Zoo Biology 27:470–487 (2008)

RESEARCH ARTICLE

Mutual Benefits of Research Collaborations Between Zoos and Academic Institutions

Eduardo J. Fernandez,* and William Timberlake*

Department of Psychological and Brain Sciences, Indiana University, Bloomington, Indiana

Zoos focus on welfare, conservation, education, and research related to animals they keep. Academic institutions emphasize description, experimentation, modeling, and teaching of general and specific animal biology and behavior through work in both laboratory and field. The considerable overlap in concerns and methods has increased interest in collaborative projects, but there is ample room for closer and more extensive interactions. The purpose of this article is to increase awareness of potential research collaborations in three areas: (1) control and analysis of behavior, (2) conservation and propagation of species, and (3) education of students and the general public. In each area, we outline (a) research in zoos, (b) research in academics, and (c) potential collaborative efforts. Zoo Biol 27:470–487, 2008. © 2008 Wiley-Liss, Inc.

Keywords: zoos; academic institutions; research; animal welfare; zoo research; academic research; academia; behavior; conservation; propagation; education

INTRODUCTION

Zoos maintain large and diverse collections of wild and endangered species, expending notable effort on the display, conservation, and propagation of these animals [Hediger, 1964; Seidensticker and Forthman, 1998]. Zoos develop programs to promote the well-being of these species, often focused on environmental

*Correspondence to: Eduardo J. Fernandez, Indiana University, Bloomington, Department of Psychological and Brain Sciences, 1101 East 10th Street, Bloomington, IN 47405.
E-mail: eduferna@indiana.edu
*Correspondence to: William Timberlake, Indiana University, Bloomington, Department of Psychological and Brain Sciences, 1101 East 10th Street, Bloomington, IN 47405.
E-mail: timberla@indiana.edu

DOI 10.1002/zoo.20215
Published online 4 November 2008 in Wiley InterScience (www.interscience.wiley.com).

enrichment and husbandry training procedures [Markowitz and Aday, 1998; Mellen and MacPhee, 2001]. In contrast, academic institutions focus most attention on research related to the biology and behavior of a set of frequently used and often special-bred species. The majority of this research is focused on questions of relevance to humans and medical conditions, though the remainder investigates the evolution, neurophysiology, and behavior of a larger number of species.

Even to a casual observer, it seems evident that there is much to be gained through interactions and collaborations between zoos and academic institutions. For example, knowledge is available about the nature and mechanisms of social and individual behavior that is relevant to housing of captive animals, relations among nearby species, and how humans can effectively interact with captive animals. Despite the many points of potential contact between zoos and academic institutions, some data show a decrease in the overlap of articles from zoos and academic collaborations in common journals. Reviewing types of studies and author's affiliations in articles published in *Zoo Biology* from 1989–1994, Hosey [1997] found that behavioral articles authored by academic researchers alone declined from 73 to 15%, as did ''basic'' research projects (from 36 to 22%). Pointing to a similar lack of overlap in 1993–1994 issues of *Animal Behavior*, Hosey found only three zoo-based studies out of 344 studies, even though 160 of these studies were conducted with animals in captivity, laboratory or otherwise.

A similar separation exists in terms of the professional ties of zoo and academic researchers. Although zoo personnel have conducted an increasing number of research projects [see Hosey, 1997; Kleiman, 1992 for recent reviews of zoo research trends], few involve ties with university researchers. In touring and conducting interviews in 16 American zoos and talking with university professors and students involved in zoo research, Hardy [1992] found that formal research collaborations between academic and zoo institutions were rare. In a similar finding, Finlay and Maple [1986] found that although 89% of 82 American zoos, aquariums, and animal parks surveyed reported that they encouraged outside scientists to conduct research at their institutions, only 21% of those institutions reported having written guidelines that researchers must follow. Even though increasing numbers of curators, directors of research, and caretakers have been academically trained, few of them have joint positions with academic institutions. From the other side, few academic researchers interact extensively with zoos.

Considering the relative wealth of diverse species housed in zoos, especially species that are uncommon or difficult to observe in field settings, the limited contact from the academic side seems puzzling. If we add the increased attempts of zoos to maintain seminaturalistic, enriched settings not generally available with captive laboratory animals, the immediate question is why aren't there more research collaborations between these institutions? As Kleiman [1992] states:

''Zoos have unique potential as sites for behavioral research because they maintain a diversity of living organisms in a standardized and controllable setting. Thus, a zoo cannot be surpassed for comparative studies of homologous behaviors (i.e., the evolution of behavioral characters from an array of closely related species)'' (p 301). One potential increase in collaborative efforts may exist in recent applied research endeavors. This will be discussed at greater length later in this article.

Ignoring for the moment the historical reasons for the separation of research in zoos and academic institutions [Bekiares, 1997; Chiszar et al., 1993], one important point is that the function of animals at each institution differs. Animals in university settings exist primarily for research and teaching. In contrast, zoos house animals for the conservation of a species in conjunction with the attraction and education of patrons visiting the zoo. Thus, in zoos, though research may be considered a contributor to the goals of displaying, breeding, and managing zoo animals, it is usually not as high a priority [Altmann, 1996]. In academics, although the understanding of an animal's interaction with its natural environment and the conservation of species are of interest, the most frequent issues are mechanisms, behavioral control, and relevance to scientific theorizing about health and disease.

Signs of Change

Collaborations between zoos and academic institutions have increased in the past several decades, particularly in the use of applied behavioral technology. In the 1980s, Georgia Institute of Technology established one of the first Ph.D. programs with an area concentration dedicated specifically to applied zoo research projects [e.g., Maple, 1995, 2006; Norton et al., 1995; Wineman et al., 1996]. Two masters programs, University of Maryland, and University of North Texas, have developed concentrations and/or laboratories that encourage students to conduct zoo or other applied captive animal research [Fernandez, 2001; University of Maryland, n.d.]. Additional recent trends in zoo research have been reviewed by other contributors to this volume.

A number of academic researchers have examined applied issues related to the training of animals for husbandry purposes, stress management (including reactions to visitors), and enrichment [Chamove et al., 1988; Grandin et. al, 1995; Mitchell et al., 1990; Moodie and Chamove, 1990]. However, this shift toward applied issues has not always been well received by researchers. For example, both Hosey [1997] and Kleiman [1992] viewed this increase in applied projects, which appeared correlated with a decrease in more traditional research, as potentially disruptive of basic research.

An historical examination of the distinctions between applied and basic research, and their role in the interaction of zoos and academic institutions is outside the scope of this article. It may be that an emphasis on applied research will help drive future basic research collaborations in zoos, but no surveys or studies at present have investigated this possibility. In this article, we will focus on how zoos and academic institutions can benefit from and contribute to each other's goals in studying and interacting with animals.

