

5 A SHORT HISTORY OF SCIENTIFIC RESEARCH IN ZOOLOGICAL GARDENS

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Most scientists and many zoo staff do not view zoos as research institutions. However, the advent of zoo biology as a scientific discipline has stimulated greater recognition that scientific research is important for advancing the husbandry and management of wildlife in captivity. Heini Hediger's (1969) book, *Wild Animals in Captivity*, was a milestone in the history of research at zoological institutions. However, research also played a more prominent role in many 19th century zoos than is often appreciated. In the early days of the Zoological Society of London, for example, research distracted the curators from their responsibilities in animal management to the extent that the Society's Secretary Chalmers Mitchell noted in 1929 (p. 77), "It was further laid down that each curator was to inspect all the animals and houses in his department daily, and subordinate any research work he might be doing to the care of the living animals." It comes as little surprise that these recommendations were made in the wake of an official enquiry into the administration of the gardens.

The situation in most zoos today is decidedly different; opportunities to increase our knowledge of wildlife far exceed the number of zoo personnel who are equal to the task, or for that matter zoo directors who appreciate the significance of scientific investigation. It is ironic that the value attached to zoological discovery may have been greater in the past because, compared to their precursors, today's modern zoos are far better settings for scientific investigation.

The purpose of this paper is to briefly summarize the history of research in zoological gardens during the past century and to show how zoological research in zoos has more or less faithfully mirrored prevailing scientific themes.

RESEARCH AS A ZOO MISSION

The "instruction and recreation of the people" was the principal objective of the oldest zoological parks, and yet scientific investigation was also an explicit goal of several early zoos and menageries. Whether Alexander the Great employed zoological collectors to stock a zoo and satisfy the scientific curiosity of Ptolemy II is debatable (Ley, 1968). The Menagerie of the Museum National de Histoire Naturelle in Paris which was established in 1793 for zoological investigation, was probably the first zoo created for scientific investigation (Mullan and Marvin, 1987). In 1817 Stamford Raffles, the founder of Singapore, voiced "the need for a collection of animals for scientific purposes as well as general interest." The Zoological Society of London was thus created, and its charter aspired to "a collection of living animals such as never yet existed in ancient or modern times...to be applied to some useful purpose, or as objects of scientific research, not of vulgar admiration" (Olney, 1980). Nevertheless, the creation of new zoos in the late 19th and early 20th centuries was motivated more by the need for public recreation and civic pride than the lofty ideals of the preceding era (ibid).

By the mid-20th century, some zoos were officially emphasizing research as part of the zoo mission. In describing research in the Antwerp Zoo since WWII, Van den Bergh (1975, p. 31) underscored the importance of research to the zoo, and remarked "that all the necessary facilities should be created to allow men of science to make the most use of the material, both living and dead." A significant number of new zoos in the 1990's include research as part of their missions and have developed detailed research mission statements and programs at the outset (e.g. Zoo Montana and new zoos in Melbourne, Florida, and [proposed] Ventura, California). Also, many modern zoos now have a formal research policy.

THREE EPOCHS OF ZOO RESEARCH

The pursuit of knowledge in zoos and aquariums can be divided into three major phases which were driven by different motivations. In the first or *prosectorial phase*¹, many species and genera were poorly known so it was logical that research was centered mainly on basic taxonomic and anatomical description. The prosector was the forerunner of the veterinarian and pathologist, but he probably had a broader understanding of contemporary zoology, and a more prolific record of scientific publication than most modern zoo veterinarians. On the down side however, the prosector seems to have rarely saved an animal's life. With academics, museum scientists and the prosector at the helm, this "prosectorial phase" of zoo research delved mainly into basic descriptive zoology. Probably few results of this early research were directly applied to the management of zoo animals.

The second phase could be called the *romantic age of research* and began about the time of the First World War, when improved transportation allowed an increasing number of zoo curators and directors to venture into the field to collect specimens and natural history information. This movement spawned a relatively large number of aspiring and successful popularizers of natural history. As a prose stylist and naturalist William Beebe was foremost amongst them (see Dee, this volume). At the same time, despite their desire to study animals under the controlled conditions of captivity, many leading academic scientists found little to commend zoos and aquariums either as laboratories or settings for research. Robert Mearns Yerkes, for example, pursued his life-long interest in primate biology through other channels, which eventually reaped the federally funded regional primate centers of the U.S. (Yerkes, 1916). However, it was also during this

¹Prosector: one who dissects dead bodies in preparation for anatomical lecture, etc. (Concise Oxford Dictionary).

phase that other scientists began to utilize zoo collections to investigate little known species, many of which were difficult or impractical to study in the wild. Many of those interested in zoo animals were scientific *carpetbaggers*—outsiders to the zoo community who appreciated the biological value of the collections, but usually paid little in return for the privilege of access to zoo specimens. While some of this information was undoubtedly of potential value to collection management, relatively little of it found its way into the everyday practices of animal management.

