

Ten Enrichment Priorities for Bats in Captivity

By Dana LeBlanc
The Lubee Foundation, Inc.
1309 NW 192nd Avenue
Gainesville, Florida 32609
Lubee2@aol.com

INTRODUCTION

Bats are managed in captivity by a variety of institutions such as zoos, living museums, and research facilities. In the wild, these unique mammals have a life that is filled with dynamic experiences such as those associated with avoiding predators, searching for and acquiring food, defending territories and producing viable offspring (Martin, 1996). Traditionally, humans have provided captive animals few choices or opportunities for activity when fulfilling their primary survival needs. Zoo animals are usually fed a basic diet at a given time of day in the same location, with emphasis being placed on nutritional requirements, economy, and ease of cleanup. This practice allows animals only the opportunity to consume their food, not search for, pursue, or process it, which can lead to boredom and the development of stereotypies (Hutchins et al. 1984). Advances in environmental enrichment and training are giving animals the freedom to make more choices in their captive environment (Martin, 1996). Environmental enrichment is an animal husbandry principle that seeks to enhance the quality of captive animal care by identifying and providing the environmental stimuli necessary for optimal psychological and physiological well-being (Shepherdson, 1998).

COMMITMENTS, ETHICS, AND ENRICHMENT

Animals managed in zoological parks, living museums and educational organizations serve the important role of being ambassadors for their species, and for this reason we owe them the best quality of life (Maple et. al., 1995). Jamieson (1995) argues in Ethics on the Ark that keeping an animal in captivity is a privilege that involves assuming special obligations for the animal's welfare. This welfare must include not only physical criteria such as longevity and freedom from disease, but also psychological criteria such as exhibition of species-typical behavior and the ability to adapt to changes in their environment (Poole, 1997; Maple et. al. 1995; Snowdon, 1991). A key to this environment and animal welfare is creating a situation in which animals feel secure (Poole, 1998). Enrichment is also a high priority for mammals that have a complex social structure, mammals that exhibit complex anti-predator behaviors, and for mammals that are adapted to environments where resource availability is highly variable (Poole, 1998; Mench, 1998). Therefore, enrichment and training have become essential tools in captive husbandry to provide them with a stimulating environment to meet both physical and psychological obligations of animal care.

THE NATAL ENVIRONMENT AND ENRICHMENT

The captive environment has an immediate effect on development of all mammals after birth. The results of this development are visible as mammals learn to exert "control" over their surroundings (Moltz, 1965; Joffe et.al. 1973; Renner, 1988; Thompson, 1996; Carlstead, 1996). The majority of captive environments are less complex than dynamic wild environments (Carlstead, 1996). Enriched environments can have positive effects on behavior, physiology, and brain morphology (Uphouse, 1980; Renner and Rosenzweig, 1986; Henderson, 1980; Carlstead and Shepherdson, 1994). The development of any complex behavior pattern is the result of extensive interaction between genetic heritage, exposure to the appropriate stimuli and experience (Polsky, 1975; Miller et. al. 1998). In considering appropriate forms of

environmental enrichment, it is therefore essential to be aware of the rearing environment of the individual. Bats that haven't received enrichment before and are housed in a more sterile environment need time to adjust and respond to this important stress. To ensure normal psychological development, a complex and stimulating rearing environment must be provided (Poole, 1998).

TEN ENRICHMENT PRIORITIES

Bats maintained in captivity belong to four different groups: plant-visiting bats, insectivorous bats, carnivorous bats, and sanguinivorous bats. The biology of each of these groups varies in their feeding strategies that range from being generalists that feed on a wide variety of resources to specialists that prey on a particular type of food item. Although each bat species has its own requirements, ten enrichment priorities can be made for all species based on their natural history, their physical design, and essential behaviors to survival.

1) Flight

Bats are the only group of mammals that can truly fly, and this trait is limited by captivity (Wilson, 1988). The Animal Welfare Act as Amended (7 USC, 2131-2156) Policy #24 states that bats must be provided with sufficient unobstructed enclosure volume to enable movement by flying and sufficient roosting space to allow all individuals to rest simultaneously. Flight is one of the most important enrichment priorities with bats, and some species may develop weight problems if not allowed to exercise in this fashion. Animals that are deprived of flight for periods of a month or more may lose the ability to fly (Wilson, 1988). The minimum caging requirements for sustained flight recommended by the AZA Bat Taxon Advisory Group (TAG) are at least eight times the wing span with a minimum width of no less than one and a half times the wing length (Fascione, 1995). Sustained flight can also be facilitated in doughnut or dumbbell shaped enclosures. If the possibility of flight does not exist, fully flighted bats can be exercised by skillful keepers who can stimulate static flight with these bats (LeBlanc, 1999a). A bat that cannot fly due to injuries has lost an integral part of its existence, but maybe able to achieve an adequate quality of life with social enrichment and training.

2) Locomotion on natural substrates and environmental complexity

All bat species move on a wide variety of substrates during foraging and roosting, and should be given opportunities for this natural locomotion. Foliage-dwelling bat species climb on vertical and horizontal branches and vines, and this helps to wear down continuously growing nails. All plant material should be non-toxic and vary in texture, diameter, and degrees of firmness. Crevice-dwelling species roost in caves, rock crevices, hollow trees, beneath tree bark, and in man-made structures. These bats are able to land and climb on vertical rock or rough cement walls. Vampire bats are able to walk and jump on the ground and have a terrestrial foraging pattern. In captivity, nail wear is limited in wire mesh caging, and nails may need to be trimmed to minimize breakage (Carpenter, 1978). Nail care management can be minimized by providing captive bats with a wide variety on natural substrates in roosting and foraging areas (Barnard, 1991).

