



# Environmental enrichment and cognitive complexity in reptiles and amphibians: Concepts, review, and implications for captive populations

Gordon M. Burghardt\*

Departments of Psychology and Ecology & Evolutionary Biology, 1404 Circle Drive, University of Tennessee, Knoxville, TN 37996, USA

## ARTICLE INFO

### Article history:

Received 2 August 2012

### Keywords:

Reptiles  
Amphibians  
Enrichment  
Controlled deprivation  
Welfare  
Behavior  
Cognition  
Emotion  
Play

## ABSTRACT

Reptiles and amphibians have been neglected in research on cognition, emotions, sociality, need for enriched and stimulating environments, and other topics that have been greatly emphasized in work on mammals and birds. This is also evident in the historic lack of enriching captive environments to reduce boredom and encourage natural behavior and psychological well-being. This paper provides those responsible for the care of reptiles and amphibians a brief overview of concepts, methods, and sample findings on behavioral complexity and the role of controlled deprivation in captive herpetological collections. Most work has been done on reptiles, however, and so they are emphasized. Amphibians and reptiles, though not admitting of easy anthropomorphism, do show many traits common in birds and mammals including sophisticated communication, problem solving, parental care, play, and complex sociality. Zoos and aquariums are important resources to study many aspects of these often exotic, rare, and fascinating animals, and rich research opportunities await those willing to study them and apply the wide range of methods and technology now available.

© 2013 Elsevier B.V. All rights reserved.

## 1. Introduction

There is increasing interest in improved methods for managing captive reptiles and amphibians (Murphy et al., 1994; Schaeffer et al., 1992; Warwick, 1990; Warwick et al., 1995). Unfortunately, there is still a serious dearth of empirical studies on most aspects of these diverse radiations. Here I will review the approaches used in the study of behavior, provide a brief overview of the kinds of behavioral complexity seen in these animals, and discuss some recent work on cognition, play, emotion, and even consciousness that should be considered by those maintaining herpetological exhibit and research collections. This is all

preparatory to a discussion of the concepts of 'environmental enrichment' and 'controlled deprivation' as a means of enhancing the psychological and behavioral well-being of captive animals and a critical review of the still sparse, but growing, literature on reptiles and amphibians. Stress and other physiological consequences of captivity are also important (e.g., Greenberg, 1992), but will not be treated here except as ancillary measures. Due to the available literature, amphibians will be less covered than nonavian reptiles; regardless, the depth of information and application guidelines found for some domesticated species (e.g., pigs, Van der Weerd and Day, 2009) can scarcely be expected. Nonetheless, I suggest that the applied training and enrichment methods used in zoos, aquariums, and wildlife parks, properly carried out and reported, can enrich academic studies of behavior as well as enhance the lives of those entrusted to our care (cf., Hosey et al., 2009).

\* Corresponding author. Tel.: +1 865 974 3300; fax: +1 865 974 9530.  
E-mail addresses: [gburghar@utk.edu](mailto:gburghar@utk.edu), [gburghar@comcast.net](mailto:gburghar@comcast.net)

## 2. Approaches to studying behavior

Ethology is the naturalistic study of behavior from an evolutionary perspective. A hallmark of ethology is that it begins with a careful description of what animals do in both field and captivity; modern technology is greatly enhancing our abilities to gather such knowledge. However, other approaches are also useful (see [Burghardt and Zippel, 2004](#)) and guides such as [Martin and Bateson \(1993\)](#) and [Lehner \(1996\)](#) should be available and consulted as new problems and species are studied. Behavior analysis is the source of many of the operant and classical conditioning training methods used in zoos for managing large and potentially dangerous animals. This field has its own set of terms, methods, jargon, and data analysis. Some of the methods have general applicability across species and contexts. Some papers in this issue illustrate this approach and so I will not cover it in any detail here. But I do want to emphasize that there are large differences within and among each major reptile and amphibian group, and many of these differences relate to sensory abilities, temperament, reproductive mode, larval and neonatal behavior, antipredator responses, social organization, and habitat selection. Such differences may be obvious in the abstract, but it is surprising how often they are ignored when in the heat of trying to solve a behavioral problem or train a response. One consequence is that animals adept in solving one kind of task or adapting to some husbandry settings may have great difficulties with others. This often frustrates and discourages people who try to use training protocols with exotic species with whom they are not intimately familiar.

This frustration is compounded by reliance upon informal anecdotal reports lacking documentation. In the early phases of an applied research field, anecdotes are often the only sources available on what other people have observed or were successful in implementing. Such reports may be with different species housed at other institutions in varying conditions. The key to the value of such reports is providing accurate details of what was done and the behavior observed. In the area of behavior analysis, often only one or a few individual animals are studied even in experiments ([Saudargas and Drummer, 1996](#)), and thus accurate small scale studies can be extremely useful.

The behavior patterns that animals perform are often organized around behavior systems such as locomotion, foraging and ingestion, body care and elimination, protection against predators, fighting and agonism, territory formation and maintenance, dominance, courtship, nesting, and parental care. The sequences of behavior in each of these categories are also important and generally can be divided into an often variable appetitive or 'stimulus searching' stage, the more stereotyped and species characteristic consummatory acts (attacking, ingesting, copulating), and a refractory or resting stage. Most of the operant training procedures used with captive animals, such as targeting and bridging, tap into the initial appetitive or anticipatory phase of behavior, with provision of food, shelter, and even human contact as consummatory 'reward' stimuli.

## 3. Comparative cognition

In approaching comparative cognition and learning in animals a major concern has been whether there are but a few principles underlying learning (such as Pavlovian and operant conditioning, with processes of association and reinforcement) or whether there is a greater typology of cognitive processes that are qualitatively distinct. The former approach underlies most of the training methods used in zoos for managing animals, getting them to 'station' for inspection and shots, transfer locations, etc. It is very powerful in initial training and is the primary method being applied in training reptiles and amphibians; both successes and failures are common, but the latter less often reported.

With the advent of ethology and its emphasis on the study of the diversity of behavior and its control, a focus on species typical behavior became extended to species typical learning often tied to specific challenges species faced in their normal lives and related to their ecology. This led to the emphasis on imprinting, vocal learning, illness-induced aversions, and other types of learning that it seemed animals were considered 'prepared' to learn, and which could vary greatly across even closely related species, or species generally considered cognitively equivalent. The cognitive modularity approach in evolutionary psychology and neuroscience are similar conceptually if not in detail, as they also postulate that cognitive and neural systems are products of evolutionary challenges. However, it is also possible that many of these systems are widespread across vertebrates due to a common core brain architecture ([Panksepp and Panksepp, 2000](#)).

Lying outside this focus on processes underlying learning is the ecological intelligence approach ([Bshary et al., 2002](#)), which views intelligence in a broader framework than just cognition. Here intelligence also includes ecological adaptations, even 'instincts,' as part of an animal's intelligence. Certainly it is important to keep in mind that an animal is not more or less smart based on how readily it accommodates to human trainers, and that adaptability to changing environments can operate at various levels including genes, development, temperament, personality, and conditioning. The Brelands discovered this in their work as the first academically trained operant conditioners to apply the methods to animals in commercial entertainment environments such as dancing chickens and token carrying pigs, among other things ([Breland and Breland, 1961](#)). They discovered that after initial training and polished performances, some animals would often revert to more species typical behavior in a process they termed instinctive drift. This process is one that should be kept in mind when engaged in target and other training with potentially dangerous animals.

Work on learning in reptiles has a long, but shallow history in comparative psychology. I was able to review quite exhaustively a century of studies in about 120 pages ([Burghardt, 1977](#)). Captive studies on amphibian learning and cognition could be reviewed, even today, in perhaps 20 pages. Nonetheless, unlike some previous ideas about reptiles and amphibians being unremittably stimulus-response creature with little between the ears

(especially snakes!), recent studies have uncovered some rather complex accomplishments.

#### 4. Examples of learning and behavioral complexity in amphibians

The sensory systems of amphibians have received much attention (Heatwole and Dawley, 1998). Frogs have for decades been known for their remarkable vocal communication abilities (Gerhardt, 1994; Ryan, 1985) and salamanders have sophisticated pheromonal communication (Houck, 1998). However, early comparative psychologists viewed amphibians as largely instinctive bound machines controlled by external stimuli (e.g., Maier and Schneirla, 1935). While their brains are small, such a conclusion was perhaps premature. Some amphibians have been shown capable of classical and instrumental conditioning, avoidance learning, habituation, extinction, and spatial orientation (e.g., Daneri et al., 2011; Elepfandt, 1985; Finkenstadt and Ewert, 1988; Muzio et al., 1994, 2006; Shibasaki and Ishida, 2012; Wenz and Himstedt, 1990). An innovative conditioning study documented that toads learn to anticipate and avoid toxic salt solutions (Daneri et al., 2007). Luthardt-Laimer (1983) found that early experience shaped visual prey recognition in salamanders. There is little evidence for object manipulation, individual recognition, social networking (outside frog choruses), or anti-predator learning, but this may also be a consequence of little creative experimental work. For example, Ferrari and Chivers (2008) uncovered social factors in predator recognition in mixed species frog communities. Murray et al. (2004) found that experience was an important factor in anti-predator responses in frogs. Spatial learning and homing have been demonstrated (e.g., Fischer et al., 2001; Shoop, 1965; Twitty et al., 1967), however, and these must involve cognitive processing that we have yet to effectively harness in captive studies. Brattstrom (1990) has shown maze learning in fire-bellied toads.

