VARIATION OF FEEDING REGIMES: EFFECTS ON GIANT PANDA (*AILUROPODA MELANOLEUCA*) BEHAVIOR

A Thesis
Presented to
The Academic Faculty

By

Estelle A. Sandhaus

In Partial Fulfillment
Of the Requirements for the Degree
Master of Science in Psychology

Georgia Institute of Technology

September, 2004

Variation of Feeding Regimes: Effects on Giant Panda (*Ailuropoda melanoleuca*) Behavior

Approved by:

Dr. Terry L. Maple, Advisor
School of Psychology
Georgia Institute of Technology

Dr. Mollie A. Bloomsmith
School of Psychology
Georgia Institute of Technology

Dr. M. Jackson Marr
School of Psychology
Georgia Institute of Technology

Date Approved: September 15, 2004

DEDICATION

This thesis is dedicated in loving memory to my grandmother, Eleanor A. O’Gorman, whose unwavering faith will be with me always.

ACKNOWLEDGEMENTS

I wish to thank my committee members, Dr.'s Terry Maple, Mollie Bloomsmith, and M. Jackson Marr, for their guidance on this endeavor. I also wish to thank Dr. Rebecca Snyder for sharing her expertise on giant panda behavior throughout the entire course of this project.

I would like to express my profound gratitude to the directors, researchers, and animal care staff at the Chengdu Research Base of Giant Panda Breeding. I am thankful for having had the rare opportunity to share in your efforts on behalf of the giant panda.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

SUMMARY

In zoos, an increased emphasis on conservation, animal welfare, and public education has fueled the drive to create captive environments that encourage the expression of natural patterns of behavior. However, captive environments are inherently less complex and/or more predictable than wild ones (Tudge, 1992). It is not uncommon for a number of abnormal behaviors to arise in environments lacking in complexity and/or predictability (Mason, 1991a, 1991b), which is one issue addressed by the principle of environmental enrichment. The giant panda (*Ailuropoda melanoleuca*) is a critically endangered species for which conservation and public education efforts are of vital importance. While most of a wild panda's time is spent foraging, processing, and eating bamboo (Schaller Jinchu, Wenshi, & Jing, 1985), captive giant pandas are typically fed discrete amounts of highly concentrated foods on a fixed schedule (Dierenfeld, Qiu, Mainka, & Liu, 1995). Captive giant pandas in various facilities routinely engage in a number of abnormal behaviors prior to the feedings of these predictable meals. These observations are consistent with the findings that members of many species when fed on fixed schedules exhibit increased arousal and activity just prior to feeding, and this is referred to as feeding anticipatory activity (Mistleberger, 1994). While the animal welfare literature abounds with recommendations to implement more temporally complex feeding schedules, few quantitative assessments of these recommendations have been made.

This study proposed to provide a quantitative analysis of the effects of meal predictability on giant panda behavior. A reversal design was planned in which the animals were to be evaluated as they were fed on their usual predictable schedule, then as

they were fed on a more unpredictable schedule, and finally as they were returned to a more predictable schedule. The goal was to allow for the objective evaluation of a management strategy that has been frequently proposed, yet infrequently investigated, in the literature.

Because dietary restrictions were imposed on the female giant pandas (each of which was possibly pregnant at the time of this study), the originally proposed diet manipulations were modified. For the female subjects, the frequency of bamboo feedings was increased (the amount was held constant to baseline levels) in the manipulation phase of the experiment. For the male subjects, the delivery of concentrated meals was, as planned, made more unpredictable in the manipulation phase. Because of housing arrangements, the males were necessarily subject to the increase in bamboo feedings that was arranged for the females.

It was hypothesized that a pattern of feeding anticipatory activity would be present in the 30-minute periods prior to the feeding of concentrated meals. It was expected that rates of stereotypic behavior would be highest in these prefeed periods and that it would be lowest during nonfeeding periods throughout the day. It was also predicted that a more species-appropriate activity budget, with a lower incidence of abnormal and stereotypic behaviors, would be observed in giant pandas when switched to the modified feeding regimes, and that when returned to the less naturalistic regime the activity budget would return to baseline levels.

Across all phases of the study, the females spent significantly more time engaged in door-directed/human-oriented behavior, stereotypic behavior, and non-stereotypic locomotion in the 30-minute periods prior to feeding of a concentrated meal when

compared to nonfeeding periods. Across all data collection categories, no significant differences were found between study phases for the above-mentioned behaviors of interest, though percentage of time engaged in stereotypy approached statistical significance. We did not find significant differences in behaviors of interest between experimental phases or observation periods in the males' data. These findings may be attributable in part to the low power inherent in the small sample size. However, some visual trends which may be indicative of increased feeding anticipatory activity were apparent. Thus, it appears that giant pandas, like many other animal species discussed in the literature, are sensitive to periodic feeding regimes. Further study is needed to determine just which modifications to current regimes will be most beneficial to captive giant pandas. Methodology of the current study is examined from an applied perspective with the goal of aiding future research.

INTRODUCTION

Conservation, Research, and Education in the Zoo

Modern zoos have become increasingly involved with wildlife conservation and public education efforts. For instance, the American Zoo and Aquarium Association (AZA) now describes itself as a "professional organization dedicated to the advancement of North American zoos and aquariums through conservation, education, scientific studies, and recreation." The mission statement of Zoo Atlanta expresses similar sentiments: "...to exhibit, interpret, study and care for wildlife in superior environments, to conserve biodiversity throughout the world, to educate, entertain, and enlighten the public...."

This increased emphasis on conservation and education of late has fueled the drive to create captive environments that encourage the expression of natural patterns of behavior. In terms of education, this is significant in that the public may derive little educational benefit from the study of animals that do not behave similarly to their wild counterparts. The implications for conservation, too, are great. Zoo animals "...must be encouraged to retain enough of their natural behaviour to make it possible for them to go back to the wilderness; or enough at least of their native wit to enable them to relearn the necessary skills" (p. 193, Tudge, 1992). The ultimate challenge before zoos, then, is to provide "...sufficiently rich environments to allow the performance and maintenance of the species-typical behaviors necessary for survival in the wild" (Shepherdson, 1988). This task is inherently difficult; captive environments rarely match the wilderness in complexity and unpredictability (Tudge, 1992). To do this effectively, we must objectively evaluate the strategies that we implement. Maple and Finlay (1989) emphasized the fundamental role of research in zoos:

> We maintain that behavioral scientists are obliged to play an active movement to improve captive environments. Solutions to the problems of animal housing and husbandry must be cost effective, and we should not waste our time and resources on techniques that have not been objectively evaluated. Further progress depends upon a sustained program of applied research. (p. 102).

The Giant Panda

The giant panda (*Ailuropoda melanoleuca*) is an animal for which issues of conservation and public education hold great urgency. While the giant panda has long held significance in Chinese culture (Schaller, Jinchu, Wenshi, & Jing, 1985), it has only recently become recognized worldwide as a precious resource. The giant panda has had significant public exposure as the icon of the World Wildlife Fund, an organization whose self-proclaimed goal is "...to stop, and eventually reverse, the worsening degradation of the planet's natural environment, and build a future in which humans live in harmony with nature." The round, black-and-white face of the giant panda is all too appropriate a symbol for the struggles of this organization. The giant panda is a critically endangered species; the most recent peer-reviewed estimate indicates that less than one thousand still live in the wild (Tougard, Chaimane, Suteethorn, Triamwichanon, & Jaeger, 1996).

After extensive DNA analysis, it has generally been agreed upon that the giant panda is a member of the bear family, *Ursidae* (Ledge & Arnason, 1996; Nash, Weinberg, Ferguson-Smith, Menninger, & O'Brien, 1988; Talbot & Shields, 1996; Waits, Sullivan, O'Brien, & Ward, 1999). Although bamboo comprises more than 99% of its diet, the giant panda has essentially retained the digestive tract of a carnivore: it has relatively short intestines and relatively long intestinal villi, lacks a special chamber to retain food, and lacks symbiotic microbes to ferment cellulose into available nutrients. (Schaller et al., 1985). However, the giant panda does possess several morphological traits that facilitate the consumption and digestion of a bamboo diet, such as relatively flat molars and posterior premolars suited to crushing stems, and an enlarged radial sesamoid and sharply curved claws that facilitate the manipulation of bamboo (Schaller et al., 1985). Adaptations to reduce energy expenditure include large body size, a thick coat with oily, springy hairs, and sparing use of calorically expensive activities (Schaller et al., 1985). Giant pandas are largely solitary, and speculations have been made that its bold black and white coloration, which is cryptic only in the snow, helps them to easily spot one another in the forest and thus avoid unwanted contact (Schaller et al., 1995).

Habitat destruction and fragmentation have caused a rapid decline in the giant panda in recent decades by separating a "...once well-integrated giant panda population into many sub-populations of small size." These small populations are susceptible to a loss of genetic diversity through inbreeding, and are particularly vulnerable to greater reduction in numbers due to further habitat loss and poaching (Zhou & Pan, 1997). During the periodic synchronous flowering and die-off that is characteristic of many temperate bamboo species, food availability can drop below carrying capacity, resulting in the starvation of giant pandas in the isolated blocks of habitat (Reid, Jinchu, Sai, Wei, & Yan, 1989). Furthermore, individuals suffer from higher mortality rates when attempting to move from one isolated block of habitat to the next (Reid et al., 1989).

Small litter sizes and high infant mortality rates further contribute to the grave status of the giant panda. Giant pandas usually give birth to one or two highly altricial cubs, and typically care for only one. Thus, captive breeding programs are an essential part of a comprehensive management plan for this species. Unfortunately, successful captive breeding remains a challenge. Some individuals are reluctant to breed, and there has been some evidence of sub-optimal maternal care in captivity (Gittleman, 1994). One tool that may be used to improve the overall physiological and psychological welfare, and subsequently the reproductive success of captive giant pandas is that of environmental enrichment.

Environmental Enrichment and Psychological Well-Being

Environmental enrichment is defined as "...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). While precisely defining the term "psychological well-being" is problematic for both practical and theoretical reasons, several factors are generally considered as indicative of psychological well-being. It should be emphasized that these factors are not necessarily independent of one another.

The absence of stress has been proposed as an indicator of psychological well-being (Moberg, 1985, cited by Novak and Suomi, 1988). Certainly, chronic or inappropriately high levels of stress can be detrimental to the physical and mental health of an organism. For instance, prolonged exposure to stress or to the adrenal steroids secreted during stress have been shown to have detrimental effects on the rodent hippocampus, and more recent findings indicate that a similar phenomenon, associated with neuropsychiatric disorders, occurs in the human hippocampus (Sapolsky, 2000).

Other findings have indicated that stress seems to precipitate or exacerbate a number of neuroinflammatory disorders (Esposito, et al., 2001). However, while the prolonged effects of stressors may induce pathological processes, the initial psychobiological activation to stressors allows for the adjustment of an organism to changes in its environment (Maschke, Rupp & Hecht, 2000). Thus, it is possible that the complete absence of stress may be detrimental to the physiological and psychological well-being of an organism. Chamove and Anderson (1989) concluded, "The literature suggests that stress levels that are markedly and persistently below those likely to be found in the wild lead to individuals who do not deal well with subsequent stressors...." (p.192). The determination of what levels of stress may be 'optimal' for captive organisms is a difficult task, indeed.

Moreover, the use of stress as a measurement of psychological well-being is further complicated by the fact that stress is neither easily defined nor easily measured (Novak & Suomi, 1988). Physiological correlates to stress, such as hypothalamic – pituitary – adrenal (HPA) axis activity, are frequently used in conjunction with behavioral measures in attempts to measure stress and assess psychological well-being. For instance, Carlstead, Brown, and Seidensticker (1993) found reduced exploration to be a behavioral indicator of chronically elevated adrenocortical activity in leopard cats, suggesting that reduced exploratory behavior is an indicator of chronic exposure to aversive environmental conditions. However, it must be emphasized that because neuroendocrine responses to stress are varied, great care must be employed when interpreting physiological correlates to stress, particularly across a variety of species.

Another approach that is frequently used to assess the psychological welfare of captive animals is to compare the behavioral repertoire of a captive animal to that of its wild counterparts. Of course, due to ethical and practical considerations, captive animals are not subject to the scope of environmental events (e.g. predation, untreated disease) that their wild counterparts are subject to. Thus, the behavioral repertoire of captive animals is necessarily limited in some capacities. Nevertheless, in comparing the behavioral repertoire of a captive animal to that of its wild counterparts, we would generally expect both the expression of a species-typical behavioral repertoire and the absence of abnormal behaviors to be indicative of psychological well-being. Indeed, these criteria are frequently cited throughout the literature. For instance, Platt and Novak (1997) stated that one of the goals of their videostimulation study on captive rhesus monkeys was "...to alter their [the monkeys'] behavioral repertoire by reducing abnormal activity and increasing species typical behavior."

Schapiro and Bloomsmith (1995) confirmed that the typical approach in examining the effects of an enrichment program is to measure changes in frequencies or durations of behaviors as a function of enrichment relative to some baseline level. They explained that when increased species-appropriate levels of predetermined 'desirable behavior' are found in the enrichment program, the program is considered beneficial to psychological well-being. Conversely, the enrichment program is considered detrimental to psychological well-being if increases in 'undesirable behavior' are observed. While the authors acknowledged that theoretical questions exist concerning the measurement of behavior as an indicator of psychological well-being, they argued that this approach has considerable face validity.