Natural substrates can also provide complexity to the bat enclosure. Environmental complexity can be increased by adding a variety of furnishings such as roosting niches, bat boxes, ropes, ladders, visual barriers, and natural ground covers (Maple and Perkins, 1996). Complexity of the environment rather than space alone may be the key to behavioral improvements (Carlstead, 1996). This complexity allows for foraging, scent-marking, hiding, and facilitates social play (Poole, 1997).

3) Secure environment and predator avoidance

All animals require a secure environment in order to prosper (Poole, 1998). This security translates into predator avoidance which means providing sufficient space in the enclosure to exceed the animal's flight distance, providing companions that help to protect the group by warning of danger, or providing concealed areas for hiding (Hediger, 1955; Carlstead et al. 1993; Shepherdson, 1997).

A special requirement for bat enclosures is a variety of roosting niches. These roosts can be subdivided into day roosts, night roosts, and feeding roosts. Roosts are secure locations that provide

concealment, a proper flight distance from potential predators, preferred temperature regimes, access to conspecifics, and resting areas. Bat roosts are varied with most species having specific requirements where they hang or rest such as rock crevices, caves, bat boxes, hollow logs, under loose bark, in foliage, and in tree canopies (Wilson, 1997). Bats will usually roost at the highest points of an enclosure, and should be given multiple roosting options that allow bats to segregate themselves into social groups such as bachelors, females with pups, and breeding animals (MacNamara et. al. 1980). The vertical dimension of these roosting niches in addition to the horizontal space is important, and may allow bats to separate themselves according to dominance. Bats also display roost loyalty for extended periods. Therefore, to provide a secure environment, bats should be given a variety of roosting opportunities and visual barriers.

Visual barriers simulate the natural screening effect of forest foliage and may have an effect on levels of aggression, roosting density, and concealment (Mckenzie et. al. 1986). Bats may seek cover and should be provided with several types of barriers to allow these bats to display natural predator avoidance (Shepherdson, 1997). Lollar and Schmidt-French (1998) provide crevice-dwelling insectivorous bats with fabric roosting pouches, which are attached to walls with Velcro®. Plywood bat boxes provide an excellent source of cover and act as visual barriers for species that roost in dark areas such as Egyptian fruit bats (*Rousettus aegyptiacus*), Jamaican fruit bats (*Artibeus jamaicensis*), and short-tailed leaf-nosed bats (*Carollia perspicillata*). Corrugated vinyl roofing sheets can be hung vertically as a simple visual barrier that is easy to clean and disinfect with large fruit bats (LeBlanc, 1999b). Commercially available shade screen can also be attached to outside walls along high traffic service areas to minimize stress to animals.

4) Social Enrichment

Each bat species has different degrees of sociability and social organization, and social groups should be modeled after wild groupings. Native foliage-roosting bats such as red bats (*Lasiurus borealis*), Seminole bats (*Lasiurus seminolus*), yellow bats (*Lasiurus intermedius*, *L. ega*, *L. xanthinus*), and hoary bats (*Lasiurus cinereus*) are noted to be solitary as adults and should be housed separately (Lollar and Schmidt-French, 1998). Neotropical false vampire bats (*Vampyrum spectrum*) are documented to live in pairs or small family groups, and they should be maintained in captivity in these units due to their monogamous nature (Vehrencamp et. al. 1977; Altringham, 1996). Wahlberg's epauletted fruit bats (*Epomophorus wahlbergi*) have a lek mating system, in which males set up breeding stations at which they perform courtship displays to attract females (Wickler and Seibt, 1976). This species is polygamous and does well in small colonies with one breeding male. Egyptian fruit bats (*Rousettus aegyptiacus*), straw-colored fruit bats (*Eidolon helvum*), and Malayan flying foxes (*Pteropus vampyrus*) are strongly colonial, and they form multi-male harem groups in large aggregations (Pierson and Rainey, 1992; Nowak, 1994). Males in these species may form male bachelor groups when not breeding. Little brown bats (*Myotis lucifugus*) form large maternity colonies of up to several thousand with mother-pup pairs as the social unit (Kunz and Pierson, 1994). While male little brown bats are usually solitary. The sexes of little brown bats are therefore separated during the day and the females invade male occupied areas at night (Altringham, 1996). Social contact in colonial species must provide a great psychological enrichment and colonial species should be housed with a natural social grouping and sex ratio (Barnard, 1995; Lollar and Schmidt-French, 1998; LeBlanc, 1999b). An abnormal number of males in a colonial breeding group or males in a maternal colony can lead to social conflicts as has been noted with common vampire bats (*Desmodus rotundus*) and big brown bats (*Eptesicus fuscus*) (Harmon, 1999; Barnard, 1989). The addition of social companions and social enrichment can introduce several potential hazards such as aggression due to territoriality, incompatibility between the sexes, and increased competition for food, water, or preferred roosting sites.

At times, bats must be separated from the group for medical reasons, and direct contact is not possible. Social enrichment can be indirect by allowing visual, vocal, and olfactory communication. Bat workers can also provide a rich source of stimulation to bats. Training and positive reinforcement may reduce animal stress during medical procedures and capture.

