The Effect of Early Rearing Experience on Adult Reproductive Behavior in Captive Giant Pandas (*Ailuropoda melanoleuca*) and Spectacled Bears (*Tremarctos ornatus*)

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The Effect of Early Rearing Experience on Adult Reproductive Behavior in Captive Giant Pandas (*Ailuropoda melanoleuca*) and Spectacled Bears (*Tremarctos ornatus*)

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SUMMARY

The present study examined the relationship between early rearing experience and reproductive competence in captive adult giant pandas (*Ailuropoda melanoleuca*) and spectacled bears (*Tremarctos ornatus*). Life history information of 52 giant pandas and 34 spectacled bears were obtained from the International Studbook and by interviewing staff at institutions housing the subjects. The early rearing experience variables included duration of mother rearing, social access within 1-yr period following maternal separation, and birth origin. Correlation, Chi-square, and logistic regression analyses were used to analyze the data. Contrary to findings from studies with other animals, the results generally suggest that early rearing experience is not related to adult reproductive success in giant pandas and spectacled bears. Alternative explanation and limitation of the study were discussed; suggestions were made for future study.

INTRODUCTION

According to the IUCN (World Conservation Union) Red List categories, the giant panda and the spectacled bear are considered endangered and vulnerable to extinction, respectively (IUCN, 2001). For the giant pandas, only about 1,600 individuals remain in the wild; moreover, the captive population is not self-sustaining (Huang, 1994; Tang & Zhang, 2001). Both captive giant panda males and females exhibit behavioral problems that lead to reproductive failures (Snyder, 2001; Snyder, Bloomsmith, Zhang, Zhang, & Maple, in press). However, factors that influence adult sexual behaviors are not yet clear (Zhu, Lindburg, Pan, Forney & Wang, 2001). For the spectacled bears, little research has been done and little is known about their reproductive behaviors, even though the captive birth rate is considered not optimal (Rosenthal, 1999). Therefore, factors that contribute to a self-sustaining captive population for both giant pandas and spectacled bears need to be identified.

One determinant of reproductive success is early rearing experience (Beach & Jaynes, 1954; King, 1958; Lindburg & Fitch-Snyder, 1994). Lack of early social experience with conspecifics has been found to affect later reproductive behavior in a variety of species, such as non-human primates (Arling & Harlow, 1967; Beck & Power, 1988; Bloomsmith, Pazol, & Alford, 1994; King & Mellen, 1994; Mason, 1963; Mitchell & Clark, 1968; Simpson, 1978), domestic cats (Mellen, 1992; Rosenblatt, 1965), rodents (Cooke, Chowanadisai, & Breedlove, 2000; Gerall, Ward, & Gerall, 1967; Hole, Einon, & Plotkin, 1986), and birds (Bambaridge, 1962; Myers, Millam, Roudybush, & Grau, 1988). Offspring reared under circumstances with sufficient social input are more likely

to contribute to breeding programs as adults, because they are less prone to develop abnormal behaviors and are more likely to demonstrate appropriate social, sexual, and maternal behavior as adults (Zhang et al., 2000). In addition, the visual, auditory, and olfactory exchanges between the dam and offspring also have profound and lasting effects on the young animal's later behavior. This study will extend the findings from past research on various species to the literature on giant pandas and spectacled bears.

Early Rearing Experience Research on Nonhuman Primates

Prior research on nonhuman primates has found relationships between early rearing experience and adult sexual behavior. For example, King and Mellen (1994) examined the effect of early rearing experience on adult copulatory behavior of zoo-born chimpanzees (*Pan trogologytes*). The results showed that 93% of the chimpanzees that were raised by their mother for at least one year copulated as adults, whereas only 44% of chimpanzees that were removed from their mothers at an early age (prior to one month of age) copulated as adults. In addition, significantly higher percentage of chimpanzees that were raised with siblings or peers (53.8%) than chimpanzees that were hand reared alone (30%) copulated as adults. These results supported the contention that certain components of early rearing experience greatly influence the sexual competence of adult chimpanzees.

Beck and Power (1988) conducted an exhaustive survey and obtained the standardized biographies of every gorilla (*Gorilla gorilla gorilla*) held in North America in order to determine the factors associated with reproductive success. The data demonstrated that when defining reproductive success as number of infants per year of

reproductive opportunity, captive-born gorillas were reproducing as well as wild-borns. However, although there was no difference between the reproductive success of mother-reared and hand-reared males, mother-reared females were reproductively more successful than hand-reared females. In addition, first-year social access to conspecifics appeared to be associated with higher reproductive success among captive-born females. Given the equal mating opportunities, reproductively unsuccessful animals were less likely to exhibit normal sexual behavior than successful ones. The investigators concluded that many cases of reproductive failure were due to lack of early social experience with conspecifics.

Similarly, early rearing experience has been found to be critical for exhibiting appropriate reproductive behavior as adults in rhesus monkeys (*Macaca mulatta*) (Arling & Harlow, 1967; Harlow, 1965; Mason, 1963; Mitchell & Clark, 1968; Simpson, 1978). Male and female captive-born rhesus monkeys that were raised in isolation from other monkeys showed deficiencies in sexual behavior (Mason, 1963, Mitchell & Clark, 1968). Inadequate early experience made it difficult or impossible for the young animals to pass from the stage of infantile sexuality into the normally subsequent stages of differential sexuality and adult heterosexuality (Harlow, 1965; Simpson, 1978). Female rhesus monkeys separated from mothers at birth and raised isolated from peers were distinctly deficient in providing maternal care compared to feral-raised females (Arling & Harlow, 1967). Furthermore, it has been demonstrated that early social deprivation influences male sexual behavior more strongly than it does female sexual behavior (Goldfoot, 1977; Sackett, 1974). It was found that all of the isolate-reared male rhesus monkeys in an

experimental group failed to copulate, whereas successful copulation was observed in 20% of the isolate-reared females in the experimental group (Sackett, 1974).

Early Rearing Experience Research on Cats

Mellen (1992) studied the effects of human rearing on adult sexual behavior of domestic cats (*Felis catus*). Female cats were randomly assigned to three different conditions: human-raised alone, human-raised with a sibling, and mother-raised with a sibling. When the subjects reached their sexual maturity, which was defined by the first estrous period, each of them was paired with a sexually experienced male, and copulatory behavior was observed. Data showed that the human-raised alone females displayed extreme aggression toward their male partners. Human-raised female cats were less likely to reproduce than mother-raised females. The researcher suggested that whenever possible, human-raising of felids should be avoided.

Early Rearing Experience Research on Birds

Myers et al. (1988) studied the influence of early rearing experience on the reproductive success of cockatiels (*Nymphicus hollandicus*). It was found that hand-reared females were more likely to lay eggs and laid more eggs than parent-reared females, but often laid them on the cage floor rather than in nest-boxes, which reduced hatching success. Pairs containing hand-reared males were less likely than pairs containing parent-reared males to produce fertile eggs, and fledging occurred only in pairs containing parent-reared males. Researchers pointed out that early rearing experience is important for males to learn characteristics of the opposite sex, and for both males and females to learn characteristics of nest-sites.