Other behavioral complexity, including sociality, is being found (Heatwole and Sullivan, 1995). Tungara frogs can adjust aspects of their calls (chucks and whines) to predatory and social contexts (Ryan, 1985). Tadpole and salamander larvae can be phenotypically plastic in morphology and behavior depending on the presence of predators. Some frogs wiggle their toes, apparently to attract prey (Murphy, 1976; Radcliffe et al., 1986). Sexual behavior can be conditioned in many species of mammals and birds (e.g., Domjan et al., 2004), which may be useful in captive breeding and conservation; in a pioneering study, Gaalema (2010) has found that a dart poison frog, *Dendrobates tinctorius* can be conditioned, to some extent, in a sexual context.

As an example of the value of long-term behavioral research on a single species in both the field and laboratory, the work by several laboratories on red-backed salamanders, *Plethodon cinereus*, but primarily that of Robert Jaeger and colleagues, is exciting and instructive. The red-backed salamander is not endangered and captive breeding is not necessary. In fact, it is undoubtedly the most common salamander in North America and perhaps the world. In north temperate forests it may have the largest biomass of

any vertebrate—pretty remarkable for a small plethodontid weighing about a gram. The species is completely terrestrial and eggs, guarded by the mother, develop directly into terrestrial animals without any post-hatching larval stage. This may be part of the reason for their success, as they are not limited by the availability of predator free streams or ponds. Females only reproduce every other year (biennial), although males can reproduce every year. This sets up some interesting conflicts of interest.

The work by Jaeger and colleagues is unusual because large numbers of animals can be collected from the field and tested (and then released) in experiments without reusing animals or having to maintain them for long periods. This is not typically possible in zoo settings where the focus is more on intensive study of small numbers of animals. Still, this work shows what is possible and, for space reasons, a few of the findings are just summarized here. A more comparative review with work from many other laboratories is also available (Bruce et al., 2000; Jaeger and Forester, 1993).

Red-backed salamanders can identify prey chemically and have preferences for high quality (termite) over less nutritious (ant) prey. Males will show greater defense of areas containing high quality prey (David and Jaeger, 1981). Substrate chemical cues allow species and sex recognition (Jaeger and Gergits, 1979). Males can identify opponents by nose-tapping fecal pellets and males advertise to females through such fecal pellets. Females are attracted to males with high quality feces (Jaeger and Forester, 1993; Lang and Jaeger, 2000)! Male and females are socially monogamous and will each defend their territory against intruders, but both sexes also may cheat. Thus, females are more antagonistic to intruding females and males more antagonistic to intruding males. Females will threaten strange females more than familiar females (Gillette et al., 2000).

Things get even more complicated. Males exposed to gravid, but not nongravid, females become more aggressive to intruding males. Males, however, allow both gravid and nongravid females into territories, in spite of the fact that nonreproductive females compete for food. Why? Jaeger and colleagues speculate that these nonreproductive females will prefer such permissive males the following year when they are reproductive. In fact, mathematical ESS (evolutionary stable strategy) models show that male permissive behavior most likely evolved in response to female preference for permissive males. Nonetheless, males will attack and stay farther from gravid females that return to home base after consorting with other males. They do not show this behavior to strange polyandrous females or naïve females (Jaeger et al., 2002; Prosen et al., 2004).

Offspring do not seem to respond preferentially to their mothers, but mothers will attack and cannibalize unrelated neonates and thus can discriminate their own from other neonates (Gibbons et al., 2003). Territorial males will allow familiar juveniles to share their feeding territories during stressful foraging periods, which also support a kin recognition model. The salamanders are able to differentially avoid chemical cues from garter snakes that have recently eaten other salamanders rather than earthworms; even sympatric congeners were effective. Furthermore, tail loss from predatory attacks is common and decreases survival.

Intruders can determine from the substrate in resident territories the status of the tail of the resident and alter their behavior accordingly (Wise et al., 2004).

Finally, red-backed salamanders can be trained to discriminate the number of prey items and prefer the larger: two over one, three over two, but not six over four or four over three (Uller et al., 2003). Truly, this is a remarkable small animal doing things that most ethologists and herpetologists would have thought ludicrous to even investigate in them. What other types of cognitive complexity in amphibians lie undiscovered in our tanks, cages, and exhibits?

## 5. Examples of learning and behavioral complexity in reptiles

In reptiles, behavior complexity is more easily seen and measured than in amphibians, but studies are still rather few compared to mammals and birds. Still, it is well-known that crocodilians have complex vocalizations, courtship, and long lasting parental care (Garrick et al., 1978); recent studies document that some Australian skinks are monogamous, live in family groups, and have a complex social organization (Chapple, 2003). Sociality can sometimes reach remarkable levels in reptiles (Doody et al., 2013). Monitor lizards may even have counting-like skills (Kaufman and Burghardt, personal observation based on Kaufman et al., 1996, and reported in Pianka and Vitt, 2003). Tortoises seem able to follow the gaze of conspecifics (Wilkinson et al., 2010) and hognose snakes monitor the gaze direction of 'predators' when death-feigning (Burghardt, 1991). Mendyk and Horn (2011) showed that the arboreal monitor lizard, *Varanus beccarii*, uses its forelimbs to extract prey hidden in logs.

Unlike with amphibians, there are several detailed reviews of reptilian learning and cognition (Brattstrom, 1978; Burghardt, 1977; Morlock, 1989; Wilkinson and Huber, 2012). Turtles, crocodilians, and lizards have all been shown to be quite adept at most traditional learning tasks if the problem accommodates their sensory abilities and behavioral repertoires. These include classical and instrumental learning, spatial and reversal learning, sensory discrimination training, habituation, and imprinting-like early experience effects. Recent well-controlled studies include those on lizards on spatial learning (Day et al., 1999), reversal learning in monitors (Gaalema, 2011), and problem solving in monitors (Manrod et al., 2008) and anoles (Leal and Powell, 2012). An outdoor enclosure study on spatial learning of retreats in Eastern water skinks, *Eulamprus quoyii* (Noble et al., 2012) could be applied to enrich the behavior of many zoo reptiles. Monitors, large tortoises, and crocodilians have all been successfully target trained in many zoos and captive settings, often with the goal of safely managing potentially dangerous animals. Augustine (2009, 2011) nicely describes such applications with crocodiles; Augustine and Baumer (2012) is a well-illustrated example of blood sampling. Group housed venomous false water cobras (*Hydrodynastes gigas*) have been target trained to aid in feeding and moving individual animals (Gerrits and

Augustine, personal communication) and so applications to snakes are possible also.

There is little learning work done on amphisbaenids or on tuataras, but that is to be expected since little behavioral work of any kind has been done with them. Snakes, however, are common in captivity and while some are reputed to be intelligent (Bowers and Burghardt, 1992), there are few traditional learning tasks, with the exception of habituation (Herzog et al., 1989), in which they have been successfully trained. The work of Holtzman et al. (1999) on escape learning is a rare exception. Work is ongoing in several zoos on using bridging and targeting in controlling the behavior of potentially dangerous snakes. Behaviors being studied include individualized feeding and movements into switch boxes. Snakes do rely on chemical cues as well as vision in feeding in rather complex ways that suggest interesting cognitive abilities that need more exploration. For example, multimodal matching may be involved in learning about noxious prey in plains garter-snakes (Terrick et al., 1995) and chemical cues can enhance the attention paid to video images of moving prey such as fish (Hansknecht and Burghardt, 2010).

Turtles have been used in studies of spatial learning (López et al., 2000, 2001). Turtles are capable of remarkable feats of homing to nest sites and will do this for many years. Recent laboratory studies have often involved North American emydid turtles. Painted turtles (*Chrysemys*), sliders (*Trachemys*) and cooters (*Pseudemys*) have been used in many (as far as reptiles go) learning studies due to their hardiness in captivity, use of visual cues, and trainability (Burghardt, 1977). Red-bellied cooters (*Pseudemys nelsoni*) can be readily trained to climb out of the water and knock over a bottle for a food pellet (Davis and Burghardt, 2007), and they can retain both the behavior and discrimination for at least 2 years without any training (Davis and Burghardt, 2012). All animals learned the task, which was broken down into five training phases. Given the annual return of females to specific nest sites on an annual basis, such retained memory is something we suspected could occur, but to demonstrate such a skill in captivity is an advance and opens up the possibility of more refined studies. Interestingly, there was even evidence of different strategies in making choice decisions.

More remarkable, perhaps, are recent demonstrations that these species are capable of learning the correct visual cues for obtaining food by merely observing a conspecific (Davis, 2009; Davis and Burghardt, 2011), an ability also found in detour learning in red-footed tortoises (Wilkinson and Huber, 2012). Such social learning in a reptile is an important finding, as it has proved, until recently, difficult to document. I suspect more examples will come to light as the social complexity of some reptile species is both recognized and investigated (Doody et al., 2013). Additional recent work on cognition in reptiles is found in the foregoing, Wilkinson and Huber (2012) and also Wilkinson et al. (2007, 2009, 2010).

## 6. Play in reptiles and amphibians

Although amphibians, and especially reptiles, may show many of the basic cognitive abilities shown by



mammals and birds, some behaviors have seemed beyond their capacities and one of these is play behavior, which has often been viewed as limited to smart endothermic vertebrates, especially mammals (Bekoff and Byers, 1981; MacLean, 1985). Curiosity has often been considered an important precursor to play (Burghardt, 2005); an early, but wide-ranging series of comparative curiosity studies in zoos seemed to show that reptiles were, by and large, a clearly non-curious group (Glickman and Sroges, 1966). These tests were not appropriate for most reptiles, however, in that chemosensory exploration was ignored and the results superseded by subsequent studies (Burghardt et al., 1996; Chiszar et al., 1976).