The third phase can be likened to an *adaptive radiation*, in that a major diversification of zoo research began in the 1960s, expanded greatly in the 1980s, and continues to expand today. Zoo research in the 1960s and 1970s was dominated by basic zoology and natural history with an emphasis on comparative animal behavior, life histories, and evolutionary biology (e.g. Morris, 1962; Wemmer, 1977). Reduced accessibility to animals from the wild seems to have been a key factor in shifting that focus onto a more applied track. The decline of imports in the mid-1960s and early 1970s and the rigorous paperwork and other impediments to importations of the 1980s also heightened the need for research aimed at improving captive breeding. Molecular studies of systematics and genetic variation became vital for long-term management of *ex situ* populations, and growing awareness of the environmental crisis by the zoo and aquarium community led to the greater body of institutional activities being defined within the framework of conservation biology. The small population paradigm has played a central theoretical role in the field with significant inputs from the zoo community (Ralls and Ballou, 1986; Meffe and Carroll, 1994; Caughley, 1994), and the Noah's Ark paradigm became part of the doctrine which emphasized the role of *ex situ* programs for conservation of endangered species (Soulé *et al.*, 1986; Seal, 1986).

Independently, the relatively small environmental engineering movement of the 1960s and 70s (Markowitz, 1975;

Markowitz and Woodworth, 1978; Hutchins *et al.*, 1983) gave way to the concept of environmental enrichment which is proceeding with vigor and addressing many welfare issues that have come to the helm (Hutchins *et al.*, in press).

In contrast to the past, most research is driven by the need for improved collection management and/or conservation goals (Kleiman, 1992). As such it is motivated more by the perceived collective needs of the profession, such as animal welfare, active exhibits, and cooperative breeding than by the intellectual curiosity of the individual curator. As this third phase has gained momentum, funding for academic research has been greatly reduced; thus, North American academics have come full circle and are now turning to zoos, and to a lesser extent to aquariums, as funding resources for scientific investigation.

THE DAWN OF MODERN ZOO RESEARCH

Van den Bergh's reference to "living and dead" is germane to the dualistic approach to zoological and biomedical research that was noted by Eisenberg (1975). Zoo research traditionally fell into these two camps, and other disciplinary approaches have been more recent. Prior to the third developmental phase however, dead animals were the focus of most zoo research.

PROSECTORS AND DEAD ANIMALS

The extent to which early zoos indulged in research was a function of their origins as cultural and scientific institutions. Throughout much of its long history, research at the Zoological Society of London centered on the prosectorium and pathology lab (Jewell, 1976). When Richard Owen was transferred from the zoological society to the British Museum Thomas Huxley took umbrage with the "deplorable wastage" of zoological material that followed. His reactions were a fitting comment

on 19th century British society, and as a result a Zootomical Committee was created to remedy the loss and "to regulate the disposal of Prosectorium material". Thus was created the post of prosector, "responsible both for the pathological routine and anatomical research" (Cave, 1976). Four Prosectors held the post between 1865 and 1915, each with his own tastes in scientific pursuit, but all were prolific zoologists. The Prosectorship was finally abolished, and until WWII was replaced with a 3-5 year Research Fellowship. It profited from a university posting that permitted the fellow to pursue part-time teaching in zoology.

Apart from London's prosectors however, much early zoo research was conducted by university or museum scholars. L.G. Goodwin's (1976) comments about the Zoological Society of London apply to many early zoos—"Animals are mortal. Their remains furnish materials for study by anatomists, taxonomists, pathologists and parasitologists, and there has been a continuous outflow of these materials to research workers in museums and university departments".

In the United States, the prosectorial model was used in developing the Penrose Research Laboratory at the Philadelphia Zoo. The first prosector, Professor Henry Chapman was an M.D. who held joint positions at the Philadelphia Zoo and Jefferson Medical College after the turn of the century (Snyder, 1974). Comparative pathology was investigated for the next four decades, but the joint chair arrangement gave way to a full time position at the zoo, which has persisted until the present. The prosector is now an outmoded title, which has been replaced by the veterinary pathologist.

Collaborative relationships between zoos and universities have been instrumental in providing bio-medical services and fostering research on zoological materials (Ratcliffe, 1974). The scientific value of unusual or rare animals, on the other hand, was usually appreciated more by academicians than those in the zoo community. D. Dwight Davis's (1964) monograph of

the giant panda for example was a labor of love that required many years of dissection. The analysis of muscular anatomy was based primarily on one specimen, Su Lin, that had lived at the Brookfield Zoo between 1937 and 1938. While the heyday of comparative anatomy has passed, a small number of anatomists continue to make use of zoo specimens for functional and comparative studies and university teaching (Grand, 1992).