5) Dietary enrichment

Dietary enrichment is the simplest form of behavioral stimulation (LeBlanc, 1999a, b). The captive diet is relatively stable and unchanging due to economics, nutritional requirements, cage restrictions and husbandry practices. Bats in the wild feed on a wide variety of resources that are unavailable in captivity. They also spend a higher proportion of their daily activity budget searching for, processing, and eating food. The key to this type of enrichment is novelty, which stimulates natural foraging behavior and exploration and minimizes boredom.

Dietary enrichment for plant-visiting bats can take many forms such as offering novel fruits, vegetables, juices, nectars, teas, browse, and flowers (LeBlanc, 1999a,b). Diet presentation can be changed by not peeling fruit, offering novel shapes, offering whole food, or offering items frozen as popsicles or mixed with gelatin to make bat jigglers.

Dietary enrichment for native insectivorous bats is more complicated since these bats show a strong preference for mealworms (Barnard, 1991; Barnard, 1995; Lollar and Schmidt-French, 1998). The following insects have been offered to captive bats: mealworms (*Tenebrio molitor*), waxmoth larvae (*Galleria mellonella*), crickets (*Acheta domestica*), silvery moths (*Autographa gamma*), angle shades (*Phologophora meticulosa*), green lacewings (*Chrysopa septempunctata*), house flies (*Musca domestica*), fruit flies (*Drosophila melanogaster*), and Carolina sphinx moths (*Manduca sexta*) (LeBlanc, 1999a; Courts, 1997; Pope, 1997). Insectivorous bats appear to be stimulated by a variety of sizes of the same insect so this should also be considered. Nocturnal insects can also be lured into outdoor enclosures with a variety of lights, but wild-caught insects may serve as intermediate hosts for parasites or contain pesticide residues (Pope, 1997; Barnard, 1991; Barnard, 1995). Several species of New World fruit bats [Jamaican fruit bats (*Artibeus jamaicensis*), short-tailed leaf-nosed bats (*Carollia perspicillata*), Palla's long-tongued bats (*Glossophaga soricina*), and Geoffroy's long-nosed bats (*Anoura geoffroyi*)] are also documented insectivores in the wild (Courts, 1998; Nowak, 1994). Recent studies with Old World fruit bats have shown that Rodrigues fruit bats (*Pteropus rodricensis*), Livingstone's fruit bats (*Pteropus livingsonii*), and Malayan flying foxes (*Pteropus vampyrus*) will consume insects in captivity (Courts, 1998; Courts, 1997; Pope, 1997). Straw-colored fruit bats (*Eidolon helvum*) and Egyptian fruit bats (*Rousettus aegyptiacus*) have also been reported to eat non-flying insects in captive diets (Carpenter, 1986; LeBlanc, 1998). Further studies on insectivory in pteropodids both in the wild and captivity are required to learn more about this aspect of their biology.

Dietary enrichment for omnivorous greater spear-nosed bats is easy because they will accept a variety of fruit, mealworms, crickets, waxworms, anoles, and rodents (Nowak, 1994). Bulldog bats are more difficult, but they respond to floating insects, pieces of fish, and fish that are allowed to float in a shallow pool (Suthers and Fattu, 1973). Common vampire bats are more restrictive in their feeding habits, and once acclimated to bovine blood they appear to prefer this source in comparison to blood of other mammals (Harmon, 1999). Other types of blood given to common vampire bats may include blood from horses, deer, sheep, goats, and swine. White-winged vampires are allowed to feed on live chickens at the Burnet Park Zoo, which is as naturalistic as possible for these avian parasites (LeBlanc, 1999a).

Water can also be an important source of dietary enrichment (LeBlanc 1999a,b). The taste of water can be altered by giving bottled water, mineral water, by adding Avimin® liquid, or by flavoring with tea. This type of enrichment can stimulate hydration and investigation while not increasing calorie consumption. Water can also be offered as ice and allowed to drip while hanging from a ceiling. Mineral blocks and salt licks can also be moved around in the enclosure to keep the bats searching for these dietary supplements.

6) Foraging Enrichment and Exploration

Exploration and foraging are two key information-gathering activities that are ingredients in the natural selection process, and these are important in environmental enrichment (Shepherdson, 1997; Mench, 1998). Both of these approaches must be sensitive to the degree of plasticity and flexibility that

different species adopt, and how difficult the enrichment task is for each group of animals. For example, puzzle feeders may be an acceptable functional alternative to more “natural” foraging situations (Shepherdson, 1997; Gilloux et. al. 1992). Novel foraging devices such as nectar feeders, log rolls, weighted plastic chain, grenade feeders, pollination poles, spinning rakes, and PVC puzzle feeders can be utilized to stimulate bats to explore, forage, and test themselves (LeBlanc, 1999 a, b). Nectarivorous bats such as long-tongued bats can also hover and forage from Oriole feeders® that are made by Opus products (Bellingham, MA).

The most popular form of foraging enrichment for plant-visiting bats is simply hanging “fruit kabobs” or whole fruit throughout the enclosure (LeBlanc, 1999a). Pieces of food can also be placed on shower curtain rings, which can be attached to plastic chain, bungee cords, ladders, ropes, swinging rakes, logs, grapevine wreaths, and branches (Atkinson, 1993; Porter, 1993, LeBlanc, 1999a). Live minnows can be offered to bulldog bats in shallow pools while fresh-killed mice can be hidden in spear-nosed bat exhibits. Blood can be offered frozen to common vampire bats.

