

To hunt or not to hunt? A feeding enrichment experiment with captive large felids

Terry Maple

Zoo Biology

Cite this paper

Downloaded from [Academia.edu](#) 

[Get the citation in MLA, APA, or Chicago styles](#)

Related papers

[Download a PDF Pack](#) of the best related papers 



[Contrafreeloading in grizzly bears: implications for captive foraging enrichment](#)

Charles Robbins

[EFFECT OF FEEDING ENRICHMENT ON BEHAVIOUR OF CAPTIVE TIGERS](#)

Arun Kumar Mishra

[Effects of Captivity on the Behavior of Wild Mammals](#)

M. Elsbeth McPhee

To Hunt or Not to Hunt? A Feeding Enrichment Experiment With Captive Large Felids

Meredith J. Bashaw,^{1,2*} Mollie A. Bloomsmith,^{1,2} M.J. Marr,² and Terry L. Maple^{1,2}

¹*TECHlab, Zoo Atlanta, Atlanta, Georgia*

²*School of Psychology, Georgia Institute of Technology, Atlanta, Georgia*

It is often difficult to promote the successful performance of feeding behaviors in zoos, especially for carnivores. Feeding enrichment provides these opportunities and often improves behavioral indications of an animal's well-being and the experience of the zoo visitor. The effectiveness of two different feeding enrichment techniques was evaluated on five subjects in two species of felids: African lions and Sumatran tigers. The activity budgets of each cat were compared before, during, and after enrichment, focusing on activity levels, frequency and variety of feeding behaviors, and occurrence of stereotypic behaviors. The presentation of live fish increased the variety and frequency of feeding behaviors, while presentation of horse leg bones increased the frequency of these behaviors. Fish reduced the tigers' stereotypic behavior from 60% of scans to 30% of scans on the day of presentation, and this change was maintained for 2 days following enrichment. Bone presentation also reduced stereotypic behavior and increased nonstereotypic activity in both species. Both of these techniques appear to have sustained effects on behavior lasting at least 2 days after presentation, which may indicate their ability to alter the animals' underlying activity patterns. *Zoo Biol* 22:189–198, 2003. © 2003 Wiley-Liss, Inc.

Key words: environmental enrichment; carcass feeding; live feeding; visitor experience; well-being

According to Maple [1995, p. 24], “zoo professionals take seriously their obligation to minimize animal stress, boredom, trauma and disease.” Feeding enrichment is designed to provide animals with an opportunity to use natural foraging strategies to obtain food in captivity. In the traditional zoo, animals were fed scheduled meals once or twice a day [Shepherdson et al., 1993]. While these foods

*Correspondence to: Meredith Bashaw, CRES/San Diego Wild Animal Park, 15500 San Pasqual Valley Road, Escondido, CA 92027-7017. E-mail: meredithjb@netzero.net

Received for publication December 19, 2000; Accepted May 31, 2002.

DOI: 10.1002/zoo.10065

Published online in Wiley InterScience (www.interscience.wiley.com).

had the appropriate nutritional content, proper feeding also includes an opportunity for animals to use their natural feeding behaviors [Holst, 1997; Lindburg, 1998]. In primates, feeding enrichment has been documented to increase foraging time [Chamove, 1981; Chamove et al., 1982; Tripp, 1985; Maple and Finlay, 1986; Bloomsmith et al., 1988; Brent and Eichberg, 1991], decrease aggression [Chamove et al., 1982; Boccia et al., 1984; Bloomsmith et al., 1988; Brent and Eichberg, 1991], and reduce abnormal behavior [Chamove et al., 1982; Gould and Bres, 1986; Bloomsmith et al., 1988; Brent and Eichberg, 1991; Bayne et al., 1992; Bloomsmith and Lambeth, 1995]. Similarly, in bears, the opportunity to work for food in a species-appropriate manner has increased activity [Forthman et al., 1992], as well as reduced passivity [Forthman et al., 1992], agonistic interactions [Markowitz, 1982], and stereotypic behavior [Carlstead et al., 1991; Forthman et al., 1992]. Scientific evaluation of feeding enrichment in felids is needed [Carlstead and Shepherdson, 1994], as the published literature contains mostly anecdotal data [e.g., Bacon, 1992; Hare and Jarand, 1998].