One particular behavioral class that indicates a departure from species-typical behavior is that of stereotypies, behaviors that are repetitive, unvarying, and lacking in obvious goal or function (Ödberg, 1987; see also Mason, 1991a, 1991b). Stereotypies have been observed in a variety of animal species in numerous circumstances. They occur in a number of captive animals, including sows (Haskell, Mendl, Lawrence, & Austin, 2000; Rushen, 1985; Terlouw et al., 1991; Terlouw, Lawrence, & Illius, 1991), bank voles (Cooper, Ödberg, & Nicol, 1996; Ödberg, 1987), mink (Bildsøe, Knud, & Jeppesen, 1991; Jeppesen, Heller, & Dalsgaard, 2000), and giant pandas (Swaisgood et al., 2000), as well as in humans suffering from such disorders as mental retardation and autism. Stereotypies can also be induced in both humans and animals by the administration of indirect-acting dopaminergic agonists such as amphetamines (Canales, Gilmour, & Iversen, 2000; Laviolette, Priebe, & Yeomans, 2000; Wallace, Gudelsky, &Vorhees, 1999), and cocaine (Quinones-Jenab, Ho, Schlussman, Franck, & Kreek, 1999; Spangler, Zhou, Schlussman, Ho, & Kreek, 1997), by direct-acting dopaminergic agonists such as apomorphine (Battisti, Uretsky, & Wallace, 1999; Canales et al., 2000), and by non-competitive NMDA antagonists (Ishmael, Franklin, & Murray, 1998; Sams-Dodd, 1998). Stereotypies are heterogeneous in nature, ranging from the rocking of an autistic human to the pacing of a captive felid.

While controversy exists concerning the nature and causal factors of stereotypies, several factors that play a role have emerged from various studies. Numerous studies have demonstrated that an organism's environment can play a key role in the development of stereotypies (Marriner & Drickamer, 1994; Pyles, Riordan, & Bailey, 1997; Spoolder, Burbidge, Edward, Simmins, & Lawrence, 1995; Saunders, Saunders, & Marquis, 1998). Stereotypies are often physically and temporally linked to suboptimal features of an animal's environment, such as barren and restrictive conditions, situations of high arousal, isolation-rearing, and periodic feeding regimes (Mason, 1991a, 1991b). With time, a stereotypy may become independent of the stimulus that initially elicited its performance (Mason, 1991a). Thus, early intervention may be especially important.

Stereotypies may be considered indicative of poor well-being for a number of reasons. Stereotypies represent a departure from species-typical behavior, frequently occur in situations that have been independently shown to cause poor well-being (e.g. Jeppesen et al., 2000), and have been associated with undesirable physiological changes, such as decreased immune function (e.g. Metz & Osterlee, 1981). Thus, environmental enrichment programs are frequently designed with the reduction of stereotypies as one of the goals.

Indeed, investigators have found species-appropriate changes in behavior, such as reductions in stereotypies and increases in foraging behavior, upon implementation of a wide variety of environmental enrichment programs. For instance, reductions in locomotor stereotypies have been seen in bank voles upon movement to enriched cages containing hay and twigs (Cooper et al., 1996). Provision of mechanical prey devices has been shown to reduce stereotypic pacing and elicit more species-typical behavior in zoo carnivores (e.g. Markowitz, Aday, & Gavazzi 1995).

Food puzzles have been successfully employed to increase foraging activities in nonhuman primates (Reinhardt, 1993). Similarly, wild bush dogs showed increases in searching behavior upon the implementation of an enrichment program in which the entire food allowance was hidden throughout the enclosures and within constructed wood-piles (Ings, Waran, & Young, 1997). In a study of feeding enrichment with captive large felids, Bashaw, Bloomsmith, Marr and Maple (2003) found that the presentation of live fish reduced stereotypic behavior from sixty percent of scans to thirty percent of scans on the day of presentation in Sumatran tigers. Furthermore, this change was maintained for two days following this enrichment. Additionally, the presentation of horse leg bones reduced stereotypic behavior and increased nonstereotypic activity in both Sumatran tigers and African lions. In another study of captive lions, enrichment techniques as diverse as provisioning frozen balls of ice containing fish and providing novel objects and scents resulted in increased behavioral diversity and increased use of habitat space (Powell, 1995).

The Role of Predictability in Animal Welfare

The reduction of complexity in a captive environment as opposed to a wild environment can be thought of as increasing the predictability of stimulation (Chamove & Anderson, 1989). This factor needs to be carefully considered in the design of captive animal management routines, for the predictability of events has been implicated as a factor influencing both the physiological and psychological well-being of organisms.

An enormous body of experimental literature is devoted to the exploration of the effects of predictability versus unpredictability on the behavior and physiology on organisms. When examining this literature it is important to keep in mind that analysis is complicated by a degree of overlap between the constructs of predictability and controllability (Foa, Zinbarg, and Rothbaum, 1992; Mineka and Kihlstrom, 1978). As my study is concerned with manipulating the timing of an event that is response independent, the focus here will be on predictability rather than control.

A large portion of predictability/controllability research has focused on the effects of aversive stimuli on laboratory animals. Much of the literature supports the notion that unpredictable and/or uncontrollable aversive events result in greater physiological and behavioral disturbances than otherwise identical predictable and/or controllable events (Kjellberg, Landström, Tesarz, Söderberg, Akerlund, 1996; Klein, L.C., Popke, E.J., & Grunberg, N.E., 1997; Lejuez, Eifert, Zvolensky, and Richards, 2000; Mineka and Kihlstrom, 1978). Minkea and Kihlstrom (1978) assert that while the relevant literature pertaining to appetitive (as opposed to aversive) events is sparse, similar although perhaps less pronounced disturbances result when such events are unpredictable and/or uncontrollable.

However, other studies have provided evidence that predictable events may be more stressful to an animal than unpredictable ones. For instance, captive animals have exhibited decreases in agonistic and abnormal behaviors upon implementation of less predictable feeding strategies in several studies. These findings may make sense in light of the fact that a captive environment is typically far more predictable than a natural one. Bloomsmith, Alford, and Maple (1988) implemented a feeding enrichment program for captive chimpanzees in which four feeding strategies were simultaneously implemented. The chimpanzees were given 1) an extra meal in the morning with foods requiring relatively high amounts of processing time, 2) food puzzle devices that required work to obtain the desired food items 3) folivore biscuits placed in outdoor dispensers (so that these food items were available all day rather than at discrete meal times), and 4) small portions of food that were scattered in the outdoor enclosures at unscheduled times daily. The implementation of these feeding enrichment procedures resulted in a reduction in agonistic and abnormal behavior in the chimpanzees. This particular experimental design, however, did not allow for the delineation of the relative effectiveness of each enrichment technique. Another point that must be considered is that the provisioning of food puzzles and scattered food made the acquisition of these food items contingent upon a response (i.e. solving the puzzle and foraging), and thus the animals may be said to have been given the opportunity to exert more control over their environments. Therefore, while the temporal and spatial locations of the some food items were made more unpredictable by providing puzzles and scatter feedings, the relative effects of or possible interaction between controllability and predictability cannot be determined.

Small felids provided with more frequent feedings of hidden food have exhibited greater behavioral diversity indices and reductions in stereotypic pacing (Shepherdson, Carlstead, Mellen, & Seidensticker, 1993) The authors point to two characteristics of the feeding manipulations that may have elicited these species-appropriate behavioral changes. One factor cited was the requirement that the animal perform "...some degree of functionally naturalistic foraging behavior to acquire food" (p. 212). The second point highlighted was the fact that "...because the food was hidden, they [the cats] could never be sure exactly how much food, if any, remained." (p.212) The first characteristic may relate to control, and as in the previous study, may confound the effects of predictability. However, it is important to note that, because the food was hidden, both the spatial and temporal locations of the rations were made more variable and thus less predictable.

Bloomsmith and Lambeth (1995) compared the behavioral effects of providing fresh produce meals to chimpanzees on a predictable versus on a more unpredictable schedule. They found that on a less predictable schedule, inactivity was less prevalent, and abnormal behavior showed a similar trend. Because behavior was altered in a species-appropriate direction, the authors assert that by that criterion, the feeding of chimpanzees on an unpredictable schedule may promote well-being. The authors note that these results may seem contrary to the findings of some investigators that unpredictable events may be more aversive. In seeking an explanation to these seemingly paradoxical results, Bloomsmith and Lambeth suggest that perhaps in instances where an organism lacks control over the delivery of an event, the ***nature*** of the upcoming event, whether appetitive or aversive, may determine whether an unpredictable or predictable schedule is more stressful. Thus, it is highly important to objectively evaluate the effects of predictability of routine events in animal facilities.

Environmental Enrichment for the Giant Panda

Because environmental enrichment may improve the reproductive potential of individual animals by affording them more of the behavioral opportunities found in the wild (Carlstead & Shepherdson, 1994), we may improve the reproductive status of captive giant pandas by implementing environmental enrichment programs as an integral part of their management. Furthermore, environmental enrichment programs have been shown to promote species-typical behavior in not only canids, felids, and primates, but in a number of bear species as well.

For instance, Carlstead, Seidensticker, and Baldwin (1991) found increases in exploration and foraging and decreases in walking and pacing upon introduction of novel, manipulable, honey-filled logs to the exhibits of sloth, brown, and black bears. Additionally, the authors found that hiding food in manipulable exhibit furnishings elicited an increase in foraging and a concomitant decrease in stereotypic pacing. Similarly, Carlstead and Seidensticker (1991) found that hiding small food items in the exhibit of an American black bear elicited a nearly complete reduction in seasonal (fall) pacing. They further demonstrated that the placement of bear odors elicited a reduction in seasonal (late spring) pacing and an increase in exploration and foraging.

To date, only one published study concerns the effects of an environmental enrichment program for giant pandas, and the results are promising. Using various objects that were expected to elicit species-typical behaviors, Swaisgood et. al. (2000) found that an enrichment program with manipulable objects was effective. The pandas spent more time active, and displayed a greater variety of both object and non-object directed behaviors when enrichment items were present.

There is reason to believe that a feeding enrichment program, too, may be instrumental in eliciting behavioral changes in a species-appropriate direction in the captive giant panda. While most of a wild panda's time is spent foraging, processing, and eating bamboo (Schaller, 1995), captive giant pandas are usually fed discrete amounts of highly concentrated foods in addition to limited amounts of bamboo and other forage in scheduled meals throughout the day (Dierenfeld, Qiu, & Mainka, 1995). It should be pointed out that providing large quantities of suitable bamboo is not always feasible due to limitations in sources and storage of bamboo. In one captive breeding facility in China, giant pandas exhibit increased vigilance toward keepers, pacing, stereotypic head tossing, rocking, and aggression during the periods just prior to the feeding of predictable meals (R. Snyder, personal communication). Similarly, in one zoological facility in the United States, giant pandas have been seen to exhibit increased vigilance toward keepers, pacing, scratching, and honking during the periods just prior to the feedings of predictable meals (personal observation). These observations are consistent with the findings that many species that are fed on fixed schedules exhibit increased arousal and activity, referred to as feeding anticipatory activity (FAA)**,** just prior to feeding (Mistleberger, 1994). Indeed, it has been well established that daily feeding schedules are capable of synchronizing many rhythmic biological functions in a variety of species (Boulos & Terman, 1979)**.**

Thus, it is of particular import to examine the effects of fixed feeding times on giant panda behavior. Hancocks, Hutchins, & Crockett (1979, cited by Hancocks, 1980) pointed out that there are two essential, basic methods of increasing environmental complexity in the zoo, spatially and temporally. Hutchins, Hancocks, & Crockett (1984) point out that temporal variation in the natural environment is apparent in daily and seasonal variations in light, temperature, humidity and food availability. The following passage (Hutchins et al.) underscores the need for controlled study of meal variability in a variety of captive species:

> "It is a fact that zoo animals are usually fed on a rigid schedule. The timing of feeding as well as the type, amount, and placement of foods are highly predictable. Behavioral stereotypes often become evident in this situation, and variety can be introduced to help reduce monotony and alleviate certain aberrant behaviors.... Some experimentation is required to learn more about this subject and to assess its potential benefits for captive animals. Food can be given at various times of the day, for example, to introduce some temporal variation. Either the food ration could be offered in a single feeding at different times each day, or the ration could be subdivided and offered at random times throughout the day. Knowledge of the natural feeding ecology would aid in selecting appropriate methods for a given species and carefully controlled behavioral observation should be made to evaluate the effects of different techniques." (pp. 35-37).

Consistent with the recommendations of Hutchins et al., the temporal manipulations originally proposed for this study were designed to facilitate a quantitative analysis of the efficacy of providing meals on a more variable schedule. These proposed manipulations were also consistent with the recommendations of the *1998 Behavior Working Group Report of the CBSG* to feed giant pandas at “different, non-fixed times during the day” (p.22) as a strategy for implementing more naturalistic feeding regimes. Due to practical constraints, the proposed manipulations were necessarily modified, albeit in a manner not as conducive to detailed analysis as was originally proposed.

It was hypothesized that a more species-appropriate activity budget, with a lower incidence of abnormal and stereotypic behaviors, would be observed in giant pandas when switched to a more naturalistic feeding regime, and that when returned to the less naturalistic regime the activity budget would return to baseline levels. Due to dietary restrictions on possibly pregnant females, the originally proposed diet manipulations were necessarily modified. For the female subjects, the frequency of bamboo feedings was increased (the amount was held constant to baseline levels) in the manipulation phase of the experiment. For the male subjects, the delivery of concentrated meals was, as planned, made more unpredictable in the manipulation phase. Because of housing arrangements, the males were necessarily subject to the increase in bamboo feedings that was arranged for the females.

METHODS

While this study was initially planned as one experiment in which the predictability of concentrated meals would be manipulated using both sexes of animals as subjects, concerns of veterinary staff about health considerations for pregnant females dictated that only slight manipulations be made to the females' diets. As a result, separate experiments were performed for females and males.

Study Site

Subjects of both experiments were housed at the Chengdu Research Base of Giant Panda Breeding in Sichuan Province, China. At the Research Base, animals typically have access to a large outdoor area (average of 2600 m^2 and an indoor bedroom area (average size of 14 m^2). The outdoor areas are enriched with live vegetation (e.g. grass, shrubs), water pools, rocks, logs, climbing structures, and tire swings. The indoor bedroom areas contain wood sleeping platforms and cement water troughs. At various times throughout the day the animals are routinely periodically confined to either the indoor or the outdoor portion of their enclosures for routine care (e.g., cleaning).

A variety of abnormal behaviors had been observed prior to this study in the giant pandas at the Research Base by animal care and research staff. Stereotypic pacing had been observed in nearly all of the animals. In many of the adults, head tossing and somersaulting had been seen to occur within pacing bouts. Several of the animals had engaged in stereotypic pirouetting and sit pirouetting. The aforementioned behaviors were typically reported when the animals were confined to a particular portion of their enclosure (e.g., indoor access only).