The key to this foraging and exploratory enrichment is to stimulate the bats to spend a higher more naturalistic proportion of their daily activity budget searching for and processing their daily diet (Allgaier, 1992). Dietary enrichment should be placed in areas where the bats have to search it out. Thus, fostering natural food retrieval behaviors rather than having bats simply taking it out of a bowl in the same location on a daily basis (Reinhardt, 1993). Items can also be offered in smaller quantities several times during a normal feeding period rather than receiving all of the food at once. In reverse lighting conditions, bats that are crepuscular could be fed both at dusk and dawn.

7) Olfactory enrichment

Bats have a well-developed sense of smell; therefore, olfactory enrichment may promote a wide variety of natural behaviors such as exploration and scent marking (Suthers, 1970; Laska, 1990; Kunz and Pierson, 1994). Olfactory enrichment also has the benefit over dietary enrichment in that it creates activity without providing calories beyond the normal diet.

Bats identify individuals in their colony by scent. Intraspecies scent marks can be placed on muslin sheets and given to bachelor groups giving them access to bats of the opposite sex (Stevens et. al. 1996). The introduction of a male scent mark may result in changes in the female estrus cycle. Male scent marks can also be given to male bachelor groups to promote territoriality and scent marking behavior. Rodrigues fruit bats were shown to display more interest in intraspecies scent marks than fruit or floral scents in their enclosure (Stevens et. al. 1996).

Olfactory enrichment also allows bats to explore other scents in their territory such as other species of bats, birds, plants, and flowers. A variety of cooking extracts, spices, fresh herbs, hunting lures, and perfumes can be utilized for enrichment with nocturnal mammals (LeBlanc, 1999b, Nicklaus, 1997; Rosenberg, 1997; Stevens et. al. 1996). Scented herbs can also be planted in window boxes or hanging baskets to allow bats to interact directly with these pungent plants which may encourage scent marking (LeBlanc, 1999b).

Snake sheds and live corn snakes (*Elaphe guttata*) are also potential sources of olfactory enrichment with Old World fruit bats (Van Wormer, 1999). These potential predator scents may stimulate natural protective behaviors. Common vampire bats may respond to scent marks and prepared hides of potential prey animals (Harmon, 1999).

8) Acoustic Enrichment

Acoustic enrichment is seldom utilized in zoos, although background noise is utilized routinely with dairy cattle to reduce stress and increase milk production. Audio recordings of bat vocalizations may be beneficial for enrichment (Livingstone, 1997). Noisy colonial bat species such as flying foxes may benefit from background noise. Some institutions report providing continuous audio enrichment

utilizing a radio, environmental theme audiotapes or by running water in a pool within the exhibit (LeBlanc, 1998). Outdoor caging offers the opportunity for a wide variety of acoustic enrichment.

9) Training enrichment

Training provides an opportunity for an animal to earn its living, not exactly as in the wild, but in a way that it can use its adaptations and senses to experience the consequences of its choices (Martin, 1996). Animal keepers utilize training daily although most do not realize it. Bats quickly learn to perform certain behaviors in response to even the most subtle cues in their environment (Martin, 1997). Effective training is based on operant conditioning. Training is also most effective if it has a purpose (Laule and Desmond, 1997). Bats can be trained to take medication from a syringe by getting them accustomed to taking juice from a syringe. Insectivorous bats can be trained to accept mealworms by hand feeding and to feed themselves out of containers (Barnard, 1991; Barnard, 1995; Lollar and Schmidt-French, 1998). Bats can also be trained with positive reinforcement to shift from one enclosure to another or to adapt to handling for educational presentations. Several species of fruit bats at the Lubee Foundation, Inc. have been target trained for public demonstrations. This training has led to a closer relationship between the keepers and the animals (Nemcik, 1998).

10) Novelty of enrichment

Novelty has been shown to affect the level of enrichment benefit over time as animals become habituated to the enrichment (Sambrook and Buchanan-Smith, 1996; Kuczaj et al. 1997). Enrichment varies in intrinsic qualities such as complexity and responsiveness. Objects that an animal can control, and which respond to the animal in some way, are utilized for longer periods of time than objects that are less responsive (Markowitz and Line, 1989). Complexity may also promote activity (Tripp, 1985). Enrichment programs should provide a variety of enrichment types that vary in complexity and responsiveness and evaluate what provides the most benefit. Rodrigues fruit bats (*Pteropus rodricensis*) are very adaptable and due to their curious nature they react quickly to new and novel enrichment ideas. Common vampire bats initially appear less curious in their reaction to enrichment, but this is an area that deserves more intensive study.

Enrichment should be scheduled to make sure that it becomes part of the animal care routine. A variety of enrichment techniques can be offered to minimize habituation to enrichment. Scheduling of enrichment is also important to ensure there is sufficient labor to install and clean up after the enrichment.

ENRICHMENT PRIORITIES

Environmental enrichment for bats should include as many of the above priorities as possible. These priorities can also act as a checklist in evaluating bat care, and deciding what types of enrichment are the most important to begin with in a particular captive colony. All enrichment techniques should be assessed for risks and benefits with each group of bats, in order to maximize benefits and minimize risks, since every animal is different and may respond differently (Carlstead, 1999).