Some simple feeding-enrichment procedures have been documented to change the behavior of felids. For example, in African lions, the provision of ice balls increased standing, locomoting, sniffing, licking, gnawing, and paw manipulation [Powell, 1995]. Several other enrichment studies on cats have revolved around elaborate devices to provide simulated hunting opportunities, and have decreased pacing, instigated hunting behavior, and increased activity, jumping, pouncing, rolling, and visibility to the public [Markowitz and LaForse, 1987; Markowitz et al., 1995]. A fishing cat (*Felis viverrina*) provided live fish showed decreased sleeping and increased hunting behaviors, behavioral diversity, and use of space after fish presentation, and hunting behaviors were still present 7 days later [Shepherdson et al., 1993]. The occasional use of live prey has been recommended as a strategy to reduce stereotypic behavior that is associated with displaced feeding behavior [Dierenfeld, 1987], and anecdotal evidence suggests that tigers, jaguars, and ocelots also perform hunting behaviors when exposed to live fish [Mellen et al., 1998].

Improving animals' well-being has been operationally defined as reducing stereotypic, undesirable, and hyper-aggressive behaviors, and increasing activity and species-specific behaviors [e.g., Markowitz and LaForse, 1987; Bloomsmith et al., 1988; Forthman et al., 1992]. In the current study, neither undesirable (but not stereotypic) behavior nor hyper-aggressive behavior were observed in the animals; therefore, they will not be used as indicators of well-being. A third measure of welfare, increased activity, is more controversial, because it may not be associated with increased welfare in every case [Mason, 1993]. In this study, increased activity as an indicator of well-being had to meet two criteria: it must not be stereotypic, and it must be changing in the direction of the activity budget of the animal's wild counterparts. Stereotypy, activity, and species-specific appetitive behaviors are used here as behavioral indices of well-being.

Appetitive behaviors make up a large portion of the behavioral repertoire of wild felids. The majority of the activity of wild cats revolves around obtaining food [Schaller, 1972; Dierenfeld, 1987], and they seem to be strongly motivated to perform appetitive behaviors [Shepherdson et al., 1993]. Lindburg [1988] divided these appetitive behaviors into four classes: 1) locating, 2) capturing, 3) killing, and 4) consuming prey. In the wild, lions and tigers usually stalk their prey and then rush from a short distance away or lie in wait and ambush prey as it walks by

[Guggisberg, 1975; Seidensticker and McDougal, 1993]. These species usually hunt at dusk or at night, presumably to provide themselves with greater camouflage in their attempts to sneak up on prey [Schaller, 1967, 1972]. Despite spending an average of 21 hr asleep, lions will “readily hunt, mate, and feed at all times of the day” [Sankhala, 1977, p. 120] in the wild, and tigers have also been observed engaged in these activities during daylight hours.

This study aimed to implement two simple enrichment procedures designed to elicit feeding behaviors common in wild cats. The presentation of live fish was tested on Sumatran tigers (*Panthera tigris sumatrae*), and bone provisioning was tested on both African lions (*Panthera leo*) and tigers. Across species, three main goals were manifest: to allow the successful use of appetitive behaviors, to increase activity, and to decrease stereotypic behaviors. We hypothesized that enrichment would increase appetitive behaviors and decrease stereotypic behaviors on the day of provision. We also expected an increase in active behaviors and a decrease in stereotypic behaviors over the day of enrichment and the following 2 days. Finally, we predicted an increase in time spent in areas associated with enrichment and visible to the zoo visitor.

METHODS

Subjects and Their Husbandry

The subjects in this experiment were one male and two female African lions, and one male and one female Sumatran tigers. All resided at Zoo Atlanta and were fed Nebraska Feline (Central Nebraska Packing, Inc., North Platte, NE) diet (ground, processed, whole-carcass horsemeat) 6 days a week. To simulate their irregular eating pattern in the wild, they were not fed on the 7th day of the week, but instead received a horse leg bone with a small amount of meat still attached. From 0900 to 1700 hr, the two tigers were housed separately in outdoor areas where they were on display to the visiting zoo public (hereafter referred to as “on-exhibit”). The three lions were housed in a similar type of outdoor area and in an indoor/outdoor area without public access (hereafter referred to as “holding”). The lions were housed separately by sex, so the male and females spent alternating days in the on-exhibit space. For this reason the lions were observed in both the on-exhibit and holding spaces. During this study, the male lion and tiger had visual and olfactory, but not tactile, access to their female conspecifics.