We will briefly examine three aspects of animal biology and behavior that appear to lend themselves to common goals and collaborative investigation by zoos and academic institutions: (1) control and analysis of behavior, (2) conservation and propagation of species, and (3) education of students and the general public. These three areas were chosen based on the American Zoos and Aquarium's (AZA) mission to achieve excellence in the care and welfare, conservation, and education of the species they house [AZA, 2006] We will examine the separate contributions of zoos and academic institutions to each area, and then consider examples of collaboration that seem likely to emerge. Through such collaboration, both institutions can further develop the current understanding of the causality and function of animal behavior, the conservation and propagation of species, and education of students and the public about the importance of conservation.

BEHAVIORAL RESEARCH: ZOO–ACADEMIC CONTRIBUTIONS

Behavioral research has had a long-standing tradition within zoos. Although recent efforts have increased focus on more applied issues, basic behavioral examinations continue to play a significant part in the research efforts conducted by zoos [Kleiman, 1992]. The following section examines some of the efforts zoological and academic institutions have made in studying animal behavior, based on samples of research in two areas: (1) studies on social behavior, and (2) training of animals. These two areas were selected because of their importance for various basic research questions in academic institutions, as well as their importance for maintaining a variety of species in captive zoo settings. Although courtship, mating, and breeding also play a significant role in behavioral research for both zoos and academia, they will be addressed later in the section on conservation and propagation.

Research on Social Behavior

The study of social factors in zoos.

A number of researchers have taken advantage of the important efforts of zoos to house animals in groups to study social organization and interactions within and among a species. For example, Collias et al. [1966] were able to study territoriality, breeding, and mobility across roosting sites in red jungle fowl (*Galus galus*) in a large housing area that allowed the birds to interact and mate freely. Similarly, Rowden [2000] was able to study social interactions in captive Bulwer's wattled pheasants (*Lophura bulweri*) by manipulating the number of species housed together. Generally, this species of bird has been housed in prearranged pairs, so knowledge of their mating systems is limited. By placing the pheasants in larger groups of initially unpaired animals, the author was able to explore and develop hypotheses about their mating systems and interactions outside captivity. This study also provided immediate suggestions for how such pheasants could be housed in other captive settings to promote their welfare.

Another study by Nimon and Dalziel [1992] took advantage of a unique zoo setting to study social interactions between zoo visitors, a long-billed corella (*Cacatua tenuirostris*), and several siamangs (*Hylobates syndactylus*). The authors observed that the corella attempted to engage in more interactions with patrons when fewer visitors were present. In contrast, the siamangs altered their behaviors based on what patrons did. If the patrons were hostile, so were the siamangs. If the patrons engaged in behaviors directed toward the siamang (e.g., reaching out to a siamang), the siamangs engaged in behaviors directed toward the patrons as well. The authors concluded that cross-species social interactions between patrons and the animals studied did occur, and that understanding these interactions could prove important for promote the welfare of animals contained in zoos.

Research on social behavior in academia.

Academic research also has focused on the importance of social factors in animal behavior. For instance, a number of efforts have been made to understand the development, organization, and function of social structure and song in brown-headed cowbirds (*Molothrus ater*), [West and King, 1988; King and West, 1977; for a review, see West et al., 2003]. Their findings included that: females can shape the courtship song in males through use of a wing-stroke in response to parts of the song; that preexisting male groups tended to physically discourage isolate-reared males from singing the songs that were most potent in eliciting copulatory postures from female cowbirds; and that isolation-reared male cowbirds appear to be less effective in gaining copulations owing to an inability to direct their songs toward female cowbirds.

A series of studies by Galef and his coworkers have examined the effects of social interaction on food preferences in Norway rats (*Rattus norvegicus*), [Galef and Beck, 1985; Galef and Wigmore, 1983; for a review, see Galef, 1996; Galef and Giraldeau, 2001]. It was found that rats prefer to eat items that other rats have eaten, based on olfactory cues, presumably transferred through their social interactions. While food preferences are learned in this way, food aversions are not [Galefet al., 1990].

Combining zoo and academia social research.

Both zoological and academic institutions share similar interests in understanding the function of social behavior in animals. The interests of zoos more often have an applied orientation, based on the need to know appropriate ways to house animals in groups, display animals to the public, and provide for their overall welfare. Academic institutions, however, are generally interested in proximate and ultimate functions of social behavior. Nevertheless, both institutions can fulfill these aims while benefiting from and contributing to the goals of the other institution. Zoos provide a unique environment for examining the functions of various behaviors with species that academicians would generally have little contact with. Likewise, by studying basic components of social behavior in zoo-housed animals, academicians can better educate zoo staff on how to display those animals.

For instance, research has been conducted on the use of conditioned taste aversion to reduce grain consumption by avian pests in zoo settings [Forthman, 1984, unpublished report; as cited in Forthman and Ogden, 1992]. A variety of pests provide an immediate health concern in zoo settings, because they can carry diseases that are lethal to zoo animals, consume large quantities of food within an exhibit, and prey on species that exist within the exhibits. Many of these pests are rodents, and methods such as poison or traps are often used to reduce their populations.

Based on research cited previously by Galef and colleagues, it is possible that zoos could use food preferences learned through social interactions to decrease the populations of rats and other pests. For instance, rats studied in the lab often show preferences for items other rats have consumed, even when the observed rat or the food itself has been poisoned [Galef and Beck, 1985; Galef et al., 1990]. Findings such as these could help personnel to better control rats, by using poisons that work more slowly, allowing rats to engage in more social interactions before perishing. In the process, academicians could test the implications of finding in field applications and how they relate to data discovered in the laboratory.

Training of Animals

Training of animals in zoos

The past several decades have seen a dramatic increase in the dramatic increase in the management of captive animals in zoos using behavioral training techniques originating from laboratory learning procedures. The need to manage the behavior of captive animals is well documented, and includes: improved cooperation for husbandry purposes, decreases in aberrant behaviors such as aggression and stereotypies, increases in species-specific behaviors, and promotion of the general "well-being" of captive populations [Desmond and Laule, 1994; Forthman and Ogden, 1992; Laule and Desmond, 1998; Markowitz, 1978]. Recent examples of the application of training techniques in captive settings include using training to decrease aggression in a male chimpanzee during feeding times [Bloomsmith et al., 1994], training a diabetic chimpanzee to allow staff to reliably obtain blood and urine samples [Laule et al., 1996], increasing voluntary movement of group-housed chimpanzees from their outdoor enclosure into an indoor enclosure [Bloomsmith et al., 1998], training an African leopard to forage near acoustic bird sounds for food rewards [Markowitz et al., 1995], and training bongo and nyala, two types of antelope, to enter a crate for husbandry purposes [Grandin et al., 1995; Phillips et al., 1998].