CONCLUSION

Bats are managed in captivity by zoos, living museums, research facilities, educational organizations, rehabilitation centers, and wildlife sanctuaries. Since wildlife conservation has been designated the highest priority of all zoological institutions, bat conservation and captive husbandry will become a higher priority as bat species suffer from human proliferation and habitat lost (Hutchins and Wiese, 1991; Stevens, 1991; Wilson, 1992). Animals managed in zoological parks, living museums, and educational centers serve the important role of being ambassadors, and for this reason we owe them the best quality of life (Maple et. al. 1995). Jamieson (1995) argues in Ethics on the Ark that keeping an animal in captivity is a privilege that involves assuming special obligations for the animal's welfare. Criteria for animal welfare must include not only physical criteria such as longevity and freedom from disease, but also psychological criteria such as exhibition of species-typical behavior and the ability to

adapt to changes in their environment (Maple et. al. 1995; Snowdon, 1991). Enrichment can be offered in many different forms to help animals display their natural behavioral repertoire and to help to reduce or eliminate abnormal behavior (Carlstead and Shepherdson, 1994). Bats have several enrichment priorities. The most important are sustained flight, climbing activities that help to manage weight and continuously growing nails, a secure environment, and a natural social grouping. Research on many species of bats is limited due to their nocturnal habits, and their ability to fly long distances. If the species record from wild data is minimal, bat workers can try to stimulate survival behaviors such as feeding and foraging, predator avoidance, and exploration, which are likely to confer a strong biological advantage in their evolutionary environment (Shepherdson, 1997; Barnard and Hurst, 1996).

REFERENCES

- Allgaier, A. 1992. Effects of spatial and qualitative variation in food availability on time budgets in *Pteropus vampyrus*. 22nd Annual North American Symposium on bat research. Universite de Sherbrooke, Quebec, Canada.
- Altringham, J.D. 1996. Bats: Biology and Behavior. Oxford University Press. Oxford, New York, Tokyo.
- Atkinson, K. 1993. Environmental enrichment for *Pteropus* at the Lube Foundation, Inc. AZA Regional Conference Proceedings. pp. 195-200.
- Barnard, S. 1989. Sexual harassment in a nursery colony of hand-raised big brown bats (*Eptesicus fuscus*). Animal Keepers Forum. Vol. 16(5): 163-165.
- Barnard, S. 1991. The Maintenance of Bats in Captivity. 6146 Fieldcrest Drive, Morrow, Georgia 30260.
- Barnard, S. 1995. Bats in Captivity. Wild Ones Animal Books. P.O. Box 275, Half Moon Bay, CA 94019.
- Barnard, C. and Hurst, J. 1996. Welfare by design: the natural selection of welfare criteria. Animal Welfare 5:405-433.
- Bloomstrand, M., Riddle, K., Alford, P., and T. Maple. 1986 Objective evaluation of a behavioral enrichment device for captive chimpanzees (*Pan troglodytes*). Zoo Biology 5:293-300.
- Brown, D.E. 1994. Vampiro: The Vampire bat in fact and fantasy. High-Lonesome Books, Silver City, NM.
- Bukojemsky, A. and Markowitz, H. 1997. Environmental enrichment as a tool for the preservation of species specific behaviors. 3rd International Conference on Environmental Enrichment. Sea World: Orlando, Florida.
- Bureau, A. 1997. Enrichment the unnatural way: It's okay. 3rd International Conference on Environmental Enrichment. Sea World: Orlando, Florida.
- Carlstead, K. 1999. Assessing and addressing animal welfare in zoos. The Shape of Enrichment. Vol. 8 (4): 6-10.
- Carlstead, K. 1996. Effects of captivity on the behavior of wild mammals. In Wild Mammals in Captivity. Editors D. Kleiman, M. Allen, K. Thompson, S. Lumpkin. The University of Chicago Press. Chicago and London. pp. 317-333.
- Carlstead, K. and Shepherdson, D. 1994. Effects of environmental enrichment on reproduction. Zoo Biology 13:447-458.
- Carlstead, K., Brown, K., and Seidensticker, J. 1993. Behavioral and adrenocortical changes in leopard cats (*Felis bengalensis*). Zoo Biology 12:321-331.
- Carpenter, R. 1986. Old World fruit bats. Zoo and Wild Animal Medicine 2nd edition. Editor: M. Fowler. W. B. Saunders company. Philadelphia, London. pp. 634-637.
- Chag, M. 1996. Give your bat grenades. The Shape of Enrichment. Vol. 5, No. 4. Nov. issue.
- Coe, C. and Scheffler, J. 1989. Utility of immune measures for evaluating psychological well-being in non-human primates. Zoo Biology Supplement 1:89-99.
- Courts, S. 1998. Dietary strategies of Old World fruit bats (Megachiroptera, Pteropodidae): how do they obtain sufficient protein? Mammal Review. 28(4):185-194.
- Courts, S. 1997. Insectivory in captive Livingstone's and Rodrigues fruit bats (*Pteropus livingstonii* and *P. rodricensis*): a behavioral adaptation for obtaining protein.
- Duncan, A. 1997. A veterinary assessment of the risks and benefits of environmental enrichment. AZA Conference Proceedings. pp. 208-215.
- Fascione, N. (Primary Editor). 1995. Fruit Bat Husbandry Manual. AZA Bat Taxon