Experimental Conditions

There were four conditions in this experiment, and each condition was 4 weeks in duration. 1) All subjects were first observed in a baseline condition, prior to any manipulation. This baseline included observations of tigers on exhibit, lions on exhibit, and lions in holding. The experimental manipulations were completed under two conditions, and there were eight presentations of each enrichment to each subject. 2) Bones were supplied to tigers and lions twice per week during the day. Observations were conducted on tigers on exhibit, lions on exhibit, and lions in holding. The bones were placed on exhibit in the area most visible to the public, before the animal came outside for the day. In the case of lions remaining in holding, bones were provided on a concrete surface before the cat was allowed access to that portion of the enclosure. 3) Live fish were supplied twice a week to tigers on exhibit,

in shallow water pools. Fish were placed beside the pools immediately before the cats were allowed access to the exhibit area. Typically, the fish flopped into the water as the cat was entering the exhibit area or shortly thereafter. The decision to place fish beside the pools rather than in them was based on the notion that the fish would go unnoticed in the water, while their movement on the bank would attract the cats' attention. 4) A final post-manipulation baseline condition was conducted for tigers only. This was done to allow assessment of possible behavioral differences associated with change in ambient temperatures from the initial baseline condition.

Preliminary data indicated that interactions of tigers with fish occurred immediately upon presentation and lasted about 10 min. The presentation of fish early in the day and the short duration of the tigers' responses suggested that the value of this form of enrichment might not be adequately represented in the planned data collection. For this reason, an extra 30 min of data were collected when tigers were provided fish, adding 8 hr of data to the dataset. Reaction to bones occurred over the hour after they were presented and lasted at least 45 min, so this was adequately represented in the data.

Data Collection

Each cat was observed for 1-hr sessions with instantaneous scans of the behavior of all individuals in an exhibit at 1-min intervals [Altmann, 1974]. As the cats were usually undisturbed from 0930 to 1630 hr, the data recording sessions were performed at 1000–1200 hr, 1200–1400 hr, and 1400–1600 hr. At least six 1-hr sessions were recorded for each cat in each time interval, location, and condition. These data were collected from the public viewing areas when the animals were on exhibit, and from the side of the enclosure or inside the holding building when they were in holding. Eleven data collectors collected a total of 540 hr of data (for ethogram, see Bashaw, 2000]. An inter-observer index of concordance between the primary observer and each of the others of 88.5% or greater was achieved in 1 hr of simultaneous data collection [Martin and Bateson, 1986].

Data Analysis

In all tests, the $P < 0.05$ criteria was used to establish statistical significance. Data from the two baselines collected on tigers were compared using within-subjects t -tests, and combined for subsequent analysis. Then, data from all cats were used to assess changes in behavior in each enrichment condition compared to baseline data. Because the data did not appear to be normally distributed, the number of subjects was small, and a repeated-measures design was used, nonparametric statistics were employed [Runyon and Haber, 1984]. The level of nonstereotypic activity was computed by calculating the number of scans in which cats were either locomoting or engaged in active behavior. The Friedman's test, the nonparametric equivalent of a repeated-measures analysis of variance (ANOVA), was used to evaluate differences in activity, visibility, and levels of stereotypic behavior under each condition, as well as to determine whether graphically apparent differences in behavior were significant. Wilcoxon signed-ranks tests, which evaluate the difference between two samples based on the magnitude and sign of the differences between each pair of scores in a correlated sample, were used to evaluate differences between baseline data and the day of enrichment presentation. Wilcoxon tests were also used to compare

morning baseline data to the morning session in which enrichment was provided [Runyon and Haber, 1984].