RESEARCH ON LIVING ZOO ANIMALS

Personal, rather than institutional choice, almost always determined the subject matter of zoo-based research, and in this regard zoos resemble many academic departments. Live animal research fell into two categories: intensive studies of single species or individuals, and comparative studies of related species, often based on limited sample sizes. We might debate the merit of scientific generalization from small sample sizes, but few "meat and potatoes zoologists" would let the artificial setting or the paltry sample size of a zoo stand in the way of studying a Stellar's sea cow (*Hydrodamalis gigas*) or a great auk (*Alca impennis*). Francis G. Benedict—Director of the Carnegie Institution of Washington—was a comparative physiologist whose research interests depended upon tractable captive animals (Figure 5.1). His physiological studies of a forgotten Asian elephant immortalized the animal in his book, *The Physiology of the Elephant* (1936). Though outdated in its metabolic methodology, it remains a classic example of how single specimen studies have influenced a field. While the zoo community can not take credit for the elephant's contribution (she was a circus animal), Benedict's work represents a fitting example of the contribution of intensive studies.



Figure 5.1 Francis G. Benedict (The Carnegie Institution photo archives)

RESEARCH DEPARTMENTS

As early as 1916 the New York Zoological Society created the Department of Tropical Research under William Beebe (Conway, 1991). It established the Institute of Animal Behavior in the 1960s—as an experimental venture with the Rockefeller University. The National Zoo formed its department in 1966, and the San Diego Zoo in 1975. However, until recently, relatively few zoos have formal research departments, preferring instead either to eschew research altogether, or rely

heavily on collaborative relationships with local medical and/or academic institutions (see below).

Over the past 5-7 years, formal research programs have proliferated among zoos. At present there are at least 31 North American members or affiliates of the Association of Zoos and Aquariums with formal research programs. Many of the these programs are administered by research scientists (Ph.D.s) whose primary responsibilities are to conduct research in their specific discipline. Some programs are led by veterinarians (often in conjunction with veterinary medicine programs) and others are headed by research coordinators, whose job it is to facilitate research by staff and researchers or collaborators from other institutions. The disciplines of zoo research have expanded beyond traditional taxonomy, morphology, behavior, and evolutionary biology to include cytogenetics, molecular genetics, reproductive physiology, applied animal behavior (e.g., behavior modification), demography, and conservation biology. Many programs focus on improved management of the displays and individual specimens in their collections, while others address the collective problems of zoos engaged in cooperative breeding and conservation projects (Hutchins *et al.*, in press). While a preponderance of modern projects are applied (Kleiman, 1992), it is important to note that modern zoos often combine strong conservation initiatives with field research in ecology, natural history, and conservation biology. For example, the Wildlife Conservation Society (founded in 1895 as the New York Zoological Society), supports conservation and research efforts in 46 countries around the world. The National Zoological Park's research on the golden lion tamarin (Kleiman, in press) or management of Royal Chitwan National Park in Nepal (Mishra and Wemmer, 1987; Dinerstein and Wemmer, 1987) are models of modern conservation and research programs.

Other zoos support research by funding projects conducted by scientists having no direct affiliation to the zoo. For example, the Lincoln Park Zoo supports conservation research

in Latin America, while the Milwaukee County Zoo, Wildlife Conservation Society, Fort Wayne Children's Zoo, and Chicago Zoological Society also support field research aimed at conservation of endangered species and their habitats.

ASSOCIATIONS BETWEEN ZOOS AND UNIVERSITIES/INSTITUTIONS

Associations with scholarly or scientific institutions have been cultivated (or tolerated) whenever science has been a strong element in a zoo's mission. Charles Darwin profited from the Zoological Garden in London to explore various ideas which ultimately appeared in *The Expression of the Emotions in Man and Animals* (1965). Evidently he spent a great deal of time questioning the keepers and Mr. Bartlett, the Superintendent, and his requests were honored to see, among other things, how the animals would react to turtles and snakes in paper bags. A quote (ibid) gives a flavor of his science, "I placed a looking glass on the floor between two young oranges...at first they gazed at their images with the most steady surprise...they then approached close and protruded their lips toward the image, as if to kiss it..."