Training research in academia.

Training research in academic institutions usually takes the form of learning procedures using respondent or operant conditioning paradigms [Catania, 1992]. Much of this research has focused on learning procedures using artificial stimuli and arbitrary responses relevant to a variety of taxa (rather than a particular species). Species-typical behaviors and stimuli are generally overlooked in favor of testing broad hypotheses about the phenomenon of learning applicable to a wide range of species [Timberlake, 2001].

However, general procedures are "tuned" to particular species to produce vigorous, reliable results. Tuning is the way in which the experimenter makes contact with niche-related mechanisms (mechanisms relevant to the survival of a particular species within its ecology), thereby clarifying that laboratory studies using food rewards engage species-typical foraging behaviors. For example, mazes used in the study of learning in rats are designed to facilitate performance and memory based on apparent search strategies of rats. The arms of elevated radial mazes have edges suitable for promoting efficient following based on whisker contact, and they are equally spaced to simplify spatial location. Hungry rats will exhaustively (and repeatedly) search such mazes in the absence of food. Further, in the classic multiple "T" mazes used in latent learning studies, the longest uninterrupted path is the correct choice [Timberlake, 2002]. Other examples include the use of keys for pigeons to peck on and movable levers for rats to press, both of which support responses related to the foraging patterns of these species [Timberlake, 1999].

Zoo-academia training research.

In short, training plays an important part in facilitating the care and welfare of animals located in zoos. Training in the laboratory, in addition to calling attention to general procedures that emphasize different kinds of learning (such as operant and respondent learning), depends to a surprising degree on identifying the way in which learning procedures interact with the niche-related stimulus sensitivities and response capabilities of a species. Because zoos necessarily deal with a great variety of species, an understanding of the interaction between laboratory-discovered learning procedures and species-typical qualities should facilitate training.

For instance, consideration of the height off the ground at which a particular primate species typically feeds, the types of sensory cues and manipulation involved, and the social feeding structure, should all be useful for guiding both the feeding and training protocols for that species of primate. From the laboratory view, theories of appetitive structures and the nature of tuning itself could profit greatly from the grounding of these concepts in the behavior of a wide variety of taxa and species. Zoos thus provide a unique environment for academicians to examine how foraging and learning related to foraging occur in multiple species.

In one example, Fernandez et al. [2004] were able to test the effects of combining training with the way food was presented on swimming time and item manipulations in two species of penguin: rockhopper (*Eudyptes chrysocome*) and magellanic penguins (*Spheniscus magellanicus*). During some conditions, food items (in the form of small fish) were placed inside two plastic balls placed in the water that allowed for them to be dispensed when contacted (fish/item condition). During other conditions, penguins were presented with fish for swimming near either of the plastic balls (training condition).

The results suggested that the rockhopper penguins were more likely to both swim and interact with the balls when the training condition was combined with the fish/item condition (combined condition). Either condition alone had little or no effect. In addition, following the combined condition, the rockhopper penguins were more likely to swim and interact with the plastic balls when compared to all previous conditions. At least for the rockhoppers, the results suggested that tuning of the stimuli and embedding them in a species-typical foraging system was critical for engaging natural foraging behaviors, and thus allowing training to be effective. As a result, the zoo could now use simple enrichment items to increase swimming times.

CONSERVATION AND PROPAGATION

One of the most important and emphasized endeavors in zoos is the conservation and propagation of the many endangered species under their control. The following section examines two research areas that play an important role in conservation and propagation efforts: (1) breeding and rearing programs, and (2) reintroduction programs.

Research on Reproduction

Breeding and rearing programs in zoos.

As noted, zoos place a considerable amount of effort on the breeding and rearing of the endangered species within their collections. One of the many programs created to promote these undertakings, the Species Survival Plan® Program (SSP), resulted in the successful breeding and reintroduction of numerous animal species that may otherwise have gone extinct [AZA, on-line]. SSPs allow studbooks to be kept for the species maintained on the program, and therefore facilitate loans of animals to other zoos for breeding purposes. By tracking reproduction, genetic diversity can be maintained in the offspring despite the limited number of individuals within a species that zoos currently house. These efforts are considered so vital, that to facilitate successful breeding, a number of animals in zoos are not publicly exhibited (R. Kinley, personal communication, July 28, 2003).

Examples of breeding programs include for the red bird of paradise (*Paradisaea rubra*) at the New York Zoological Park [Hundgen et al., 1991], artificial insemination programs for Asian elephants (*Elephas maximus*) at the National Zoological Park [Brown et al., 2004], breeding and rearing of the Tarictic hornbill (*Penelopides panini*) at the Jurong Bird Park, [Buay, 1991], behavioral management and breeding programs for giant pandas (*Ailuropoda meanoleuca*) at the Wolong Breeding Center [Zhang et al., 2004], artificial incubation of bird eggs at the Zoological Society of San Diego, [Kuehler and Good, 1990], breeding programs for several species of duikers at the Los Angeles Zoo [Barnes et al., 2002], and hand-rearing of the secretary bird (*Sagittarius serpentarius*) at the Oklahoma City Zoo, [Todd, 1988].

Observations are often made to document courtship, mating, nesting, rearing, and new-born diet and development. In one such case, Myers [2000] observed all of these variables with the Writhe-billed hornbill (*Aceros leucocephalus*) at the Audubon Park and Zoological Garden. As a result of this program, five of nine hatchlings survived, and could be donated to the European Endangered Species Programme. Farrellet al. [2000] examined the breeding behavior of a large group of Chilean flamingos (*Phoenicopterus chilensis*) over a 3-month period of observation. A number of measures were taken, including which members of the group copulated, and the total length of time each parent incubated the eggs. They found that the majority of the flamingos only mated within a pair-bond, and that both males and females spent a considerable portion of their time incubating the eggs.

Carlstead et al. [1999] examined numerous environmental variables correlated with the breeding success of black rhinoceros (*Diceros bicornis*). Twenty-three zoos were surveyed for variables such as enclosure size, frequency of chlorine use, and noise level. The authors found that reproductive success was positively correlated with the size of the rhinos' enclosure, and that zoos with two or more females had a lower reproductive rate. In a similar study, Taylor and Poole [1998] surveyed both Western zoos and Asian elephant centers to assess their Asian elephant breeding success. The survey included variables relating to reproductive behavior and husbandry practices, as well as several environmental factors. They found significantly higher rates of breeding success in the Asian sites, along with lower percentages of stillbirths and infant mortality. They also found that the elephants at the Asian centers reached sexual maturity later than those found in Western zoos. Some variables correlated with these findings included (1) males and females at Western sites had access to each other, and (2) that elephants found in Western zoos were significantly heavier than those found at the Asian centers.