RESULTS

Although visual trends were apparent in much of the data, few significant differences were detected, perhaps in part because of the low power inherent in the small sample size. Comparing baseline, treatment day, and each of the two subsequent days, no statistically significant differences were found for fish presentations (see Fig. 1), though graphs reveal an approximately 50% reduction in pacing maintained across the 2 days following treatment for these two animals. With only two animals, we can not claim statistical significance ($P=0.308$), but had we observed six animals, and all had shown a similar decrease, such results would be significant at the 0.05 level. For bone presentations, data for all cats reveal no

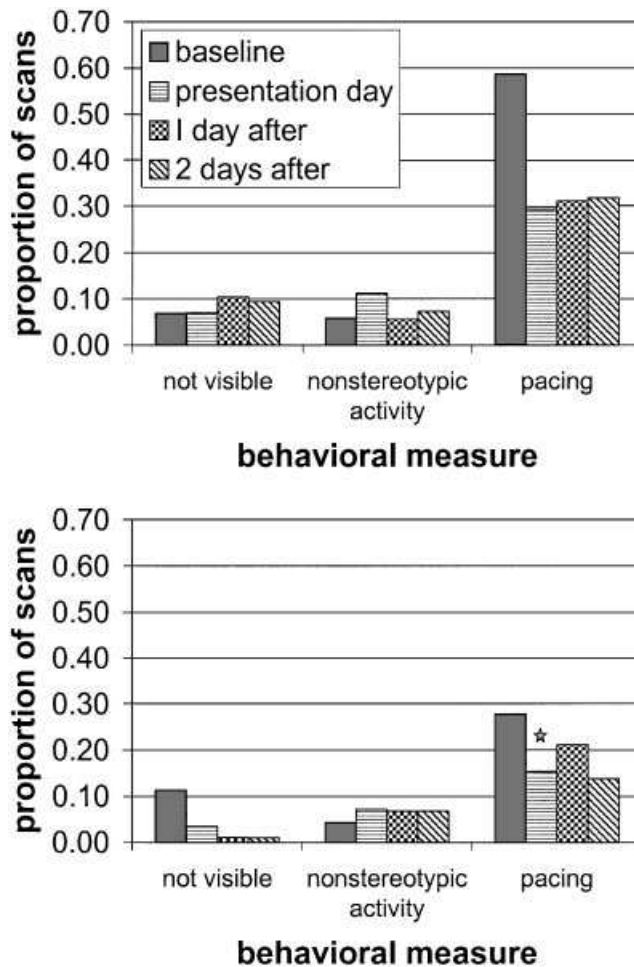


Fig. 1. Effects of provision of live fish to tigers (top), and bones to lions and tigers (bottom) on behavior. Stars represent significant differences from baseline.

significant differences (see Fig. 1), although trends toward effects on stereotypy ($P=0.095$) and nonstereotypic activity ($P=0.077$) were apparent. Data for the lions only showed decreased resting the day of presentation (from 38% of scans in baseline to 30%), followed by increased resting the next 2 days (44% and 50% of scans, respectively, $P=0.042$). Lions also showed increased nonstereotypic activity (from 3% in baseline to 9% the day of presentation and 5% each of the next 2 days, $P=0.045$) and a nonsignificant trend toward a difference in consumption (3% of scans on presentation days, never observed on other days, $P=0.082$). When data for the day of presentation were isolated, fish had no effect, whereas bones significantly reduced stereotypic behavior (Fig. 1, $P=0.043$). On the morning of presentation, bone presentation increased the proportion of scans spent resting but awake (from 38% to 65%, $P=0.045$), increased standing (5% to 14%, $P=0.045$), and increased consumptive behavior (from none to 3%, $P=0.045$), but fish caused no significant change in overall behavior patterns. Morning fish sessions, however, saw the occurrence of several appetitive behaviors never observed in the other conditions: crouching, pouncing, swiping, and biting. Watching, holding, and eating, which were not observed in the baseline, were seen in both bone and fish morning observations. In addition, carrying was observed with bones but not with fish or in the baseline.

DISCUSSION

Providing bones and live fish successfully elicited behavioral changes in captive lions and tigers. Consumptive behaviors increased with bone provision, and live fish presentation elicited capturing, killing, consumptive, and caching behaviors on the morning of presentation. There was also a nonsignificant trend toward reduced pacing with both fish and bone presentations, and a trend toward an increase in nonstereotypic activity with bone presentation. Although these findings did not reach statistical significance, changes were as much as 50% from baseline values. The trend toward an increase in time spent visible to zoo visitors with bone presentation may be large enough to have practical significance for the visitor experience. The enriched conditions had a few long-term effects, including a significant effect on resting in lions when they were given bones. Nonsignificant long-term trends were also present in stereotypic behavior (for both species and both conditions), in visibility (for both species and both conditions), in activity (for both species in the bone condition), and in consumption (for lions in the bone condition).