- Advisory Group. Published by the Lube Foundation, Inc. and the American Zoo and Aquarium Association Bat Taxon Advisory Group.
- Fleming, T. 1993. Plant-visiting bats. *American Scientist*, Volume 81:460-467.
- French, B. 1997. False vampires and other carnivores. *BATS*. Vol 15(2): 11-14.
- Funakoshi, K, Watanabe, H, and Kunisaki, T. 1993. Feeding ecology of the northern Ryukyu fruit bat (*Pteropus dasymallus dasymallus*) in a warm-temperate region. *Journal of Zoology*, London, 230:221-230.
- Gavazzi, A. and Markowitz, H. 1994. Evaluation of environmental enrichment projects. *AZA Regional Conference Proceedings*. pp. 192-194.
- Gilloux, I., Gurnell, J., and D. Shepherdson. 1992. An enrichment device for great apes. *Animal Welfare* 1:279-289.
- Graydon, M. and Giorgi, P. 1987. Vision in flying foxes (Chiroptera: Pteropodidae). *Australian Mammalogy* 10: 101-106.
- Greenhall, A.M. and U. Schmidt (eds.) 1988. Natural History of Vampire Bats. CRC Press, Boca Raton, Florida.
- Guerrero, D. 1997. Enrichment 101: A basic overview. *Tracks Magazine*. Website: <http://www.arkanimals.com/E/Enrich101.html>
- Hancocks, D. 1995. Lions and tigers and bears, Oh no! In Ethics of the Ark. Editors: B. Norton, M. Hutchins, E. Stevens, and T. Maple. Smithsonian Institution Press. Washington and London. pp. 31-37.
- Harmon, L. 1999. Vampire bat husbandry manual. Bat Taxon Advisory Group. American Zoo and Aquarium Association. Silver Spring, MD 20910.
- Hediger, H. 1950. Wild Animals in Captivity. London: Butterworth & Co.
- Hediger, H. 1955. Studies of the Psychology and Behavior of Captive Animals in Zoos and Circuses. London: Butterworths.
- Hediger, H. 1969. Man and Animal in the Zoo. London: Routledge and Kegan Paul.
- Henderson, N. 1980. Effects of early experience upon the behavior of animals: the second twenty-five years of research. In Early behavior: Implications for Social Development, Editor: E.C. Simmel. New York: Academic Press.
- Hutchins, M.D., Hancocks, D., and Crockett, C. 1984. Naturalistic solutions to the behavioral problems of captive animals. *Zoologische Garten* 54:28-42.
- Hutchins, M. and Wiese, R. 1991. Beyond genetic and demographic management: The future of the Species Survival Plan and related AAZPA conservation efforts. *Zoo Biology* 10:285-292.
- ISIS Mammal Abstracts. 1999. International Species Information System. Apple Valley, MN. USA. September issue.
- Jamieson, D. 1995. Zoos revisited. In Ethics of the Ark. Editors: B. Norton, M. Hutchins, E. Stevens, and T. Maple. Smithsonian Institution Press. Washington and London. p. 52-56.
- Joffe, J., Rawson, R., and J. Mulick. Control of their environment reduces emotionality in rats. *Science* 180:1383-1384.
- Kreger, M.D., Hutchins, M., and Fascione, N. 1998. Context, ethics, and environmental enrichment in zoos and aquariums. In Second Nature: Environmental Enrichment for Captive Animals. Editors: D.J. Shepherdson, J.D. Mellen, and M. Hutchins. Smithsonian Institution Press. Washington and London. pp. 59-82.
- Kuczaj, S., Lacinak, C., Tompkins, C. and O. Fad. 1997. Why do environmental enrichment devices become less enriching? 3rd International Conference on Environmental Enrichment. Sea World: Orlando, Florida.
- Kunz, T. and Diaz, C. 1994. Folivory in fruit-eating bats, with new evidence from *Artibeus jamaicensis* (Chiroptera: Phyllostomidae). *Biotropica*.
- Kunz, T and Ingalls, K. 1994. Folivory in bats: an adaptation derived from frugivory. *Functional Ecology* 8:665-668.
- Kunz, T. and Pierson, E. 1994. Bats of the world: an introduction. In Walker's Bats of the World. Editor: Ronald Nowak. The John Hopkins University Press. Baltimore and London. pp. 1-46.
- Laska, M. 1990. Olfactory discrimination ability in short-tailed fruit bat (*Carollia perspicillata*). *Journal of chemical ecology*, 16(12):3291-3299.