Prior to this study, feeding anticipatory behavior prior to the predictable feeding of concentrated meals had been informally observed in nearly all of the pandas at the Research Base. In the pair-housed animals, an increased incidence of aggressive behavior, such as moaning and paw-swatting, had been observed. Increased human-oriented behavior was reported to be seen regularly in nearly all of the animals prior to feeding. Stereotypic behaviors, including rocking, teeth clicking, and muzzle pushing had been observed in several animals prior to feeding. Animals had also been observed to repetitively reach through the cage bars prior to feeding, in both the presence and absence of humans. In addition to this reaching behavior, some animals had been observed to repetitively flick the cage padlocks with their paws. An increased frequency of bleating had been observed in many animals prior to feeding, as well. Two adult females, Cheng Cheng and Qing Qing, had been known to engage in stereotypic reingestion and regurgitation following the initial consumption of their concentrated meals, but this had not been observed in any of the males.

One aim of this study was to document existing feeding practices at the Research Base. The experimenter was initially told that a concentrated meal was fed in the bedroom area within approximately thirty minutes of 0930 hours. A concentrated meal consisted of several items: a milk “gruel,” provided to the animals in metal bowls, 1-3 cone-shaped masses of “bread,” which was comprised of wheat flower, rice flower, corn flower, powdered milk concentrate, egg, a vitamin/mineral supplement, and sometimes meat powder. Fruit, usually apple, was provided after the animals had finished both gruel and bread. Pair- and group- housed animals were sometimes separated into different areas for these meals; at other times they were simply fed at opposite ends of a shared enclosure.

Experiment 1

Subjects

Subjects of this experiment were seven adult female giant pandas: Bing Bing (studbook # 314), Er Ya Tou (studbook # 401), Jiao Zi (studbook # 425), Qing Qing (studbook # 278), Su Lan (studbook # 407), Su Su (studbook # 312), and Ya Ya (studbook # 362).

Adult females are generally housed in pairs and sometimes trios at the Research Base, though they are housed alone when pregnancy is suspected. This was the case for the subjects of Experiment 1. In the Baseline phase, the following animals were pair-housed: Bing Bing and Qing Qing, Su Su and Ya Ya, Jiao Zi and Su Lan. Eryatou spent time with Lan Lan (mating opportunities, as she had a late estrous that year) and alone. One week after the feeding changes were implemented in the Treatment phase (but on the very first day of data collection for this phase), the following animals were moved to solitary enclosures due to signs of pregnancy: Bing Bing, Su Su, Ya Ya. Lan Lan and Eryatou spent more time together for mating opportunities during the treatment phase, after which Qing Qing and Eryatou shared an enclosure with Lan Lan for at least one observation session, after which Qing Qing and Eryatou spent the rest of the Treatment phase together. This pair remained together during the Second Baseline phase, as did Jiao Zi and Su Lan. Bing Bing, Su Su, and Ya Ya remained alone during the Second Baseline

Phase.

Procedure

Both Experiments 1 and 2 were introduced, discussed, and modified at an animal care staff meeting at the Research Base in Chinese via an interpreter, and keeper staff (most of whom had been present at the meeting) were subsequently provided with both oral and written instructions in Chinese via an interpreter.

During the Baseline condition, animal care staff were asked to continue with their “usual” feeding and animal care regimes. The animals had presumably been on the same feeding schedules for a number of years, and this study aimed to document the existing feeding practices. During the entire study, the single experimenter tried to remain as unobtrusive as possible in her observations, so as not to unduly influence the animal care routines.

Due to possible pregnancies in the females, the Research Base’s team of veterinarians and scientists decided that the females’ concentrated diet should be held constant. Thus, in the manipulation phase of the study the females were given only more frequent portioning of fresh bamboo (amount held constant). No modifications made to the delivery of their concentrated diet. Fresh bamboo provisioning was increased from approximately 3 times (as determined in the Baseline phase) to 5 times during daylight hours, with the total volume of bamboo held constant. Table 1 summarizes the observation (i.e., data collection) times and bamboo provisioning times for each housing cluster of females in the baseline phase of the study.

Table 1. Observed Baseline Bamboo Feeding Times for Each Housing Cluster of Females.

	Early AM			**10-11 AM**			**1-2 PM**			**2-3 PM**			**Late PM**		
	Date	*Prov Time*	*Obs Time*	*Date*	*Prov Time*	*Obs Time*	*Date*	*Prov Time*	*Obs Time*	*Date*	*Prov Time*	*Obs Time*	*Date*	*Prov Time*	*Obs Time*
Eryatou (Housed with Lan Lan)	6/2/2001	none	7:50-9:13	6/14/2001	none	10:00	6/20/2001	1:41,1:52	1:00	6/12/2001	none	2:08	6/2/2001	none	3:41-5:00
	6/12/2001	7:40, 9:07	7:40-9:15	6/15/2001	none	10:00	6/23/2001	none	1:11	6/15/2001	2:22	2:19	6/8/2001	4:33	3:42-4:53
	6/14/2001	7:38,9:21	7:38-9:52							6/25/2001	2:35	2:23	6/18/2001	4:31	3:41-4:52
	6/27/2001	7:58	7:45-9:24												
Su Su/Ya Ya	6/9/2001	8:56	7:52-8:59	6/7/2001	none	10:00	6/12/2001	none	1:00	6/2/2001	2:55	2:19	6/12/2001	3:43,4:16,4:33	3:31-4:57
	6/19/2001	8:45	7:49-9:09	6/8/2001	none	10:00	6/14/2001	none	1:11	6/23/2001	2:44	2:22	6/13/2001	4:00, 4:27	3:35-4:51
	6/23/2001	8:51	7:51-9:16	6/18/2001	none	10:00									
				6/22/2001	none	9:59									
Jiao Zi/Su Lan	5/30/2001	8:52	7:40-9:10	6/2/2001	none	10:00	6/9/2001	none	1:00	6/8/2001	14:22	2:02	6/7/2001	4:48	3:52-4:55
	6/7/2001	9:11	7:53-9:26	6/19/2001	none	10:02	6/19/2001	none	1:06	6/14/2001	2:22,3:11	2:12	6/15/2001	3:47,4:06,4:24	3:40-4:54
	6/18/2001	9:01	7:50-9:31										6/23/2001	4:17	3:41-4:53
	6/22/2001	9:02	7:49-9:16												
Bing Bing/Qing Qing	6/4/2001	7:58	7:48-9:08	6/12/2001	none	10:00	5/31/2001	1:21	12:59	6/8/2001	2:54	2:17	5/30/2001	4:02,4:41	3:45-5:01
	6/6/2001	8:17	7:52-9:04	6/23/2001	10:03	10:00	6/15/2001	1:10	1:04	6/9/2001	2:28	2:12			
	6/15/2001	8:38	7:53-9:00	6/26/2001	none	10:00	6/25/2001	1:20	1:08						
	6/20/2001	8:51	7:52-9:07												

After examining baseline feeding practices, it was determined that an additional feeding manipulation was needed during the experimental phase of the study. During the Baseline phase it had become apparent that animals were sometimes moved to an empty enclosure without having their bamboo being moved (i.e., no bamboo was in the new enclosure). In the first week of the feeding manipulation (before data collection for that phase had commenced), this was observed to interfere with the two newly scheduled bamboo provisionings because animals would sometimes be given a scheduled feeding and then very soon afterwards moved away from the bamboo (usually into a separate enclosure for the concentrate). The experimenter decided that the manipulation in these cases could not be deemed a manipulation (i.e., the animals being moved away from the bamboo would be nearly equivalent to not having received it at all), and so the additional stipulation was made that the scheduled bamboo feedings were to be made in the enclosure in which the concentrated food was to be fed. Thus, the feeding manipulation in the treatment phase was not limited to a change in bamboo feeding frequency in and of itself. Ideally a separate manipulation phase would have been added (i.e. feed bamboo on the "usual" schedule but with the stipulation that the bamboo was to be always present in the enclosure in which the concentrate was to be fed), but time did not allow for this. It should be noted that ethical considerations were involved in the decision to add the aforementioned stipulation to the feeding manipulation. When the animals were moved to an empty enclosure before feeding in the baseline phase, it appeared that a number of undesirable behaviors were regularly performed. The extent to which this was dependent on the temporal aspects of the feeding, and/or on the spatial problem (i.e. absence of food in the new enclosure) could not be determined without a separate manipulation phase as mentioned above. However, it was thought that adding the stipulation (as opposed to making no changes in light of the “lack-of-manipulation” issue) might do more to encourage species-appropriate behavior in those times before feeding.

Data Collection

Observational data were collected during each of the experimental phases (dates). Mealtime data collection periods (subsequently referred to as “observation periods”) consisted of the thirty minutes prior to the feeding of a concentrated meal (“Prefeed”) and the thirty minutes immediately after the provisioning of a concentrated meal (“Postfeed”). Additionally, animals were observed for sixty-minute “Nonfeed’ time blocks between 1000 and 1500. Thus, observer presence should not have served as a discriminative stimulus for the arrival of meals.

Note that while modification of the delivery of the concentrated meal was not carried out as originally planned, it was deemed appropriate to continue to center observations around the concentrated mealtimes, as this was when feeding anticipatory activity was thought to occur. The more frequent bamboo feedings were expected to elicit behavioral changes that would be present in the time periods surrounding the provisioning of concentrated food.

The observer watched from a position outside of the pandas’ enclosures. When observing indoors this distance was usually 1-3 meters, while when observing outdoors this distance was more typically 5-10 meters. Animals were randomly assigned (without replacement) to observation periods, with the exception that no animal was to be observed for more than two back-to-back observation periods of a particular type (i.e., Prefeed, Postfeed, Nonfeed) on the same day. Three sampling methods (i.e. all-occurrence, instantaneous, and one-zero) with one-minute intervals were used simultaneously to collect behavioral data on a single animal during each session (Crockett, 1996). A stopwatch was used to emit an audible signal at one-minute intervals. Approximately 146 hours of data were collected for Experiment 1. The ethogram employed for this study (Appendix A) was adapted from those already utilized at San Diego Zoo, Wolong Reserve, Zoo Atlanta, and Chengdu Zoo and Research Base of Giant Panda Breeding, so that behavioral data might be compared if so desired in the future. Behaviors recorded included: stereotypies, aggression, locomotion, resting, and feeding.

Data Analysis

Activity budgets based on estimated mean percent time spent in various activities were calculated for each subject and study phase using data collected via instantaneous sampling. Hourly rates of behaviors likely to be affected by the changes in feeding routine, such as stereotypies and aggressive interactions, were calculated for each subject and study phase using data collected via all-occurrence sampling. The percentages of intervals in which selected vocalizations occurred were calculated from data collected via one-zero sampling.

The following all-occurrence behaviors were collapsed for analysis: 1) state-like event stereotypies (Head Nod, Head Shake, Lick Mouth, Muzzle Push, Pirouette, Reach, Rock, Stereotypic Roll, Sway, Teeth Click, Weave) and 2) Olfactory Investigation of different substrates.

The following instantaneous behaviors were collapsed for analysis: stereotypies

(Door-Directed when characterized by stereotypy, Head Nod, Head Shake, Stereotypic Lick/Bite, Lick Mouth, Muzzle Push, Rock, Stereotypic Scratch, Pace, Sway, Quasi-Stereotypic Pace, Stereotypic Self Bite) feeding on bamboo (Feed Leaves, Feed Stem, Feed Shoots, Feed Whole Bamboo) , feeding on other matter (Feed bread, Feed Fruit, Feed Gruel, Feed Other Vegetation, Feed Other, Feed Unknown,), inactivity (Rest, Stationary Alert), door-directed and human-oriented (Door Directed, Human Oriented), olfactory investigation (includes all substrates), and maintenance behaviors (Scratch, Lick/Bite, Lick/Bite Forepaws).

Because the data were strongly suspected to violate parametric assumptions, and a non-parametric counterpart to a two-way within-subjects multiple analysis of variance (MANOVA) could not be found, the assumption of no interactions was made and the nonparametric Friedman's two-way analysis of variance (ANOVA) was used to evaluate whether measurements of behaviors of interest differed between 1) study phase and 2) observation period. Where significant differences were revealed by a Friedman test, a multiple comparison procedure, the Wilcoxon signed-ranks test, was employed (Siegel and Castellan, 1988; Hollander and Wolfe 1999). To maintain an experimentwise error rate of $\alpha = 0.05$, the critical values for the multiple comparison procedure were modified as specified in Hollander and Wolfe (1999). All analyses were carried out with SPSS 11.0 for Windows.

Experiment 2

Subjects

Subjects of this experiment were two adult males, Kobi (studbook # 386) and Lan Lan **(**studbook # 287). Of the two subjects studied, Kobi had been reported by Research Base staff to be a frequent pacer. Lan Lan was not generally considered by Research Base staff to exhibit high levels of stereotypic behavior. It should also be noted that for a period of years, Lan Lan was the only breeding male at the Chengdu institutions. By contrast, Kobi had reputedly shown signs of aggression that prevented pairing with females for breeding.

Kobi was housed individually throughout the duration of the study, though he was moved from a solitary building to one shared by two additional adult males (Lan Lan and Xiao Ping Ping (studbook # 342)). During this time period Kobi periodically had visual access to Lan Lan through a barred cement tunnel. Kobi also presumably had the auditory and olfactory contact with the other animals that is inherent to sharing a building. During the Baseline phase Lan Lan was given access to an estrous female, Er Ya Tou, as described in the Methods section for Experiment 1. Also as described, for Experiment 1, for at least one observation day he shared an enclosure area with both Qing Qing and Eryatou in the Treatment phase. Lan Lan had reportedly shared enclosures uneventfully with this pair of females for many prior years (R. Snyder, personal communication).

Procedure

A reversal design was employed to examine the effects of modifying the frequency and timing of feedings. During baseline conditions, the daily feeding routine was simply observed. Table 2 summarizes the observed Baseline concentrated feeding times for each male.

Table 2. Mean Baseline Concentrated Feeding Times ± Std Dev for Each Male.