Another major problem was being able to identify play if it occurs in reptiles, for existing definitions were of limited use in identifying play in organisms or contexts where one was already predisposed to label behavior as play. Thus, in order to identify play in organisms not already considered playful I developed a set of five criteria that to be met before it can be stated confidently that a particular behavior is play. The short definition is this: "Play is repeated, incompletely functional behavior differing from more serious versions structurally, contextually, or ontogenetically, and initiated voluntarily when the animal is in a relaxed or low stress setting" (Burghardt, 2005, p. 82).

Using this definition, evidence clearly exists for object play in some turtles and lizards, and perhaps in crocodilians. For example, Nile softshell turtles bat around basketballs and plastic bottles, swim through and manipulate hoops and rings, and even play tug of war with their keepers and the fill hose (Burghardt et al., 1996; Burghardt, 1998). Monitor lizards manipulate, shake, and carry about objects such as rings, plastic disks, buckets, and so forth and can have close attachments with their keepers, such as approaching them, climbing on them, and even soliciting rubbing and other tactile stimulation (Burghardt et al., 2002). Such attachments have been found in other reptiles as well (Bowers and Burghardt, 1992).

Precocial courtship in some turtles and squamate reptiles has characteristics similar to play fighting in rodents (Kramer and Burghardt, 1998). There is less evidence for amphibians, but tadpoles of the Vietnamese mossy frog *Theloderma coricale* (Hylidae) repeatedly allow themselves to be swept up in airstreams and 'harmless fighting' in adult dart poison frogs suggests that some amphibians also play fight (Burghardt, 2005; Hurme et al., 2003). The conclusion is that environmental features and social partners may be useful components of 'enrichment' in reptiles and amphibians. The problem is that due to physiological and life history constraints, play may be less evident and less frequent in many poikilothermic species (Burghardt, 2005).

## 7. Controlled deprivation and environmental enrichment

If reptiles and amphibians play, then that is added incentive to provide rich, stimulating environments for them. While often this is called enrichment, even the best captive environments are less spacious and stimulus rich than natural ones; thus, we at best are providing animals necessarily depauperate environments in which we try,

based on limited knowledge, to provide the most important features of nature (with the exception of disease and predators). The term controlled deprivation is a more accurate descriptor than is environmental enrichment (Burghardt, 1996). The latter implies that we are providing something beyond what is adequate and normal when, in fact, we are basically trying to implement trial and error methods to improve the psychological, behavioral, and physiological well-being of captive animals by approximating the most necessary features of nature. The most appropriate term for this may be that put forth by Greenberg (1995): ethologically informed design. To a large extent most environmental enrichment today is equivalent to providing 'enriched white bread' to school children in the middle of the last century. Clearly better for them than standard white bread, it was nutritionally far inferior to whole grain bread. The lesson here is that we do not want to make too many claims for the superior job being done through most enrichment procedures. While I will use the term enrichment from here on out in its conventional sense, please keep in mind the caveats.

The first systematic advocate and researcher of enrichment in captive animal settings was Hal Markowitz, who worked for many years at the San Francisco Zoo (Markowitz, 1982; Markowitz and Gavazzi, 1996). Markowitz established the field by focusing on getting animals to be active in locomotion, foraging, and other species typical behaviors through the use of ingenious operant techniques. Unfortunately, these procedures often were very hard to maintain and trained staff were needed. The history, terminology, and implementation of enrichment are covered in many recent articles in this journal and elsewhere, but those by King (1993), Mench (1998), and Mellen and MacPhee (2001) are still excellent sources. Maple and Perdue (2013) provide an updated review of animal welfare in zoos and include information on enrichment in many species, including reptiles. Kuppert (2013) carried out a number of studies on enrichment in amphibians and reptiles at the National Zoo (DC) that indicate the potential for the kinds of work that need to be done. Her focus was on the role of sensory cues (visual and chemical), especially in foraging and social interactions. She devised and executed a number of experimental observations on species as diverse as crocodiles, monitors, iguanas, basilisks, chameleons, hellbenders, and rattlesnakes that indicate the kinds of systematic studies that can be readily carried out in zoos, replicating and extending laboratory and field studies and raising possibilities for implementing methods of improving captive well-being.

## 8. Research studies on environmental enrichment for amphibians

Hayes et al. (1998) called for zoos and others to include amphibians and reptiles in their enrichment schemes, which had rarely been considered relevant due to the limited cognitive and emotional needs these animals were deemed to require. Fleming (2007) lists some abnormal behaviors in frogs that may warrant interventions. Generally, amphibian exhibits are not usually formally labeled as being enriched, perhaps because successful maintenance of

them often involves providing naturalistic, often quite specific, conditions such as proper humidity, cage structures, and live prey and thus are already maintained in environmentally complex settings that are expensive and difficult to emulate in larger species. In other words, for many amphibians successful breeding and maintenance require attention to specific microclimate and structural details that are often less necessary for feeding and breeding most mammals. However, there is scope for study here, as shown in work on developing behaviorally appropriate settings for bullfrogs (Bang and Mack, 1998) and dendrobatid dart poison frogs (Hurme et al., 2003; McRobert, 2003). Since frogs have been used in much physiological and biomedical research, it is important that such research is not compromised due to keeping the animals in crowded inappropriate housing and until the time they are needed for often terminal experiments. Fortunately, modern amphibian exhibits often strive for better conditions for long-term captives and breeding.

One of the species often used in biomedical research as well as exhibits is *Xenopus laevis*, the aquatic South African clawed frog. Not only are there detailed captive housing manuals available (Reed, 2005; Schultz and Dawson, 2003) but also some empirical research on evaluating enrichment. Brown and Nixon (2004) found that adding cover objects to group housing tanks did not enhance reproduction. On the other hand, a study in which refuge pipes were added to tanks containing many frogs led to both universal use of the pipes as hiding places and about a 90% reduction in bite wounds, including among females (Torreilles and Green, 2007). Cannibalism is also a problem and they recommended segregation of animals by size class. As discussed below, it is likely that many interventions, more or less systematic, have been carried out in zoos to enhance the quality of life in captive amphibians, but have not been always disseminated through archival publication venues.

## 9. Research studies on environmental enrichment for reptiles

With reptiles, studies of enrichment have been more common, though still quite rare. Fleming (2007) has briefly outlined abnormal behaviors in a number of reptiles that suggest the need to provide enrichment as well as training (conditioning), stating that “The key to an optimal captive environment is to facilitate animals’ opportunities to make associations that enhance their well-being” (Fleming, 2007, p. 1541). Skurski (2010) lists numerous suggestions for making exhibits for reptiles more conducive to complex and natural behavior (see also Kuppert, 2013). Many of these are gaining currency such as providing retreats and thermal gradients, varying diets and how they are presented, accommodating circadian cycles, and so forth. Behavioral development in terms of growth, diet, maturation, and experience may often be a critical concern (e.g., Burghardt and Layne, 1995; Waters and Burghardt, 2013). Alberts (2007) has excellently reviewed the behavioral issues that should be addressed in preparing headstarted iguanas for release in conservation programs and the need for empirical evaluation of success; discussion of these issues is becoming common for many taxa involved in

reintroduction or translocation projects. Indeed, behavioral competence in captive populations, including snakes, is worth systematic study (e.g., Chiszar et al., 1993). However, here I will limit discussion to several experimental and quantitative studies of enrichment procedures and their effects on captive animals, providing enough details in order to encourage replications and extensions. This detail is needed to alert readers to the need for careful methodology and to some of the controversies that may arise as this field develops.

### 9.1. Turtles

In turtles, the initial observations of the value and use of introduced objects such as balls, hoses, and sticks in Nile soft-shelled turtles to reduce self-injurious behavior and, perhaps, boredom (Burghardt et al., 1996), were replicated in terms of object interaction independently in other captive *Trionyx triunguis* (Krause et al., 1999). A study of object provisioning in sea turtles, hatchling loggerheads and a blind green, by Therrien et al. (2007) built on this initial work. The loggerheads were tested with four objects and observed for 20 min with each over several days as well as comparable periods without any enrichment. The enrichment devices were PVC pipe configurations, a water cooler jug with holes and filled with just water or filled with fish and squid that could be extracted, or flowing water from an outlet above the water surface. For the blind green turtle the water jug filled with food was replaced with a lettuce feeder device and the water flow replaced by tactile carapace stimulation by a keeper. All were voluntarily available to the turtles. Eight categories of behavior were recorded and the study is admirable in the detailed data provided for individual animals. Although there were some interesting individual and enrichment device differences, the main findings were that resting and stereotyped ‘pattern’ swimming decreased and more random swimming as well as behavior directed at the objects, other features of the tank, and self (e.g., flipper directed) increased. Neither aggression nor hiding behavior changed. Therrien et al. (2007) viewed their study as a success and highly adaptable to exhibit animals. The inclusion of the blind turtle raises the issue of taking seriously the needs of the often disabled, injured, aged, and other special needs animals that may be increasing components of zoo collections.