In another study, focal pairs of parakeet auklets (*Cyclorrhynchus psittachula*) were observed with and without the presence of a potential nest attendant present [Grimes and Logan, 2001]. They found that pairs with an attendant present spent significantly greater time feeding and bathing. Additionally, because the attendant bird helped in protecting the nest and incubating the eggs, the pair had to spend less time with intruders. In a similar study of variables affecting breeding, Blay and Cote [2001] examined breeding success for Humboldt penguins (*S. humboldti*) in 16 British zoos as a function of a number of variables, such as nesting materials, size of pool, and enclosure substrate. They found that nesting boxes lined with gravel and sand, large-sized pools, and enclosures with concrete floors produced the greatest per capita breeding success.

Research on reproduction in academia.

Courtship and mating have also been of academic research. We focus here on the effects of learning on breeding success. For example, Hollis et al. [1997] examined the effects of a Pavlovian conditioning procedure on reproductive behavior in a male blue gourami (*Trichogaster trichopterus*). These fish are typically territorial, and when protecting territories, often repel potential mates as well as other males. Fish in the experimental group received a 10 sec presentation of a light (conditioned stimulus: CS) followed by a 5 min presentation of a female (unconditioned stimulus: US). Males in the experimental group spent significantly less time trying to bite females and more time nestbuilding and clasping them, as well as showing a significantly lower latency to spawn with females, when compared with controls not receiving the pairings. As a result, the males in the experimental group produced more offspring than those in the control group.

In another study, Domjan et al. [1998] used a similar Pavlovian conditioning procedure with Japanese quail (*Coturnix japonica)*. Male quail were placed in a distinct experimental chamber (CS), and 2 min after were presented with a female quail (US) they could copulate with. During testing, the males in this experimental group spent significantly more time near a female probe, had greater semen volume, and a greater number of spermatozoa when compared with controls.

Female mate choice has also been examined in the laboratory. More recently, social factors that effect how females select mates have been studied. This particular area of research on sexual selection began largely with guppies [Dugatkin, 1992] and has continued most recently with quail [see Galef and White, 2000]. Similar to other academic research on reproduction, respondent conditioning procedures are often used to test how such procedures will affect female mate choice.

Potential zoo–academia interaction in breeding and rearing research.

Breeding and rearing of endangered species will continue to be one of the primary goals of most zoos. However, few current breeding programs have considered potentiating the reproductive process of males found in zoos [Wildt, 1996]. It seems worthwhile to attend to observations of natural breeding interactions as well as laboratory work [see above] showing how respondent conditioning manipulations of males (exposing them to cues predicting the availability of a receptive female) can facilitate courtship behaviors and semen production. This could increase the likelihood of successfully breeding endangered species in zoos, as well as provide a larger context for testing mechanisms and theories developed in the laboratory.

Zoos also may provide an opportunity to further deal with the issue of female choice of male mates, particularly as a function of females observing the choices of other females. Research mentioned previously, such as that of Dugatkin [1992], could help facilitate how to improve female mating patterns and successful pregnancies. Comparative studies of breeding and rearing practices, both from observations conducted in the zoo's seminaturalistic environments, and from experiments conducted on manipulating breeding and rearing successes in various zoo animals, could markedly increase the data available to academicians interested in theories of breeding behavior and mate selection, while also providing data to guide zoo breeding practices in the process.

Reintroduction Programs

Zoo-based reintroduction programs.

An important aim of many breeding and rearing programs in zoos is to reintroduce animals bred in captivity back into the wild. Most reintroduction programs face critical difficulties: susceptibility to disease, lack of habitat availability, inability to interbreed with existing populations, and financial limitations on transportation and initial supervision, to name but a few [Kleiman, 1996]. Even with these formidable limitations, zoos have been able to successfully reintroduce a number of captive bred species into the wild, and collect various measures of success in the process.

In one example, the endangered black-footed ferret (*Mustela nigripes*) was extensively studied and adapted to potential wild conditions, before being permanently released into the wild [Miller et al., 1998]. Ferret enclosures were designed to mimic many features of the wild, such as a burrow system, and the ability to come in contact with prey. A related species, the Siberian ferret (*M. eversmanii*) was used to test hypotheses on prerelease conditioning, development, and release techniques. Siberian ferrets (after sterilization) were also released into the wild to study natural hunting strategies. By measuring and considering the results of these procedures, the authors were eventually able to successfully reintroduce this species back into the wild.

In another example, golden lion tamarins (*Leontopithecus rosalia*) were extensively trained and studied in captivity for release into the wild [Castroet al., 1998]. Golden lion tamarins bred and raised in captivity were housed in enriched environments that included presentations of predator models, and naturalistic foraging requirements. The authors extensively tested two hypotheses: (1) enrichment earlier to reintroduction enhances survival rates, and (2) there will be significant differences between captive-born and wild golden lion tamarins. In the first case, the hypothesis was not supported, and in the second case, few differences between the captive-born and wild tamarins were found. Still, both the collection of behavioral measures, and the use of training and enrichment may have been useful for eliminating potentially unhealthy tamarins that would not be ideal for reintroduction.

Reintroduction research in academia.

In academic institutions, little has been done to examine the effects of releasing captive-born animals back into the wild. As noted previously, academic institutions are primarily interested in the functional aspects of animal behavior, whereas reintroduction is almost exclusively an applied conservation goal. Academic research, however, has been interested in differences between captive-bred and wild animals. Much of this research has been focused on understanding potential biological mechanisms (such as avoidance responses to natural predators) lost or inhibited by captivity, [Boice, 1970; Clark and Galef, 1977; Vilhunen et al., 2005].

For instance, McPhee [2003] examined the effects of releasing oldfield mice (*Peromyscus polionotus subgriseus*) into a wild-like testing arena. Oldfield mice were collected from the wild and bred in captivity for 35, 14, or 2 generations. In addition, mice caught from the wild were also tested in the arena. A modified open-field arena consisting of a 55-gallon tank with burrow and bedding substrate was used to assess behavioral differences between the groups. Overall, the mice 35 generations removed from the wild showed the least amount of exploratory behavior, and the greatest amount of time in the burrow. Although the mechanisms underlying these changes are unknown, the data still suggest that animals bred in captivity for multiple generations can show significant changes in behavior relative to their wild counterparts.

Zoo-academia reintroduction research.