Giant Pandas

In general, giant pandas are inefficient at reproducing offspring, which may contribute to their status as endangered species (Wang, Kai, & Tan, 1993). The reproductive inefficiency observed in giant pandas may be partially attributed to the following ontogenetic characteristics. Giant panda females only come into estrus once a year, during the spring. The entire estrous period may last from 12-25 days, but the receptive period (also called peak estrus) only lasts for about 2-7 days (Domico, 1988; Schaller, Hu, 2001; Hu, Pan, & Zhu, 1985; Wang et al., 1993). Moreover, giant pandas are very particular about their sexual partners, which makes mating difficult even if a panda is in heat (Wang et al., 1993). Further, quite a few females do not let out any fertile ovum when in heat (Wang et al., 1993). They have a delayed embryo implantation for several months. That is, the fertilized ovum only develops to the blastocyst stage and then floats free in the uterus for one to three-and-a-half months before implanting (Domico, 1988; Schaller, Hu, Pan, & Zhu, 1985). In addition, the giant panda newborn is extremely tiny and weak, requiring profound maternal cares from the mother. It typically weighs about 2.6-5.3 ounces (75-150 grams), which is only one thousand percent of its mother's weight. The cub is blind at birth and is almost naked. It opens its eyes at around six weeks of age, and it cannot see until 120 days after birth. The cub is fully furred at about 25 days of age, and it starts to walk at 4 months of age (Hu, 2001; Wang et al., 1993; Zhu, Lindburg, Pan, Forney, & Wang, 2001). The mother holds the cub to her breast with her forepaws almost continuously for the first three weeks of the cub's life and provides an amazing amount of care and attention (Domico, 1988; Schaller et al., 1985). Above 50% of the time, the female will give birth to twins. However, due to the extremely high

levels of maternal care needed by the newborns, the giant panda mother is unable to take care of two cubs at the same time. Typically, only one of them survives, while the other is usually abandoned and starves to death or becomes accidentally crushed beneath the weight of the mother's body (Domico, 1988; Schaller et al., 1985; Wang et al., 1993; Zhang et al., 2000). Finally, male giant pandas have a very short penis (Domico, 1988; Wang et al., 1993), and they seldom reach sexual climax. The amount of their seminal fluids is small, and the sperm malformation rate is high (Wang et al., 1993). Due to the above facts, giant pandas face dramatic reproductive difficulties in general. As such, a long-term goal of developing a self-sustaining captive population of giant pandas has been established in order to support a long-term, viable population in the wild (Zheng, Zhao, Xie, Wildt, & Seal, 1997). However, both female and male captive giant pandas exhibit behavioral problems that reduce the likelihood of reproduction success (Snyder, 2001, Zheng et al, 1997).

The primary problem for captive females is that the majority does not display normal behavioral estrus (Zheng et al., 1997). The Chinese zoo personnel stated that an unacceptable number of captive adult females failed to demonstrate overt signs of estrus (Zheng et al., 1997). In addition, for those who were paired with males but failed to complete copulation, the behavioral problems included being timid toward the male, incorrect mating postures such as not showing lordosis, not holding the tail up, and not standing still to let the male mount (Snyder et al., in press). For captive males, the main behavioral problems include lacking sexual interest in estrus females, being either too aggressive or too meek toward females (Zheng et al., 1997). However, antecedents

accounting for the behavioral failure of both female and male captive giant pandas have not been successfully identified.

In the wild, giant panda cubs have been reported to remain with their mothers for 1.5 to 2.5 years, sometimes even up to three years (Hu, 2001; Schaller et al., 1985; Zhu et al., 2001). This suggests that giant panda cubs may learn social behaviors from their mothers that are important for successful conspecific interactions in adulthood (Zoo Atlanta Giant Panda Application). However, in captivity, giant panda cubs are often permanently removed from mother at six-month of age or earlier. This has become a standard management practice in Chinese zoos, which allows the females to enter the next reproductive cycle earlier than the natural condition (Snyder et al., in press). Although this management strategy increases the potential birthrate of a female in a fixed number of years, the shortened mother rearing duration may not provide the cubs with sufficient opportunities to learn species-specific behaviors from mothers that are important for their later social interactions with conspecifics. Thus, the insufficient mother rearing duration may exert long-term effects on various aspects of the animals' behavior including reproductive success within the entire captive population (Snyder et al, in press), which may severely impede the process of establishing a self-sustained captive population. Therefore, if the acceleration of female pandas' reproductive cycle is necessary in captivity, the least and optimum duration of mother rearing need to be determined.

In the captive giant panda population, a lower proportion of males than females have successfully reproduced offspring (Lindburg, Huang, and Huang, 1997). According to the newest issue of the giant panda studbook (Xie & Gipps, 2001), of the

30 living captive males of breeding age (six-year old or above), only seven males worldwide have ever produced offspring via natural copulation, and only one of these was captive-born. Another two males reproduced only through artificial insemination. These nine males constituted 30% of all adult males alive at the end of 2001. Historically, only 31 (29.3%) of all adult males have reproduced, whereas 34.9% of the adult females have reproduced (Zheng et al, 1997). Lindburg et al. (1997) examined a variety of factors that were thought to impact the reproductive performance of captive males. It was found that larger enclosure size and presence of reproductive rival (i.e. other males) favor the reproductive success of captive males. Early rearing and social experience remained unexplored. However, researchers suggested that early rearing deficiencies could be a possible factor contributing to mating dysfunction in adult males (Lindburg et al., 1997).

Spectacled Bears

Spectacled bears, also called Andean bears, are the only bear species living in South America. They inhabit the Andes Mountains, ranging from Venezuela, Colombia, Ecuador, Peru, to Bolivia (Domico, 1988; Peyton, 1999; Nowak, 1999). Spectacled bears can be found from coastal deserts at 180m up to the snow line where the altitude is about 4,200m (Domico, 1988). However, the optimum habitat appears to be the lower part of cloud forests between 1,900m and 2,350m (Nowak, 1999). The name of "spectacled" is given rise by the white or yellowish markings that encircle their eyes (Domico, 1988; Nowak, 1999; Peyton, 1999). These markings are unique to each individual (Peyton, 1999).

Spectacled bears are the only survivors of the short-faced bear subfamily (Domico, 1988). They have the shortest relative snout length and the largest zygomatic mandibularis muscles to body size ratio among all bear species. These two features are shared most similarly with the giant pandas, which allow them to chew and crush fibrous vegetation, and hence enable the spectacled bears to rival the giant pandas as the most herbivorous of bears (Peyton, 1999).

Spectacled bears reach sexual maturity between four and seven years of age (Peyton, 1999). In the wild, mating usually occurs in April, May and June, and pairs stay together for a week or two, with copulation occurring several times (Domico, 1988). Gestation periods vary between five and a half to eight months. This implicates that the females may be capable of delayed implantation, which allows the timing of births to coincide with the fruit season (Domico, 1988; Nowak, 1999; Peyton, 1999). Similar to the giant pandas, the spectacled bear females den in a nest under boulders or tree roots before giving birth (Domico, 1988; Schaller et al., 1985). The cubs are generally born from November through February, with most births in January. Litter sizes range from one to three with two being the most common. The newborn weights about 1/300 of its mother's weight (Domico, 1988; Nowak, 1999; Peyton, 1999), and it opens its eyes in about 25 days and start to move about at 3 months of age (Domico, 1988). Cubs remain with mother for up to a year after birth (Peyton, 1999). Mothers and cubs were found to communicate through various vocalizations (Domico, 1988; Elowson, 1988; Peyton, 1999).

Due to the animals' isolated and inhospitable habitats, the wild population of the spectacled bear is not yet clear. The estimation of the wild population varies from a few

thousand (Domico, 1988) to more than 10, 000 (Peyton, 1999). Although the accurate population estimates of the spectacled bear are currently unavailable, it is believed that the wild population is rapidly declining because of habitat destruction and hunting (Peyton, 1999). According to the IUCN Red list categories (IUCN, 2001), the spectacled bear is listed as vulnerable to extinction and is protected against trade.

In captivity, historically 607 spectacled bears have been housed in zoological institutions worldwide, and by the end of 1999, 293 living animals were housed at 99 institutions worldwide (Rosenthal, 1999). Although a few studies have been conducted on the captive population, such as environmental enrichment studies (Altman, 1999; Renner and Lussier, 2002) and mother-cub vocal communication study (Elowson, 1988), the relationship between early rearing experience and later reproductive behavior remains unexplored. According to the newest issue of the international studbook of the spectacled bear (Rosenthal, 1999), "births in the population have been limited." Therefore, it is time to take advantage of the currently sufficient captive population of the spectacled bear to conduct scientific studies to gain more knowledge about this species.