	Kobi	Lan Lan (Housed w/Eryatou)
AM Bread	9:27±0:07	8:47±0:11
AM Gruel	9:20±0:02	8:51±0:21
PM Bread	4:19±:0:00	4:32±0:12
PM Gruel	4:17±0:00	4:23±0:08

In the manipulation phase of the study, the males were simultaneously given 1) their twice-daily concentrated meals on a more unpredictable schedule and 2) more frequent portioning of fresh bamboo (although the daily volume of provisioned food was held constant). The latter manipulation, while not initially planned, was unavoidable for Lan Lan because he was at times housed with two subjects of Experiment 1. For consistency, this manipulation was given to Kobi also. As in Experiment 1, animal care staff were given both oral and written instructions in Chinese (via an interpreter) both prior to and during the manipulation phase. Meals were fed on an unpredictable schedule: either -60, 0, or +60 minutes to the Baseline mean feeding time. Because of management practicalities, a greater variation in meal times was not possible.

During the third phase of the study, the animals were returned to the baseline feeding schedule. The daily amount and content of provisioned food remained constant for all phases.

Data Collection

Data collection methods for Experiment 2 were the same as for Experiment 2 are the same as were described in the Methods section for Experiment 1. Approximately 67 hours of data were collected for Experiment 2.

Data Analysis

The following all-occurrence behaviors were collapsed for analysis: state-like event stereotypies (Cage Climb, Head Nod, Head Shake, Lick Mouth, Muzzle Push, Reach, Rock, Stereotypic Roll, Sway), olfactory investigation (all substrates), and anogenital marking (Leg-Cock Mark, Handstand Mark).

The following instantaneous behavior were collapsed for analysis: stereotypies (Door Directed when characterized by stereotypy, Head Nod, Head Shake, Stereotypic Lick/Bite, Lick Mouth, Muzzle Push, Rock, Stereotypic Scratch, Pace, Sway, Quasi-Stereotypic Pacing, Stereotypic Self Bite, feeding on bamboo (Feed Leaves, Feed Stem, Feed Shoots, Feed Whole Bamboo), feeding on other matter (Feed Other Vegetation, Feed Bread, Feed Fruit, Feed Gruel, Feed Other, Feed Unknown), inactivity (Rest, Stationary Alert), olfactory investigation (all substrates), door-directed and human-oriented (Door Directed, Human Oriented), and maintenance (Scratch, Lick/Bite, Lick/Bite Forepaws).

The statistical analyses for Experiment 2 were performed in the same manner as those described in the Methods section for Experiment 1.

RESULTS

Experiment 1

Differences Between Study Phases

Table 1 presents hourly rates of behaviors of interest for each of the experimental phases averaged across all observation periods.

Table 3. Mean Hourly Rate ± Std Dev of Behaviors of Interest for each Experimental Condition

Behavior	**Baseline**	**Treatment**	**Second Baseline**
Bouts of Stereotypy*	3.86±3.90	4.96±3.67	9.09±5.91
Head Toss	16.96±34.26	0.84±1.50	5.35±7.66
Olfactory Investigation	0.93±0.92	0.43±0.44	1.37±1.16
Anogenital Mark	0.21±0.41	0.00±0.00	0.71±1.54

*includes those stereotypies measured as bouts of behavior rather than those measured as discrete events

A Friedman test revealed that the hourly rate of bouts of stereotypies defined as state-like-events in the ethogram differed between study phases (χ^2=6.889 ,p=0.032). Based on a Wilcoxon Test, the rate of such bouts was higher in the Second Baseline than in the Baseline phase (Z=-2.201, p=0.028). No significant differences were detected between the Baseline and Treatment phases, or between the Treatment and Second Baseline phases.

No significant differences were found between study phases for the following behaviors: Head Toss, Olfactory Investigation, and Anogenital Mark.

Table 2 presents the mean percentage of time spent in behaviors of interest for each of the experimental phases, averaged across all observation periods.

Table 4. Mean Percent Time ± Std Dev of Behaviors of Interest for each Experimental Condition

Behavior	**Baseline**	**Treatment**	**Second Baseline**
Door Directed and Human Oriented	6.47±2.40	5.55±4.98	7.10 ±3.25
Stereotypy	9.86±7.61	3.05±2.50	9.03±6.41
Inactive	22.13±11.58	49.01±20.97	51.08±23.41
Feed Concentrated Food	10.21 ±4.80	11.52 ±6.04	11.37±7.14
Forage Other	0.00±0.00	0.32± 0.44	1.16± 1.80
Feed Bamboo	37.53±8.36	17.51±8.51	6.93±6.63
Locomote	2.56±1.09	1.95±1.92	2.14±1.17
Maintenance	2.14±2.09	3.46±3.44	3.66±5.13
Olfactory Investigation	0.21±0.25	0.13±0.23	0.24±0.28

A Friedman test indicated differences between phases in percent time spent in Forage Other (χ^2=6.000, p=0.050), but none of the pairwise comparisons were significant. Feed Bamboo differed across phases (χ^2=10.286, p=0.006), occupying a greater percentage of the animals' time in the Baseline than in both the Treatment (Z=-2.197, p=0.028) and the Second Baseline (Z=-2.366, p=0.018) phases.

No significant differences were found between experimental phases for the following behaviors: Door Directed and Human Oriented, Inactive, Feed Concentrated, Locomote, Maintenance, and Olfactory Investigation, and Stereotypies, though rates of the latter behavior may represent a meaningful trend (χ^2=5.856, p=0.054).

Differences Between Observation Periods

Table 3 presents the hourly rates of behaviors of interest for each of the observation periods (i.e., Prefeed, Postfeed, Nonfeed) averaged across all experimental phases.

Table 5. Mean Hourly Rate ± Std Dev of Behaviors of Interest for each Observation Period

Behavior	**Prefeed**	**Postfeed**	**Nonfeed**
Bouts of Stereotypy*	11.22±9.09	5.37±4.67	1.32±1.13
Head Toss	18.35±30.90	2.60±5.90	2.20±3.12
Olfactory Investigation	1.18±1.35	0.84±0.82	0.70±0.52
Anogenital Mark	0.66±1.55	0.21±0.34	0.05±0.09

*includes those stereotypies measured as bouts of behavior rather than as discrete events.

A Friedman test revealed that the hourly rate of bouts of stereotypies defined as state-like-events in the ethogram also differed between observation periods (χ^2=6.000, p=0.050). A Wilcoxon test detected that, the rate of such bouts was higher in the Prefeed observation period than in the Nonfeed observation period (Z=-2.366, p=0.018). The hourly rate of head tosses differed significantly between observation periods (χ^2=6.462,p=0.040), with the animals showing a significantly higher hourly rate in the Prefeed than in the Nonfeed period (Z=-2.028, p=0.043). The hourly rate of head-tossing did not differ between the Prefeed and Postfeed periods, nor between the Postfeed and Nonfeed periods.

Significant differences were not found between observation periods for Olfactory Investigation and Anogenital Mark.

Table 4 presents the mean number of occurrences of agonistic interactions per observation session for each observation period in the Baseline phase. A Friedman test did not show significant differences between the three observation periods. Because individual differences may be present, Figure 1 presents the mean number of occurrences of agonistic interactions for each pair of females.

Table 6. Mean number of agonistic interactions per observation session during Baseline

Observation Period	**Mean±SD**
Prefeed	5.28±4.63
Postfeed	1.56±0.32
Nonfeed	0.98±0.64

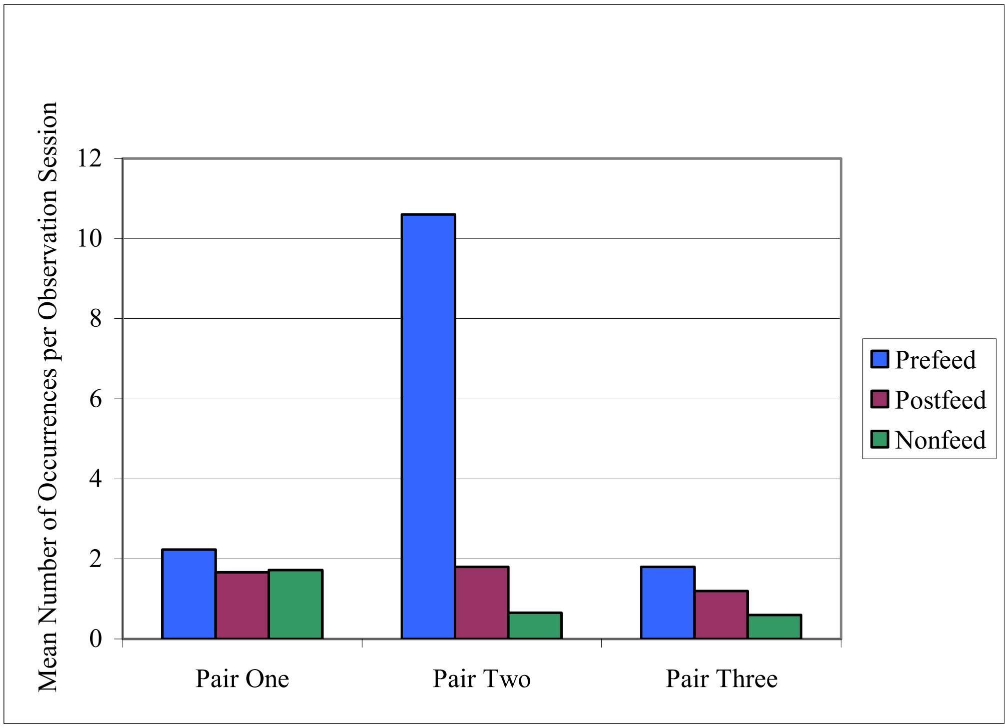

Figure 1. Mean number of occurrences of agonistic interactions for each pair of females in the Baseline phase

Table 5 presents the mean percentage of time spent in behaviors of interest for each of the observation periods, averaged across all study phases.

Table 7. Mean Percent Time ± Std Dev of Behaviors of Interest for each Observation Period

Behavior	**Prefeed**	**Postfeed**	**Nonfeed**
Door Directed and Human Oriented	12.00±6.26	5.38±4.41	1.74±1.63
Stereotypy	12.00±8.12	8.11±9.97	1.83±1.76
Inactive	32.67±17.05	21.40±17.31	68.14±19.00
Feed Concentrated Food	0.48±0.88	30.57±12.33	2.06± 2.34
Forage Other	0.34±0.49	0.08±0.21	1.05±1.85
Feed Bamboo	25.40±6.43	17.08±5.77	19.49±12.62
Locomote	3.83±2.18	1.61± 0.94	1.22±1.06
Maintenance	1.23±0.96	7.29±10.08	0.73±0.58
Olfactory Investigation	0.13±0.24	0.34±0.46	0.12±0.11

A number of behavioral categories differed significantly between observation periods. A Friedman Test of Door Directed and Human Oriented (χ^2=8.857, p=0.012) behavior and a subsequent Wilcoxon signed-ranks test revealed that the animals spent a greater mean percent time engaged in this behavior in the Prefeed than in the Nonfeed period (Z=-2.366, p=0.018). Significant differences in Door Directed and Human Oriented behavior were not found between the Prefeed and Postfeed periods nor between the Postfeed and Nonfeed periods. Stereotypic behavior differed significantly between observation periods (χ^2=11.185, p=0.004), with the animals spending a greater percentage of time engaged in stereotypy in the Prefeed than in the Nonfeed period (Z=-2.366, p=0.018) and in the Postfeed than in the Nonfeed period (Z=-2.366, p=0.018). Significant differences were not found in stereotypic behavior between the Prefeed and Postfeed periods. The percentage of time the animals spent inactive also differed between observation periods (χ^2=14.000, p=0.001). The greatest percentage of time spent in inactivity was seen in the Nonfeed period; this differed significantly from the time spent inactive in both the Prefeed (Z=-2.371, p=0.018) and the Postfeed (Z=-2.366, p=0.018) periods. Additionally, a greater percentage of time was spent inactive in the Prefeed than in the Postfeed period (Z=-2.366, p=0.018). A Friedman Test of Feed on Concentrated Food (χ^2=12.000, p=0.002) and a subsequent Wilcoxon signed-ranks test revealed that this category of behavior occurred more frequently in the Postfeed than in the Prefeed (Z=-2.366, p=0.018) and the Nonfeed (Z=-2.366, p=0.018) observation periods. No significant differences were revealed between the Prefeed and the Nonfeed observation periods. The percentage time engaged in Non-Stereotypic Locomotion, too, was significantly different between observation periods (χ^2=10.571, p=0.005). The pandas spent more time locomoting in the Prefeed than in the Postfeed (Z=-2.366, p=0.018) and in the Nonfeed (Z=-2.366, p=0.018) observation periods. Significant differences were not found between the Postfeed and Nonfeed observation periods.

No significant differences were found between observation periods for the following behaviors: Forage Other, Feed Bamboo, Maintenance, and Olfactory Investigation.

Experiment 2

Differences Between Study Phases

Table 6 presents the hourly rates of behaviors of interest for each of the experimental phases, averaged across all observation periods.

Table 8. Mean Hourly Rate ± Std Dev of Behaviors of Interest for each Experimental Condition

Behavior	**Baseline**	**Treatment**	**Second Baseline**
Bouts of stereotypy*	0.38±0.59	3.79±3.48	3.47±1.41
Head Toss	5.58±7.90	12.01±16.99	8.10±11.45
Olfactory Investigation	0.54±0.06	1.18±0.43	0.76±0.09
Anogenital Mark	0.25±0.35	0.03±0.05	0.17±0.25

*includes those stereotypies measured as bouts of behavior rather than those measured as discrete events

No statistically significant differences between study phases were detected for the all-occurrence behaviors examined for Experiment 2: Stereotypy (bouts), Head Toss, Olfactory Investigation, and Anogenital Mark. However, a visual inspection of each individual's behavior reveals that Kobi's mean hourly rate of bouts of stereotypy increased from 0.42 in the Baseline phase to 6.25 in the Treatment phase, with a final reduction to 4.28 in the Second Baseline phase (Figure 2). A similar pattern emerged for head-tossing - Kobi's mean hourly rate of head-tosses increased from 11.17 in the Baseline phase to 24.02 in the Treatment phase and then decreased to 16.19 in the Second Baseline phase (Figure 3).