A study more focused on overall living arrangements involved preference of box turtles for a barren or ‘enriched’ environment containing mulch substrate, shredded paper, and a hide box (Case et al., 2005). Turtles were 38 adults, either wild-caught or long-term captives. After given an initial choice of spending time in either the barren or provisioned environment, they were housed in one of the two environments for a month and then their preferences again assessed. In addition, blood counts, fecal corticosterone, body weights, and video recorded behavior samples were evaluated. Diets were the same for both groups. Virtually all animals preferred the enriched over the barren environment both initially and irrespective of the housing experience. Heterophil to lymphocyte ratios (H/L) were lower in animals kept in the enriched environment as compared to the barren housed animals, although there was

no change in corticosterone concentrations. While overall weight change did not differ based on housing treatment, the wild-caught animals gained more weight than the long-term captives. In terms of behavior, filmed half way through the 1-month period on both feeding and non feeding days for 6 h each, barren housed animals spent more time trying to escape and less time resting and engaging in non-escape movements (Case et al., 2005).

## 9.2. Lizards

Lizards have been used in a few systematic experiments. A Komodo monitor was, as noted previously, the first lizard to have play behavior clearly documented and analyzed, although anecdotal records go back almost 80 years. The responses to a variety of objects including shoes, rings, Frisbees, buckets, etc. were videotaped and then quantified in numerous sessions over many months before, during, and after presentation of the objects with and without the presence of a familiar human caretaker (Burghardt et al., 2002; Manrod, 2003). The diversity of responses, the level of exploration and curiosity, and the rapidity of learning were quite remarkable; many reptile curators are discovering that these animals seem to be in a psychologically different place than other lizards. As these animals are becoming more common as trophy reptiles in zoos, they can easily become the great ape of the squamate reptile world (Burghardt, 2005).

Other monitors, as discussed in the learning section, have shown remarkable learning abilities, including animals from a study of 16 black-throated monitors (*Varanus albigularis*) reared from hatching at the Dallas Zoo in off-exhibit housing (Manrod, 2003; Manrod et al., 2008). Here eight animals were raised in standard cages and fed dead prey while the other eight were given cages in which they could climb, eat live prey, and given periodic exposure to a problem to solve (retrieving mice from a clear tube by opening a small door), a ball with small mice running around inside that they could see, smell, and hear but not capture, and periodic social experience with one of their siblings. While no group comparisons were made (the problem task exposure was part of the enrichment scheme), the enriched animals all solved the problem tube on the first trial in an average of less than 5 min and greatly improved by the second trial, showing remarkable one trial learning. Noninvasive MRI brain scans of animals before and after experience resulted in a trend for larger forebrains in the enriched animals, but the small number of animals and low resolution of the then available equipment led to no definitive conclusions (Burghardt, Hartdegen, and Alml, unpublished observation).

Two more recent studies of enrichment in lizards have appeared. Phillips et al. (2011) studied blue-tongued skinks (*Tiliqua scincoides*), a popular pet and exhibit species. Two experiments were carried out with eight or nine captive bred juveniles. In the first experiment, on food enrichment, all animals were kept in individual 60 cm × 40 cm enclosures outfitted with water and food bowl, 20 cm pipe for shelter, a brick, paper substrate and natural as well as supplemental UV light. All animals rotated through three conditions that lasted 30 days each. One involved

'randomly' scattering six live mealworms in the cage, one involved placing the live mealworms in small ball with two 4 mm holes, and the other a control with no live food. Timelapse video recordings of all animals were taken for 5 h after feeding, noting behaviors involving feeding, active on paper, climbing, hiding in pipe, and others. Weight gain was also measured. Results showed that animals eating the live mealworms gained more weight, spent more time eating the mash ration in addition to eating the mealworms, were more active on the open paper substrate, and engaged in more walking and nose rubbing on the wall. The food ball context led to quicker ingestion of the mealworms than did foraging on the scattered mealworms. A second experiment took place a year later in which eight animals rotated through four conditions of 2 weeks each with behavior video recorded for 6 h a day and classified into similar categories as in Experiment 1 except for the live food related behaviors. The four conditions were all combinations of large and small enclosures at either hot or cool temperatures based on field data. All enclosures contained the same items. Results showed more walking in the large enclosures, especially on the first day. More hiding in shelters occurred with the large enclosures as well as in hot ones. Eating, drinking, and some other behaviors were not affected by either temperature or space. Animals in small enclosures gained more weight. The authors make suggestions encouraging feeding live prey and larger enclosures. Since all animals rotated through all conditions no long-term welfare or behavioral consequences could be expected from this design, in spite of the admirably large data set collected (Phillips et al., 2011).

The last study to be discussed did attempt to measure longer term consequences using larger numbers of lizards (Rosier and Langkilde, 2011a) in a study that explicitly asked the question: Does environmental enrichment really matter? Hatchling Eastern fence lizards (*Sceloporus undulatus*) were raised in groups of four siblings in either enriched or control 30 cm × 20 cm tubs. There were 12 replicates of each condition. The tubs were similarly outfitted fairly sparsely with one difference: the enriched container had an elevated wooden platform (13.5 cm high) on which they could climb or jump. The control tubs contained the same size wood platform on the sand substrate. This was under the light bulb that provided heat for basking. The height was adjusted for the two conditions. Animals were measured at hatching and at 34 weeks of age when the experiment ended. At 28 weeks of age a small blood sample was taken for corticosterone analysis. As animals died, they were replaced by siblings. Behavior observations occurred once for each lizard at an unspecified age and involved recording at hourly intervals if the animal was active, basking, or hiding (and not visible). Behavior was not video recorded. The results, based on individual scores, can be simply stated: there were no effects of enrichment on any behavior, growth, corticosterone, or survival measure. Although the authors mention that other types of enrichment may be valuable as well as other measures of behavior, such as sprint speed or stamina, they emphasize that more research is needed, especially for animals "more phylogenetically unrelated to humans" (Rosier and Langkilde, 2011a: 76).

This paper led to a critique by Kanaan and Hötzel (2011) who pointed out problems of the narrowness of how enrichment was conceived (primarily to reduce abnormal behavior and stress), lack of specific hypotheses and predictions, the use of toe clipping for individual recognition, lack of information on when the behavioral measurements were taken, and the lack of using enclosure, rather than individual, in the statistical analysis. They also pointed out the provocative nature of the title and that no data were presented that the lizards even used the platform. Rosier and Langkilde (2011b) responded by pointing out that the active category included climbing, jumping and basking involved the platform (though these points were not made in the original paper). The use of toe clipping was defended as less stressful than PIT tagging and more permanent than paint marks. The statistics were defended as more powerful, cage ID was a random factor in the model, and using cage as the unit led to qualitatively similar results. The authors end by claiming that Kanaan and Hötzel (2011) seem to want to use anthropomorphic criteria, not objective measures, for assessing 'quality of life' for a lizard. This exchange is valuable as it indicates that the field is gaining maturity and more detailed analyzes of methods, results, and implications are being incorporated into this work.

### 9.3. Snakes

The work of Chiszar and colleagues has been invaluable in identifying and measuring a large number of psychologically relevant phenomena in snakes including chemosensory curiosity, self-recognition, effects of cage cleaning and object rearranging, and competence of performing species typical behavior (e.g., Chiszar et al., 1976, 1993, 1995) and it is disappointing that more studies have not followed up on these often simple and elegant studies easily carried out in zoo settings. Social experience can also alter grouping and other behavior in snakes and such effects might well be incorporated into group housing designs (Yeager and Burghardt, 1991).

One study did formally study the effects of enrichment in altering the behavior of yearling rat snakes (*Pantherophis*) (Almli and Burghardt, 2006). We used 16 snakes from two clutches of eggs from both yellow ratsnakes and black ratsnakes. Half of each clutch were raised with more complex environments with substrate for burrowing and branches for climbing and fed live mice; the other half were raised in standard situations with dead prey, no climbing opportunities, and a solid substrate. The sizes of the enclosures were the same for both groups. After 8 months all snakes were tested on feeding, exploratory, and escape tasks. The major findings were that the animals in the enriched conditions captured and consumed prey more quickly, more readily habituated in the exploratory task (an effect found in rodent enrichment studies (Zimmermann et al., 2001) and generally considered a sign of more intelligence), and more quickly escaped, over repeated trials, in a circular arena with 12 holes, 11 of which were blocked (based on Holtzman et al., 1999). Using measures from all three tasks a discriminant analysis showed that all 16 snakes could be correctly assigned to their housing group based on their behavioral scores alone. This was in spite of

the large differences in behavior between the two clutches (e.g., the yellow rat snakes were far more nervous about feeding and had to be tested in the dark or when no one was around). Snakes, in spite of their reputation as sedentary animals of limited behavioral flexibility as compared to turtles, lizards, and crocodilians, may be just far more subtle in their responses and require more innovative interventions than other reptiles (Almli and Burghardt, 2006).

### 9.4. Other reptiles

No formal studies have appeared on tuatara, amphibians, or even, most surprisingly, crocodilians, in spite of the latter's ability to learn, frequent subjects of target training, and highly developed social behavior, parental care, and communication. Crocodilian farming operations would seem to be good settings to carry out some studies as the crowded conditions, atypical diets, and other consequences of being reared for rapid commercial harvest must have deleterious consequences. Here, as with other species of amphibians and reptiles, the alien nature of their morphology and behavior has seemed to desensitize our ability to identify behavioral and psychological stress and abnormalities (Warwick et al., 1995).