Spectacled bears and giant pandas share similarities in both reproductive physiology and reproductive behaviors. For example, both giant panda mothers and spectacled bear mothers exhibit behavior of holding cubs to their breasts with front limbs (Domico, 1988; Schaller et al., 1985). Moreover, the spectacled bear mother is observed to hold the cub against her body with one paw as she runs on three legs (Domico, 1988). As solitary species, both spectacled bear mothers and giant panda mothers solely take the responsibility of raising the cubs and provide high levels of maternal care (Domico, 1988; Peyton, 1999; Schaller et al., 1985). A comparison of the biological background and

behaviors of these two species is provided in Table 1. Based on the knowledge about the reproduction of these two species, we have reason to assume that early rearing experience could be one of the factors that affect the animals' sexual behavior as adults. In addition, the various similarities between these two species make the comparison a reasonable one.

Table 1. Comparison of the Biological Background and Behaviors of Giant Pandas and Spectacled Bears

	Giant pandas	Spectacled bears
Body length	5.25-6 feet	4.25-6.25 feet
Weight	175-275 pounds	175-275 pounds
Diet	primarily bamboo, but also eat meat when given the opportunities	primarily vegetarian, but also small animals if given the opportunities
Habitat altitude	4,000- 13, 250 feet	600-13,800 feet
Hibernation	no	no
Social structure	solitary	solitary
Age at sexual maturity	male 6 years female 5 years	male 4-7 years female 4-7 years
Mating season	mid-March to May	April to June
Gestation period	3.5-5.5 months	5.5-8 months
Delayed implantation	yes	yes
Litter size	1-2 cubs	1-3 cubs, with 2 the most
Cub weight	3-5 ounces (1/900 of dam weight)	11-18 ounces (1/300 of dam weight)
Age cub opens eyes	42 days	25 days
Age cub moves about	4 months	3 months
Duration cub remains with mother	1.5-2.5 years	up to one year

In summary, early rearing and social experience was found to be critical for reproductive success as adults in many species. Although past studies have examined various factors that might exert influences on giant panda reproduction success (Kleiman, 1983; Lindburg, Huang, & Huang, 1997; Snyder, 2001; Swaisgood, Lindburg, Zhou, & Owen, 2000), there has been little to no research on the relationship between early rearing experience and adult sexual behavior for both the giant pandas and the spectacled bears. The present study focused on how the early rearing and social experiences would affect the sexual behavior of giant pandas and spectacled bears as adults. First, we hypothesized that the duration of mother rearing would be positively correlated with the likelihood of reproductive success for both species. That is, the earlier the animals are removed from mothers, the more disturbed is the reproductive behavior. In addition, we hypothesized that animals that were housed with conspecifics within the one-year period following permanent maternal separation would be more likely to reproduce as adults than animals that were housed alone during the corresponding period. Third, we hypothesized that for giant pandas, the relationship between duration of mother rearing and reproductive behavior would be stronger for males than for females. Findings from this study could provide insight into the development of management protocols that facilitate rearing conditions to enhance reproductive success. Further, in comparison with the early rearing studies of different species, this study may help us to answer the question of whether organisms with different genetic backgrounds respond alike to the same early rearing experience.

METHOD

Subjects

For the giant pandas, data of 58 animals were collected initially. However, review of the data suggested that among animals that had never copulated, six of them never had available mates. In other words, these animals were never given the opportunity to display copulatory behavior because institutions housing these animals were unable to provide them with any potential mates. Therefore, we removed these six animals from the subject pool, and data from 52 subjects (18 males, 34 females) were analyzed in the current study. The 52 giant pandas were housed at 10 locations in China, Germany, Japan, and the United States.

For the spectacled bears, data of 41 animals were collected initially. However, among animals that had never copulated, seven of them never had available mates. Therefore, 34 spectacled bears (14 males, 20 females) were included in the final subject pool, and they were housed at 21 locations in the United States, Russia, Germany, Switzerland, and Venezuela.

For the giant pandas, 58% (30 of 52) subjects had copulated as adults. Of this total, 56% of males (10 of 18) and 59% of females (20 of 34) had copulated as adults. For the spectacled bears, 79% (27 of 34) had copulated as adults. Of this total, 71% of males (10 of 14) and 85% of females (17 of 20) had copulated as adults (see Table 2).

Table 2. Percentage and Number of Giant Pandas and Spectacled Bears that Copulated as Adults

	Female		Male		Total	
	%	N	%	N	%	N
Giant Panda						
Wild-born	50%	8 of 16	60%	6 of 10	54%	14 of 26
Captive-born	67%	12 of 18	50%	4 of 8	62%	16 of 26
Total	59%	20 of 34	56%	10 of 18	58%	30 of 52
Spectacled bear						
Wild-born	N/A		N/A		N/A	
Captive-born	85%	17 of 20	71%	10 of 14	79%	27 of 34

Note. There were no wild-born spectacled bears in this study.

Measurements

Independent variables. First, the duration of mother rearing was recorded as an open-ended response. The duration of mother rearing was also converted into categorical data. In the 1996 Giant Panda Captive Management Planning Workshop (Zheng et al, 1997), ordinal categories were recommended by the Reproduction, Behavior, and Management Working Group to help identify the range of hand-rearing. Thus, the subjects were assigned to one of the following rearing categories: (1) being removed from mother at birth (less than or equal to one day old), (2) being removed from mother between one day and one month of age, (3) being removed from mother between one and

four months of age, (4) being removed from mother between four and six months of age, (5) being removed from mother between six months and one year of age, (6) being removed from mother after one year of age. It is important to note that categorizing continuous data results in a loss of information. As such, both continuous data of the duration of mother rearing and categorical data were analyzed. Second, the origin of the subjects, which refers to captive born or wild born, was recorded. Third, the subject's social access within the one-year period following its permanent separation from mother was assessed (i.e., whether or not the subject was housed with peers or other adult conspecifics in the same enclosure after it was separated from its mother). Fourth, the sex of the subjects was recorded.

Dependent variables. First, whether the subject has ever copulated during its adult life was recorded. Second, the number of different years in which the subject copulated was recorded. Third, the number of living cubs produced by the subject (defined by 100-day survival) was recorded, and whether breeding occurred following natural mating or artificial insemination was identified.

Since artificial insemination has been widely used in captive giant panda reproductive management, in many cases, the production of offspring was the result of solely artificial insemination, which means the animals could have produced offspring even they were incapable of natural mating; in some other cases, the dam underwent both natural mating and artificial insemination, making it difficult to determine the sire of the offspring. Therefore, compared to *the number of cubs produced by the subject*, we believe that *the number of different years in which the subject copulated* can better represent the giant panda's reproductive competence. However, the ages of the giant

panda subjects ranged from 6 to 30, and thus, younger animals have had less potential years to display copulatory behavior than older animals. In order to control for potential copulation opportunities, we computed the *copulation rate* for each subject. More specifically, we divided the number of different years in which the subject copulated by its years of copulation opportunity, which was obtained by subtracting 5 from females' ages and 6 from males' ages. For example, suppose a female giant panda was 20 years old, and had previously display copulatory behavior in 10 different years. Thus, her *copulation rate* would be 10/ (20-5) = 0.67. We computed the *copulation rate* for each giant panda subject, and examined the effect of various independent variables on the *occurrence of successful copulation* (i.e., whether the subject has ever copulated as adult) and the *copulation rate*.