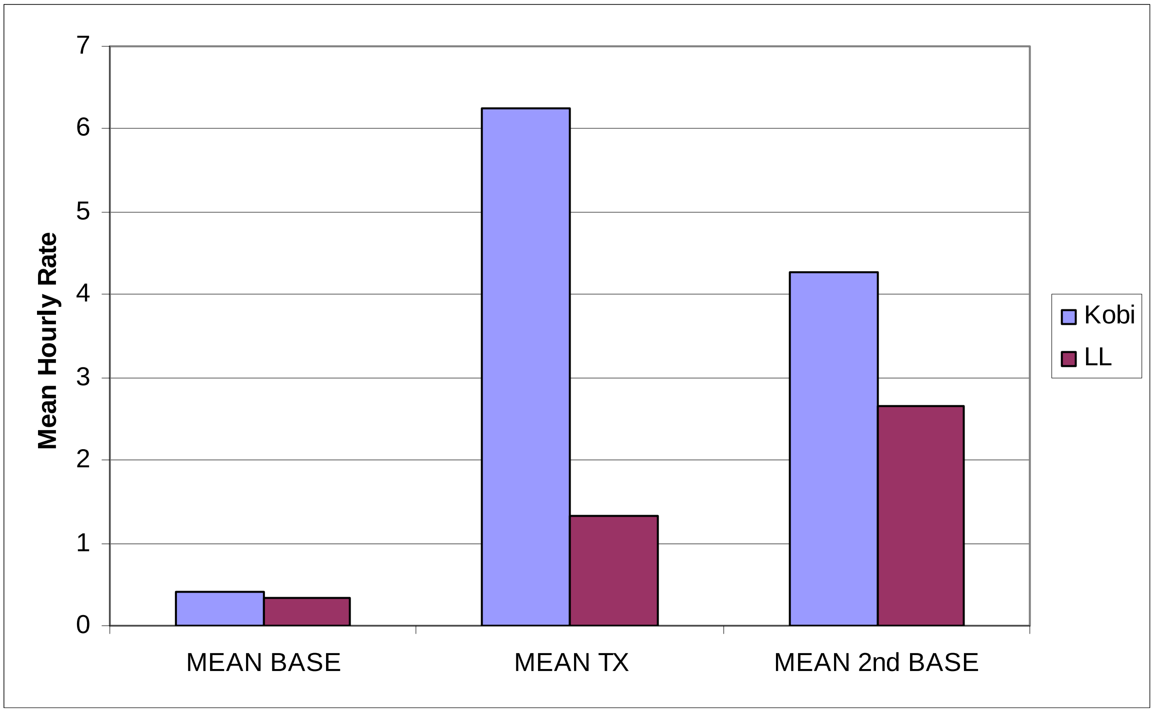

Figure 2. Mean hourly rate of bouts of stereotypy for each experimental phase

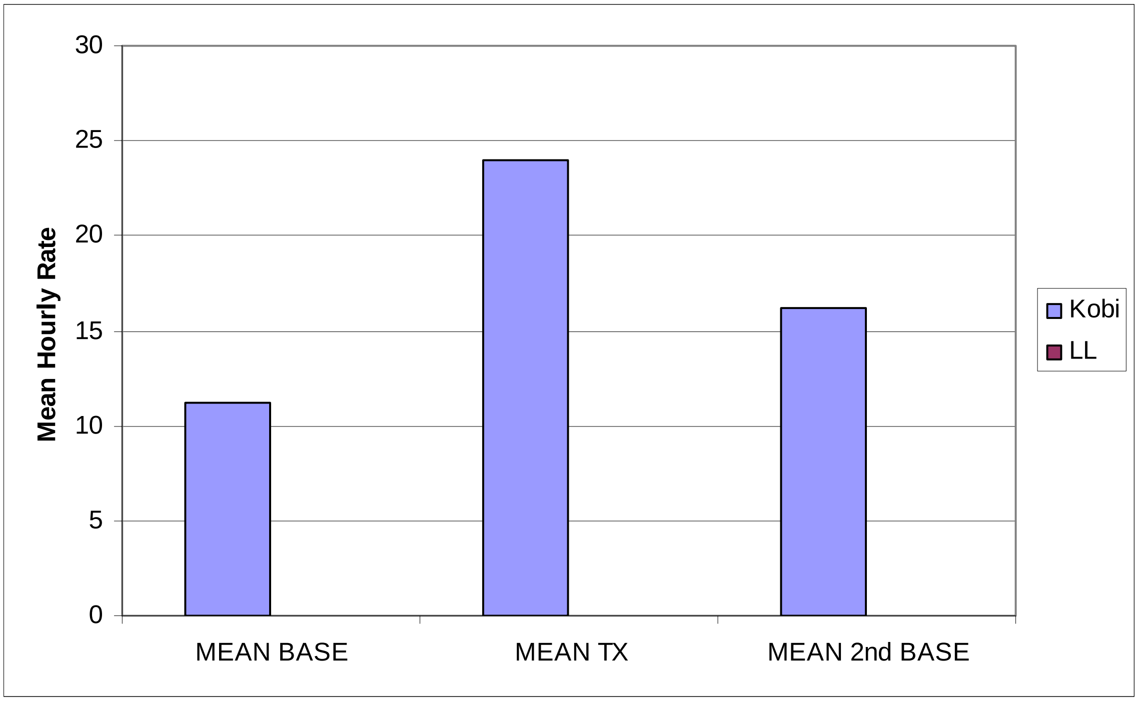

Figure 3. Mean hourly rate of head-tosses for each experimental phase

Table 7 presents the mean percentage of time spent in behaviors of interest for each of the experimental phases, averaged across all observation periods.

Table 9. Mean Percent Time ± Std Dev of Behaviors of Interest for each Experimental Condition

Behavior	**Baseline**	**Treatment**	**Second Baseline**
Stereotypy	7.08±10.02	7.77±7.06	5.34±6.38
Feed Bamboo	48.75±14.14	25.11±5.57	38.52±14.49
Feed Other	13.88±2.57	10.76±3.64	10.17±1.02
Locomote	0.88±0.07	0.94±0.43	1.03±0.11
Inactive	18.76±2.63	38.16±5.82	28.41±2.63
Olfactory Investigation	0.37±0.52	0.32±0.17	0.06±0.08
Door Directed and Human Oriented	3.01±2.03	6.37±0.17	7.71±4.45
Maintenance	3.15±1.83	5.22±3.51	5.78±5.90

No statistically significant differences between study phases were detected for the instantaneous behaviors examined for Experiment 1: Stereotypy, Feed Bamboo, Feed Other, Locomotion, Olfactory Investigation, Door Directed and Human Oriented, and Maintenance.

Differences Between Observation Periods

Table 8 presents the hourly rate of behaviors of interest for each of the observation periods, averaged across all experimental phases.

Table 10. Mean Hourly Rate ± Std Dev of Behaviors of Interest for each Observation Period

Behavior	**Prefeed**	**Postfeed**	**Nonfeed**
Bouts of stereotypy*	4.67±1.90	1.61±0.97	1.37±1.81
Head Toss	23.32±32.98	0.10±0.15	2.27±3.21
Olfactory Investigation	1.19±0.39	0.46±0.27	0.83±0.40
Anogenital Mark	0.46±0.65	0.00±0.00	0.00±0.00

*includes those stereotypies measured as bouts of behavior rather than those measured as discrete events

No statistically significant differences between observation periods were detected for the all-occurrence behaviors examined for Experiment 1. However, both males did appear to exhibit a trend towards higher rates of stereotypy in the Prefeed than in the Nonfeed and Postfeed periods (Figure 4).

Table 9 presents the mean percent time spent in behaviors of interest for each of the observation periods, averaged across all experimental phases.

No statistically significant differences between observation periods were detected for the instantaneous behaviors examined for Experiment 1. However, as shown in Figure 5, Kobi spent more time engaged in stereotypy in the Prefeed observation period than in the other observation periods.

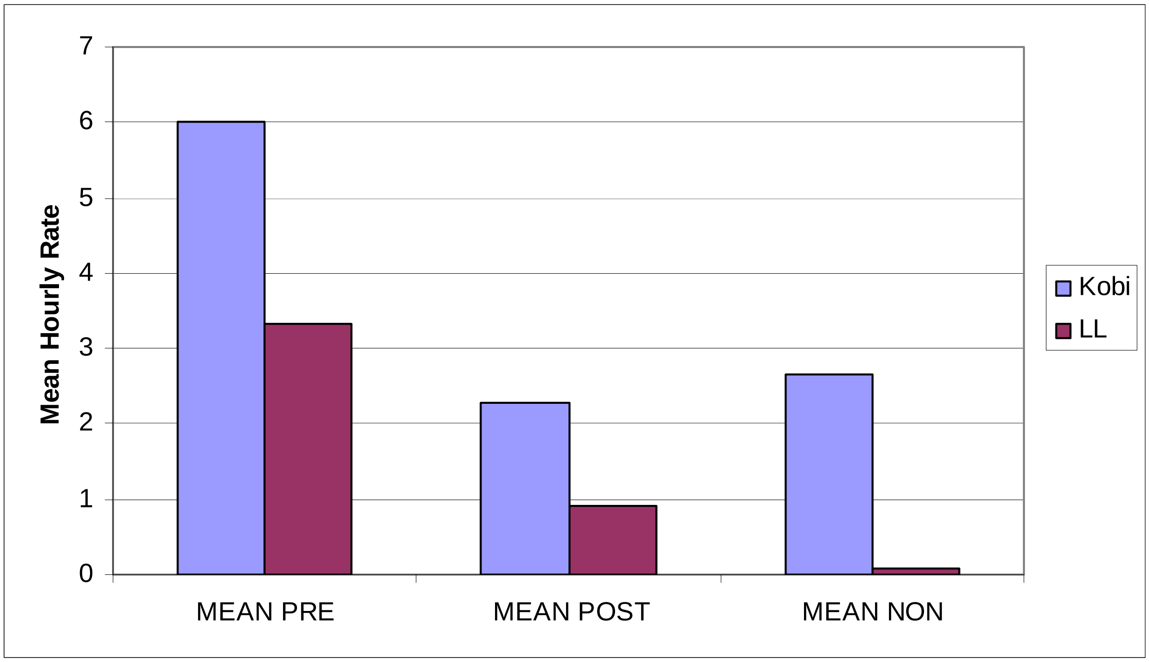

Figure 4. Mean hourly rate of bouts of stereotypy for each observation period

Table 11. Mean Percent Time ± Std Dev of Behaviors of Interest for each Observation Period

Behavior	**Prefeed**	**Postfeed**	**Nonfeed**
Stereotypy	15.65±20.94	1.81±1.60	2.74±0.92
Feed Bamboo	46.00±17.39	38.83±18.67	27.56±1.87
Feed Other	1.39±1.85	32.37±9.18	1.04±0.10
Locomote	1.68±0.34	0.51±0.09	0.66±0.18
Inactive	16.72±3.24	9.78±4.12	58.84±3.67
Olfactory Investigation	0.51±0.35	0.00±0.00	0.24±0.08
Door Directed and Human Oriented	10.00±4.19	2.98±0.71	4.11±2.83
Maintenance	1.45±1.21	10.52±13.89	2.18±1.43

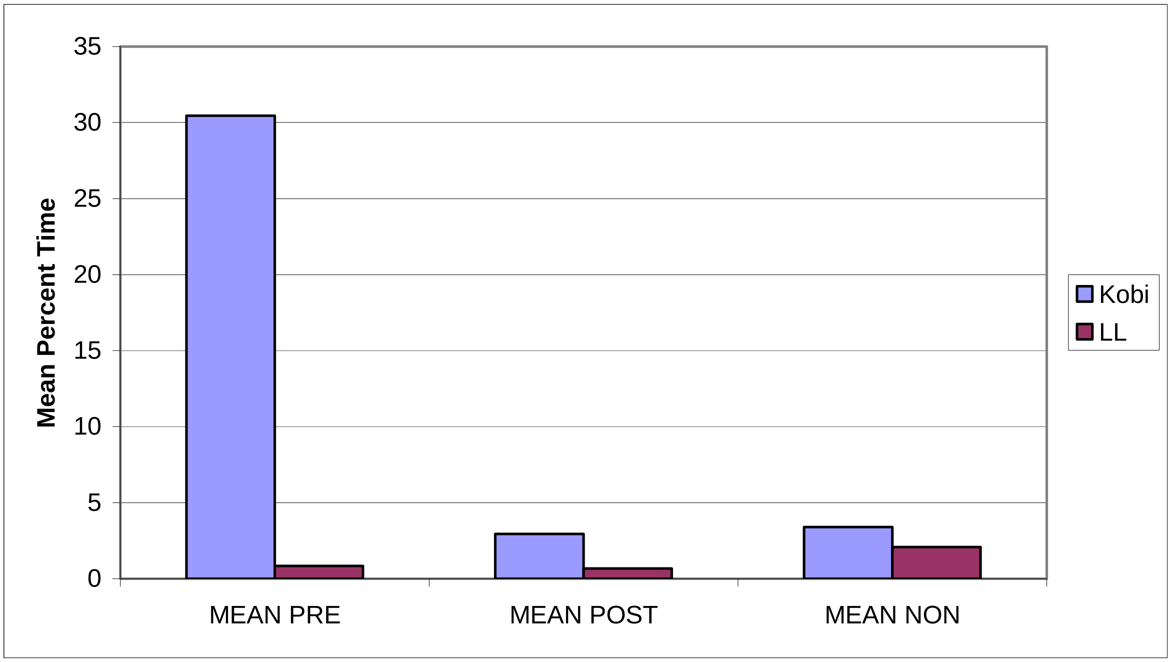

Figure 5. Estimated percent time engaged in stereotypy for each observation period.

DISCUSSION

In Experiment 1, the giant pandas spent significantly more time engaged in (and/or showed a higher rate of) a number of undesirable and locomotor behaviors in the 30-minute periods prior to feeding of a concentrated meal when compared to nonfeeding periods. This finding agrees with observations of feeding anticipatory activity in other animal species (see review in Mistleberger, 1994).