Dr. Erna Mohr (Figure 5.2) was also a "zoo outsider"—a fish systematist at the Hamburg Zoological Museum—whose scholarly use of zoological collections generated a vast contribution to zoology (Kosswig, 1969; Herre, 1968). During her long career she painstakingly photo-documented the development of zoos in Germany and neighboring countries, and pioneered the use of wild animal studbooks. She produced the first studbook for the wisent (*Bison bonasus*) in 1925, and later initiated the Przewalski horse (*Equus przewalskii*) studbook. She was a prolific writer with a maximum output of 20 publications per year (in German, English and Danish). But her real talent was remarkable observational skills which generated valuable contributions on a wide range of obscure species and sometimes esoteric morphological topics. Her papers on comparative morphology covered adaptive variation



Figure 5.2 Dr. Erna Mohr (photo provided by Dr. Harald Schliemann)

in mammalian horns, tails, ears, and marsupial pouches, and she never missed an opportunity to document the biology of little known or rare species such as the solendon (*Solenodon paradoxus*), hutias (*Capromys* and *Plagiodontia*), the fossa (*Cryptoprocta ferax*), and the pacarana (*Dinomys branickii*).

The call of herpetology has beckoned a variety of souls to the zoological park, and Lawrence Klauber (Figure 5.3) was one who pursued a highly successful career as both scientist and businessman. Educated as an electrical engineer, he quickly moved through the ranks of the San Diego Gas and Electric Company, from salesman to President and Chairman. He is an example of the outsider who benefitted from zoo association, as his ties with the San Diego Zoo were strong. An inventor of some note and a statistical wizard, he was a productive scholar without pretension, who considered himself



Figure 5.3 Lawrence Klauber (photo provided by San Diego Zoological Society)

dedication he produced the two volume classic—*The Rattlesnakes* (1956), which is now in its second printing.

A number of zoos and aquariums have established collaborative research linkages with local universities and institutes (Finlay and Maple, 1986). These relationships vary in nature. Zoo curators, for example may have adjunct status on university faculties which facilitate graduate student research at the zoo and allow zoo involvement in advanced education. Consortia are an organizational means of promoting research. Recently, four zoos and aquariums, and the University of Washington's Institute for Environmental Studies joined to create the Center for Wildlife Conservation which promotes wildlife conservation in the Pacific Northwest through applied research and environmental education. The Dutch National Foundation for Research in Zoological Gardens is somewhat similar, but functions as the science bureau of the Dutch Federation of Zoos. Both of these organizations are managed by small staffs, and supported by annual contributions of member institutions with supplementary funding from federal and private grants. Recently, the AZA created a broad-based scientific advisory group as a consultative resource for Species Survival Plans (Hutchins *et al.*, in press).

One excellent example of the latter involves the Woodland Park Zoo in Seattle. Through a strong linkage with the University of Washington's Psychology Department, Woodland Park Zoo has fostered intensive research within the zoo. The publication of *Applied Behavioral Research at the Woodland Park Zoological Gardens* (Crockett and Hutchins, 1977) demonstrated how exhibition and management could profit from research. Interactions between the university and the zoo led to a training course which was originally a credit course and then developed into a zoo course which is still being given today (Crockett and Hutchins, 1988; Stevens and Hutchins, 1993).

Finally, the Consortium of Aquariums, Universities and Zoos (CAUZ) is an informal North American network for

sharing information and ideas for "the mutual benefit of the participants" (Hardy, 1993). At the time of writing the network includes over 600 members from 300 institutions in 19 countries. The directory is basically a listing of members, sorted by institution and taxonomic interest.

FIELD RESEARCH

Field work for many North American and European zoos meant collecting animals (see Dee, this volume), but as early as the 1950s a number of large zoos became involved in wildlife field studies. Best known among these people were Bernard Grzimek of the Frankfurt Zoo, and his son Michael (Hayes, 1976). Grzimek's work in the Serengeti and the untimely death of his son there had a powerful effect upon his commitment to conserve African wildlife, and set the stage for the Frankfurt Zoo's continuing support of research in East Africa and other tropical countries. The Serengeti Research Institute was created as a result of Michael Grzimek's death in an airplane accident. The approach to African conservation espoused by Grzimek has been recently criticized (Adams and McShane, 1992), but its fundamental benefit in securing protected areas can not be questioned.

The support of wildlife research and conservation is not widespread in the zoo community, but has had a measurable impact in parts of the developing world. Early in its history the New York Zoological Society developed a highly successful model of wildlife conservation assistance which fosters training and research, and helped found over 90 protected areas around the world (Conway, 1991). The National Zoological Park and its sister bureaus in the Smithsonian Institution have trained over a 1000 developing country nationals from over 60 countries (Rudran *et al.*, 1990; Wemmer *et al.*, 1993). The AZA's Faunal Interest Groups (FIGs) are another mechanism designed to promote *in situ* zoo and aquarium research collaboration with developing countries (Wemmer and Anderson, 1991).