These effects corroborate and extend the results of several other enrichment procedures evaluated on felids. First, they emphasize that although they spend much of their time sleeping or engaged in stereotypic behavior, big cats do benefit from enrichment opportunities. Two advantages of these techniques are their small demand on keeper time and the lack of a mechanical apparatus, which obviates the need for repairs or maintenance by keepers on a tight schedule [Hutchins et al., 1984]. The presentation of bones and fish in this experiment also allowed the appetitive behaviors expressed to be rewarded with feeding opportunities. The increase in appetitive behaviors over those observed in baseline indicates that our enrichment procedures provided the cats with an opportunity to successfully express appetitive behaviors. The presentation of live fish was the more effective of the two techniques at increasing the variety of appetitive behaviors performed. These empirical data on the response of tigers to live fish, previously only anecdotally

described [Mellen et al., 1998], suggest that the presentation of live fish should be evaluated in a larger population to increase the generalizability of the results.

This study provides an example of the importance of evaluating the long-term effects of enrichment. In addition to studying the reaction of an animal to the enrichment procedure or device when it is present, evaluation of behavioral changes that occur in the animals' overall activity budgets is also important. In this study, the increase in feeding behaviors constitutes a reaction to the physical addition of the enrichment, but the changes in stereotypic behavior, used in part to monitor welfare, were not limited to periods in which the enrichment was present. Without evaluation at times when enrichment is not present, it is impossible to distinguish between procedures that cause a temporary behavior change only while they are present and those that cause sustained change outside the time at which enrichment is present. Forthman and colleagues [1992] identified an example of a temporary enrichment effect when Kodiak and polar bears provided with ice blocks and "fishcicles" showed dramatic behavior changes during enrichment, but no effect 5 hr later. However, Moodie and Chamove [1990] identified a sustained effect: brief presentations of predator silhouettes or removal of a group member resulted in changes in tamarins' behavior for the remainder of the day. In the current study, bone provision is an example of a more sustained and generalized enrichment effect, as the resulting changes in resting and trends in stereotypic pacing, nonstereotypic activity, consumption, and visibility over the 3-day period of observation suggest that bone provision altered the underlying behavior pattern of the cats.

Long-term evaluation is rarely performed because it is very time-consuming and frequently reveals little effect. Schapiro and colleagues [1995, 1996] collected 4,700 hr of data to discover a lack of overall behavioral effect from the presence or absence of enrichment over a 3-year period. However, important differences in behavior, including differences in mother-infant behavior in rhesus macaques under varying levels of foraging demand [Rosenblum and Pauly, 1984] and increased locomotion/exploring behavior when leopard cats were fed multiple hidden meals [Shepherdson et al., 1993], would not have been revealed had the sustained effects of enrichment not been evaluated. Because behavior is never altered in isolation, future studies should continue to document the effects of enrichment outside of the time in which it is presented.

Enrichment in zoos must strike a balance between the optimal living conditions of the animals and the quality of the visitor experience. The effect of enrichment projects must therefore be evaluated on both of these scales. Stereotypic behavior and inactivity may indicate compromised animal well-being and produce a compromised visitor viewing experience. The decrease in stereotypic behavior and the trend toward increased nonstereotypic activity in our study should affect both sides of this balance. It has been suggested that stereotypies arise in environments that do not allow the performance of a highly motivated behavior pattern to reach its endpoint [Hughes and Duncan, 1988]. If stereotypies result from a lack of connection between an animal's behavior and its environment, it is not surprising that creating an environment in which the reward of eating is contingent upon hunting behavior (as in nature) reduces the performance of these stereotypies.

The increase in variety and occurrence of appetitive behaviors with the presentation of fish, and the increase in frequency of appetitive behaviors with the presentation of bones are also positive changes for the animals' well-being. Many of

the anecdotal accounts of carnivore enrichment have highlighted the feeding of whole- or partial-carass meat [e.g., Hare et al., 1996]. The physiological consequences of feeding only processed meat diets include reduced influence of the jaw and neck muscles on skull shape in development [Duckler, 1998], greater gingival health problems, greater plaque formation, and more focal palatine erosion [Fitch and Fagan, 1982; Lindburg, 1988]. All of these problems are alleviated by carcass feeding opportunities. Carcass feeding has been demonstrated to increase feeding behaviors and decrease stereotypic behavior [McPhee, 1998], increase approaching, feeding, exploring, and processing food [Bond and Lindburg, 1990], and increase feeding duration and produce a wider variety of feeding behaviors [e.g., Ziegler, 1995; Hare et al., 1996]. Considering the similarity of these behavioral results to those obtained with bone presentation in this study, bones may function as a simplified and convenient form of carcass feeding.