The finding that the pandas spent a significantly greater percentage of time inactive in nonfeeding periods than in periods within 30 minutes of the provisioning of a concentrated meal also concurs with studies of feeding anticipatory behavior. However, the finding that the pandas spent a greater percentage of time inactive in the Prefeed than in the Postfeed period seems at odds with the notion of increased arousal prior to the feeding of meals.

Bloomsmith and Lambeth (1995) similarly found increased inactivity in captive chimpanzees prior to the feeding of predictable meals. In addition to the considerations above, these findings relating to activity budgets underscore the need to consider the myriad of contextual variables present for each captive animal. If for instance, under a particular management regime, a group of captive animals is provisioned food only when sitting quietly, then their activity budgets may change over time to reflect that particular reinforcement contingency. Could this have been the case in Bloomsmith and Lambeth's (1995) study, in which they remarked that it "…seemed that the subjects were 'waiting' for the meal to be fed." (p. 71)? Perhaps studies of keeper-animal interaction will lend more insight into the role of keepers' training, whether intentional or not, of their animals in certain situations.

The increased inactivity seen in the 1995 study may be seen as an undesirable behavioral change in the context of captive management strategies for captive primates (in part due to obesity problems as noted by the authors). However, when the distribution of activities over time is considered in the physiological and ecological contexts of the giant panda, this assessment may change. The degree to which the aforementioned change coincides with the activity budget of a free-ranging counterpart may be very different from species to species – it may be more appropriate in those contexts for some species than for others. For the giant panda, which when free-ranging spends its time alternating between bouts of sleeping and foraging on bamboo, it may be appropriate to see captive activity cycles which include bouts of inactivity immediately prior to feeding.

An unexpected finding was that of a higher rate of bouts of stereotypy in the Second Baseline phase than in the Baseline phase, with no other significant differences in this behavior being detected between phases. This was not consistent with our prediction that a higher rate of bouts of stereotypy would be found in the Baseline and Second Baseline phases than in the Treatment phase. We did not expect to find differences between the Baseline and Second Baseline phases. Interestingly, a general increase in this behavioral category is seen across the phases – from 3.86 in the Baseline phase to 4.96 in the Treatment phase to 9.09 in the Second Baseline phase. Thus, it appears possible that the changes seen in this behavioral category may have been due to the influence of an uncontrolled variable not related to this study. It seems likely that housing changes necessitated by pregnancy and pseudopregnancy played a role here. First, the housing transfers themselves may have been disturbing to the animals. Further, the features of the animals' new enclosures may have been suboptimal in some way in comparison to their original enclosures. Importantly, the animals spent more time indoors- in arguably less environmentally complex enclosures -during the hotter summer months.

This finding may also be explained in part by a possible increase in stereotypic mouth licking (LM) in two of the females, Jiao Zi and Su Lan, towards the end of the summer (noted independently by keeper staff and by the experimenter). It is interesting to note that the two animals tended to engage in this behavior simultaneously. Temporal contingencies may have been a factor here but it would be interesting to examine whether social facilitation played any role. Indeed, Mason (1991b, citing Palya and Zacny 1980, and Kiley-Worthington, 1983) points out that "the rate of development of stereotypies may be accelerated if an animal's neighbours show the behaviour." (p. 105) Also interesting to note is the experimenter's observation that this same pair of animals tended to engage in a similar pattern of stereotypic and quasi-stereotypic pacing simultaneously. It is interesting to note that Jiao Zi and Su Lan were the only females kept together for the entire duration of the study. These two animals may have been forced to spend more time in close proximity with one another because summer heat necessitated that they be kept in a smaller indoor enclosure for much of the time. Thus, it is possible that increased social stress may have influenced rates of stereotypic behavior. Perhaps a change to solitary housing for the hotter months of the year would be beneficial for pair-housed female giant pandas.

Regarding the females' higher rate of bouts of stereotypy in the Second Baseline phase than in the Baseline phase, it is also possible that measuring some of the shorterduration stereotypies, such as teeth-clicking, as bouts did not accurately capture the behavior. Extensive videotape analysis of the frequency and morphology of the variety of stereotypies shown by individual giant pandas may lend insight into this question.

None of the analyses conducted for Experiment 2 yielded significant results; this may be attributable in part to the low power inherent in the small sample size. However, in examining the behavior of each male separately, a number of individual differences were evident. For instance, graphs reveal a 90 % increase in Kobi’s estimated percent time spent engaged in stereotypic behavior in the prefeed condition relative to the Postfeed and Nonfeed conditions. By contrast, graphs reveal little change in Lan Lan’s percent time engaged in stereotypy between the each condition. This is not surprising, as a number of individual differences are thought to play a role in an animal’s tendency to develop stereotypy (see Mason, 1991b, for a review).This underscores the need for the careful, controlled analysis of individual animals who exhibit stereotypies. Through this, it may be possible to carefully tease out the relevant variables for each individual animal.

While Kobi and Lan Lan exhibited different trends in the estimated percent time engaged in stereotypy, *both* males appear to exhibit a trend towards higher rates in the Prefeed condition of those stereotypies measured as bouts of behavior. While this result concords with our predictions, it must be considered in light of the individual differences previously discussed. Is there something categorically different about the stereotypies that were measured as bouts of behavior, as compared to those longer duration stereotypies that were estimated as a percentage of time? Or are these differing trends a reflection of individual differences between the males’ individual repertoires of stereotypic behavior? Further research with more animals and more data points per animal is needed to answer these questions.

The increased levels of stereotypic activity found in the Prefeed conditions support reports in the experimental literature linking stereotypies to periodic feeding regimes (e.g., Mason 1991a, 1991b).However, the data are less clear as to whether the specific feeding manipulations performed in this study were helpful towards solving the problem of periodic feeding regime-related undesirable behavior in giant pandas.

The visual trends that indicated increased stereotypic activity for Kobi during the treatment phase may be consistent with the notion that the feeding manipulations may have exacerbated feeding-related stereotypic behavior in this animal. It seems possible that for Kobi, the disruption of the heretofore predictable feeding schedule may have been a source of distress. Indeed, in a discussion of feeding schedules and behavioral conditioning, Lindburg (1998) points out that when food is available less than continuously, “human-imposed schedules have a conditioning effect that may become a source of stress if ignored.” (p. 273)

As discussed in the introduction, an environmental enrichment program is considered beneficial to an animal’s psychological well-being if an enrichment program results in increases in species-appropriate behavior, while it is considered detrimental to an animal’s psychological well-being if increases in ‘undesirable’ behavior are observed (Schapiro and Bloomsmith, 1995). Because we did not find statistically significant reductions in undesirable behavior and/or increases in species-appropriate behavior with our feeding enrichment program, we cannot conclude that this program was beneficial to the giant pandas’ psychological well-being. However, it must be noted that the visual trends previously discussed may indicate that with larger sample sizes we may have obtained statistically significant behavioral changes that would have reflected an improvement in the female giant pandas’ psychological well-being.

One statistically significant decrease in species-appropriate behavior was seen with implementation of the feeding enrichment program with the females – a decrease in the amount of time spent feeding on bamboo. However, this value was also significantly lower in the second baseline phase, indicating that perhaps the feeding enrichment program was not responsible for the decline. Indeed, it seems more likely that the females were simply spending less time eating during their pregnancies and pseudopregnancies, when appetite decline is expected. Since other statistically significant increases in undesirable behaviors and/or decreases in desirable behaviors were also not observed, we cannot conclude that the feeding enrichment had a detrimental effect on the giant pandas’ psychological well-being. Yet, it must be underscored that regarding the males, Kobi’s trend towards increased bouts of stereotypy in the treatment phase may be indicative of decreased psychological well-being associated with the feeding regime changes.

Therefore, while the specific feeding manipulations performed in this study may not have resulted in the desired statistically significant behavioral changes, the data do demonstrate that periodic feeding times appear to play a role in the expression of stereotypic behavior in giant pandas. While I cannot recommend at this time that the specific feeding modifications examined in this study be implemented, further investigation of these and alternate feeding regimes with a greater number of animals is certainly warranted. It is important to note that while the males may have responded unfavorably to the sudden change in feeding schedule (from fixed to less predictable), this does not tell us whether this change in schedule may or may not have been beneficial in the long run. The animals, particularly Kobi, may have been going through an initial learning period. Had we monitored the animals for a longer period of time, we may have seen beneficial changes.

Further, it is essential to consider that the methodological approach to changing feeding schedules may be of great significance. It is possible that shifting the animals suddenly from a strictly predictable feeding schedule to a random one may have had long-lasting effects.

In the study of captive animals of an endangered species, a number of methodological limitations are to be expected. Small sample sizes, such as seen in both experiments 1 and 2, limit the generalizability of findings. When a planned subject pool is necessarily reduced as was the case for experiment 2, it may be more enlightening to run a separate single subject experiment for each animal. Indeed, this approach may have helped us to understand some of the individual differences apparent between Kobi and Lan Lan.

Another major difficulty in the study of a captive endangered species relates to the issue of reproductive management. For the giant panda, a slow and infrequent reproducer for whom a self-sustaining captive population has yet to be reached, any risks to reproductive success are not to be taken lightly. As a result, experimental manipulations may be at times severely limited, as they were for the female subjects of the planned feeding predictability study. Further, control over a number of independent variables, such as social partners, may necessarily be lost during an experiment. This was indeed the case for both Experiments 1 and 2; social partners were changed in lieu of first mating and then parturition requirements.

Accompanying the aforementioned changes in social partner were changes in housing location and in animal care staff. Concern existed as to whether these management changes would affect the outcome of the study. Specifically, territorial behavior (as evidenced by foot scraping) unseen in the earlier parts of the study emerged in Kobi upon moving. Clearly a different dimension of social behavior was being expressed, but the relation between this newly emerged (for the study period at least) social behavior and the dependent variables of interest is unclear. Additionally, in that particular complex Kobi was unable to go outside at all during his residence there (the barriers in the outdoor yard were not sufficient for his size). Thus, Kobi was confined to a much smaller area than he was accustomed to. Because Kobi had an observed history of pacing near boundaries, I was particularly concerned that we might see behavioral changes related to being confined in a smaller, less enriched environment, such as increases in stereotypy (Draper and Bernstein, 1963) accompanying this move. Because of the timing of the move, it was not possible to delineate the effects of the move relative to the effects of the experimental manipulation. Clearly, it would have been ideal if the housing situation could have remained stable for the duration of the study. For future cases in which it is unavoidable to maintain such stability, it may be helpful to repeat the experiment at different times of year to assess whether seasonal management changes (as dictated by the animals' reproductive cycles) affect study outcome.

Changes in staff-animal assignments, too, may have been problematic for both Experiments 1 and 2. Staff hours and assignments necessarily changed throughout the entire Research Base during the time of parturition. Most animal care staff moved temporarily to living quarters on the Research Base so that the pandas could be carefully monitored and cared for on a 24-hour basis. As a result, small groups of 2-4 keepers who were previously assigned to 1-4 pandas in separate complexes were instead assigned to work with all of the females in the nursery complex. However, it had become apparent in the Baseline phase of both Experiments 1 and 2 that each group of keepers kept its own set routine. This was all changed when the animals moved to the nursery complex and the care of the animals was redistributed over nearly the entire group of keepers. An example of a change that may have had direct influence over the dependent variables of interest is the manner in which the group of keepers previously assigned to the building of Jiao Zi, Su Lan, Ya Ya, and Su Su provided gruel. In both the morning and the evening, when performing animal care duties, bowls of gruel were placed in front of the animals' enclosures, just out of arm's reach, and left sitting there for up to 20 minutes before actually being provisioned to the animal. Often the animals were visibly agitated by this and could be seen reaching out of the enclosure bars towards the food. Unfortunately, this different feeding routine was inadvertently introduced to *all* of the animals on some days of the week (those days in which that group of keepers were responsible for feeding all of the animals). It seemed possible that the agitation of animals previously unaccustomed to this practice may have been more pronounced than that of the animals who had been subject to this practice for many weeks before. Further, the animals previously exposed to this feeding practice every day of the week were now receiving it on only several days of the week. This underscores the need to carefully document and maintain a particular management style throughout the duration of a study if at all possible.

At least two other factors may have influenced the animals' activity budgets.

When a female giant panda is in pseudopregnancy or pregnancy, her activity level declines substantially. However, for this group of animals, summer is one of the most feasible times of year for this study in relation to breeding and birthing seasons. It may have been helpful to collect hormonal data on the females. Perhaps being able to detect hormonal changes associated with pregnancy and pseudo pregnancy would enable us to rule out whether certain behavioral changes were related to the experimental manipulation, or if they were chiefly related to the reproductive cycle. In a similar vein, hormonal analyses may be used to help determine whether males are undergoing behavioral changes at particular points in time in the breeding season that may be affecting behavior.

One particular limitation of this study is that the rearing histories of individual animals were not considered. In this vein, Marriner and Drickamer (1994) found that rearing method (hand versus mother) was a more important factor in the frequency of stereotyped behavior than were present environmental conditions. This is not surprising, as detrimental effects of early weaning have been documented in a variety of species.

It became apparent during the course of the study that a number of simple feeding strategy modifications may produce some desirable behavioral changes if consistently implemented. It was mentioned earlier that in the Baseline phase, bamboo was not always provided in the enclosure in which animals were to be confined for their concentrated feedings. As this was one of the manipulations in the experiment, and as there is some evidence that positive behavioral changes were elicited in the Treatment phase, there is reason to believe that this is a beneficial change to feeding regime. Thus, it is recommended that bamboo be always provided in the location of concentrated feeding.

Of particular note was that in certain pairs of females, aggressive interactions, which appeared to be a result of food competition, occurred almost daily. Not until vocal and sometimes physical aggression had commenced were the animals separated. This practice may make more sense when considered in light of the fact that during shifting, animals not infrequently had agonistic interactions (two of a pair would rush the shift door simultaneously). Thus, more precise shift training might enable animal care staff to regularly shift animals before meals without incident. This situation may underscore the need for continuing education programs for staff in animal care facilities; perhaps too wide a gap exists between the formal study of behavioral principles and the application of these principles.

APPENDIX A

Giant Panda Ethogram. Adapted from Giant Panda Ethogram, San Diego (R. R. Swaisgood) and Zoo Atlanta Giant Panda Subadult Ethogram (R. J. Snyder).