SCIENTIFIC DISCOVERY

Serendipity has spawned a number of notable scientific discoveries in zoos and aquariums. The discovery of arrested growth and ecophenotypes in salmonids is an example with a flavor of masterpiece theater (Greenwood, 1976). The first Professor at the ZSL was a dour Scotsman named James Murie, who resolutely declared that the inadequate attentions of curators and keepers were to blame for the deaths of most specimens. For the rest of his career he was labeled a curmudgeon, an identity he lived with quite comfortably. The scope of scientific interest in those days was broad, but jealous rivalry sometimes ran amok. Murie made a significant discovery at the society's so-called Fish House—that when salmon (*Salmo salar*) are denied salt water at the appropriate age of seaward migration, their physical development is delayed. When his paper was published, he was bitterly challenged by a jealous contemporary, Albert Gunther of the British Museum, and the finding, which is still valid, was rejected by the scientific community. Because of Gunther's stature as the unchallengeable leader of British ichthyology, appreciation of the significance of Murie's contribution was delayed until much later.

The zoological garden undoubtedly contributed to Darwin's discovery of the three principles of emotional expression (Darwin, 1965). The best known of these—the *principle of antithesis* posits that antithetical expressions of vertebrate behavior parallel different underlying emotional substrates, such as fear and aggression.

Zoological gardens have been a source of research material for biologists of diverse backgrounds, but many biologists have disdained zoos as unacceptable settings for research—they were simply never equated with museums for cultural or scientific sophistication. Curiously, some of the biologists who dared to break with this tradition have challenged the conventional wisdom with their findings. Concern with

genetic background and the genetic relationship among individuals and populations within zoos stimulated karyological and molecular investigations. Two examples will suffice.

The chromosomal basis of infertility emerged as a scientific discovery largely as a result of zoo research. It had long been a tradition of certain zoo directors to hybridize species, especially in some of the German zoos, like Munich where extensive collections of related species were held. In the 1960s, geneticists looked to zoos for hybrids to examine the basis of infertile crosses, and as a result discovered that hybrid infertility was a consequence of the multiple complex chromosomal rearrangements which caused meiotic breakdown, i.e. failure to produce viable germ cells (Benirschke and Kumamoto, 1987).

But it was in the 1980s that zoo biologists and their academic brethren began an escalated examination of taxonomic relationship. The advent of the Species Survival Plan (SSP) and Europaisches Erhaltungszucht Program (EEP) was the impetus. Scientific breeding of small populations of rare exotic species demanded careful evaluation of the genetic relationships of the captive population. Soon it was discovered that the provenance of many species in zoos was unknown, and the physical variation within a population suggested that several subspecies were represented (Ryder, 1987). The antiquated taxonomy of many species was of little help. Only one conclusion could be drawn—the taxonomy of these groups had to be re-examined. A mini-renaissance of systematic research was the consequence (Ryder, 1987, 1992). This new wave of work interested molecular biologists far more than traditional museum taxonomists who pour over skins and skulls, and part of the reason was that a blood sample was sufficient for the analysis of genetic makeup. As a result of these studies it was discovered that chromosomal differences distinguish orangutans from Sumatra and Borneo (Ryder and Chemnick, 1993), and that there are seven chromosomally

distinct populations of dik dik within the two named species (*Madoqua guentheri* and *kiriki*) (Ryder *et al.*, 1989). These are only a few of the studies that challenged notions of evolutionary relationship that had been resting peacefully for years. Molecular technology also made possible the identification of the genetic contribution to captive populations of genetically distinct founders. While not a major contribution to science itself, this has been invaluable to captive propagation by clarifying the affinities of the captive gene pool (O'Brien *et al.*, 1987; Fogle, 1990).

Environmental enrichment is a final example of the contribution of research to the improvement of captive conditions. Traditionally, behavioral enrichment or modification was accomplished via trial and error, as animal care staff performed *ad hoc*, qualitative assessments of enrichment protocols. Over the past 10 years, scientific studies to determine the effectiveness of various behavioral modification schemes have increased dramatically (Carlstead *et al.*, 1991). Although early studies of enrichment often involved researchers from outside zoos, the recent attention to enrichment has been driven by behaviorists working within the zoo community. At least two zoos, Washington Park in Portland, Oregon, and San Diego, currently employ researchers whose primary responsibility is to conduct research on, and implement, protocols for behavioral enrichment.

DATA BASES

With the increasing availability of computers since the Second World War, several notable efforts were initiated to establish comprehensive databases on zoo-generated information. The best known is ISIS, which is discussed in this volume (see Chapter 7). The Veterinary Records in Zoo Animals Program (VRZA) was developed in 1968; it is a supplemental database to the Veterinary Medical Data Program

devised by the National Cancer Institute of the National Institutes of Health in Bethesda, Maryland (Appleby, 1974). Contributors to the database submit abstracts in a standardized format and the data are stored at the Royal Veterinary College, London.