Because of the increasing importance of dealing with critically endangered species, a collaboration between zoos and academia on issues of reintroduction and handling seems worthwhile. Understanding the behavior of animals in the wild can play an important role in the success of such efforts. Academic research based on field observations of various animals may facilitate reintroduction efforts, and provides an important cornerstone in any reintroduction program.

In addition to research on mating and sexual selection, academics could also conduct extensive observations on free-ranging animals in the wild to help ensure the success and survival of animals released into the wild. For instance, in one study, female mate choice in the field was examined in European kestrels (*Falco tinunculus*) [Hakkarainen et al., 1996]. The authors found that female kestrels chose smaller male kestrels, as evidenced by tarsus length and body mass. The authors also found that lighter, shorter-winged male kestrels had better hunting success. Through similar studies, zoos could match animals on SSPs to selectively breed traits that would make those offspring more viable for reintroduction programs.

Likewise, understanding the behavior of released animals can be greatly facilitated by studies of animals in seminaturalistic settings, such as those often found in zoos. Historically, field scientists have elected to utilize zoological settings to hone their observational skills prior to entering the field [e.g., Carpenter, 1937; Schaller, 1963]. In some cases, zoos also can be used as a test site to pilot apparatus and measurement codes with animals before attempting such methods in the wild. For instance, Simeon et al. [2002] were able to test data-loggers on the general activity of captive Humboldt penguins (*S. humboldti*). This allowed them both to test the data-loggers themselves (which were eventually used in a study with wild Humboldt penguins), and to test for any adverse behavioral effects on the penguins.

Furthermore, the investigators found that the penguins habituated to the data-loggers generally within a day, as seen by return to baseline levels of activity and lack of attempts to peck at the device. The obvious implications of such research is that they can ensure that the energetic cost of the devices to the Humboldt penguins, which are one of the most endangered penguin species, will be relatively low, and thereby less likely to increase mortality rates of penguins wearing such a device in the wild. In the process, they can prevent the loss of expensive apparatus, and test for any potential mechanical failures before actual implementation. It is worth noting they did not document the long-term energy demands of wearing the loggers, but they were able to show the penguins demonstrated no differences in the typical behaviors of feeding, swimming, social behaviors.

EDUCATION

A primary goal of zoological institutions is to provide information on the species they exhibit. Whether this is through educating the public about a particular species, conserving the planet's diversity of life, or teaching students interested in learning about zoos and research, zoos put a considerable amount of effort into educating people about animals. In many zoos, education is viewed as a primary means of helping people understand why zoos exist and of promoting greater knowledge about the plight of less well-known endangered species. The following section examines the contributions both zoos and academia have on animal education.

Animal Education at the Zoo

Education of patrons at the zoo.

Zoos spend a considerable amount of time on public education in a variety of forms. Below we consider the areas of: human–animal interactions, exhibit design, visitor perception, and animal influences on zoo visitors.

Human– animal interactions.

One way that zoos educate visitors is by providing opportunities for close human–animal interactions in the form of educational demonstrations, children's zoos, and public feedings [Kreger and Mench, 1995]. In some cases, benefits are achieved by presenting people with access to animal training demonstrations, such as publicly exhibiting trained husbandry behaviors in Asian small-clawed otters [Anderson et al., 2003].

Exhibit design.

Over the past several decades, promoting visitor education and the welfare of the animals have been achieved by designing and creating more naturalistic exhibits. The context the animals are viewed in is considered to be an important factor in influencing how patrons perceive and appreciate the nature of the animals [Coe, 1996]. One study found that subjects rated slides of animals in naturalistic exhibits closer on 11 semantic differential scales (e.g., free vs. restricted, active vs. passive) to ratings given to slides of wild animals than to slides of animals in more traditional caged zoo environments [Finlay et al., 1988]. By presenting animals in such exhibits, the goal is to increase natural behaviors shown by the animals, and therefore to help patrons understand how the animals behave in the wild. Finally, by displaying animals in naturalistic habitats, patrons can be better educated about the importance of habitat protection for wildlife conservation [Coe, 1985].

A second contribution of exhibit design has been in the area of organized and hands-on displays that promote knowledge about various aspects of animal behavior. For instance, Brookfield Zoo had previously developed an interactive zoo exhibit, in which visitors could learn how birds fly. Through the interactive exhibit, visitors learned that many birds use figure-8 wing movements instead of showing a simple flapping motion [Birney, 1988].

A third contribution has to do with the organization of the exhibits either sequentially or in groups of different animals that might be found together in particular ecologies. This is also achieved by presenting mixed-species exhibits, where two or more species are housed within the same exhibit [Thomas and Maruska, 1996].

Patron perception.

One crucial educational goal for most zoos is to change the perception of patrons about specific animals and about zoos in general. Given that zoos are often interested in the conservation of endangered species in the wild, it is difficult to promote such a message if persons outside the zoo community do not feel zoos adequately met the needs of their own animals. In one study, it was found that, though persons surveyed outside a zoo setting believed conservation was the main goal of zoos, they had a number of negative perceptions of the animals zoos exhibit, such as the animals being bored [Reade and Waran, 1996]. In contrast, it was found that persons surveyed inside the zoo had a more positive view of how animals were exhibited. In contrast, it was found that persons with an interactive experience with an elephant were more likely to support continuing a trade moratorium on elephant ivory than those who did not interact with an elephant [Swanagan, 2000]. Swanagan's study is another good example of zoo–university collaboration at the student level. His research fulfilled his thesis requirements for a master's degree at the Georgia Insitute of Technology under the supervision of environmental ethicist, Brian Norton. Swanagan was enrolled in graduate study while employed at Zoo Atlanta where he was encouraged to collaborate with academics.

Animal influences on patrons

Other researchers have examined how the behaviors of the animals directly influence the behaviors of the patrons. Altman [1998] found that persons viewing exhibits in which the animals were engaged in nonstereotyped activity were more likely to have conversations with others about the animals or the animals' behaviors while viewing the exhibit, as opposed to conversations about nonanimal topics. In a similar study, it was found that visitors tended to stay in front of an exhibit longer and the number of total visitors in front of an exhibit was greater when several species of cats were active rather than inactive [Margulis et al., 2003].

Animal Education in Academia

Clearly one of the primary goals of academic institutions is the education of persons attending that institution. In various animal-based programs and departments on university campuses, this is often accomplished through various lecture and laboratory courses, research assistant work, and university-based internship programs. For example, our own institution, Indiana University, offers numerous courses at both the undergraduate and graduate student level that involve some aspect of animal biology and behavior, including Biology of Birds, Animal Behavior, Bioanthropology, Ecology and Environmental Biology, Neural Science, and so on [Indiana University, n.d.]. In addition, Indiana University offers numerous laboratories across several different departments that help educate students about various research projects on some particular aspect of animal biology and behavior.