Contrary to the captive giant panda reproductive management, artificial insemination was never reported to be used among the captive spectacled bear population. Therefore, *the number of cubs produced by the subject* remains to be a strong measure for the spectacled bear's reproductive competence. Again, in order to control for years of reproductive opportunity between animals of different ages, we computed the *reproduction rate*. More specifically, we divided the subject's number of cubs by its years of reproductive opportunity, which was obtained by subtracting 4 from ages of both male and female subjects. Thus, if a spectacled bear (male or female) was 20 years old and had produced 8 cubs, its *reproduction rate* would be 8/(20-4) = 0.5. We computed the reproduction rate for each spectacled bear subject, and examined the effect of various independent variables on the *occurrence of successful copulation* and the *reproduction rate*.

Procedure

Survey and archival methods were used in the present study. Data were collected either by interviewing staff at institutions housing the animals, or by mailing questionnaires to institutions housing the animals. A complete questionnaire is shown in the appendix. The questionnaires for giant pandas and spectacled bears were identical.

Life history information such as wild-born or captive-born and offspring information was obtained from the International Studbook. Survey responses were compared to information contained in the International Studbook to ensure the accuracy of the data.

For captive-born giant pandas, the duration of mother rearing was obtained from the questionnaire response. Because giant panda cubs in the wild typically remain together with their mothers for 1.5 to 2.5 years (Schaller et al., 1985; Zhu et al, 2001), we used 1.5 years (18 months) as the duration of mother rearing for wild-born subjects if the estimated age at capture was beyond 1.5 years old; if the animal was capture prior to 1.5 years old, the estimated age at capture was used as the duration of mother rearing.

For the giant pandas, an adult female was defined as being at least five years old; an adult male was defined as being at least six years old (Shaller et al, 1985; Hu, 2001). For both the spectacled bear males and females, an adult was defined as being at least four years old (Peyton, 1999).

Data analysis

Correlational analyses were used when examining the relationship between the independent variables and continuous measures of dependent variables. This includes the dependent variables of copulation rate and reproduction rate. Second, Chi-square

analyses were used to examine the relationship between two categorical measures. This included the relationship between birth origin (i.e., captive-born vs. wild-born) and the occurrence of successful copulation, as well as between the categorical measure of duration of mother rearing and the occurrence of successful copulation. Third, logistic regression analysis was used to determine the relationship between the continuous measure of duration of mother rearing and the occurrence of successful copulation.

The dichotomous variables were dummy coded for these analyses. For birth origin, “0” represents wild born and “1” represents captive born. For social access, “0” represents housed alone and “1” represents housed with at least 1 conspecific. For whether successful copulation occurred, “0” represents no and “1” represents yes.

RESULTS

Duration of Mother Rearing

We first examined the effect of duration of mother rearing on reproductive success.

Giant Pandas. In this sample, duration of mother rearing ranged from 0–18 months. One animal remained with its mother for less than one day, one animal remained with its mother for one month, four animals remained with their mothers between one and four months, 20 animals remained with their mothers between four and six months, three animals remained with their mothers between six and 12 months, and 23 animals were separated from their mothers after 12-month of age. Table 3 presents the distribution of subjects' durations of mother rearing and whether they had copulated as adults.

Table 3. Number of Giant Panda Subjects within each Duration of Mother Rearing Condition and Their Copulation Status

	Whether copulated as adult			
Duration of mother Rearing (in month)	No	Yes	Total	Percentage of subjects copulated
0		1	1	100%
1		1	1	100%
2	1		1	0%
3	1	1	2	50%
4	1		1	0%
4.5		1	1	100%
5	2	11	13	85%
6	4	2	6	33%
8		1	1	100%
12	1	1	2	50%
13	2	2	4	50%
18	10	9	19	47%
Total	22	30	52	58%

We first examined the relationship between duration of mother rearing and the occurrence of successful copulation. Figure 1 shows the percentage of subject that had copulated as adults under each duration of mother rearing condition.

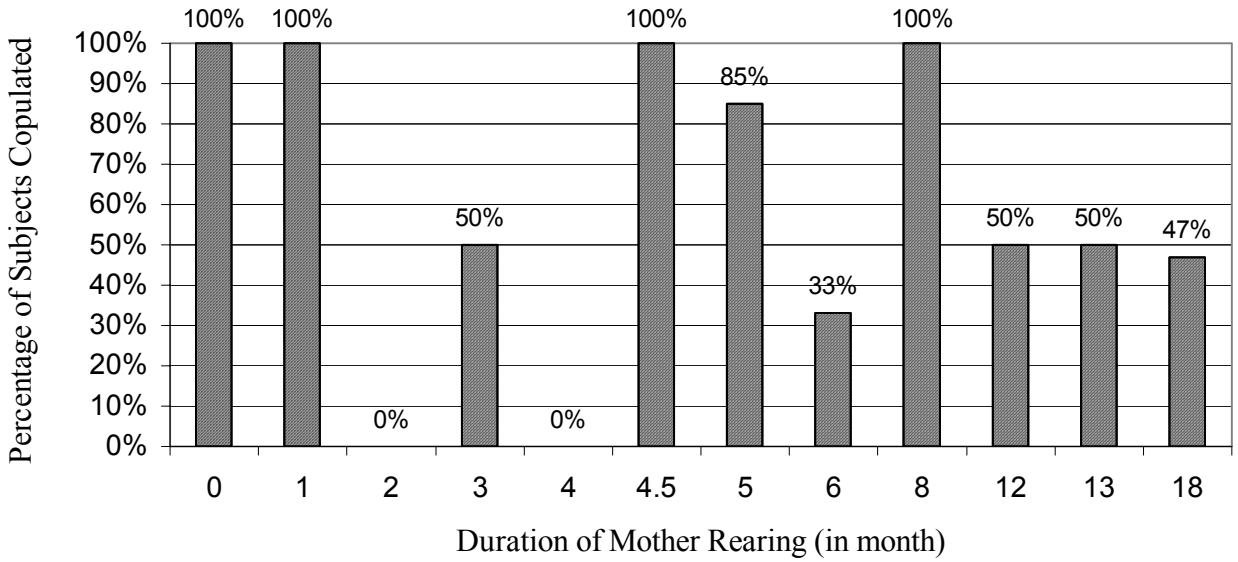

Figure 1. Percentage of Giant Panda Subjects Copulated in each Duration of Mother Rearing Condition.

Since duration of mother rearing is a continuous variable, and the dependent variable (whether the subject copulated as adult) is a categorical variable, logistic regression analysis was used to determine the ability of duration of mother rearing at predicting occurrence of successful copulation. Contrary to our hypothesis, the regression

analysis shows that adding duration of mother rearing into the regression equation did not significantly improve the prediction of copulatory behavior (Chi-square test for the overall model fit, $\chi^2 = 1.857$; df = 1; p = .173); duration of mother rearing was not a significant predictor for copulatory behavior (Wald test for b-weight, Wald = 1.816, df = 1, p = .178). Consistent with the regression analysis results, the correlation between duration of mother rearing and copulatory behavior was not significant (Spearman correlation, r = -.199, p = .158) (Table 4).

Second, we examined the effect of duration of mother rearing on copulation rate. The relationship between duration of mother rearing and copulation rate was graphed in Figure 2. Visual inspection did not reveal a discernable trend. Further correlation analysis shows that there was not a significant relationship between duration of mother rearing and copulation rate (Spearman correlation, r = -.211, p = .138) (Table 4). These results do not support our hypothesis that duration of mother rearing is positively correlated with the likelihood of copulatory behavior. Thus, cubs removed from their mothers at an early age (e.g., less than one day) did not differ from those that remained with mothers for longer period of time (e.g., 18 months) in the likelihood of exhibiting copulatory behavior.