Although the changes associated with bone provision are beneficial, the behaviors elicited by this opportunity, much like those elicited by carcass feeding, have all been associated with the consumption of food [Lindburg, 1988]. It would be more desirable to elicit behaviors from other categories of appetitive behavior, as accomplished by presentation of live prey, such as the live fish used in the present experiment and in other anecdotal reports [e.g., Hare et al., 1996; Hammond, 1998]. Providing live food may also be more educational for the public, who would get an opportunity to see carnivores engaged in the hunting and consumption of prey.

The time the animals spent in areas visible to zoo visitors in this study may have increased because the on-exhibit manipulations all rewarded the cats for going to the area of their exhibit where they were most easily seen. In fact, the intermittent nature of the presence of the stimuli may have resulted in a greater increase in visibility than continuous reinforcement for being in the same area would have. That the trend toward increased visibility was present even with bone presentation is especially interesting, since the bones were not restricted to visible areas of the exhibit. The cats could easily have picked up the bones and moved them to a different resting place, but anecdotal observation suggests that the animals spent most of their day where the enrichment was placed.

The results of this study support prior investigations into the role of feeding enrichment in improving the psychological well-being of animals and the visitor viewing experience. Carnivores in zoos should continue to be provided with their food in ways that allow the successful expression of a variety of appetitive behaviors to promote more naturalistic behavior. This naturalistic behavior will help educate the public about how these animals interact with their environment in the wild, thereby promoting conservation of not only the animals, but also their habitat [Maple, 1995]. In addition, maintaining a more complete behavioral repertoire is a contribution to preserving behaviorally competent animals in zoos, in case these animals should be needed to reinforce the wild population [Foose, 1987; Castro et al., 1998].

CONCLUSIONS

1. Bone presentation increased the performance of consumptive behaviors in lions and tigers, and its effects on behavior extended beyond the time when bones were present.

2. The presentation of live fish to tigers increased the frequency of a variety of appetitive behaviors in all categories, and also may have had sustained behavioral effects.
3. Long-term evaluation of enrichment can be used to distinguish between temporary effects from enrichment and procedures that result in sustained and generalized behavioral changes that affect an animal's overall activity budget.
4. Feeding enrichment for lions and tigers improves both the well-being of the cats and the experience of the zoo visitor.

ACKNOWLEDGMENTS

This study was completed as a portion of Meredith Bashaw's Master's thesis in the School of Psychology, Georgia Institute of Technology, and was approved by the IACUC of Zoo Atlanta. It should be noted that the feeding of live vertebrate animals to carnivores is illegal in some countries. Special thanks are extended to the animal-care staff: Glenn Goodman, Tim Nichols, Cilinia Powell, and Elise Varnadoe. These data could not have been collected without the concerted effort of a team of volunteers. Kate Alexander, Natasha Kennedy, Robin Keough, Sharon LeMeer, Melissa Loree, Jeanne Peters, Missy Snyder, Lorie Tarou, and Tiffany Willis all collected data for this project. Thanks also to the Zoo Atlanta veterinarians, Dr. Rita McManamon and Dr. Maria Crane.