Code	S-E	Activity	Definition
NV	S	Not Visible	Animal moves temporarily out of view.
FD	S	Feed	Animal is processing or consuming food. Note food type.
LC	S	Locomote	Short bout of directional travel between two points, or sustained locomotion in a non-stereotyped manner.
DD	S	Door-directed	Panda at the door/gate, behavior oriented toward food, keeper, or adjacent enclosure. Supersedes most behaviors that may be embedded in door-directed behavior (e.g. SA, OI). However, the following behaviors should be scored within each bout of door-directed behavior: *Stereotypies (e.g. MP, RK) *SCR
DD1	At Beep	Door-directed mild	Panda waits at the door with mild restlessness. This includes investigating the door, stationary alert at the door, scratching itself, or looking towards the other side of the door.
DD2	At Beep	Door-directed high	Panda is door-directed with a high degree of restlessness. This would include pacing back and forth in front of the door, pushing and manipulating the door, shifting posture frequently while waiting, vocalizing frequently, or other behaviors that indicate a high anticipatory level of food, keepers, etc.
PC	S	Stereotypic Pacing	Back and forth or perimeter locomotion in a repetitive, sustained, stereotyped pattern. Must travel the same route at least 3 times in a row. Includes travel patterns interrupted by other repetitive behaviors. At the beep, score PC-d if the panda is within one body length of the door/gate.
QPC	S	Quasi-stereotypic Pacing	As in Stereotypic Pacing, except animal need not take the same path 3 or more times in a row; any pacing in which a predictable pattern emerges. There may be variations in the routine or the animal may alternate between a limited number of travel paths. At the beep, score QPC-d if the panda is within one body length of the door/gate.
CL	SLE	Climb	Vertical ascent or descent, as into trees or structures. All four limbs must leave the ground.
		Stereotypies:	Animal engages in invariant, repetitive acts that have no obvious goal or function.
CC	SLE	Cage Climb	Animal stands bipedally and sways or makes climbing motions, as if attempting to escape.
HT	E	Head-toss	Animal abruptly lifts head upward and/or to the side in a swinging movement; often occurs during pacing (especially during turning). Each individual head-toss is counted.

MP	SLE	Muzzle-push	Animal pushes muzzle through enclosure bars, often accompanied by the opening and closing of the mouth. Often seems to occur in anticipation of feeding.
PI	E	Pirouette	Animal stands on hind legs and spins at least 90 degrees.
RR	SLE	Regurgitation and Reingestion	Animal vomits and reingests vomit repeatedly. Only score for habitual regurgitators, not the occasional bout of illness.
RK	SLE	Rock	Animal shifts weight from side to side, but remains stationary. Often occurs in anticipation of feeding.
SB	SLE	Self-biting	Animal bites itself repeatedly in a stereotyped manner (not grooming).
SPI	E	Sit Pirouette	Hindquarters are resting on the ground, torso is erect, and animal spins at least 90 degrees.
SU	E	Sit-up	Animal lies on back, then sits upright. May repeat more than once. This behavior must be part of a (quasi)stereotypic pacing pattern.
SMA	S	Stereotyped Masturbation	Animal masturbates repetitively and rigidly for extended periods; may be manual or oral.
SUC	S	Suck Chest	Repetitive, sustained sucking of the chest area (not grooming).
SUP	S	Suck Paw	Repetitive, sustained sucking of the toes/paw (not grooming).
SW	SLE	Sway	Animal swings head back and forth, but does not exhibit the undulating movements associated with weaving.
TC	SLE	Teeth Click	Repetitive opening and closing of the mouth so that the teeth click together loudly. Differs from chomp in that it is not directed towards other animals, and the teeth clicking sound is much louder.
LM	SLE	Lick Mouth	Animal flicks tongue out, licking its mouth repeatedly.
TS	E	Truncated Somersault	Places head to ground as if to do a somersault, but does not complete action; often part of a stereotyped motor routine.
WV	SLE	Weave	Animal 'weaves' back and forth, undulating the front portion of the body, somewhat reminiscent of a fish's swimming movements.
		Maintenance:	Comfort behaviors.
SCR	S	Scratch	Scratch self with paws.
SS	Beep	Scratch against surface	Animal rubs a small part of its body repetitively back and forth against an object, as if 'to scratch an itch."
DB	Beep	"Dirt" bathe	Animal rolls on ground, scratching body on surface; may use paws to throw dirt or other substrate over body.
LIB	S	Licks/bites	Licks or bites self to clean or maintain pelage. Sometimes occurs after feeding on bread or gruel.
LBF	S	Licks/bites forepaws	Licks or bites forepaws in a non-stereotypic, non-play context. Sometimes occurs after feeding on bread or gruel.
LP	SLE	Locomotor Play	Solitary, superfluous, apparently purposeless activity such as gamboling, frisking, somersaulting, rolling, and leaping.
OP	SLE	Object Play	Dragging, batting, or tossing objects with excessive energy. Animal appears to be using object for entertainment rather than investigating object.
WP	SLE	Water Play	Animal is splashing and/or rolling in water.
SOP	SLE	Social Play	Any "playful" interaction: characterized by lack of apparent purpose, exaggerated and vigorous movements, frequently repeated motor patterns, etc.
RS	S	Rest	Animal is lying or sitting, either awake or asleep.

		Anogenital Mark: (substrate)	Rubs anogenital region (tail up) against object or substrate.
SM	SLE	Squat	In squatting posture. More common in females.
LM	SLE	Leg Cock	With one hind leg raised.
RM	SLE	Reverse	Backs into a vertical surface before marking. More common in males.
HM	SLE	Handstand	Elevates hind quarters vertically, hands support weight; both hind feet must leave the ground. Only seen in males.
UR	S	Urinate	Animal voids urine.
BR	SLE	Body Rub (substrate)	Other than anogenital mark, rubs areas of body (head, neck, chest) against structures or substrate in a smooth, fluid motion in which the animal rubs a large portion of its back, especially the neck and shoulders and sometimes the tail, against an object in a way that seems to be intended to impart scent onto the object. Often associated with social interaction or olfactory investigation.
OI	SLE	Olfactory Investigation (substrate)	Places nose close to a substrate or object and sniffs and/or appears attentive for >1 sec. Does not include sniffing bamboo or the air. Note if the following occur during the OI bout: -fle = "flehmen' = raises lips, exposing teeth and/or opens mouth while investigating scent. Usually only occurs when an animal is investigating another's scent. The animal opens its mouth and sucks air into its oral cavity, often drools prolifically, and is intently focused on the scent. Score flehmens in a one-zero manner per minute. -lick = licks area that it is sniffing.
OE	S	Object Examine (substrate)	Animal manipulates and explores by grasping, chewing, sniffing, etc. Usually does not apply to bamboo, unless manipulative behavior is not part of a feeding bout.
CO	S	Carry Object (substrate)	Animal travels (walking, trotting, or climbing) from one point to another while using its mouth to carry or drag an object. Usually does not apply to bamboo, unless this behavior is not part of a feeding bout.
SAN	SLE	Scent Anoint	Picks up object with paws and rubs object over body. Note that dirt is not considered an object.
DE	S	Defecate	Animal voids feces.
ST	E	Startle	Sudden, intense movement such as whole body jerk, indicative of surprise or fear. This is not a response to another panda but to an inanimate object or sound. Indicate disturbance or preceding event which elicited response.
WD	E	Withdraw	Any form of attempted distancing from an outside stimulus (not another panda), e.g., rapid retreat, cringe, hide. Indicate disturbance or preceding event which elicited response.
SA	S	Stationary Alert	Alert, standing quadrupedally, sitting or lying quietly, but remaining attentive, moving head from side to side and/or sniffing air, perhaps attending to external stimuli. This behavior lies on a continuum with rest.
SAW	S	Stationary Alert in Water	Sits, stands or lies quietly in water; no water play. Must have at least one paw in the water.

BI	S	Bipedal (substrate)	Stands on hind feet; often accompanied by sniffing movements (directed to air, not substrate) and exploratory behavior. Panda's entire rear end must be off the ground.
DR	S	Drink	Ingests water.
		Vocalizations:	
BL	One-Zero	Bleat	A twittering, goat-like call of variable length (1-3 s). Contact call, appeasing, non-aggressive.
CH	One-Zero	Chirp	Short, tonal, high-pitched, descending in pitch toward end. Most common during estrus. Affiliative, promotes social proximity.
BA	One-Zero	Bark	Short (0.1-0.3s), fairly noisy, similar to dog bark. Threat, causes withdrawal by receiving animal.
MO	One-Zero	Moan	Low-pitched, low to medium amplitude call of variable duration Often grades with barks, chirps, and bleats. Mild threat, often used by female to discourage approach by male.
GR	One-Zero	Growl	Long, noisy, low-pitched growl similar to a dog's. Aggressive, often accompanies or precedes fighting. Only used by attacking animal.
HK	One-Zero	Honk	Short (<0.5s), tonal, low pitched, nasal, falling pitched, produced repetitively in a series. Often used when stressed or frustrated.
RO	One-Zero	Roar	Very loud, intense, harsh (highest level threat).
CM	One-Zero	Chomp	Alternate rapid opening and closing of mouth, with teeth coming together audibly. Defensive (e.g., when the female avoids the male's approach), mild threat.
HU	One-Zero	Huff	Audible expulsion of air through open mouth (anxious, mild threat).
SN	One-Zero	Snort	More intense expulsion of air through nose (threat, apprehension).
SQ	One-Zero	Agonistic Squeal	Short, high-pitched, open-mouthed call. Often used by subordinate animal in a fight or in response to pain.
FSC	E	Foot scrape	Rapid scraping of hind feet back and forth on substrate while standing in place; aggressive act.
DG	S	Digging	Animal digs in dirt or loose substrate with forepaws
CW	S	Chewing	Animal chews on wood or other non-mobile substrate, such as logs, trees, and doors.
HO	S	Human Oriented	Approach and observe person closely; may stand bipedally or interact with human in any way. Does not include simply looking toward visitors.

Transactional social behaviors (to be recorded for interactions between adults).

I	E	Initiates Interaction	Always record who initiates an interaction.
t	E	Terminates Interaction	Always records who terminates an interaction.

TE	SLE	Territorial	Panda footscrapes while interacting with another panda. TE accompanied by any vocalization should be scored according to the appropriate category for that vocalization.
N1	SLE	Non-contact Aggression, Level 1	Agitated. Interaction which includes mild threats which are primarily defensive, connoting alarm, distress, apprehension, aversion. Vocalizations include huff, snort, chomp, and honk.
N2	SLE	Non-contact Aggression, Level 2	Threatening. Interaction which includes moderate threats. Actions include paw swats without contact and charge/lunge. Vocalizations include moan, bark, growl, and roar.
C1	SLE	Contact Aggression, Level 1	A non-sustained (less than five seconds) aggressive interaction of moderate intensity, including actions such as paw swat, bite, grab, and dominance mount. "Moderate intensity" is defined as aggressive acts which have low potential for inflicting serious injury, e.g. drawing blood. Generally accompanied by vocalizations discussed in N2.
C2	SLE	Contact Aggression, Level 2	Sustained aggression, including vigorous and potentially injurious physical contact (fighting, attacking), such as bite, grab, paw swat, wrestle, chase with contact. Intensity of aggression is high, as indicated by injury, duration, or vocalizations such as roar and squeal.
SI	SLE	Shows Interest	Animal appears "eager" to interact with the other panda, as suggested by pushing and pulling at fence separating the pandas, sniffing at the other panda, greeting, pacing back and forth in close proximity to the other panda, or circling the other panda with attention clearly focused on the other panda. Score SI when no vocalization has occurred and behavior is clearly not neutral. SI accompanied by any vocalization should be scored according to the appropriate category for that vocalization, rather than as SI.
AF	SLE	Affiliative	Animal approaches or attempts to interact in a "friendly" manner, as evinced by vocalizations such as bleat, sex squeal, chirp.
SX	SLE	Sexual	Animal approaches or attempts to interact in a proceptive or receptive manner. Generally accompanied by one or more of the vocalizations described in AF. SX takes priority over other transactional behaviors.
IG	SLE	Ignore/Neutral	Panda shows no overt response to proximity or behavior of another panda. Should be scored when proximity lasts more than 5 sec and none of the behaviors described in the other categories occur. An ignore may end an interaction sequence.
AM	SLE	Ambivalent	Behavior during transaction includes both friendly and aggressive elements i.e., includes elements of N1, N2, or C1 and AF or SX.
AV	E	Avoid	Behavior intended to prevent or avoid interaction. Panda turns away, backs off, or redirects its travel path to avoid interacting with another panda in proximity (<2 BL). Behavior serves to increase inter-animal distance or avoid close proximity. An avoid may end an interaction sequence.

RT	E	Retreat	Same as AV, except panda is "forced" to increase the distance between itself and the other panda, i.e., in response to aggressive activity by the opposing party, such as that discussed in N1, N2, C1, C2, AM. A retreat may end an interaction sequence.
SUB	SLE	Submission	Animal adopts a submissive posture (facing away from the other panda, crouched with head down) or simply turns whole body away from the other panda, not increasing social distance. SUB accompanied by any vocalization should be scored according to the appropriate category for that vocalization.
AP	E	Approach	Panda moves to <1 body lengths from other panda. An approach often begins an interaction sequence.
DP	E	Depart	Panda moves to >1 body lengths from the other panda. A depart often ends an interaction sequence. If a panda "departs" for less than 10 secs and then "re-approaches" the other panda, a depart is not scored and the interaction continues.

REFERENCES

Bashaw, M.J., Bloomsmith, M.A., Marr, M.J., & Maple, T.L. (2003). To hunt or not to hunt? A feeding enrichment experiment with captive large felids. *Zoo Biology, 22,* 189-198.

Bloomsmith, M.A., Alford, P.L, & Maple, T.L. (1988). Successful feeding enrichment for captive chimpanzees. *American Journal of Primatology, 16,* 155-164.

Bloomsmith, M.A. and S.P. Lambeth (1995). Effects of predictable versus unpredictable feeding schedules on chimpanzee behavior. *Applied Animal Behaviour Science, 44,* 65-74.