## 10. Consciousness and emotion

It is important to assess how the animal perceives, interprets, and experiences its environment, what I have termed the aim of private experience (Burghardt, 1997, 2005). Although whether or not reptiles and amphibians are conscious or have emotions is perhaps not directly relevant to what we do in training and enrichment, these questions do have implications for how we perceive them, treat them, address their needs, and alleviate physical and psychological disorders (Warwick et al., 1995), as well as how we educate the public about them. The discussion of the fence lizard study raises the issue of what emotions, if any, reptiles and amphibians may experience and how they could possibly be measured. We cannot use simplistic evaluations of behavior viewed through our human-centered lens, since poikilothermic vertebrates operate at different time scales, lack readily interpreted facial and vocal signals of internal states, and rely on sensory cues, often chemical, outside the range of those we can readily evaluate with our mammalian infrastructure (Bowers and Burghardt, 1992; Rivas and Burghardt, 2002). For example, chemical cues are often particularly salient and yet chemosensory enrichment is often ignored, as a critical review documents (Clark and King, 2008; see also Chiszar et al., 1995).

The occurrence of play and cognitively adept behavior, rapid learning, acute evaluation of social and other stimuli, and decision making in many reptiles and amphibians suggest that they should not be arbitrarily excluded from such attributions. As consciousness is a notoriously difficult concept to pin down in animals, even in the great apes (e.g., see the entries in Bayne et al., 2009), it is not surprising that most workers with non-mammalian vertebrates have avoided the topic. One who has not is Michel Cabanac (1999). In a series of papers (e.g., Cabanac and Cabanac, 2000), he has presented and reviewed data that



he feels supports the view that reptiles are both conscious and have emotions, while amphibians (and thus certainly fish and invertebrates) lack both. It should be pointed out that since he argues that having emotions means being conscious, the link he makes between the two is not surprising. Setting aside the argument for consciousness, let us look at the evidence for claiming reptiles, but not amphibians, have emotions. First, there is neural data suggesting that emotions are mediated by the limbic system in the telencephalon and this is found in reptiles but not, apparently, in amphibians, who also lack virtually any neocortex. Second, my experience, and that of many zookeepers is that some reptiles, such as monitors, iguanas, tortoises, and crocodilians do seem to recognize different people, approach to be stroked or to make contact, and seem to enjoy various sensations, such as flowing water (Bowers and Burghardt, 1992; Burghardt et al., 1996). So, emotional experience in reptiles is quite possible, contradicting the eminent comparative neuroscientist Paul MacLean (1985), who argued that reptiles lack positive socially bonding emotions based on his flawed appreciation of maternal care and social bonds in diverse reptiles.

Cabanac argues that four lines of evidence support the dichotomy between reptiles and amphibians. One is that reptiles, but not amphibians, display delayed illness-induced food aversions (Paradis and Cabanac, 2004). The second is that iguanas but not amphibians will go to a cold area of a cage to get a favored food but will not do so for a nutritious but unpalatable food, suggesting that reptiles, but not amphibians, experience pleasure (Balasko and Cabanac, 1998). The third is that handling produces 'emotional fever' in reptiles but not amphibians (Cabanac and Cabanac, 2004). Emotional fever is increasing your preferred body temperature when stressed (endothermic vertebrates can increase their body temperature internally). Fourth, reptiles, but not amphibians, increase their heart rate when handled (Cabanac and Cabanac, 2000).

This work is very useful and challenges our conceptions with empirical data. Still, caution in interpretation is needed. First, only a few species have been tested for any of these phenomena. Second, the essential link between these four phenomena and emotion is not proven. Certainly we can anthropomorphically relate to the fact that we feel nauseous after eating tainted novel food and may then feel sick just thinking about it. When scared or nervous our heart rate may indeed increase. We may also develop a higher body temperature when stressed. But there is no reason why the linkage in us has to be the same or even present at all in other species and stronger evidence is needed to make sure our conclusions are critically anthropomorphic. Nevertheless, it is interesting to note that there are fewer studies dealing with training or enrichment with amphibians. While this may indicate that amphibians are more intractable than reptiles, it is also relevant to note that most training with reptiles has involved large or dangerous species and the most studied amphibians are dart poison frogs. However, in this case their sensitivity to handling seems to have been a major motivation for working with them in addition to their relatively high rates of activity that increase training success rates.

As for consciousness in reptiles and amphibians, the issue is one of defining consciousness, which can range from simply being awake and alert to having a sense of self-reflection. At this point, there are too many unknowns; as work proceeds in training and evaluating the well-being of amphibians and reptiles through enrichment and training, we should be in prime situations to uncover fascinating and crucial data to help answer these questions. Nonetheless, the possible depth of the emotional and cognitive lives of both amphibians and reptiles need to be part of the framework of herpetological welfare studies as they mature.

## 11. Some implications

In conclusion, those privileged to work with exotic species are in a key position to collect novel data and evaluate new findings. My suggestion is to keep extending the reach of this important work and trying out new ideas. Provide and evaluate responses to, and use of, varying kinds of shelters, structures, prey, feeding schedules, social groupings, and mixed species housing. Putting heat sources in different locations or changing them, even hourly, will enhance activity. Similarly, altering which retreats are open is a way of enhancing exploratory behavior, as is introducing/changing odoriferous objects to snakes and other chemosensory reactive species. Even simple operations such as cleaning cages or replacing substrates can have major impact on behavior (Chiszar et al., 1995). Evaluate responses to different keepers and handling. Systematically reward a wide range of behavior patterns in addition to movements and stationing. Also, keep aware of what is being done with other species. Reserve time to simply watch and record, in notes and on video, these remarkable animals and not rush too quickly to design experiments that may not be appropriate or conducive to answering the questions asked. Finally, write up and report your observations and data, being as quantitative as possible. Just because work is motivated by solving practical problems with exhibit or colony animals, does not mean that it may not be valuable and relevant to others. The American Association of Zoo Keepers Forum has addressed some herpetological topics and, hopefully, more will be forthcoming. However, issues of interobserver reliability and blind testing should be incorporated whenever possible (Burghardt et al., 2012) and guides such as Martin and Bateson (1993) and Lehner (1996) should be available and consulted as new problems and species are studied.

Reptiles have generally been left out of zoo concern with environmental enrichment. While reptile exhibits are becoming more naturalistically appearing, in order to better convey the ecological environments they inhabit and simulate natural lighting, temperature, humidity, substrates, and structural complexity, this rarely is based on the idea that these animals need such stimulation for developing species typical behaviour or enhancing their psychological well-being. Off exhibit caging, as well as most research laboratory housing, is typically sparse. This is often due to limited staffing, funding, and available space as well as outmoded building designs that did not take into account the need for breeding arrangements and

rearing of offspring. Feeding of live prey other than insects is too often rarely done even with obligate carnivores such as snakes. This is often justified on practical, aesthetic, possible predator injury, legal and animal welfare grounds, even for snakes and other reptiles that are obligate vertebrate carnivores (Burghardt, 1996). But, as noted above, experiments have shown that snakes with experience with live prey have better foraging skills. Plasticity in terms of adapting to efficient foraging on different types of prey with experience is also present (Burghardt and Krause, 1999). Perhaps their morphology and physiology are affected, in addition, such as adapting to different gut microflora.

As many now recognize, environmental “enrichment” is not an extra benefit that we may choose to provide as a luxury if the budget permits; it may be essential for proper management, even for reptiles. We need to realize that no captive environments can ever hope to fully simulate or mimic those lived in by wild animals, even the smallest and most sedentary species. All we can really do in zoos and aquariums is to work within the parameters of controlled deprivation. We have to identify, out of all the behavioural, social, and ecological needs of animals, those most essential for facilitating expression of their normal behavioural repertoire, reproduction (e.g., breeding for conservation projects), and development of normal phenotypes (e.g., body size and shape, bone structure, coloration). Clearly, with a group as large and diverse as reptiles, this poses great challenges and much essential information is lacking. Still, great progress can be made through utilizing existing data and a critically anthropomorphic attitude (Burghardt, 1991) to create and test housing, nutrition, environmental complexity, temporal variation, and other schemes to improve behavioural and psychological welfare of reptiles. To this end it is important that we not view reptiles and their individuality through a lens coloured by an uncritical mammalcentric bias (Rivas and Burghardt, 2002). As the studies reported here suggest, such a bias stereotypes them mentally and underestimates their need for stimulation, their individual and species level temperament and personality differences, and their cognitive and learning capacities.

Many laboratories and zoos are documenting the value of systematic observation and experimentation to test out the best ways to enhance the lives of reptiles in captivity as well as to provide more educational and ecologically appropriate exhibits. A preoccupation with large numbers is not necessary for good science worthy of publication. This reminder is needed to encourage persons who are working with small numbers of large, rare, endangered, if not potentially dangerous, animals to record and publish their endeavors. This work has just begun, but may be increasingly necessary, not just to enhance the lives of captive animals, but for ensuring the survival of animals in conservation efforts (c.f. Alberts, 2007).

## Acknowledgments

This paper is dedicated to David Chiszar in memory of his pioneering research in both zoo and academic settings that uncovered many remarkable phenomena, especially

in snakes, that will enrich applications to enhance how they are maintained and studied in captivity for many years to come. My work and that of my students has been supported for many years by NSF, NIH, the University of Tennessee (including the Science Alliance), several zoos (National, Dallas, San Diego, Brookfield, Columbus, Cleveland, and Knoxville) and other outside sources including Strachan and Vivien Donnelly of the Center for Humans and Nature. Some of the text is based on sections of Burghardt and Zippel (2004) and Burghardt (2005). Earlier versions of this paper were presented at the Reptile and Amphibian Training and Enrichment conference in Orlando, FL in 2005, the International Environmental Enrichment Conference in Torquay, England in 2008, and the American Psychological Association conference symposium on zoo research in Washington, DC in 2011.