Although an extensive review of such efforts is beyond the scope of this article, it seems clear that universities put a considerable effort into educating students about numerous animal-related topics. Although the focus of animal education for students may differ than the conservation-geared educational efforts of zoos, both institutions' goals of educating people about aspects of animal biology and behavior allow for various collaborative efforts to be examined.

Academia and Zoo Interactions in Education

Because zoos contain a diversity of animals in relatively controlled seminaturalistic enclosures, a number of academic institutions have used zoos to teach students about animal behavior and research. In one such case, students taking an animal behavior course were given the opportunity to learn about the generality of operant conditioning by training one of several species of animals located at the zoo [Lukas et al., 1998]. In other settings, students have been used to help researchers collect data on various zoo research projects [Fernandez, 2001]. The logic behind using students in both capacities is simple. Students, when appropriately trained, make excellent observers and research assistants, are relatively inexpensive, are enthusiastic about participating in animal projects (especially in zoo settings), and gain first-hand knowledge about species they would otherwise not have [Beck, 1975].

Thus, zoos can extend their education efforts by offering their facilities to undergraduate university students as a place to learn about animal research, while at the same time gaining valuable resources in the form of volunteer research assistants for their current research projects. Finlay and Maple [1986] have shown that many zoos both allow students to participate in zoo/aquarium research, and that many also encourage outside researchers to conduct research within their institution. By incorporating university students into existing research in-house projects, zoos can help promote the education of these students, and increase the likelihood of creating more zoo–academia collaborations.

In turn, academic institutions gain animal facilities that would serve as animal education sites for their students. These zoo sites offer students first-hand experience with a diverse range of animals the students would otherwise not have the ability to experience and learn about.

THE FUTURE OF ZOO–ACADEMIA COLLABORATIONS

Zoos continue to play important, if not critical roles, in animal research, conservation, propagation, and education in current society. Given an increasing trend toward applied research in zoo settings, it is likely that many future animal studies will help merge the three areas distinguished within this article: animal behavior, conservation and propagation, and education. Clearly, advancement of animal conservation and education will require research becoming a primary tool used to help evaluate the effectiveness of breeding programs, the changes in behavior based on the ways in which animals are exhibited, and the attitudes of patrons encountering various zoo exhibits.

Behavioral research programs can serve both functional purposes for the animals, as well as gain important information about species often difficult to access [Markowitz, 1978]. This emergence of the dual applied/basic approach to zoo research will likely continue, and help promote both a better understanding of animal behavior, and enhanced conservation of animals both within the zoo and in the wild. Similarly, as efforts continue in breeding and reintroducing animals into the wild, behavioral research will likely help promote a better understanding of the variables necessary to produce effective outcomes.

Research collaborations between academic and zoological institutions can also help promote the conservation and education goals of zoos. By experimentally examining and manipulating the environments that contain zoo animals, we are more likely to discover important species-specific mechanisms that will encourage successful breeding programs. In the process, we may also discover the conditions necessary for producing naturalistic behaviors in various captive species, thereby promoting active, healthy zoo animals for visitors to view. By accomplishing this, we can help zoo visitors to understand the significance of conserving the animals we still have. This would help promote the re-introduction and survival of captive-bred zoo animals that could thrive in the wild once again.

This article outlines just a few of the advantages of zoos and academic institutions working together to provide experimental and observational knowledge that promotes education, welfare, conservation, and a greater understanding of how and why animals behave in particular ways. We hope that the current increase in applied zoo research will foster further collaborations, as well as promote a greater understanding of animal behavior.

REFERENCES

Altmann J. 1996. Summary, looking forward. In: Burghardt GM, Bielitzki JT, Boyce JR, Schaeffer DO, editors. The well-being of animals in zoo and aquarium sponsored research. Greenbelt, MD: Scientists Center for Animal Welfare. p 133–135.

Altman JD. 1998. Animal activity and visitor learning at the zoo. Anthrozoos 11:12–21.

American Zoos and Aquariums. Species Survival Plan® Program. [On-line]. http://www.aza.org/ConScience/ConScienceSSPFact/.

American Zoos and Aquariums. 2006. Our Mission. [On-line]. http://www.aza.org/AboutAZA/MissionVision/.

Anderson US, Kelling AS, Pressley-Keough R, Bloomsmith MA, Maple TL. 2003. Enhancing the zoo visitor's experience by public animal training and oral interpretation at an otter exhibit. Environ Behav 35:826–841.

Barnes R, Greene K, Holland J, Lamm, M. 2002. Management and husbandry of duikers at the Los Angeles Zoo. Zoo Biol 21:107–121.

Beck BB. 1975. Student behavioral research. Research in zoos and aquariums. Washington, D.C.: National Academy of Sciences. p 91–102.

Bekiares NA. 1997. Book review: a primer for zoo and aquarium research. Zoo Biol 16:369–371.

Birney BA. 1988. Brookfield zoo's "Flying Walk" exhibit: formative evaluation aids in the development of an interactive exhibit in an informal learning setting. Environ Behav 20:416–434.

Blay N, Cote IM. 2001. Optimal conditions for breeding of captive Humboldt penguins (*Spheniscus humboldti*): a survey of British zoos. Zoo Biol 20:545–555.

Bloomsmith MA, Laule GE, Alford PL, Thurston RH. 1994. Using training to moderate chimpanzee aggression during feeding. Zoo Biol 13: 557–566.

Bloomsmith MA, Stone AM, Laule GE. 1998. Positive reinforcement training to enhance the voluntary movement of group-housed chimpanzees within their enclosures. Zoo Biol 17:333–341.

Boice R. 1970. Effect of domestication on avoidance learning in the Norway rat. Psychon Sci 18:13–14.

Brown JL, Goritz F, Pratt-Hawkes N, Hermes R, Galloway M, Graham LH, Gray C, Waler SL, Gomez A, Moreland R, Murray S, Schmitt DL, Howard J, Lehnhardt J, Beck B, Bellem A, Montali R, Hildebrant TB. 2004. Successful artificial insemination of an Asian elephant at the National Zoological Park. Zoo Biol 23: 45–63.

Buay J. 1991. Breeding and hand-rearing the Tarictic hornbill *Penelopides panini* at Hurong Bird Park, Singapore. Int Zoo Yearbook 30: 180–187.

Carlstead K, Fraser J, Bennett C, Kleiman DG. 1999. Black rhinoceros (*Diceros bicornis*) in US zoos: II. Behavior, breeding success, and mortality in relation to housing facilities. Zoo Biol 18:35–52.

Carpenter CR. 1937. An observational study of two mountain gorillas (*Gorilla berengi*). Hum Biol 9:175–196.