Battisti, J.J., Uretsky, N.J., Wallace, L.J. (1999). Sensitization of apomorphine-induced stereotyped behavior in mice is context-dependent. *Psychopharmacology, 146,* 42-48.

Bildsøe, M., Knud, E.H., Jeppesen, L.L. (1991). Effects of immobility stress and food restriction on stereotypies in low and high stereotyping female ranch mink. *Behavioural Processes, 25,* 179-189.

Carlstead, K., Brown, J.L., & Seidensticker, J. (1993). Behavioral and adrenocortical responses to environmental changes in leopard cats (*Felis bengalensis*). *Zoo Biology, 12,* 321-331.

Carlstead, K., & Seidensticker, J. (1991). Seasonal variation in stereotypic pacing in an American black bear *Ursus americanus*. *Behavioural Processes, 25,* 155-161.

Carlstead, K., & Shepherdson, D. (1994). Effects of environmental enrichment on reproduction. *Zoo Biology, 13,* 447-458.

Chamove, A.S., & Anderson, J.R. (1989). Examining environmental enrichment. In E.F. Segal (Ed.), *Housing, Care and Psychological Wellbeing of Captive and Laboratory Primates.* (pp.183-202). Park Ridge, NJ: Noyes Publications.

Canales, J.J., Gilmour, G., Iversen, S.D. (2000). The role of nigral and thalamic output pathways in the expression of oral stereotypies induced by amphetamine injections into the striatum. *Brain Research, 856,* 176-183.

Cooper, J., Ödberg, F., Nicol, C. (1996). Limitations on the effectiveness of environmental improvement in reducing stereotypic behaviour in bank voles (*Clethrionomys glareolus*) *Applied Animal Behaviour Science, 48,* 237-248.

Coulton, L.E., Waran, N.K., & Young, R.J. (1997). Effects of foraging enrichment on the behaviour of parrots. *Animal Welfare, 6,* 357-363.

Crockett, C. (1996). Data collection in the zoo setting, emphasizing behavior. In D. Kleiman, M. Allen, K. Thompson, & S. Lumpkin (eds.), *Wild Mammals in Captivity,* pp. 545-565. Chicago: University of Chicago Pres.

Dierenfeld, E.S., Qiu, X., Mainka, S.A., & Liu, W. (1995). Giant panda diets fed in five Chinese facilities: an assessment. *Zoo Biology, 14,* 211-222.

Draper, W.A., & Bernstein, I.S. (1963). Stereotyped behavior and cage size. *Perceptual and Motor Skills, 16,* 232-234.

Esposito, P., Gheorghe, D., Kandere, K., Pang, X., Connoly, R., Jacobson, S., Theoharis, C. (2001). Acute stress increases permeability of the blood-brain barrier through activation of brain mast cells. *Brain Research, 888,* 117-127.

Foa, E.B., Zinbarg, R., & Rothbaum, B.O. (1992). Uncontrollability and unpredictability in Post-Traumatic Stress Disorder: An animal model. *Psychological Bulletin, 112,* 218-238.

Gittleman, J.L. (1994). Are the pandas successful specialists or evolutionary failures? *Bioscience, 44,* 456-464.

Hancocks, D. (1980). Bringing nature into the zoo: Inexpensive solutions for zoo environments. *International Journal for the Study of Animal Problems, 1,* 3, 170-177.

Hancocks, D., Hutchins, M., & Crockett, C. (1979)). Naturalistic solutions to the behavioral problems of captive animals. *AAZPA 1978 Annual Conference Proceedings* (pp. 108-113). Wheeling, West Virginia.

Haskell, M.J., Mendl, M.T., Lawrence, A.B., & Austin, E. (2000). The effect of delayed feeding on the post-feeding behaviour of sows. *Behavioural Processes, 49,* 85-97.

Hughes, B.O., & Duncan, I.J.H. (1988). The notion of ethological 'need', models of motivation and animal welfare. *Animal Behaviour, 36,* 1696-1707.

Hutchins, M., Hancocks, D., & Crockett, C. (1984). Naturalistic solutions to the behavioral problems of captive animals. *Der Zoologische Garten 1/2,* S, 28-42.

Ings, R., Waran, N.K., & Young, R.J. (1997). Effect of wood-pile feeders on the behaviour of captive bush dogs (*Speothos venaticus*). *Animal Welfare, 6,* 145-152.

Ishamel, J.E., Franklin, P.H., Murray, T.F. (1988). Dextrorotatory opoids induce stereotyped behavior in Sprague-Dawley and Dark Agouti rats. *Psychopharmacology, 140,* 206-216.

Jeppesen, L.L., Heller, K.E., & Dalsgaard, T. (2000). Effects of early weaning and housing conditions on the development of stereotypies in farmed mink. *Applied Animal Behaviour Science, 68,* 85-92.

Kiley-Worthington, M. (1983) Stereotypies in horses. *Equine Practice, 5,* 34-40.

Kjellberg, A., Landström, U., Tesarz, M., Söderberg, L, & Akerlund, E. (1996). The effects of nonphysical noise characteristics, ongoing task and noise sensitivity on annoyance and distraction due to noise at work. *Journal of Experimental Psychology, 16,* 2, 123-136.

Klein, L.C., Popke, E.J., & Grunberg, N.E. (1997). Sex differences in effects of predictable and unpredictable footshock on fentanyl self-administration in rats. *Experimental and Clinical Psychopharmacology, 5,* 99-106.

Laviolette, S.R., Priebe, R.P.M., Yeomans, J.S. (2000) Role of the laterodorsal tegmental nucleus in scopolamine- and amphetamine-induced locomotion and stereotypy. *Pharmacology Biochemistry and Behavior, 65,* 163-174.

Ledge, C., Arnason, U. (1996). Phylogenetic relationships within caniform carnivores based on analyses of the mitochondrial 12S rRNA gene. *Journal of Molecular Evolution, 43,* 641-649.

Leguez, C.W., Eifert, G.H., Zvolensky, M.J., & Richards, J.B. (2000). Preference between onset predictable and unpredictable administrations of 20% carbon-dioxide-enriched air: Implications for better understanding the etiology and treatment of panic disorder. *Journal of Experimental Psychology: Applied, 6,* 349-358.

Levine, S. (1985). A definition of stress? In G.P. Moberg (Ed.), *Animal Stress* (pp. 51-71). Baltimore, MD: Williams & Wilkins.

Lindburg, D.G. (1998). Enrichment of captive mammals through provisioning. In D.J. Shepherdson, J.D. Mellen, & M. Hutchins (Eds.), *Second Nature. Environmental Enrichment for Captive Animals* (pp. 262-276). Washington and London: Smithsonian Institution Press.

Maple, T.L., & Finlay, T.W. (1989). Applied primatology in the modern zoo. *Zoo Biology Supplement 1,* 101-116.

Markowitz, H., Aday, c., & Gavazzi, A. (1995). Effectiveness of acoustic "prey": environmental enrichment for a captive African leopard (*Panthera pardus*). *Zoo Biology, 14,* 371-379.

Marriner, L.M., & Drickamer, L.C. (1994). Factors influencing stereotyped behavior of primates in a zoo. *Zoo Biology, 13,* 267-275.

Maschke, C., Rupp, T., Hecht, K. (2000). The influence of stressors on biochemical reactions—a review of present scientific findings with noise. *International Journal of Hygiene and Environmental Health, 203,* 1, 45-53.

Mason, G.J. (1991a). Stereotypies: a critical review. *Animal Behaviour, 41,* 1015-1037.

Mason, G.J. (1991b). Stereotypies and suffering. *Behavioural Processes, 25,* 103-115.

Mineka, A., & Kihlstrom, J.F. (1978). Unpredictable and uncontrollable events: A new perspective on experimental neurosis. *Journal of Abnormal Psychology, 87,* 2, 256-271.

Mistleberger, R.E. (1994). Circadian food-anticipatory activity: Formal models and physiological mechanisms. *Neuroscience and Biobehavioral Reviews, 18,* 171-195.

Moberg, G. (1985). Biological response to stress: Key to assessment of animal well-being. In G. Moberg (Ed.), *Animal Stress* (pp. 27-50). Baltimore, MD: Williams & Wilkins.

Nash, W.G., Weinberg, J., Ferguson-Smith, M.A., Menninger, J.C., & O'Brien, S.J. (1998). Comparative genomics: tracking chromosome evolution in the family Ursidae using reciprocal chromosome painting. *Cytogenetics and Cell Genetics, 83,* 182-192.

Novak, M., & Suomi, S.J. (1988). Psychological well-being of primates in captivity. *American Psychologist, 43,* 10, 765-773.

Ödberg, F.O. (1987). The influence of cage size and environmental enrichment on the development of stereotypies in bank voles (*Clethrionomys glareolus*). *Behavioural Processes, 14,* 155-173.

Palya, W.L., & Zacny, J.P. (1980). Stereotyped adjunctive pecking by caged pigeons. *Animal Learning and Behavior, 8,* 293-303.

Platt, D.M., & Novak, M.A. (1997). Videostimulation as enrichment for captive rhesus monkeys (*Macaca mulatta*). *Applied Animal Behaviour Science, 52,* 139-155.

Powell, D.M. (1995). Preliminary evaluation of environmental enrichment techniques for African lions (*Panthera leo*). *Animal Welfare, 4,* 361-370.

Quinones-Jenab, V., Ho, A., Schlussman, S.D., Franck, J., Kreek, M.J. (1999). Estrous cycle differences in cocaine-induced stereotypic and locomotor behaviors in Fischer rats. *Behavioral Brain Research, 101,* 15-20.

Reid, D.G., Hu, J., Dong, S., Wang, W., & Huang, Y. (1989). Giant panda *Ailuropoda melanoleuca* behaviour and carrying capacity following a bamboo die-off. *Biological Conservation, 49,* 85-104.

Reinhardt, V. (1993). Enticing nonhuman primates to forage for their standard biscuit ration. *Zoo Biology, 12,* 307-312.

Rushen, J.P. (1985). Stereotypies, aggression and the feeding schedules of tethered sows. *Applied Animal Behaviour Science, 14,* 137-147.

Sams-Dodd, F. (1998). Effects of dopamine agonists and antagonists on PCP-induced stereotyped behaviour and social isolation in the rat social interaction test. *Psychopharmacology, 135,* 182-193.

Sapolsky, R.M. (2000). Glucocorticoids and hippocampal atrophy in neuropsychiatric disorders. *Archives of General Psychiatry, 57,* 10, 925-935.

Schaller, G.B, Hu, J., Pan, W., & Zhu, J. (1985). *The Giant Pandas of Wolong.* Chicago: The University of Chicago Press.

Shepherdson, D.J. (1998). Tracing the path of environmental enrichment in zoos. In D.J. Shepherdson, J.D. Mellen, & M. Hutchins (Eds.), *Second Nature: Environmental Enrichment for Captive Animals* (pp. 1-12). Washington, DC & London: Smithsonian Institution Press.

Shepherdson, D.J, Carlstead, K., Mellen, J.D., & Seidensticker, J. (1993). The influence of food presentation on the behavior of small cats in confined environments. *Zoo Biology, 12,* 203-116.

Spangler, R., Zhou, Y., Schlussman, S.D., Ho, A., Kreek, M.J. (1997). Behavioral stereotypies induced by 'binge' cocaine administration are independent of drug-induced increases in corticosterone levels. *Behavioral Brain Research, 86,* 201-204.

Spoolder, H.A.M, Burbidge, J.A., Edward, S.A., Simmins, H.P., Lawrence, A.B. (1995). Provision of straw as a foraging substrate reduces the development of excessive chain and bar manipulation in food restricted sows. *Applied Animal Behaviour Science, 43,* 249-262.

Swaisgood, R.R., White, A.M., Zhou, X., Zhang, H., Zhang, G., Wei, R., Hare, V.J., Tepper, E.M., & Lindburg, D.G. (2001). A quantitative assessment of the efficacy of an environmental enrichment programme for giant pandas. *Animal Behaviour, 61,* 447-457.

Talbot, S.L., & Shields, G.F. (1996). A phylogeny of the bears (Ursidae) inferred from complete sequences of three mitochondrial genes. *Molecular Phylogenetics and Evolution, 5,* 567-575.

Terlouw, E.M.C., Lawrence, A.B., & Illius, A.W. (1991). Influences of feeding level and physical restriction on development of stereotypies in sows. *Animal Behaviour, 42,* 981-991.

Terlouw, E.M.C., Lawrence, A.B., Ladewig, J., De Passille, A.M., Rushen, J., & Schouten, W.G.P.(1991). Relationship between plasma cortisol and stereotypic activities in pigs. *Behavioural Processes, 25,* 133-153.

Tougard, C., Chaimanee, Y., Suteethorn, V., Triamwichanon, S., & Jaeger, J.J. (1996). Extension of the geographic distribution of the giant panda (*Ailuropoda*) and search for the reasons for its progressive disappearance in Southeast Asia during the Latest Middle Pleistocene. *C.R. Acad. Sci. Paris, 323,* 973-979.

Tudge, C. (1992). *Last animals at the zoo: How mass extinction can be stopped.* Washington, D.C.: Shearwater Publications.

Waits, L.P., Sullivan, J., O'Brien, S.J., & Ward, R.H. (1999). Rapid radiation events in the family Ursidae indicated by likelihood phylogenetic estimation from multiple fragments of mtDNA. *Molecular Phylogenetics and Evolution, 13,* 82-92.

Wallace, T.L., Gudelsky, G.A., Vorhees, C.V. (1999). Methamphetamine-induced neurotoxicity alters locomotor activity, stereotypic behavior, and stimulated dopamine release in the rat. *The Journal of Neuroscience, 19,* 9141-9148.

Whitmore, K.D. & Marzluff, J.M. (1988). Hand-rearing corvids for reintroduction: importance of feeding regime, nestling growth, and dominance. *Journal of Wildlife Management* 62(4), 1960.

Xie, Z. & Gipps, J. (1999). The 1999 international studbook for giant panda (*Ailuropoda melanoleuca*). Beijing: China Association of Zoological Gardens.

Zhou, Z., & Pan, W. (1997). Analysis of the viability of a giant panda population. *Journal of Applied Ecology, 34,* 363-374.