## References

- Alberts, A.C., 2007. Behavioral considerations of headstarting as a conservation strategy for endangered Caribbean rock iguanas. *Appl. Anim. Behav. Sci.* 102, 380–391.
- Almli, L.M., Burghardt, G.M., 2006. Environmental enrichment alters the behavioral profile of ratsnakes (*Elaphe*). *J. Appl. Anim. Welf. Sci.* 9, 85–109.
- Augustine, L., 2009. Husbandry training with an exceptional South African crocodile. *ABMA Wellspring* 10 (3), 2–3.
- Augustine, L., 2011. Putting training to work in large animal capture. *ABMA Wellspring* 12, 36–37.
- Augustine, L., Baumer, M., 2012. Training a Nile crocodile to allow for collection of blood at the Wildlife Conservation Society's Bronx Zoo. *Herpetol. Rev.* 43, 432–435.
- Balasko, M., Cabanac, M., 1998. Behavior of juvenile lizards (*Iguana iguana*) in a conflict between temperature regulation and palatable food. *Brain Behav. Evol.* 52, 257–262.
- Bang, D., Mack, V., 1998. Enriching the environment of the laboratory bullfrog (*Rana catesbeiana*). *Lab Anim.* 27 (6), 41–42.
- Bayne, T., Cleeremans, A., Wilkens, P. (Eds.), 2009. *Oxford Companion to Consciousness*. Oxford University Press, Oxford, UK.
- Bekoff, M., Byers, J.A., 1981. A critical reanalysis of the ontogeny and phylogeny of mammalian social and locomotor play: an ethological hornet's nest. In: Immelmann, K., Barlow, G.W., Petrinovich, L., Main, M. (Eds.), *Behavioral Development: The Bielefeld Interdisciplinary Project*. Cambridge University Press, Cambridge, pp. 296–337.
- Bowers, B.B., Burghardt, G.M., 1992. The scientist and the snake: relationships with reptiles. In: Davis, H., Balfour, D. (Eds.), *The Inevitable Bond*. Cambridge University Press, Cambridge, pp. 250–263.
- Brattstrom, B., 1978. Learning studies in lizards. In: Greenberg, N., MacLean, P.D. (Eds.), *Behavior and Neurology of Lizards*. National Institute of Mental Health, Bethesda, MD, pp. 173–181.
- Brattstrom, B.H., 1990. Maze learning in the fire-bellied toad, *Bombina orientalis*. *J. Herpet.* 24, 44–47.
- Breland, K., Breland, M., 1961. The misbehavior of organisms. *Am. Psychol.* 16, 681–684.
- Brown, M., Nixon, R.M., 2004. Enrichment for the captive environment—the *Xenopus laevis*. *Anim. Tech. Welf.* 3, 87–95.
- Bruce, R.C., Jaeger, R.G., Houck, L.D. (Eds.), 2000. *The Biology of Plethodontid Salamanders*. Springer, New York.
- Bshary, R., Wickler, W., Fricke, H., 2002. Fish cognition: a primate's eye view. *Anim. Cogn.* 5, 1–13.
- Burghardt, G.M., 1977. Learning processes in reptiles. In: *Ecology and Behavior*, In: Gans, C., Tinkle, D. (Eds.), *The Biology of the Reptilia*, vol. 7. Academic Press, New York, pp. 555–681.
- Burghardt, G.M., 1991. Cognitive ethology and critical anthropomorphism: a snake with two heads and hognose snakes that play dead. In: istau, C.A. (Ed.), *Cognitive Ethology: The Minds of Other Animals*. Erlbaum, San Francisco, pp. 53–90.
- Burghardt, G.M., 1996. Environmental enrichment or controlled deprivation? In: Burghardt, G.M., Bielitski, G.M., Boyce, J.T., Schaefer, J.R.D.O. (Eds.), *The Well-Being of Animals in Zoo and Aquarium Sponsored Research*. Scientists Center for Animal Welfare, Greenbelt, MD, pp. 91–101.