- Laule, G. and Desmond, T. 1997. Purposeful enrichment. 3rd International Conference on Environmental Enrichment. Sea World: Orlando, Florida.
- LeBlanc, D. 1997. Nectar feeding as an enrichment technique with island flying foxes (*Pteropus hypomelanus*). *Animal Keepers' Forum*, Vol. 24, No. 1. Pp. 18-26.
- LeBlanc, D. 1998. Horticulture options for fruit bat enrichment. AZH National Conference. Indianapolis, Indiana.
- LeBlanc, D. 1999a. Bat enrichment survey. *Animal Keepers' Forum*. 26(7) 267-285.
- LeBlanc, D. 1999b. Bat enrichment guidelines. Enrichment Notebook 2nd edition. American Association of Zoo Keepers. Topeka, KS 66606.
- Livingstone, K. 1997. The potential for utilizing acoustic communication as a form of behavioral enrichment. 3rd International Conference on Environmental Enrichment. Sea World: Orlando, Florida.
- Lollar, A. and Schmidt-French, B. 1998. Captive care and medical reference for the rehabilitation of insectivorous bats. A Bat World Publication. Mineral Wells, Texas. 76067.
- Lyndaker, A.J. and Houck, B. 1998. Hand Preference in the Malayan flying fox (*Pteropus vampyrus*). AZA National Conference Proceedings. Boston, Mass.
- MacNamara, M. Doherty, J., Viola, S., and A. Schacter. 1980. The management and breeding of hammer-headed bats at the New York Zoological Park. *International Zoo Yearbook*: 260-264.
- Maple, T., McManamon, R., and E. Stevens. 1995. Defining the good zoo: Animal care, maintenance, and welfare. In Ethics of the Ark. Editors: B. Norton, M. Hutchins, E. Stevens, and T. Maple. Smithsonian Institution Press. Washington and London. p. 219-234.
- Maple, T. and Perkins, L. 1996. Enclosure furnishings and structural environmental enrichment. In Wild Mammals in Captivity: Principles and Techniques. Editors: D. Kleiman, M. Allen, K. Thompson, and S. Lumpkin. The University of Chicago Press. Chicago and London. pp. 212-222.
- Markowitz, H. and Line, S. 1989. Primate research models and environmental enrichment. In: E. Segal (Editor). Housing, Care and Psychological Well-being of Captive and Laboratory Primates. Noyes Publications. New Jersey. Pp. 203-212.
- Marshall, A. 1983. Bats, flowers and fruit: evolutionary relationships in the Old World. *Biological Journal of the Linnean Society*, 20:115-135.
- Marshall, A. 1985. Old World phytophagous bats (Megachiroptera) and their food plants: a survey. *Zoological Journal of the Linnean Society*, 83:351-369.
- Martin, S. 1996. Training as enrichment. AZA regional conference proceedings. Pp. 139-143.
- Martin, S. 1997. Training: A critical component of enrichment programs. AAZK Annual Conference Proceedings. pp. 381-385.
- McKenzie, S., Chamove, A., and Feistner, A. 1986. Floor coverings and hanging screens alter arboreal monkey behavior. *Zoo Biology* 5:339-348.
- Mench, J.A. 1998. Environmental enrichment and the importance of exploratory behavior. In Second Nature: Environmental Enrichment for Captive Animals. Editors: D.J. Shepherdson, J.D. Mellen, and M. Hutchins. Smithsonian Institution Press. Washington and London. pp. 30-46.
- Mickleburgh, S., Hutson, A., and Racey, P. 1992. Old World Fruit Bats: An Action Plan for their Conservation. IUCN/SSC Chiroptera Specialist Group. Published by The World Conservation Union (IUCN), Gland, Switzerland. Printed by Information Press, Oxford, UK.
- Mickleburgh, S. and Carroll, J. 1994. The role of captive breeding in the conservation of Old World fruit bats. In Olney, P., Mace, G., and A. Feistner (Editors). Creative Conservation: Interactive management of wild and captive animals. Chapman & Hall, London. Pp. 352-364.
- Miller, B., Biggins, D., Vargas, A., Hutchins, M., Hanebury, L., Godbey, J., Anderson, S., Wemmer, C., and J. Oldemeier. 1998. The captive environment and reintroduction: The Black-footed ferret as a case study with comments on other taxa. In Second Nature: Environmental Enrichment for Captive Animals. Editors: D.J. Shepherdson, J.D. Mellen, and M. Hutchins. Smithsonian Institution Press. Washington and London. pp. 97-112.
- Moltz, H. 1965. Contemporary instinct theory and the fixed action pattern. *Psychological Review* 72:27-47.
- Moodie, E. and Chamove, A. 1990. Brief threatening events beneficial for captive tamarins? *Zoo Biology* 9(4):275-286.

- Morris, D. 1964. The response of animals to a restricted environment. *Symposia of the Zoological Society of London* 13:99-118.
- Nemcik, L. 1998. Target training Malayan flying foxes (*Pteropus vampyrus*): A beginners perspective. *Proceedings of the National AAZK Conference*. Indianapolis, Indiana. Pp. 115-118.
- Nicklaus, F. 1997. Olfactory enrichment in many species. *AZA regional conference proceedings*. pp. 567-569.
- Novak, M., Kinsey, J., Jorgensen, M., and T. Hazen. 1998. Effects of puzzle feeders on pathological behavior in individually housed rhesus monkeys. *American Journal of Primatology* 46:213-227.
- Novick, A. 1977. Acoustic orientation. Editor: W, Wimsatt, Biology of bats, Vol. 3, Academic Press, New York.
- Nowak, R. 1994. Walker's Bats of the World. The John Hopkins University Press. Baltimore and London. pp. 1-46.
- Parry-Jones, K. and Augee, M. 1992. Insects in flying fox diets. *Bat Research News*. 33:9-11.
- Pierson, E.D. and Rainey, W.E. 1992. The Biology of flying foxes of the genus *Pteropus*: A review. In Proceedings of the Pacific Island Flying Fox Conservation Conference, Editors: D. Wilson and G. Graham. USFWS Biol. Rept. No. 90, Washington, D.C., pp. 1-17.
- Polsky, R.H. 1975. Developmental factors in mammalian predation. *Behavioral Biology* 15:353-382.
- Poole, T. 1997. Identifying the behavioral needs of zoo mammals and providing appropriate captive environments. *Ratel* (24) 200 – 210.
- Poole, T. 1998. Meeting a mammal's psychological needs. In Second Nature: Environmental Enrichment for Captive Animals. Editors: D.J. Shepherdson, J.D. Mellen, and M. Hutchins. Smithsonian Institution Press. Washington and London. pp. 83 – 94.
- Pope, B., Kirkpatrick, M. and LeBlanc, D. 1997. Fruit bats, sticks, flight, and non-food enrichment. *The Shape of Enrichment*. Vol. 6, No. 3. August issue.
- Pope, B. 1997. Insectivory as enrichment with Old World fruit bats. 3rd International Conference on Environmental Enrichment. Sea World: Orlando, Florida.
- Porter, B. 1993. The "Spinning Rake": Stimulating foraging behavior in bats. *The Shape of Enrichment*. Volume 2, No. 4. November issue.
- Reinhardt, V. 1993. Foraging enrichment for caged macaques: A review. *Laboratory Primate Newsletter* 32:4.
- Renner, M. 1988. Learning during exploration: The role of behavioral topography during exploration in determining subsequent adaptive behavior. *International Journal of Comparative Psychology* 2:43-56.
- Renner, M. and Rosenzweig, M. 1986. Object interactions in juvenile rats (*Rattus norvegicus*): Effects of different experimental histories. *Journal of Comparative Psychology* 100:229-236.
- Rosenberg, L. 1997. Enrichment of nocturnal animals. *AZA regional conference proceedings*. pp. 116-119.
- Ryan, M.J. and Tuttle, M.D. 1983. The ability of the frog-eating bat to discriminate among novel and potentially poisonous frog species using acoustic cues. *Animal Behavior* 31:827-33.
- Ryan, R.M, Tuttle, M.D., and Barclay, R.M.R. 1983. Behavioral responses of the frog-eating bat (*Trachops cirrhosus*) to sonic frequencies. *Journal of Comparative Physiology, ser. A*, 150:413-18.
- Sambrook, T. and H. Buchanan-Smith. 1996. What makes novel objects enriching? A comparison of the qualities of control and complexity. *Laboratory Primate Newsletter*. Volume 35. Pp. 2-7.
- Seyjagat, J. 1994. Principal aspects of enclosure design for flying fox. *AZA Regional Conference Proceedings*. Pp. 158-159.
- Seyjagat, J. 1998. The pollination pole. *The Shape of Enrichment*. Vol. 7, No. 4, Nov. issue.
- Shepherdson, D. 1997. The animal's perspective: Developing strategies for successful enrichment. *AZA Annual conference proceedings*. pp. 486-489.
- Shepherdson, D. 1998. Tracing the path of environmental enrichment in zoos. In Second Nature: Environmental Enrichment for Captive Animals. Editors: D.J. Shepherdson, J.D. Mellen, and M. Hutchins. Smithsonian Institution Press. Washington and London. pp. 1-12.
- Snowdon, C.1991. Naturalistic environments and psychological well-being. In Through the