Castro MI, Beck BB, Kleiman DG, Ruiz-Miranda CR, Rosenberger AL. 1998. Environmental enrichment in a reintroduction program for golden lion tamarins (*Leontopithecus rosalia*). In: Shepherdson DJ, Mellen JD, Hutchins M, editors. Second nature: environmental enrichment for captive animals. Washington: Smithsonian Institution Press. p 113–128.

Catania AC. 1992. Learning. 3rd ed. Englewood Cliffs, NJ: Prentice-Hall.

Chamove AS, Hosey GR, Schaetzel P. 1988. Visitors excite primates in zoos. Zoo Biol 7:359–369.

Chiszar D, Murphy BB, Smith HM. 1993. In search of zoo–academic collaborations: a research agenda for the 1990s. Herpetologica 49: 388–500.

Clark MM, Galef BG. 1977. The role of the physical rearing environment in the domestication of the Mongolian gerbil (*Meriones unguiculatus*). Anim Behav 25:298–316.

Coe JC. 1985. Design and perception: making the zoo experience real. Zoo Biol 4:197–208.

Coe JC. 1996. What's the message? Education through exhibit design. In: Kleiman DG, Allen ME, Thompson KV, Lumpkin S, editors. Wild mammals in captivity: principles and techniques. Chicago: The University of Chicago Press. p 167–174.

Collias NE, Collias EC, Hunsaker D. 1966. Locality fixation, mobility and social organization within an unconfined population of red jungle fowl. Anim Behav 14:550–559.

Desmond T, Laule G. 1994. Use of positive reinforcement training in the management of species for reproduction. Zoo Biol 13:471–477.

Domjan M, Blesbois E, Williams J. 1998. The adaptive significance of sexual conditioning: Pavlovian control of sperm release. Psychol Sci 9:411–415.

Dugatkin LA. 1992. Sexual selection and imitation: females copy the mate choice of others. Am Nat 139:1384–1389.

Farrell MA, Barry E, Marples N. 2000. Breeding behavior in a flock of Chilean flamingos (*Phoenicopterus chilensis*) at Dublin zoo. Zoo Biol 19:227–237.

Fernandez EJ. 2001. ORCA: a new kind of lab. Clicker J Mag Anim Trainers 51:18–23.

Fernandez EJ, Kinley R, Timberlake W. 2004. Training penguins to interact with enrichment items for lasting effects. Paper presented at the Animal Behavior Management Alliance, Baltimore, MD.

Finlay T, James LR, Maple TL. 1988. People's perceptions of animals: the influence of zoo environment. Environ Behav 20:508–528.

Finlay TW, Maple TL. 1986. A survey of research in American zoos and aquariums. Zoo Biol 5:261–268.

Forthman DL, Ogden JJ. 1992. The role of applied behavior analysis in zoo management: today and tomorrow. J Appl Behav Anal 25: 647–652.

Galef BG. 1996. Social enhancement of food preferences in Norway rats: a brief review. In: Heyes CM, Galef BG, editors. Social learning in animals: the roots of culture. San Diego, CA: Academic Press. p 49–64.

Galef BG, Beck M. 1985. Aversive and attractive marking of toxic and safe foods by Norway rats. Behav Neural Biol 43:298–310.

Galef BG, Giraldeau LA. 2001. Social influences on foraging in vertebrates: causal mechanisms and adaptive functions. Anim Behav 61:3–15.

Galef BG, White DJ. 2000. Evidence of social effects on mate choice in vertebrates. Behav Process 51:167–175.

Galef BG, Wigmore SW. 1983. Transfer of information concerning distant foods: a laboratory investigation of the ''information-centre'' hypothesis. Anim Behav 31:748–758.

Galef BG, McQuoid LM, Whiskin EE. 1990. Further evidence that Norway rats do not socially transmit learned aversions to toxic baits. Anim Learn Behav 18:199–205.

Grandin T, Rooney MB, Phillips M, Cambre RC, Irlbeck NA, Graffam W. 1995. Conditioning of Nyala (*Tragelaphus angasi*) to blood sampling in a crate with positive reinforcement. Zoo Biol 14:261–273.

Grimes J, Logan C. 2001. Nest attendants in parakeet auklets. Zoo Biol 20:271–277.

Hakkarainen H, Huhta E, Lahti K, Lundvall P, Mappes T, Tolonen P, Wiehn J. 1996. A test of male mating and hunting success in the kestrel: the advantages of smallness? Behav Ecol Sociobiol 39:375–380.

Hardy DF. 1992. The consortium of aquariums, universities and zoos. Int Zoo News 39:7–20.

Hediger H. 1964. Wild animals in captivity. London, UK: Dover.

Hollis KL, Pharr VL, Dumas MJ, Britton GB, Field J. 1997. Classical conditioning provides paternity advantage for territorial male blue gouramis (*Trichogaster trichopterus*). J Comp Psychol 111:219–225.

Hosey GR. 1997. Behavioural research in zoos: academic perspectives. Appl Anim Behav Sci 51:199–207.