REFERENCES

- Altmann J. 1974. Observational study of behavior: sampling methods. *Behavior* 48:227–265.
- Bacon RC. 1992. N.O.A.H. (naturalized operant animal habitat). In: Hare VJ, Worley KE, editors. *Proceedings of the Third International Conference on Environmental Enrichment*. Orlando, FL: Shape Enrich 1:6–7.
- Bashaw MJ. 2000. To hunt or not to hunt: a feeding enrichment experiment with captive wild cats. Master's thesis, Georgia Institute of Technology, Atlanta. 88 p.
- Bayne K, Dexter S, Mainzer H, McColly C, Campbell G, Yamada F. 1992. The use of artificial turf as a foraging substrate for individually housed rhesus monkeys (*Macaca mulata*). *Anim Welfare* 1:39–53.
- Bloomsmith MA, Alford PL, Maple TL. 1988. Successful feeding enrichment for captive chimpanzees. *Am J Primatol* 16:155–64.
- Bloomsmith MA, Lambeth SP. 1995. Effects of predictable versus unpredictable feeding schedules on chimpanzee behavior. *Appl Anim Behav Sci* 44:65–74.
- Boccia ML, Laudenslager M, Reite M. 1984. Spatial distribution of food and dominance related behaviors in bonnet macaques: a laboratory study. *Am J Primatol* 6:399.
- Bond JC, Lindburg DG. 1990. Carcass feeding of captive cheetahs (*Acinonyx jubatus*): the effects of a naturalistic feeding program on oral health and psychological well-being. *Appl Anim Behav Sci* 26:373–82.
- Brent L, Eichberg JW. 1991. Primate puzzleboard: a simple environmental enrichment device for captive chimpanzees. *Zoo Biol* 10:353–60.
- Carlstead K, Seidensticker J, Baldwin R. 1991. Environmental enrichment for zoo bears. *Zoo Biol* 10:3–16.
- Carlstead K, Shepherdson D. 1994. Effects of environmental enrichment on reproduction. *Zoo Biol* 13:447–58.
- 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, D.C.: Smithsonian Institution Press. p 113–28.
- Chamove AS. 1981. Establishment of a breeding colony of stump-tailed monkeys. *Lab Anim* 15:251–9.
- Chamove AS, Anderson JR, Morgan-Jones SC, Jones SP. 1982. Deep woodchip litter: hygiene, feeding, and behavioral enhancement in eight primate species. *Int J Stud Anim Prob* 3:308–17.
- Dierenfeld ES. 1987. Nutritional considerations in captive tiger management. In: Tilson RL, Seal US, editors. *Tigers of the world: the biology, biopolitics, management, and conservation of an endangered species*. Park Ridge, NJ: Noyes Publications. p 149–60.
- Duckler GL. 1998. An unusual osteological formation in the posterior skulls of captive tigers (*Panthera tigris*). *Zoo Biol* 17:135–42.