PUBLICATIONS

Much of the knowledge generated by zoos in the past did not meet the scholarly standards of scientific publication. Needless to say, the early research produced by the Zoological Society of London was an exception. The Society's long history of publication began in 1831 with what became the *Proceedings of the Zoological Society* (Edwards, 1976). In 1965 the proceedings gave way to the *Journal of Zoology*, and the scope of the journal increased to include a wide variety of zoological topics. The *International Zoo Yearbook*, while conceived in 1830, did not materialize until 1959, and caters specifically to the broader aspects of zoo biology, management, exhibition, and conservation (Edwards, 1976).

A small number of journals however were created to specifically cater to the zoo community. In 1907 the New York Zoological Society began publication of the journal *Zoologica* which continued until the winter of 1973; the journal published works on a variety of zoological topics beyond the scope of zoos, but went out of print for lack of subscriptions, and was replaced by *Wildlife Conservation*.

Symposium series were established by the Zoological Society of London in 1959, and by the U.S. National Zoological Park in 1978. Both publish irregularly.

The secular nature of zoo research has sometimes hampered acceptance of papers for publication in traditional biological journals. In general, the limitation has been most strongly felt in the organismic journals; molecular and biochemical journals have been more inclined to accept appropriate papers on zoo research.

Trade journals have also emerged in particular zoo disciplines, such as the *Journal of the American Association of Zoo Veterinarians*, and the *American Association of Zoo Keepers*.

CONCLUSION

Zoos have been decried as entertainment centers, but there is ample evidence of significant contributions to the biology of vertebrates and invertebrates. The identity problem which beleaguers most zoos is a consequence of their mixed bureaucratic and political origins, and their primary creation for human entertainment and recreation as opposed to intellectual stimulation and enlightenment. Until the public achieves a more enlightened perspective and places greater value on education, the situation is unlikely to change for the better. The message is clear—zoos must play an even more serious role in promoting public education, not only of environmental problems through public relations, but through a dedicated and united commitment to excellence.

REFERENCES

- Adams, Jonathan and Thomas O. McShane. 1992. *The myth of wild Africa, conservation without illusion*. W.W. Norton and Co., New York.
- Appleby, E.C. 1974. The V.R.Z.A. International Program for zoo data recording and retrieval--some preliminary results. In *The Centennial Symposium on Science and Research*, pp. 106-118. Philadelphia Zoo, Philadelphia, Pennsylvania.
- Benedict, F.G. 1936. *The physiology of the elephant*. Carnegie Institute of Washington, Washington D.C.
- Benirschke, K. and A.T. Kumamoto. 1987. Challenges of Artiodactyl cytogenetics. *La Chromosoma*, II: 1468-1478.

- Carlstead, K., J. Seidensticker, R. Baldwin. 1991. Environmental enrichment for zoo bears. *Zoo Biology*, 10(1):3-16.
- Caughley, G. 1994. Directions in conservation biology. *Journal of Applied Animal Ecology*, 63:215-244.
- Cave, A.J.E. 1967. The Zoological Society and Nineteenth Century Comparative Anatomy. *Symposia of the Zoological Society of London*, 40:49-66.
- Conway, W.L. 1991. A zoo-based international conservation program: Wildlife Conservation International. In *AAZPA Annual Conference Proceedings*, pp.381-385.
- Crockett, C and M. Hutchins. 1977. *Applied Behavioral Research at the Woodland Park Zoological Gardens, Seattle, Washington*. Pike Press, Seattle.
- Darwin, Charles. 1965. *The expression of the emotions in man and animals*. Phoenix Books, University of Chicago Press, Chicago.
- Davis, D. Dwight. 1964. The giant panda, a morphological study of evolutionary mechanisms. *Fieldiana: Zoology Memoirs*, Volume 3, Chicago Natural History Museum.
- Dinerstein, E., and C. Wemmer. 1987. Fruits *Rhinoceros* Eat: Dispersal of *Trewia nudiflora* (Euphorbiaceae) in Lowland Nepal. *Ecology*, 69(6):1768-1774.
- Edwards, M.A. 1976. The library and scientific publications of the Zoological Society of London: Part II. *Symposia of the Zoological Society of London*, 40:253-266.