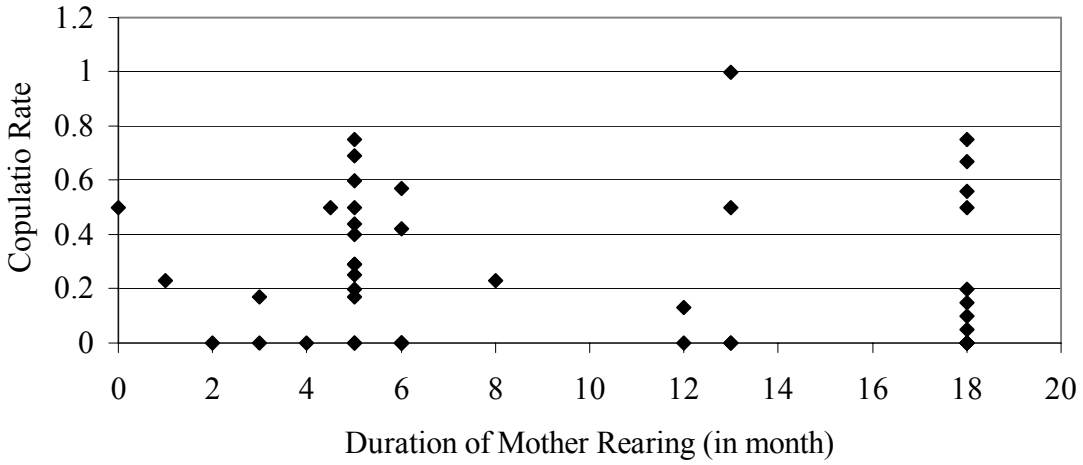

Figure 2. Relationship between Duration of Mother Rearing and Copulation Rate of the Giant Pandas.

Table 4. Spearman Correlations between Various Independent Variables and Reproductive Success in Giant Pandas

	Occurrence of copulation		Copulation rate	
Independent Variable	Correlation	P	Correlation	P
Duration of mother rearing	-.199	.158	-.211	.138
Categorical duration	--	--	-.134	.349
Birth origin	--	--	.142	.321
Social access	--	--	.152	.522
Sex of subjects	--	--	-.033	.816

As stated previously, we converted the duration of mother rearing into categorical data based on the recommendation given at the 1996 Giant Panda Captive Management Planning Workshop (Zheng et al, 1997). As depicted in Figure 3, 100% of subjects that remained with their mothers for less than one day (one of one) and for one month (one of one) copulated as adults, 25% (one of four) of subjects that were mother-reared for 1-4 months copulated, 70% (14 of 20) of subjects that were mother-reared for 4-6 months copulated, 67% (two of three) of subjects that were mother-reared for 6-12 months copulated, and 48% (11 of 23) of subjects that were mother-reared for more than 12 months copulated. No significant difference was found for the occurrence of successful copulation under different mother rearing conditions (Chi-square test, $\chi^2 = 5.476$; df = 5; p = .361) (Table 5). The correlation between mother rearing conditions and copulation rate was also not significant (Spearman correlation, r = -.134, p = .349) (Table 4). These results are consistent with the analyses using the continuous variable of duration of mother rearing, which do not support our hypothesis that duration of mother rearing is positively correlated with reproductive success.

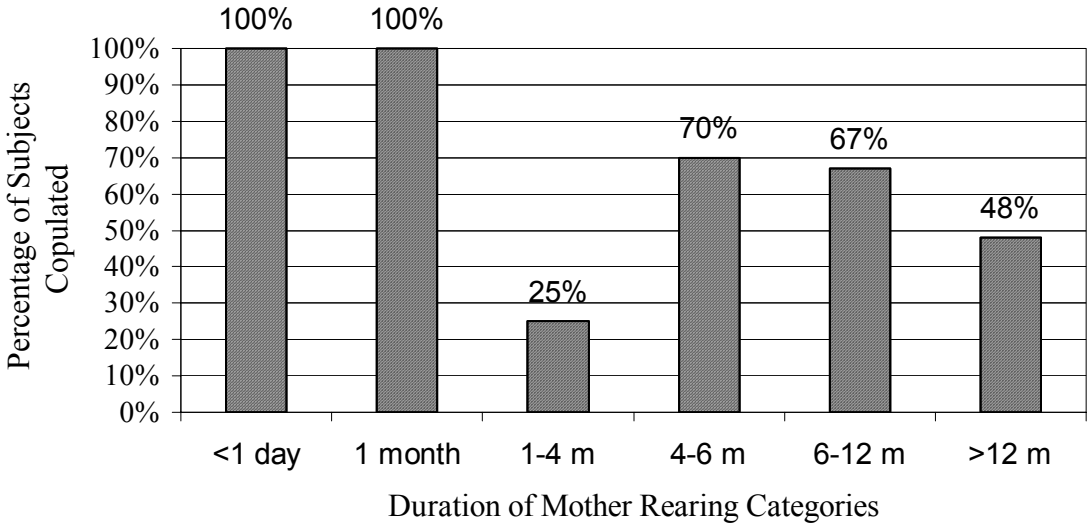

Figure 3. Percentage of Giant Panda Subjects Copulated in each Duration of Mother Rearing Category.

Table 5. Chi-square Test for Relationship between Various Independent Variables and the Occurrence of Successful Copulation in Giant Pandas

Variable	Percentage	N	χ^2	df	P
Duration of mother rearing			5.476	5	.361
categories:					
≤ 1 day	100	1 of 1			
> 1 day and ≤ 1 month	100	1 of 1			
> 1 month and ≤ 4 months	25	1 of 4			
> 4 months and ≤ 6 months	70	14 of 20			
> 6 months and ≤ 12 month	67	2 of 3			
>12 months	48	11 of 23			
Birth origin:			.315	1	.575
captive-born	62	16 of 26			
wild-born	54	14 of 26			
Social access:			.020	1	.888
housed with at least one conspecific	67	6 of 9			
housed alone	64	7 of 11			
Sex of subject:			.051	1	.820
male	56	10 of 18			
female	59	20 of 34			

Spectacled Bears. Of the 34 spectacled bear subjects, accurate information about duration of mother rearing was only obtained for 16 subjects. Therefore, the subsequent data analyses only included 16 spectacled bears. In this sub-sample, duration of mother rearing ranged from 7-35 months, and 75% of subject (12 of 16) had copulated as adults. Table 6 and Figure 4 present the distribution of subjects' durations of mother rearing and whether they had copulated as adults.

Table 6. Number of Spectacled Bear Subjects within each Duration of Mother Rearing Condition and Their Copulation Status

	Whether copulated as adult			
Duration of mother Rearing (in month)	No	Yes	Total	Percentage of subjects copulated
7		1	1	100%
10		2	2	100%
11	1	1	2	50%
13	1		1	0%
14	1	2	3	67%
15		1	1	100%
16		2	2	100%
18		1	1	100%
24	1	1	2	50%
35		1	1	100%
Total	4	12	16	75%

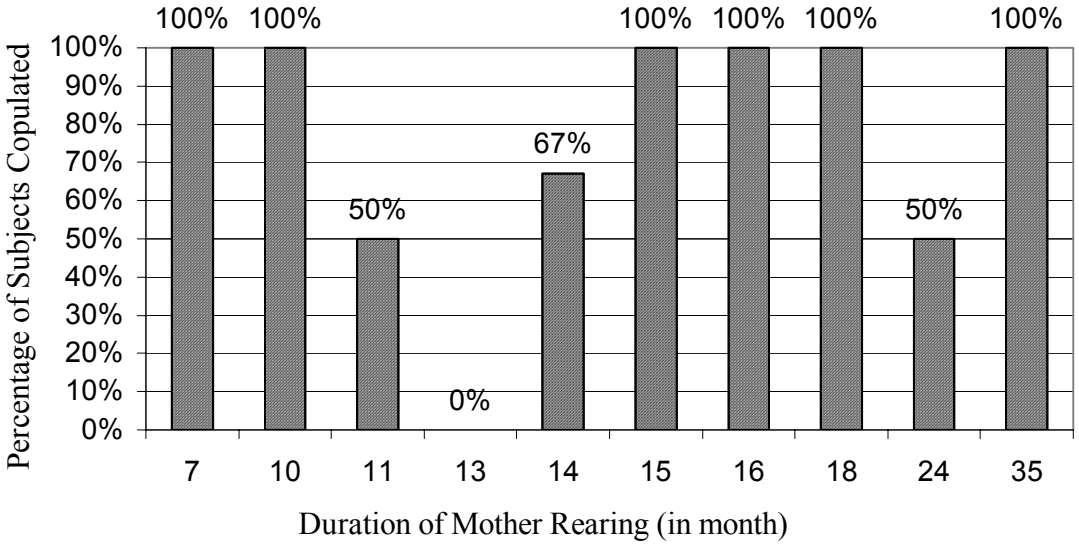

Figure 4. Percentage of Spectacled Bear Subjects Copulated in each Duration of Mother Rearing Condition.