- Fitch H, Fagan DA. 1982. Focal palatine erosion associated with dental malocclusion in captive cheetahs. *Zoo Biol* 1:295–310.
- Foose TJ. 1987. Species survival plans and overall management strategies. In: Tilson RL, Seal US, editors. *Tigers of the world: the biology, biopolitics, management, and conservation of an endangered species*. Park Ridge, NJ: Noyes Publications. p 304–16.
- Forthman DL, Elder SD, Bakeman R, Kurkowski TW, Noble CC, Winslow SW. 1992. Effects of feeding enrichment on three species of captive bears. *Zoo Biol* 11:187–95.
- Gould E, Bres M. 1986. Regurgitation and reingestion in captive gorillas: description and intervention. *Zoo Biol* 5:241–50.
- Guggisberg CAW. 1975. *Wild cats of the world*. New York: Taplinger Publishing Company. 328 p.
- Hammond JP. 1998. Give 'em a life. In: Hare VJ, Worley KE, editors. *Proceedings of the Third International Conference on Environmental Enrichment*. Orlando, FL: Shape Enrich 7:4–6.
- Hare VJ, Herren R, Hawk K. 1996. Quick and easy mammal enrichment at Sun Bear forest. In: Hare VJ, Worley KE, editors. *Proceedings of the Third International Conference on Environmental Enrichment*. Orlando, FL: Shape Enrich 5:3–6.
- Hare VJ, Jarand P. 1998. Artificial prey that fights back (and other tales of tiger enrichment). In: Hare VJ, Worley KE, editors. *Proceedings of the Third International Conference on Environmental Enrichment*. Orlando, FL: Shape Enrich 7:1–4.
- Holst B. 1997. The ethics of environmental enrichment. In: Hare VJ, Worley KE, editors. *Proceedings of the Third International Conference on Environmental Enrichment*. Orlando, FL: Shape of Enrichment. p 45–8.
- Hughes BO, Duncan IJH. 1988. The notion of ethological need, models of motivation and animal welfare. *Anim Behav* 36:1696–707.
- Hutchins M, Hancocks D, Crockett C. 1984. Naturalistic solutions to the behavioral problems of captive animals. *Zool Garten* 54:28–42.
- Lindburg DG. 1988. Improving the feeding of captive felines through application of field data. *Zoo Biol* 7:211–8.
- Lindburg DG. 1998. Enrichment of captive mammals through provisioning. In: Shepherdson DJ, Mellen JD, Hutchins M, editors. *Second nature: environmental enrichment for captive animals*. Washington, D.C.: Smithsonian Institution Press. p 262–76.
- Maple TL. 1995. Toward a responsible zoo agenda. In: Norton BG, Hutchins M, Stevens EF, Maple TL, editors. *Ethics on the ark*. Washington, D.C.: Smithsonian Institution Press. p 20–30.
- Maple TL, Finlay TW. 1986. Evaluating the environments of captive nonhuman primates. In: Benirschke K, editor. *Primates: the road to self-sustaining populations*. New York: Springer-Verlag. p 479–88.
- Markowitz H. 1982. *Behavioral enrichment in the zoo*. New York: Van Nostrand Reinhold Company, 210p.
- Markowitz H, LaForse S. 1987. Artificial prey as behavioral enrichment devices for zoo felines. *Appl Anim Behav Sci* 18:31–43.
- Markowitz H, Aday C, Gavazzi A. 1995. Effectiveness of acoustic “prey”: environmental enrichment for a captive African leopard (*Panthera pardus*). *Zoo Biol* 14:371–9.
- Martin P, Bateson P. 1986. *Measuring behavior: an introductory guide*. Cambridge, UK: Cambridge University Press, 200p.
- Mason GJ. 1993. Forms of stereotypic behaviour. In: Lawrence AB, Rushen J, editors. *Stereotypic animal behaviour—fundamentals and applications to welfare*. Wallingford: CAB International. p 7–40.
- McPhee ME. 1998. *Behavioral research on captive mammals: its purpose, effectiveness, and perception*. Master's thesis, University of Michigan, Ann Arbor, Michigan. 120 p.
- Mellen JD, Hayes MP, Shepherdson DJ. 1998. Captive environments for small felids. In: Shepherdson DJ, Mellen JD, Hutchins M, editors. *Second nature: environmental enrichment for captive animals*. Washington, D.C.: Smithsonian Institution Press. p 184–201.
- Moodie EM, Chamove AS. 1990. Brief threatening events beneficial for captive tamarins? *Zoo Biol* 9:275–86.
- Powell DM. 1995. Preliminary evaluation of environmental enrichment techniques for African lions (*Panthera leo*). *Anim Welfare* 4:361–70.
- Rosenblum LA, Paulty GS. 1984. The effects of varying environmental demands on maternal and infant behavior. *Child Dev* 55:305–14.
- Runyon RP, Haber A. 1984. *Fundamentals of behavioral statistics*. 5th ed. Reading, MA: Addison-Wesley Publishing Company. 494 p.
- Sankhala K. 1977. *Tiger! The story of the Indian tiger*. New York: Simon & Schuster. 220 p.
- Schaller GB. 1967. *The deer and the tiger*. Chicago: University of Chicago Press. 370 p.
- Schaller GB. 1972. *The Serengeti lion: a study of predator-prey relations*. Chicago: University of Chicago Press. 480 p.
- Schapiro SJ, Bloomsmith MA, Porter LM, Suarez SA. 1995. Long-term effects of inanimate environmental enrichment on young rhesus monkeys. *Am J Primatol* 36:154.
- Schapiro SJ, Bloomsmith MA, Porter LM, Suarez SA. 1996. Enrichment effects on rhesus monkeys successively housed singly, in pairs, and in groups. *Appl Anim Behav Sci* 48:159–72.
- Seidensticker J, McDougall C. 1993. Tiger predatory behavior, ecology, and conservation. *Symp Zool Soc Lond* 65:105–25.
- Shepherdson DJ, Carlstead K, Mellen JD, Seidensticker J. 1993. The influence of food presentation on the behavior of small cats in confined environments. *Zoo Biol* 12:203–16.
- Tripp JK. 1985. Increasing activity in captive orangutans: provision of manipulable and edible materials. *Zoo Biol* 4:225–34.
- Ziegler G. 1995. An alternative to processed meat diets: carcass feeding at wildlife safari. *Shape Enrich* 4:1–5.