- Burghardt, G.M., 1997. Amending Tinbergen: A fifth aim for ethology. In: Mitchell, R.W., Thompson, N.S., Miles, H.L. (Eds.), *Anthropomorphism, Anecdotes, and Animals*. SUNY Press, Albany, NY, pp. 254–276.
- Burghardt, G.M., 1998. The evolutionary origins of play revisited: Lessons from turtles. In: Bekoff, M., Byers, J.A. (Eds.), *Animal Play: Evolutionary, Comparative, and Ecological Perspectives*. Cambridge University Press, New York, pp. 1–26.
- Burghardt, G.M., 2005. The Genesis of Animal Play: Testing the Limits. MIT Press, Cambridge, MA.
- Burghardt, G.M., Bartmess-LeVasseur, J.N., Browning, S.A., Morrison, K.E., Stec, C.L., Zachau, C.E., Freeberg, T.M., 2012. Minimizing observer bias in behavioral studies: a review and recommendations. *Ethology* 118, 511–517.
- Burghardt, G.M., Chiszar, D., Murphy, J.B., Romano, J., Walsh, T., Manrod, J., 2002. Behavioral complexity, behavioral development, and play. In: Murphy, J.B., Ciofi, C., Panouse, C., de La, Walsh, T. (Eds.), *Komodo Dragons: Biology and Conservation*. Smithsonian Institution Press, Washington, DC, pp. 78–118.
- Burghardt, G.M., Krause, M.A., 1999. Plasticity of foraging behavior in garter snakes (*Thamnophis sirtalis*) reared on different diets. *J. Comp. Psychol.* 113, 277–285.
- Burghardt, G.M., Layne, D.G., 1995. Effects of ontogenetic processes and rearing conditions. In: Warwick, C., Frye, F.L., Murphy, J.B. (Eds.), *Health and Welfare of Captive Reptiles*. Chapman & Hall, London, pp. 165–185.
- Burghardt, G.M., Ward, B., Roscoe, R., 1996. Problem of reptile play: Environmental enrichment and play behavior in a captive Nile soft-shelled turtle, *Trionyx triunguis*. *Zoo Biol.* 15, 223–238.
- Burghardt, G.M., Zippel, K., 2004. Amphibian behavior. In: Odum, A., Zippel, K. (Eds.), *Amphibian Biology and Management*. Association of Zoos and Aquariums, Silver Spring, MD, pp. 1–20.
- Cabanac, M., 1999. Emotion and phylogeny. *J. Conscious. Stud.* 6, 176–190.
- Cabanac, A., Cabanac, M., 2000. Heart rate response to gentle handling of frog and lizard. *Behav. Proc.* 52, 89–95.
- Cabanac, A.J., Cabanac, M., 2004. No emotional fever in toads. *J. Thermal Biol.* 29, 669–673.
- Case, B.C., Lewbart, G.A., Doerr, P.D., 2005. The physiological and behavioural impacts of and preference for an enriched environment in the eastern box turtle (*Terrapene carolina carolina*). *Appl. Anim. Behav. Sci.* 92, 353–365.
- Chapple, D.G., 2003. Ecology, life history, and behavior in the Australian scincid genus *Egernia*, with comments on the evolution of complex sociality in lizards. *Herpetol. Monogr.* 17, 145–180.
- Chiszar, D., Carter, T., Knight, L., Simonson, L., Taylor, S., 1976. Investigatory behavior in the plains garter snake and several additional species. *Anim. Learn. Behav.* 4, 272–278.
- Chiszar, D., Smith, H.M., Radcliffe, C.W., 1993. Zoo and laboratory studies on the behavior of snakes: assessments of competence in captive-reared animals. *Am. Zool.* 33, 109–116.
- Chiszar, D., Tomlinson, W.T., Smith, H.M., Murphy, J.B., Ratcliffe, C.W., 1995. Behavioural consequences of husbandry manipulations: indicators of arousal, quiescence, and environmental awareness. In: Warwick, C., Frye, F.L., Murphy, J.B. (Eds.), *Health and Welfare of Captive Reptiles*. Chapman & Hall, London, pp. 186–204.
- Clark, F., King, A.J., 2008. A critical review of zoo-based olfactory enrichment. In: Hurst, J.L., Beynon, R.J., Roberts, S.C., Wyatt, T.D. (Eds.), *Chemical Signals in Vertebrates*, vol. 11. Springer, New York, pp. 391–398.
- Daneri, M.F., Casanave, E., Muzio, R.N., 2011. Control of spatial orientation in terrestrial toads (*Rhinella arenarum*). *J. Comp. Psychol.* 125, 296–307.
- Daneri, M.F., Papini, M.R., Muzio, R.N., 2007. Common toads (*Bufo arenarum*) learn to anticipate and avoid hypertonic saline solutions. *J. Comp. Psychol.* 121, 419–427.
- David, R.S., Jaeger, R.G., 1981. Prey location through chemical cues by a terrestrial salamander. *Copeia* 1981, 435–440.
- Davis, K.M., 2009. Sociality, cognition and social learning in turtles (Emydidae). Unpublished doctoral dissertation. University of Tennessee, Knoxville, TN.
- Davis, K., Burghardt, G.M., 2007. Training and long-term memory of a novel food acquisition task in a turtle (*Pseudemys nelsoni*). *Behav. Proc.* 75, 225–230.
- Davis, K.M., Burghardt, G.M., 2011. Turtles (*Pseudemys nelsoni*) learn about visual cues indicating food from experienced turtles. *J. Comp. Psychol.* 125, 404–410.
- Davis, K.M., Burghardt, G.M., 2012. Long-term retention of visual tasks by two species of emydid turtles, *Pseudemys nelsoni* and *Trachemys scripta*. *J. Comp. Psychol.* 126, 213–223.
- Day, L.B., Crews, D., Wilczynski, W., 1999. Spatial and reversal learning in congeneric lizards with different foraging strategies. *Anim. Behav.* 57, 393–407.
- Domjan, M., Cusato, B., Krause, M., 2004. Learning with arbitrary versus ecological conditioned stimuli: evidence from sexual conditioning. *Psychon. Bull. Rev.* 11, 232–246.
- Doody, J.S., Burghardt, G.M., Dinets, V., 2013. Breaking the social-nonsocial dichotomy: A role for reptiles in vertebrate social behaviour research? *Ethology* 119, 95–103.
- Elepfandt, A., 1985. Naturalistic conditioning reveals good learning in a frog (*Xenopus laevis*). *Naturwissenschaften* 72, 492–493.
- Ferrari, M.C.O., Chivers, D.P., 2008. Cultural learning of predator recognition in mixed-species assemblages of frogs: the effect of tutor-to-observer ratio. *Anim. Behav.* 75, 1921–1925.
- Finkenstadt, T., Ewert, J.-P., 1988. Stimulus-specific long-term habituation of visually guided orienting behavior toward prey in toads: A  $^{14}\text{C}$ -2DG study. *J. Comp. Physiol. A: Neuroethol. Sensory Neural Behav. Physiol.* 163, 1–11.
- Fischer, J.H., Freake, S.C., Borland, S.C., Phillips, J.B., 2001. Evidence for the use of magnetic map information by an amphibian. *Anim. Behav.* 62, 1–10.
- Fleming, G.J., 2007. Reptile behavioral problems, enrichment, and training. *Proc. N. Am. Vet. Conf.* 21, 1539–1541.
- Gaalema, D.E., 2010. Sexual conditioning in the dyeing poison dart frog (*Dendrobates tinctorius*). Unpublished doctoral dissertation. Georgia Institute of Technology, Atlanta, GA.
- Gaalema, D.E., 2011. Visual discrimination and reversal learning in rough-necked monitor lizards (*Varanus rudicollis*). *J. Comp. Psychol.* 125, 246–249.
- Gerhardt, H.C., 1994. The evolution of vocalization in frogs and toads. *Ann. Rev. Ecol. Syst.* 25, 293–324.
- Garrick, L.D., Lang, J.W., Herzog, H.A., 1978. Social signals of adult American alligators. *Bull. Am. Mus. Nat. Hist.* 160, 155–192.
- Gibbons, M.E., Ferguson, A.M., Lee, D.R., Jaeger, R.G., 2003. Mother-offspring discrimination in the red-backed salamander may be context dependent. *Herpetologica* 59, 322–333.
- Gillette, J.R., Jaeger, R.G., Peterson, M.G., 2000. Social monogamy in a territorial salamander. *Anim. Behav.* 59, 1241–1250.
- Glickman, S.E., Sroges, R.W., 1966. Curiosity in zoo animals. *Behaviour* 26, 151–188.
- Greenberg, N., 1992. The saurian psyche revisited: lizards in research. In: Schaeffer, D.O., Kleinow, K.M., Krulish, L. (Eds.), *The Care and Use of Amphibians, Reptiles, and Fish in Research*. Scientists Center for Animal Welfare, Bethesda, MD, pp. 75–91.
- Greenberg, N., 1995. Ethologically informed design in husbandry and research. In: Warwick, C., Frye, F.L., Murphy, J.B. (Eds.), *Health and Welfare of Captive Reptiles*. Chapman & Hall, London, pp. 239–262.
- Hansknecht, K.A., Burghardt, G.M., 2010. Stimulus control of lingual predatory luring and related foraging tactics of Mangrove Salt-marsh Snakes (*Nerodia clarkii compressicauda*). *J. Comp. Psychol.* 124, 159–165.
- Hayes, M.P., Jennings, M.R., Mellen, J.D., 1998. Beyond mammals: environmental enrichment for amphibians and reptiles. In: Shepherdson, D.J., Mellen, J.D., Hutchins, M. (Eds.), *Second Nature: Environmental Enrichment for Captive Animals*. Smithsonian Institution Press, Washington, DC, pp. 205–234.
- Heatwole, H., Dawley, E.M. (Eds.), 1998. *Amphibian Biology*, vol. 3. Sensory Perception Surrey, Beatty & Sons, Chipping Norton, NSW.
- Heatwole, H., Sullivan, B.K. (Eds.), 1995. *Amphibian Biology*, vol. 2. Social Behaviour Surrey, Beatty & Sons, Chipping Norton, NSW.
- Herzog Jr., H.A., Bowers, B.B., Burghardt, G.M., 1989. Development of antipredator responses in snakes: IV. Interspecific and intraspecific differences in habituation of defensive behavior. *Dev. Psychobiol.* 22, 489–508.
- Holtzman, D.A., Harris, T.W., Aranguren, G., Bostock, E., 1999. Spatial learning of an escape task by young corn snakes, *Elaphe guttata guttata*. *Anim. Behav.* 57, 51–60.
- Hosey, G., Melfi, V., Pankhurst, S., 2009. *Zoo Animals. Behaviour, Management, Welfare*. Oxford University Press, Oxford.
- Houck, L.D., 1998. Integrative studies of amphibians: from molecules to mating. *Am. Zool.* 38, 108–117.
- Hurme, K., Gonzalez, K., Halversen, M., Foster, B., Moore, M., Chepko-Sade, D.D., 2003. Environmental enrichment for dendrobatid frogs. *J. Appl. Anim. Welf. Sci.* 6, 285–299.
- Jaeger, R.G., Forester, D.C., 1993. Social behavior of plethodontid salamanders. *Herpetologica* 49, 163–175.
- Jaeger, R.G., Gergits, W.F., 1979. Intra- and interspecific communication in salamanders through chemical signals on the substrate. *Anim. Behav.* 27, 150–156.