Logistic regression analysis results showed that duration of mother rearing was not a significant predictor for the occurrence of successful copulation (Chi-square test for the overall model fit, $\chi^2 = .008$; df = 1; p = .931; Wald test for b-weight, Wald = .007, df = 1, p = .931). Consistent with the regression analysis results, the correlation between duration of mother rearing and copulatory behavior was not significant (Spearman correlation, r = .031, p = .908) (Table 7). Further, we examined the effect of duration of mother rearing on reproduction rate (Figure 5). The correlation between duration of mother rearing and reproduction rate was not significant (Spearman correlation, r = -.012,

p = .965) (Table 7). These results do not support our hypothesis that duration of mother rearing is positively correlated with reproductive success of the spectacled bears.

Table 7. Spearman Correlations between Various Independent Variables and Reproductive Success in Spectacled Bears

	Occurrence of copulation		Reproduction rate	
Independent Variable	Correlation	P	Correlation	P
Duration of mother rearing	.031	.908	-.012	.965
Social access	--	--	.252	.547
Sex of subjects	--	--	-.098	.580

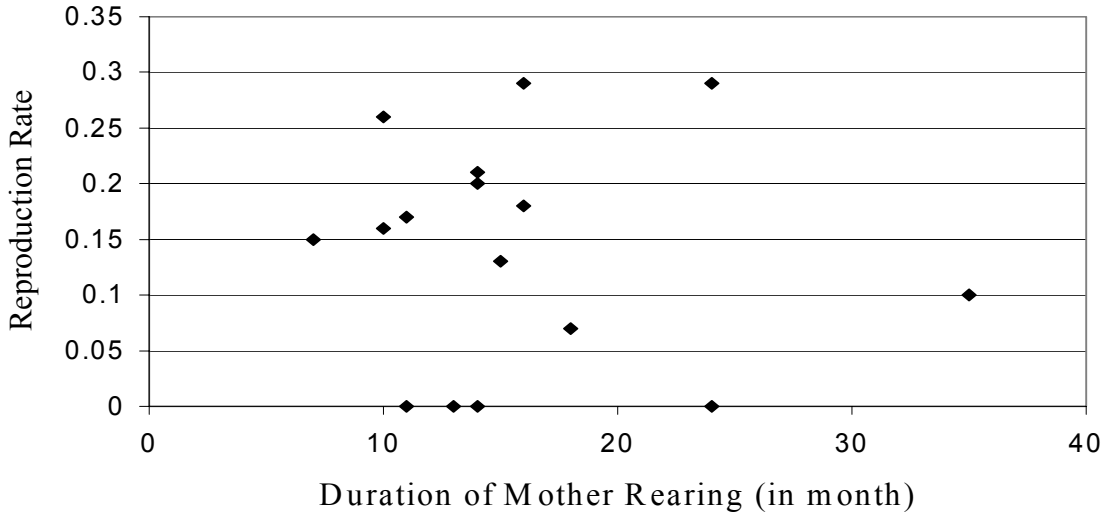

Figure 5. Relationship between Duration of Mother Rearing and Reproduction Rate of the Spectacled Bears.

Origins of Subjects: Captive-Born/Wild-Born

We next examined the effect of birth origin (i.e., captive-born vs. wild-born) on reproductive success. Since all of the spectacled bear subjects were captive-born, the analyses were only conducted on the giant pandas.

Of the 52 giant panda subjects, 26 of them (9 males, 17 females) were wild-born, and 26 of them (8 males, 18 females) were captive-born. 62% of captive-born subjects and 54% of wild-born subjects copulated as adults (see Figure 6). This difference in the occurrence of successful copulation between captive-born and wild-born subjects was not significant (Chi-square test, $\chi^2 = .315$; df = 1; p = .575) (Table 5). Thus, captive-born individuals are as likely to copulate as wild-born individuals.

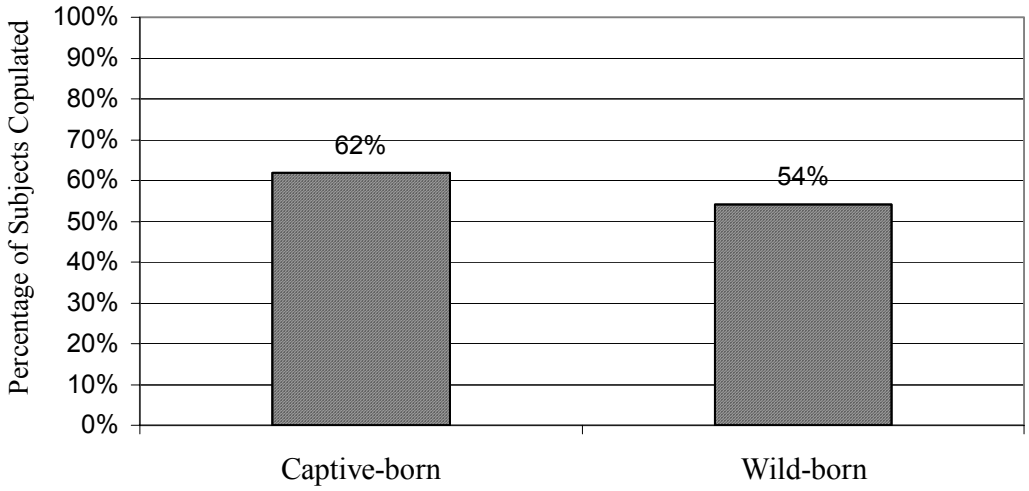

Figure 6. Percentage of Wild-born vs. Captive-born Subjects that had Copulated as Adults.

We further looked at the effect of birth origin on copulation rate. One wild-born female subject was captured in 2002 when she was 18 years old. Although she did not exhibit copulatory behavior in captivity, anogenital examination suggested that she had prior given birth to offspring in the wild. Since we were unable to estimate the number of different years this female had copulated in the wild, and hence could not compute her copulation rate, we only included 51 subjects in the current analysis. The copulation rate ranged from zero to one among the 51 subjects. The correlation between birth origin and copulation rate was not significant (Spearman correlation, $r = .142$, $p = .321$) (Table 4). Thus, captive-born giant pandas copulated as frequently as wild-born giant pandas.

Social access within One Year after Maternal Separation

Giant Pandas. Because the social experience within the one-year period following permanent maternal separation for wild-born subjects is unknown, we only examine the effect of early social experience among captive-born subjects. Of the 26 captive-born subjects, 11 of them were housed alone, 9 of them were housed with at least one peer within the one-year period following permanent maternal separation. We did not have information for 6 of the captive-born subjects. Therefore, only 20 subjects were included in the data analyses. 64% (7 of 11) subjects that were housed alone copulated as adult, and 67% (6 of 9) of those that were housed with at least one peer copulated as adult. The difference between two housing conditions on the occurrence of successful copulation was not significant (Chi-square test, $\chi^2 = .020$; $df = 1$; $p = .888$) (Table 5), and the correlation between housing condition and copulation rate was not significant (Spearman correlation, $r = .152$, $p = .522$) (Table 4). Thus, social access within the one

year period following permanent maternal separation does not significantly affect copulatory behavior in adulthood.