- Eisenberg, J.F. 1975. Design and administration of zoological research programs. In *Research in zoos and aquariums*, pp. 12-18. National Academy of Sciences, Washington, D.C.
- Finlay, T.W. and T.L. Maple. 1986. A Survey of Research in American Zoos and Aquariums. *Zoo Biology*, 5:261-268.
- Fogle, T. 1990. Role of cytogenetics for breeding management of squirrel monkey colonies. *Zoo Biology*, 9:373-383.
- Goodwin, L.G. 1976. Research. *Symposia of the Zoological Society of London*, 40:215-222.
- Grand, T.I. 1992. Altricial and precocial mammals: a model of neural and muscular development. *Zoo Biology*, 11(1):3-15.
- Greenwood, P.H. 1976. The Zoological Society and Ichthyology, 1826-1930. *Symposia of the Zoological Society of London*, 40:85-103.
- Hardy, D.F. 1993. *Directory of the Consortium of Aquariums, Universities and Zoos, 1993-1994*. University of California, Northridge, California.
- Hayes, H.H.P. 1976. *The last place on earth*. Stein & Day, New York.
- Hediger, H. 1969. *Man and animal in the zoo: zoo biology*. Seymour Lawrence/Delacorte Press, New York.
- Herre, W. 1968. Erna Mohr, Rede zur Trauerfeier. *Zeitschrift für Säugetierkunde*, 33:257-261.
- Hutchins, M. 1988. On the design of zoo research programs. *International Zoo Yearbook*, 27:9-18.

- M. Hutchins, B. Norton, E. Stevens, and T. Maple (eds.). In press. *Ethics on the Ark, Zoos, Animal Welfare and Wildlife Conservation*. Smithsonian Institution Press, Washington, DC.
- Hutchins, M., C. Wemmer, and B. Dresser. In press. Ethical considerations in zoo and aquarium research. In *Ethics on the Ark, Zoos, Animal Welfare and Wildlife Conservation*, edited by M. Hutchins, B. Norton, E. Stevens, and T. Maple. Smithsonian Institution Press, Washington, DC.
- Jewell, P. 1976. The Contribution of the Zoological Society of London to Field Studies and Prospects for the Future. In *Symposia of the Zoological Society of London*, 40:269-280.
- Klauber, L.M. 1956. *Rattlesnakes, their habits, life histories, and influence on mankind*. 2 volumes. University of California Press, Berkeley and Los Angeles.
- Kleiman, D.G. 1992. Behavior research in zoos: past, present and future. *Zoo Biology*, 11:301-312.
- Kleiman, D.G. (ed.). In press. *A Case Study in Conservation Biology: The Golden Lion Tamarin*. Smithsonian Institution Press, Washington, DC.
- Kosswig, C. 1969. Dr. h.c. Erna Mohr 11.7.1894--10.9.1968. *Mitteilungen Hamburg Zool. Mus. Inst.*, 66:7-23
- Ley, W. 1968. *The dawn of zoology*. Prentice-Hall, Inc., Englewood Cliffs, New Jersey.
- Markowitz, H. 1975. Analysis and control of behavior in the zoo. In *Research in Zoos and Aquariums*, pp. 77-90. National Academy of Sciences, Washington, D.C.

- Markowitz, H. and G. Woodworth. 1978. Experimental analysis and control of group behavior. In *Behavior of Captive Wild Animals*, edited by H. Markowitz and V.J. Stevens, pp. 107-131. Nelson-Hall, Chicago, Illinois.
- Meffe, G.K. and C.R. Carroll. 1994. *Principles of Conservation Biology*. Sinauer Associates, Sunderland, Massachusetts.
- Mishra, H. and C. Wemmer. 1987. The Comparative Breeding Ecology of Four Cervids in Royal Chitwan National Park, Nepal. In *Biology and Management of the Cervidae*, edited by Chris Wemmer, pp. 259-271. Symposia of the National Zoological Park, Smithsonian Institution Press, Washington, D.C.
- Mitchell, P. Chalmers. 1929. *Centenary History of the Zoological Society of London*. Zoological Society of London, London.
- Morris, D. 1962. The behaviour of the green acouchi. In *Patterns of Reproductive Behaviour: Collected papers by Desmond Morris*, pp. 454-489. McGraw-Hill Book Company, New York.
- Mullan, B. and G. Marvin, 1987. *Zoo culture*. Weidenfeld & Nicholson, London.
- O'Brien, S.J., et al. 1987. Evidence for African origins of founders of the Asiatic lion Species Survival Plan. *Zoo Biology*, 6:99-116.
- Olney, P.J.S. 1980. London Zoo. In *Great Zoos of the world: their origins and significance*, edited by Solly Zuckerman, pp. 35-48. Weidenfeld & Nicholson, London.
- Ratcliffe, H. L. 1974. Retrospect and prospect. In *The Centennial Symposium on Science and Research*, pp. 256-259. Philadelphia Zoo, Philadelphia, Pennsylvania.