- Looking Glass: Issues of Psychological Well-Being in Captive Nonhuman Primates, ed. M.A. Nowak and A.J. Petts. Washington, D.C.: American Psychological Association.
- Snowdon, C. 1997. Significance of animal behavior research. Animal Behavior Society. www.cisab.indiana.edu/ABS/valueofanimalbehavior.html.
- Stevens, B., LeBlanc, D. and R. Gutman. 1996. The nose knows: Olfactory enrichment for fruit bats. *The Shape of Enrichment*. Vol. 5, No. 2. May issue.
- Stevens, W. K. 1991. Species loss: Crisis or false alarm. *New York Times*, 20 August, sec. C.
- Stevenson, M. and Poole, T. 1982. Playful interactions in family groups of the common marmoset (*Callithrix jacchus jacchus*). *Animal Behavior* 30:886-900.
- Suthers, R. 1970. Vision, olfaction, and taste. In Wimsatt, W. A., ed., Biology of bats, vol.2, Academic Press, New York, pp. 265-309.
- Suthers, R.A. and Fattu, J.M. 1973. Fishing behavior and acoustic orientation by the bat (*Noctilio labialis*). *Animal Behavior* 21:61-66.
- Thomas, P. and McCann, C. 1997. The effectiveness of cortisol as a physiological marker of well-being in zoo animals. *AZA Annual Conference Proceedings*. pp. 524-529.
- Thompson, K. 1996. Behavioral development and play. In Wild Mammals in Captivity. Editors D. Kleiman, M. Allen, K. Thompson, S. Lumpkin. The University of Chicago Press. Chicago and London. pp. 317-352-371.
- Tripp, J. 1985. Increasing activity in captive orangutans. *Zoo Biology*, 4:225-234.
- Uphouse, L. 1980. Reevaluation of mechanisms that mediate brain differences between enriched and impoverished animals. *Psychological Bulletin* 88:215-232.
- Van Wormer, K. 1999. Stimulating natural protective behaviors with short term natural stress. *The Shape of Enrichment* Vol. 8, No. 1. February issue.
- Vehrencamp, S.L., F.G. Stiles, and J.W. Bradbury. 1977. Observations on the foraging behavior and avian prey of the neotropical carnivorous bat, *Vampyrus spectrum*. *Journal of Mammalogy*. 58:469-478.
- Wickler, W., and U. Seibt. 1976. Field studies of the African fruit bat, *Epomophorous wahlbergi*, with special reference to male calling. *Z. Tierpsychol.* 40:345-376.
- Wilson, D. 1997. Bats in Question – The Smithsonian Answer Book. South China Printing Co. Hong Kong.
- Wilson, D. 1988. Maintaining bats for captive studies. In Ecological and Behavioral Methods for the Study of Bats. Editor: Thomas Kunz. Smithsonian Institution Press. Washington, D.C. and London. pp. 247-263.
- Wilson, E.O. 1992. The Diversity of Life. Cambridge: Harvard University Press, Belknap Press.
- Wimsatt, W.A. 1986. Vampire Bats. In: Zoo and Wild Animal Medicine, 2nd edition, Editor: M.E. Fowler. W.B. Saunders Co., Philadelphia, Pp. 644-649.