Spectacled Bears. Of the 34 spectacled bear subjects, information about social access within the one-year period following maternal separation was only obtained for 8 subjects. Two of the 8 subjects were housed alone, and 6 of them were housed with one peer within the one-year period following maternal separation. 50% (1 of 2) of subjects that were housed alone, and 100% of subjects that were housed with one peer copulated as adult. This difference approached significance (Chi-square test, $\chi^2 = 3.429$; df = 1; p = .064) (Table 8). However, the correlation between post-separation housing condition and reproduction rate was not significant (Spearman correlation, r = .252, p = .547) (Table 7). These results together suggest that spectacled bears that were housed with one peer following maternal separation were more likely to display copulatory behavior as adults, but they did not produce more offspring than spectacled bears that were housed alone. These analyses should be particularly interpreted with caution because of the small sample size.

Table 8. Chi-square Test for Relationship between Various Independent Variables and the Occurrence of Successful Copulation in Spectacled Bears

Variable	% mated	N	χ^2	df	P
Social access:			3.429	1	.064
housed with at least one conspecific	100	6 of 6			
housed alone	50	1 of 2			
Sex of subject:			.928	1	.335
male	71	10 of 14			
female	85	17 of 20			

Duration of Mother Rearing by Sex of Subject

Giant Pandas. Of the 52 subjects, 18 were males, and 34 were females. As stated previously, 56% of males (10 of 18) and 59% of females (20 of 34) had copulated as adults. This difference between males and females was not significant (Chi-square test, χ^2 = .051; df = 1; p = .820) (Table 5). In addition, the correlation between copulation rate and sex was not significant (Spearman correlation, r = -.033, p = .816) (Table 4). Thus, giant panda males and females are equally likely to copulate as adults. In order to test our hypothesis that reproductive behavior of giant panda males is more severely affected by rearing experiences than is female behavior, we tested the relationship between duration of mother rearing and reproductive behavior (i.e., the occurrence of successful copulation and copulation rate) in males and females separately. However, the effect of rearing

experience was not significant either in males (Logistic regression analysis for the occurrence of successful copulation, Wald = .762, df = 1, p = .383; Spearman correlation analysis for copulation rate, r = -.209, p = .405) or in females (Logistic regression analysis for the occurrence of successful copulation, Wald = 1.064, df = 1, p = .302; Spearman correlation test for copulation rate, r = -.176, p = .328).

Spectacled Bears. Of the 34 subjects, 14 were males, and 20 were females. 71% of males (10 of 14) and 85% of females (17 of 20) copulated as adults. This difference was not significant (Chi-square test, $\chi^2 = .928$; df = 1; p = .335) (Table 8). In addition, the correlation between sex and reproductive rate was not significant (Spearman correlation, r = -.098, p = .580) (Table 7). Thus, spectacled bear males and females do not differ in exhibiting copulatory behavior as adults and in the number of offspring they produce.

DISCUSSION

Both giant pandas and spectacled bears are under the threat of extinction in the wild (IUCN 2001), and a self-sustaining captive population needs to be established for both species. However, the captive birthrates for both species are not optimal (Rosenthal, 1999; Zheng et al., 1997), and factors causing reproductive failures are not yet clear. Previous studies on many other species revealed that early rearing and social experience was important for reproductive success in later adulthood (Arling & Harlow, 1967; Beck & Power, 1998; King & Mellen, 1994; Mason, 1963; Simpson, 1978), while little to no research has been conducted on giant pandas and spectacled bears to examine the relationship between early rearing experience and adult reproductive behavior. Therefore, the purpose of the present study was to investigate how the early rearing and social experiences affect the reproductive behavior of giant pandas and spectacled bears as adults.

We first hypothesized that the duration of mother rearing would be positively correlated with reproductive success for both the giant pandas and the spectacled bears. However, the data did not provide support for this hypothesis. For the spectacled bears, no relationship was found between the duration of mother rearing and reproductive success. Given that most of the spectacled bear subjects had stayed with their mothers for at least one year or longer, which is the typical length that wild spectacled bear mothers raise their cubs (Peyton, 1999), it is not surprising that the majority of the subjects have successfully copulated as adults and produced offspring. In other words, zoos housing spectacled bears generally allow the cubs to stay with mothers for an adequate among of

time, which may have greatly enhanced their reproductive success. In fact, our feedback from zoo staff suggested that spectacled bears bred very well in captivity, and the suboptimal number of births in the past 10-15 years have been due to a lack of space rather than reproductive deficiency (personal communication). Thus, the failure of detecting a relationship between duration of mother rearing and reproductive success is likely to be due to the lack of variance in the data.

For the giant pandas, we also found no effect of duration of mother rearing on adult reproductive behavior. That is, subjects that remained with their mothers for different durations did not differ in the likelihood of displaying copulatory behavior as adults. Our data suggest that a large number of the wild-born subjects, whose duration of mother rearing was estimated to be the highest 18 months, had never copulated. According to staff at institutions housing the animals, some wild-born giant pandas were rescued and captured as adults due to illness or injury in the wild. Although these animals were assumed to have stayed with their mothers for a species-typical length of time (18 months), their traumatic experiences might have impacted their later reproductive behavior in captivity. For example, some wild-born animals that were captured as adults displayed extreme timidity toward other animals, which appeared to be a factor that contributed to copulation failures. Thus, the varied backgrounds of wild-born animals might have confounded our analyses. To eliminate the potential confounds brought in by wild-born animals, we analyzed data from captive-born animals separately. However, no significant effect of rearing experience was found among captive-born animals either.

Although previous research on social animals such as nonhuman primates have demonstrated profound effects of early rearing experience on later reproductive success

(Arling & Harlow, 1967; Beck & Power, 1988; King & Mellen, 1994; Mason, 1963, Mitchell & Clark, 1968; Simpson, 1978), research on solitary animals have shown mixed results. Mellen (1992) demonstrated the differences between sexual behavior of mother-reared, human-reared with sibling, and human-reared alone female domestic cats. However, she did not find a relationship between early rearing experience and reproductive success using 20 species of small captive exotic felids (Mellen, 1991). Again, mixed results were found in Rosenblatt's (1965) study on male cats. Two male cats were isolated at birth, and four were isolated at two-months old. At 15 months of age, all six subjects were tested for mating behavior. The two birth isolates showed reduced sexual activity (i.e., it took them longer time to initiate mating, and they mated for shorter amount of time). Two of the four males that were isolated at two months failed to show mating behavior completely, the other two males exhibit quite normal mating behavior. This study appeared to demonstrate the possibility of individual differences on the animals' reactions to early social isolation. Wielebnowski (1999) studied the behavioral attributes of the solitary captive cheetahs as predictors of reproductive competence. No significant difference was found between behavioral component scores of hand-reared and mother-reared cheetahs. These findings along with results from the current study suggest that the relationship between early rearing experience and reproductive success of solitary animals may not be as remarkable as it is in social animals.

We also hypothesized that animals housed with at least one conspecific within the one-year period following maternal separation would reproduce better than animals that were housed alone. Beck and Power's (1988) gorilla study showed that captive-born

females that had first-year social access to conspecifics were significantly more likely to conceive than females that did not have first-year social access. However, the differences in the likelihood of copulation and giving birth were not significant between the two groups. Mellen (1992) studied the effect of housing condition on reproductive behavior, and found that the human-raised with sibling female cats were intermediate in exhibiting sexual behavior when compared to the human-raised alone and mother-raised with sibling cats. Mellen (1992) stated that human-raised with sibling females were better able to adjust to the environment than the human-raised alone females. However, findings of the present study did not show a significant difference between reproductive success of giant panda subjects that were housed with or without conspecifics. For the spectacled bears, although a trend was found that animals housed with peers were more likely to copulate than animals housed alone, this could be due to sampling error because the sample size was small.