- Rudran, R., C. Wemmer, and M. Singh. 1990. Teaching applied ecology to nationals of developing countries. In *Race to Save the Tropics: Ecology and Economics for a Sustainable Future*, edited by E.R. Goodland, pp. 125-140. Island Press, Washington D.C.
- Ryder O.A. 1987. Species conservation and systematics: the dilemma of subspecies. *Trends in Ecology and Evolution*, 1:9-10.
- Ryder, O.A. 1992. DNA investigative technologies: Application to endangered species preservation. *Clinical Chemistry*, 38(3):458-459.
- Ryder, O.A. and L.G. Chemnick. 1990. Chromosomal and molecular evolution in Asiatic wild asses. *Genetica*, 83:67-72.
- Ryder, O.A. and L.G. Chemnick. 1993. Chromosomal and mitochondrial DNA variation in orang utans. *Journal of Heredity*, 84(5):405-409.
- Ryder, O.A., A.T. Kumamoto, B.S. Durrant and K. Benirschke. 1989. Chromosomal divergence and reproductive isolation in dik-diks (genus *Madoqua*, Mammalia, Bovidae). In *Speciation and Its Consequences*, edited by D. Otte and J.A. Endler, pp. 225-228. Sinauer Assoc., Sunderland, Massachusetts.
- Seal, U.S. 1986. Goals of propagation programmes for the conservation of endangered species. *International Zoo Yearbook*, 24/25:174-179.
- Snyder, R.L. 1974. Introduction. In *The Centennial Symposium on Science and Research*, pp. 1-3. Philadelphia Zoo, Philadelphia, Pennsylvania.
- Soulé, M., M. Gilpin, W. Conway, and T. Foose. 1986. The millenium ark: how long a voyage, how many staterooms, how many passengers? *Zoo Biology*, 5:101-113.

- Stevens, E.F., and M. Hutchins. 1993. The "Applying Behavioral Research to Zoo Animal Management" Workshop. In *AAZPA Annual Conference Proceedings*, pp. 41-45.
- van den Bergh, W. 1975. Long-term experience of a European zoo in research endeavors. In *Research in zoos and aquariums*, pp. 30-38. National Academy of Sciences, Washington, D.C.
- Wemmer, C. 1977. Comparative ethology of the large-spotted genet, *Genetta tigrina*, and related viverrid genera. *Smithsonian Contributions to Zoology*, No. 239, 98 pp.
- Wemmer, C. and D. Anderson. 1991. Faunal interest groups: zoo conservation with a regional focus. In *AAZPA Annual Conference Proceedings*, pp. 395-402.
- Wemmer, C., R. Rudran, F. Dallmeier, and D. Wilson. 1993. Training developing country nationals is the critical ingredient to conserving global diversity. *BioScience*, 43(11):762-767.
- Wildt, D.E. 1989. Reproductive research in conservation biology: priorities and aims for support. *Journal of Zoo and Wildlife Medicine*, 20(4):391-395
- Yerkes, R.M. 1916. Provision for the study of monkeys and apes. *Science*, XLIII(1103):231-234.
- Zuckerman, S. (ed.). 1976. *The Zoological Society of London, 1826-1976 and beyond*. Symposia of the Zoological Society of London, No. 40.
- Zuckerman, S. 1932. *The social life of monkeys and apes*. Kegan Paul, Trench, Trubner & Company, Ltd.

6 THE EVOLUTION OF ZOO ANIMAL EXHIBITS

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Zoos, like all cultural institutions, must adapt to changing environments or perish. An awareness of the past and anticipation of the future can help to guide this adaptation. Zoological parks are undergoing major redevelopment and change. The mission of these facilities is rapidly shifting from popular entertainment to conservation education and long-term management of small populations of rare animals. Retracing the historical path that has brought zoological parks to their current mission may help to chart a wise course through a troubling future.

Human attitudes toward nature and wildlife have evolved through the ages. Early hunter-gatherers saw themselves as part of nature. Pastoralists, farmers, and the city residents they supported, often contested wild, uncontrolled nature for their livelihood. Some great empires, distant from wild frontiers, represented a more intellectual and artistic approach. Exceptional leaders in China and India taught harmony with nature and used tame animals in naturalistic gardens. More commonly, zoos and menageries reflected the cultural attitude, usually with religious sanction, of a human-dominated universe. Captive wildlife were objects of curiosity, ornament or sport.

Evolving attitudes, including more awareness about environmental and ethical concerns, are changing the way zoos operate as well as public perception of them. Importantly, these changes seem to be taking place within the zoological and related community at a faster rate than in society at large. Zoos are now in the novel position of leading rather than following popular attitudes about wildlife.

This paper examines the history of wild animal collections in two separate time lines. First, collections are