- Jaeger, R.G., Gillette, J.R., Cooper, R.C., 2002. Sexual coercion in a territorial salamander: males punish socially polyandrous female partners. *Anim. Behav.* 63, 871–877.
- Kanaan, V.T., Hötzel, M.J., 2011. Letter to the Editor. Does environmental enrichment really matter? A case study using the eastern fence lizard, *Sceloporus undulatus*. *Appl. Anim. Behav. Sci.* 135, 169–170.
- Kaufman, J.D., Burghardt, G.M., Phillips, J.A., 1996. Sensory cues and foraging decisions in a large carnivorous lizard, *Varanus albigularis*. *Anim. Behav.* 52, 727–736.
- King, C., 1993. Environmental enrichment: is it for the birds? *Zoo Biol.* 12, 509–512.
- Kramer, M., Burghardt, G.M., 1998. Precocious courtship and play in emydid turtles. *Ethology* 104, 38–56.
- Krause, M., Burghardt, G.M., Lentini, A., 1999. Object provisioning for Nile soft-shelled turtles (*Trionyx triunguis*). *Lab. Anim.* 28, 38–41.
- Kuppert, S., 2013. Providing enrichment in captive amphibians and reptiles: is it important to know their communication? Smithsonian Herpetological Information Service No. 142.
- Lang, C.D., Jaeger, R.G., 2000. Defense of territories by male-female pairs in the red-backed salamander (*Plethodon cinereus*). *Copeia* 2000, 169–177.
- Leal, M., Powell, B.J., 2012. Behavioural flexibility and problem-solving in a tropical lizard. *Biol. Lett.* 8, 28–30.
- Lehner, P.N., 1996. *Handbook of Ethological Methods*, second ed. Cambridge University Press, Cambridge.
- López, J.C., Rodríguez, F., Gómez, Y., Varagas, J.P., Broglio, C., Salas, C., 2000. Place and cue learning in turtles. *Anim. Learn. Behav.* 28, 360–372.
- López, J.C., Gómez, Y., Rodríguez, F., Broglio, C., Varagas, J.P., Salas, C., 2001. Spatial learning in turtles. *Anim. Cogn.* 4, 49–59.
- Luthardt-Laimer, G., 1983. Ontogeny of preferences to visual prey stimulus parameters in salamanders. *J. Herpetol.* 17, 221–227.
- MacLean, P., 1985. Brain evolution relating to family, play and the separation call. *Arch. Gen. Psychiatry* 42, 405–417.
- McRobert, S.P., 2003. Methodologies for the care, maintenance, and breeding of tropical poison frogs. *J. Appl. Anim. Welf. Sci.* 6, 95–102.
- Maier, N.R.F., Schneirla, T.C., 1935. *Principles of Animal Psychology*. McGraw-Hill, New York.
- Manrod, J.D., 2003. Play behavior and enrichment in two species of monitor lizards (*Varanus*). Unpublished M.S. Thesis. University of Tennessee, Knoxville.
- Manrod, J.D., Hartdegen, R., Burghardt, G.M., 2008. Rapid solving of a problem apparatus by juvenile black-throated monitor lizards (*Varanus albigularis albigularis*). *Anim. Cogn.* 11, 263–267.
- Maple, T.L., Perdue, B.M., 2013. *Zoo Animal Welfare*. Springer-Verlag, Berlin/Heidelberg.
- Markowitz, H., 1982. *Behavioral Enrichment in the Zoo*. Van Nostrand Reinhold, New York.
- Markowitz, H., Gavazzi, A.J., 1996. Definitions and goals of enrichment. In: Burghardt, G.M., Bielitski, G.M., Boyce, J.T., Schaefer, J.R.D.O. (Eds.), *The Well-Being of Animals in Zoo and Aquarium Sponsored Research*. Scientists Center for Animal Welfare, Greenbelt, MD, pp. 85–90.
- Martin, P., Bateson, P., 1993. *Measuring Behavior: An Introductory Guide*, second ed. Cambridge University Press, Cambridge.
- Mellen, J.D., MacPhee, M.S., 2001. Philosophy of environmental enrichment: past, present, and future. *Zoo Biol.* 20, 211–226.
- Mench, J.A., 1998. Environmental enrichment and the importance of exploratory behavior. In: Shepherdson, D.J., Mellen, J.D., Hutchins, M. (Eds.), *Second Nature: Environmental Enrichment for Captive Animals*. Smithsonian Institution Press, Washington, DC, pp. 30–46.
- Mendyk, R.W., Horn, H.-G., 2011. Skilled forelimb movements and extractive foraging in the arboreal monitor lizard *Varanus beccarii* (Doria, 1874). *Herpetol. Rev.* 42, 343–349.
- Morlock, H., 1989. Learning. In: Harless, M., Morlock, H. (Eds.), *Turtles: Perspectives and research*. Robert E. Krieger, Malabar, FL, pp. 455–474.
- Murphy, J.B., 1976. Pedal luring in the leptodactylid frog, *Ceratophrys calcarata*. *Herpetologica* 32, 339–341.
- Murphy, J.B., Adler, K., Collins, J.T. (Eds.), 1994. *Captive Management and Conservation of Amphibians and Reptiles*. Society for the Study of Reptiles and Amphibians, Ithaca, NY.
- Murray, D.L., Roth, J.D., Wirsing, A.J., 2004. Predation risk avoidance by terrestrial amphibians: The role of prey experience and vulnerability to native and exotic predators. *Ethology* 110, 635–647.
- Muzio, R.N., Segura, E.T., Papini, M.R., 1994. Learning under partial reinforcement in the toad (*Bufo arenarum*): Effects of lesions in the medial pallium. *Behav. Neural Biol.* 61, 36–46.
- Muzio, R.N., Ruetti, E., Papini, M.R., 2006. Determinants of instrumental extinction in terrestrial toads (*Bufo arenarum*). *Learn. Motiv.* 37, 346–356.
- Noble, D.W.A., Carazu, P., Whiting, M.J., 2012. Learning outdoors: male lizards show flexible spatial learning under semi-natural conditions. *Biol. Lett.* 8, 946–948.
- Panksepp, J., Panksepp, J.B., 2000. The seven sins of evolutionary psychology. *Evol. Cogn.* 6, 108–131.
- Paradis, S., Cabanac, M., 2004. Flavor aversion learning induced by lithium chloride in reptiles but not in amphibians. *Behav. Proc.* 67, 11–18.
- Phillips, C.J.C., Jiang, Z., Hatton, A.J., Tribe, A., Bouar, M.le., Guerin, M., Murray, P.J., 2011. Environmental enrichment for captive Eastern blue-tongue lizards (*Tiliqua scincoides*). *Anim. Welf.* 20, 377–384.
- Pianka, E.R., Vitt, L.J., 2003. *Lizards: Windows to the Evolution of Diversity*. University of California Press, Berkeley.
- Prosen, E.D., Jaeger, R.G., Lee, D.R., 2004. Sexual coercion in a territorial salamander: females punish socially polygynous male partners. *Anim. Behav.* 67, 85–92.
- Radcliffe, C.W., Chiszar, D., Estep, K., Murphy, J.B., Smith, H.M., 1986. Observations on pedal luring and pedal movements in leptodactylid frogs. *J. Herpetol.* 20, 300–306.
- Reed, B.T., 2005. *Guidance on the Housing and Care of the African Clawed Frog *Xenopus laevis**. Research Animals Department, RSPCA, West Sussex, England.
- Rivas, J., Burghardt, G.M., 2002. Crotalophormism: a metaphor for understanding anthropomorphism by omission. In: Bekoff, M., Allen, C., Burghardt, G.M. (Eds.), *The Cognitive Animal: Theoretical, Methodological, and Empirical approaches*. MIT Press, Cambridge, MA, pp. 9–17.
- Rosier, R.L., Langkilde, T., 2011a. Does environmental enrichment really matter? A case study using the eastern fence lizard, *Sceloporus undulatus*. *Appl. Anim. Behav. Sci.* 131, 71–76.
- Rosier, R.L., Langkilde, T., 2011b. In response to the letter to the editor regarding the article: Does environmental enrichment really matter? A case study using the eastern fence lizard, *Sceloporus undulatus*. *Appl. Anim. Behav. Sci.* 135, 171–172.
- Ryan, M.J., 1985. *The Túngara Frog*. University of Chicago Press, Chicago.
- Saudargas, R.A., Drummer, L.C., 1996. Single subject (small N) research designs and zoo research. *Zoo Biol.* 15, 173–181.
- Schaeffer, D.O., Kleinow, K.M., Krulish, L. (Eds.), 1992. *The Care and Use of Amphibians, Reptiles, and Fish in Research*. Scientists Center for Animal Welfare, Bethesda, MD.
- Schultz, T.W., Dawson, D.A., 2003. Housing and husbandry of *Xenopus* for oocyte production. *Lab Anim.* 32 (2), 34–39.
- Shoop, C.R., 1965. Orientation of *Ambystoma maculatum*: movements to and from breeding ponds. *Science* 149, 558–559.
- Shibasaki, M., Ishida, M., 2012. Effects of overtraining on extinction in newts (*Cynops pyrrhogaster*). *J. Comp. Psychol.* 126, 368–371.
- Skurski, M., 2010. Reptile enrichment: thinking outside the pillowcase. *Proc. N. Amer. Vet. Conf.* 24, 1693–1694.
- Terrick, T.D., Mumme, R.L., Burghardt, G.M., 1995. Aposematic coloration enhances chemosensory recognition of noxious prey in the garter snake, *Thamnophis radix*. *Anim. Behav.* 49, 857–866.
- Therrien, C.L., Gaster, L., Cunningham-Smith, P., Manire, C.A., 2007. Experimental evaluation of environmental enrichment of sea turtles. *Zoo Biol.* 26, 407–416.
- Torreilles, S.L., Green, S.L., 2007. Refuge cover decreases the incidence of bite wounds in laboratory South African clawed frogs (*Xenopus laevis*). *J. Am. Assn. Lab. Anim. Sci.* 46 (5), 33–36.
- Twitty, V.C., Grant, D., Anderson, O., 1967. Amphibian orientation: an unexpected observation. *Science* 155, 352.
- Uller, C., Jaeger, R., Guidry, G., Martin, C., 2003. Salamanders (*Plethodon cinereus*) go for more: rudiments of number in an amphibian. *Anim. Cogn.* 6, 105–112.
- Van der Weerd, H.A., Day, J.E.L., 2009. A review of environmental enrichment for pigs housed in intensive housing systems. *Appl. Anim. Welf. Sci.* 116, 1–20.
- Warwick, C., 1990. Reptilian ethology in captivity: observations of some problems and an evaluation of their aetiology. *Appl. Anim. Behav. Sci.* 26, 1–13.
- Warwick, C., Frye, F.L., Murphy, J.B. (Eds.), 1995. *Health and Welfare of Captive Reptiles*. Chapman & Hall, London.
- Waters, R.M., Burghardt, G.M., 2013. Prey availability influences the ontogeny and timing of chemoreception-based prey shifting in the striped crayfish snake, *Regina alleni*. *J. Comp. Psychol.* 127, 49–55.
- Wenz, E., Himstedt, W., 1990. Telencephalic structures are involved in learning and memory in the newt *Triturus alpestris*. *Naturwissenschaften* 77, 239–240.
- Wilkinson, A., Chan, H.-M., Hall, G., 2007. Spatial learning and memory in the tortoise (*Geochelone carbonaria*). *J. Comp. Psychol.* 121, 412–418.



- Wilkinson, A., Coward, S., Hall, G., 2009. Visual and response-based navigation in the tortoise (*Geochelone carbonaria*). *Anim. Cogn.* 12, 779–787.
- Wilkinson, A., Huber, L., 2012. Cold-blooded cognition: Reptilian cognitive abilities. In: Vonk, J., Shackelford, T.K. (Eds.), *The Oxford Handbook of Comparative Evolutionary Psychology*. Oxford University Press, New York, pp. 129–143.
- Wilkinson, A., Mandl, I., Bugnyar, T., Huber, L., 2010. Gaze following in the red-footed tortoise (*Geochelone carbonaria*). *Anim. Cogn.* 13, 765–769.
- Wise, S.E., Verret, F.D., Jaeger, R.G., 2004. Tail autonomy in territorial salamanders influences scent marking by residents and behavioral responses of intruders to resident chemical cues. *Copeia* 2004, 165–172.
- Yeager, C., Burghardt, G.M., 1991. The effect of food competition on aggregation: Evidence for social recognition in the plains garter snake (*Thamnophis radix*). *J. Comp. Psychol.* 105, 380–386.
- Zimmermann, A., Stauffacher, M., Langhans, W., Würbel, H., 2001. Enrichment-dependent differences in novelty exploration in rats can be explained by habituation. *Behav. Brain Res.* 121, 11–20.