In the present study, one captive-born giant panda female (Studbook# 425) that was removed from mother permanently within the first day after birth and was housed alone for the subsequent year successfully copulated in 2 different years, and reproduced two living offspring by age 9. Another female (Studbook# 314) that was removed from mother at one month of age and was housed alone afterwards copulated in 3 different years, and produced 6 living offspring by age 18. In addition, the majority (70%) of subjects that remained with mother for 4-6 months, which was the typical length that cubs were kept with mothers in Chinese zoos, had reproduced regardless of their social access following maternal separation. Thus, prolonged duration of mother rearing and social access do not appear to be the absolute requirement for successful reproduction.

However, the lower percentage (25%) of reproductive success in the 1-4 months mother rearing group may suggest that less than 4 months of mother rearing would impair the giant panda's reproductive competence. It should be noted that sample size for the 1-4 months group was small (4 subjects); therefore, conclusion should be drawn with caution.

Although results of the present study suggest that, under the current captive management protocol (i.e., remove cubs from mothers at 4-6 months of age), giant pandas could reproduce fairly well, it does not mean that longer duration of mother rearing would not further improve the giant panda's reproductive success. For example, captive giant pandas in general start to breed at a later age than their wild counterparts (Snyder et al., in press). The reason for delayed initiation of breeding is unknown. In our study, one captive-born male (studbook# 467) that had remained with mother for 13 months successfully copulated at age 6. In contrast, for the rest of males that stayed with mother for shorter period of time (i.e., between 3-8 months) and had copulated, their first time copulation occurred at 11 years old on average. This difference suggest that longer duration of mother rearing helps to lower the age at which the animal first copulate. Therefore, we should continue to expand the sample size in the 12 months or above mother rearing group, and compare their reproductive behavior with animals of similar ages but stayed with mother for shorter period of time to see if subjects in the long duration group start to breed earlier and breed more successfully.

Hediger (1965) pointed out that reproductive success is the result of a complex combination of biological elements, and that this combination is specific for different species. While early social and rearing experience may be the determining element for reproductive success of social animals such as nonhuman primates, for the solitary giant

pandas, there may be elements in addition to early experience that play important roles in determining reproductive success. For example, Lindburg and colleagues (1997) reported that wild-born males captured as adults may exhibit motivational deficiency in copulation. This indicates that even adequate mother rearing under natural circumstances does not guarantee reproductive success. Rather, early rearing experience may interact with other factors in determining reproductive success.

One potential cause for reproductive failure in giant panda may be abnormal hormonal processes. As mentioned previously, the major problems that hinder captive males' reproductive success include lacking sexual interest in estrus females (Lindburg et al, 1997; Zheng et al, 1997), asynchronous libido with female reproductive cycle (Wang et al., 1993), and being too aggressive toward potential mates (Lindburg, et al, 1997; Zheng et al, 1997). Meanwhile, quite a few captive females do not let out fertile ovum during estrous (Wang et al., 1993). These behavioral and physiological problems may be related to hormonal abnormality.

Another important element for insuring reproductive success is physical health. In captivity, the giant panda is subject to various digestive, respiratory, neurological, circulatory, and kidney diseases (Hu, 2001; Wang et al, 1993). Moreover, seven species of entozoic and 16 species of ectozoic parasites have been found in the giant pandas (Hu, 2001). In many cases, the animals were never paired with potential mates due to poor health (Lindburg, et al, 1997).

Third, chemical communication appears to play an important role in giant panda reproduction. Swaisgood and colleagues (2000) studied giant pandas discrimination of conspecific odors. They found that males showed a greater preference for female odors

than male odors, and responded more to estrus than anoestrus female odors. They also found that anoestrus females licked more and estrus females vocalized more when encountering male than female odors. They suggested that the low natural mating observed in captive giant pandas might be attributed in part to the failure of providing sufficient opportunities for chemical communication.

Fourth, the giant pandas are very particular about their sexual partners (Feng & Li, 2000; Wang, et al., 1993). There have been many incidents that when given access to multiple sexually competent and experienced mates, the giant panda chose to mate with some individuals but not others (Feng & Li, 2000). After intense study on the pair of giant pandas at the National Zoo, Kleiman (1983) suggested that the prior compatibility with partner before paring is essential for successful copulation.

Fifth, the presence of sexual rivals may play a role in displaying successful sexual behavior, especially for giant panda males. It has been observed by numerous researchers in the wild that during breeding season, several male giant pandas gather around one estrous female, and compete for the opportunities to mate with the female (Domico, 1988; Hu, 2001; Schaller et al, 1985). In captivity, sexual competition is generally absent; males never have to fight for breeding access. Lindburg and colleagues (1997) studied the sexual performance of captive giant panda males and found that all the breeding males in their sample have had at least one other male in adjoining enclosures. This may indicate that the presence of sexual rival stimulates sexual drive and is a positive factor for the reproductive success of male giant pandas.

Finally, the appropriate physical captive environment is the bottom line for reproductive success. In the wild, giant panda remain active for more than 12 hours daily,

foraging and roaming in a relatively large area full of environmental stimuli (Hu, 2001; Schaller et al, 1985). In comparison, captive environments provide limited space, and lack complexity and novelty, which may compromise the animals' physical and psychological well-being (Swaisgood et al., 2001), and hence affect their reproductive performance. Swaisgood and colleagues (2001) demonstrated that environmental enrichment significantly improved the giant panda subjects' activity levels and the complexity of their behaviors. It also reduced stereotypic behaviors among the subjects. The relationship between reproductive success and psychological well-being remains unexplored.

Future research should consider examining the effect of above factors on reproductive success in depth. In addition, during the past few years, captive giant panda breeding has been improved, and the number of animals, especially males that successfully copulated has increased. This indicates that some aspect of the captive conditions must have changed. Thus, future study should evaluate and compare various aspects of captive environment across different time to examine changes that are possibly associated with the improvement of captive breeding.

APPENDIX A

Questionnaire on the Giant Panda/Spectacled Bear Rearing and Breeding History

1 Studbook # _____ 2 Name _____ 3 Sex _____4 Date of Birth _____

5 Current location _____ 6 Time transferred between locations _____

7 Captive born or wild born? _____ If wild born, estimated age at capture _____

8 Age at permanent separation from mother? (In days or weeks) _____

9 Was this animal housed in the same enclosure with other animals in the one-year period following the permanent separation from its mother? Yes _____ No _____

If yes, please list the sexes and approximate ages of other bears this animal was housed with each year.

1990	1991	1992	1993	1994	1995	1996	1997

10 Has this animal ever copulated? Yes _____ No _____

11 Please rate the strength of this animal's estrous behavior for each year. If you don't know because this animal was at a different institution that year, write NA = not applicable. 0 = no estrous; 1 = weak; 2 = moderate; 3 = strong

2002	2001	2000	1999	1998	1997	1996	1995	1994	1993

12 Please indicate by writing "yes" or "no" if this animal was given access to an opposite sex animal during estrus and if this animal had successfully copulated. If yes, list the other animal's studbook number. If the animal had the opportunity to mate, but copulation didn't occur or wasn't successful, please indicate what were the reasons that

might account for the copulation failure. For example, 1 = being timid toward the other animal; 2 = being aggressive toward the other animal; 3 = having no sexual interest in the other animal; 4 = incorrect mating postures. If there were other reasons, please briefly describe. If you don't know because this animal was at a different institution that year, write NA = not applicable.

Year	2001	2000	1999	1998	1997
Was introduced to another animal?					
Successfully copulated?					
Studbook # of the other animal					
Reasons for copulation failure					

13 Please list the breeding information of the animal for each year.

Offspring studbook #	Date of birth	Sex	Alive/dead	Natural mate/AI	How long had the focal animal nursed her offspring (days or weeks) (Skip this category if the focal is a male)

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