Hundgen K, Hutchins M, Sheppard C, Bruning D, Worth W. 1991. Management and breeding of the red bird of paradise *Paradisaea rubra* at the New York Zoological Park. Int Zoo Yearbook 30:192–199.
Indiana University. 2006. Center for the integrative study of animal behavior: member course offerings. Retrieved March 5th, 2006, from http://www.indiana.edu/~animal/academics/seminars/Courseoffering-F03.html.
King AP, West MJ. 1977. Species identification in the North American cowbird: appropriate responses to abnormal song. Science 195: 1002–1004.
Kleiman DG. 1992. Behavior research in zoos: past, present, and future. Zoo Biol 11:301–312.
Kleiman DG. 1996. Reintroduction programs. In: Kleiman DG, Allen ME, Thompson KV, Lumpkin S, editors. Wild mammals in captivity: principles and techniques. Chicago: The University of Chicago Press. p 297–305.
Kreger MD, Mench JA. 1995. Visitor–animal interactions at the zoo. Anthrozoos 8: 143–158.
Kuehler C, Good J. 1990. Artificial incubation of bird eggs at the Zoological Society of San Diego (California, USA). Int Zoo Yearbook 29: 118–136.
Laule G, Desmond T. 1998. Positive reinforcement training as an enrichment strategy. In: Shepherdson DJ, Mellen JD, Hutchins M, editors. Second nature: environmental enrichment for captive animals. Washington: Smithsonian Institution Press. p 302–313.
Laule GE, Thurston RH, Alford PL, Bloomsmith MA. 1996. Training to reliably obtain blood and urine samples from a diabetic chimpanzee (*Pan troglodytes*). Zoo Biol 15:587–591.
Lukas KE, Marr J, Maple TL. 1998. Teaching operant conditioning at the zoo. Teach Psychol 25:112–116.
Maple TL. 1995. Toward a responsible zoo agenda. In: Norton BG, Hutchins M, Stevens EF, Maple TL, editors. Ethics on the ark. Washington, DC: Smithsonian Institution Press. p 20–30.
Maple TL. 2006. Tales of an Entrepreneurial Animal Psychologist. Observer 19:11–13.
Margulis SW, Hoyos C, Anderson M. 2003. Effect of felid activity on zoo visitor interest. Zoo Biol 22:587–599.
Markowitz H. 1978. Engineering environments for behavioral opportunities in the zoo. Behav Anal 1:34–47.
Markowitz H, Aday C. 1998. Power for captive animals: contingencies and nature. In: Shepherdson DJ, Mellen JD, Hutchins M, editors. Second nature: environmental enrichment for captive animals. Washington: Smithsonian Institution Press. p 47–58.
Markowitz H, Aday C, Gavazzi A. 1995. Effectiveness of acoustic "prey": environmental enrichment for a captive African leopard (*Panthera pardus*). Zoo Biol 14:371–379.
McPhee ME. 2003. Effects of captivity on response to a novel environment in the oldfield mouse (*Peromyscus polionotus subgriseus*). Int J Comp Psychol 16:85–94.
Mellen J, MacPhee S. 2001. Philosophy of environmental enrichment: past, present, and future. Zoo Biol 20:221–226.
Miller B, Biggins D, Vargas A, Hutchins M, Hanebury L, Godbey J, Anderson S, Wemmer C, Oldemeier J. 1998. The captive environment and reintroduction: the black-footed ferret as a case study with comments on other taxa. In: Shepherdson DJ, Mellen JD, Hutchins M, editors. Second nature: environmental enrichment for captive animals. Washington: Smithsonian Institution Press. p 97–112.
Mitchell G, Obradovich S, Sumner D, DeMorris K, Lofton L, Minor J, Cotton L, Foster T. 1990. Cage location effects on visitor attendance at three Sacramento Zoo mangabey enclosures. Zoo Biol 9:55–63.
Moodie EM, Chamove AS. 1990. Brief threatening events beneficial for captive tamarins? Zoo Biol 9:275–286.
Myers MS. 2000. Breeding the Writhe-billed hornbill *Aceros leucocephalus* at Audubon Park and Zoological Garden, New Orleans. Int Zoo Yearbook 37:345–354.
Nimon AJ, Dalziel FR. 1992. Cross-species interaction and communication: a study method applied to captive siamang (*Hylobates syndactylus*) and long-billed corella (*Cacatua tenuirostris*) contacts with humans. Appl Anim Behav Sci 33:261–272.
Phillips M, Grandin T, Graffam W, Irlbeck NA, Cambre RC. 1998. Crate conditioning of bongo (*Tragelaphus eurycerus*) for veterinary and husbandry procedures at the Denver Zoological Gardens. Zoo Biol 17:25–32.
Reade LS, Waran NK. 1996. The modern zoo: how do people perceive zoo animals? Appl Anim Behav Sci 47:109–118.
Rowden J. 2000. Behavior of captive Bulwer's wattled pheasants, *Lophura bulweri* (Galliformes: Phasianidae). Zoo Biol 20:15–25.
Schaller G. 1963. The mountain gorilla: ecology and behavior. University of Chicago Press.
Seidensticker J, Forthman DL. 1998. Evolution, ecology, and enrichment: basic considerations for wild animals in zoos. In: Shepherdson DJ, Mellen JD, Hutchins M, editors. Second nature: environmental enrichment for captive animals. Washington: Smithsonian Institution Press. p 47–58.
Simeone A, Wilson RP, Knauf G, Knauf W, Schutzendube J. 2002. Effects of attached data-loggers on the activity budgets of captive Humboldt penguins. Zoo Biol 21:365–373.
Swanagan JS. 2000. Factors influencing zoo visitors' conservation attitudes and behavior. J Environ Educ 31:26–31.

Taylor VJ, Poole TB. 1998. Captive breeding and infant mortality in Asian elephants: a comparison between twenty Western zoos and three Eastern zoos elephant centers. Zoo Biol 17: 311–332.

Thomas WD, Maruska EJ. 1996. Mixed-species exhibits with mammals. In: Kleiman DG, Allen ME, Thompson KV, Lumpkin S, editors. Wild mammals in captivity: principles and techniques. Chicago: The University of Chicago Press. p 204–213.

Timberlake W. 1997. An animal-centered, causal-system approach to the understanding and control of behavior. Appl Anim Behav Sci 53:107–129.

Timberlake W. 1999. Biological behaviorism. In: O'Donohue W, Kitchener R, editors. Handbook of behaviorism. New York: Academic Press. p 243–284.

Timberlake W. 2001. Integrating niche-related and general process approaches in the study of learning. Behav Process 54:79–94.

Timberlake W. 2002. Niche-related learning in laboratory paradigms: the case of maze behavior in Norway rats. Behav Brain Res 134: 355–374.

Todd WT. 1988. Hand-rearing the secretary bird *Sagittarius serpentarius* at the Oklahoma City (Oklahoma, USA) Zoo. Int Zoo Yearbook 27:258–263.

University of Maryland. 2006. CONS. Retrieved February 20th, 2006, from http://www.life.umd.edu/CONS/.

Vilhunen S, Hirvonen H, Laakkonen MV. 2005. Less is more: social learning of predator recognition requires a low demonstrator to observer ratio in Arctic charr (*Salvelinus alpinus*). Behav Ecol Sociobiol 57:275–282.

West MJ, King AP. 1988. Female visual displays affect the development of male song in the cowbird. Nature 334:244–246.

West MJ, King AP, White DJ. 2003. Discovering culture in birds: the role of learning and development. In: de Waal FBM, Tyack PL, editors. Animal social complexity: intelligence, culture, and individualized societies. Cambridge, MA: Harvard University Press. p 470–492.

Wildt DE. 1996. Male reproduction: assessment, management, and control of fertility. In: Kleiman DG, Allen ME, Thompson KV, Lumpkin S, editors. Wild mammals in captivity: principles and techniques. Chicago: The University of Chicago Press. p 429–450.

Wineman J, Piper C, Maple TL. 1996. Zoos in transition: enriching conservation education for a new generation. Curator 39:94–107.

Zhang G, Swaisgood RR, Zhang H. 2004. Evaluation of behavioral factors influencing reproductive success and failure in captive giant pandas. Zoo Biol 23:15–31.