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The Influence of Activity Space on the Behavior of Giant Pandas (*Ailuropoda melanoleuca*) in Captivity

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Abstract: We studied the impact of activity space on the estrous behaviors of 11 healthy adult female and 3 adult male giant pandas with natural mating ability from the Beijing, Lanzhou, and Chengdu Zoos, and the Chengdu Giant Panda Breeding Center during their non-mating and mating seasons from November of 1999 to May of 2003. We compared the frequencies of estrous behavior and activities of giant pandas that were kept in activity spaces of various sizes during their estrous period. We found that the frequency of estrous behavior and other activities of the female and male giant pandas kept in a large activity space were significantly higher than those of the pandas kept in small pens ($P < 0.05$). When the giant pandas were kept in small pens (< 12 m^2), estrous behavior occurred less frequently. Once the captive giant pandas were released into a larger playground (> 200 m^2), their estrous behaviors were expressed at higher frequencies. If the giant pandas were again confined in small pens, the frequency of their estrous behaviors would decrease. This reversibility of estrous behavior of the giant pandas proved that a small activity space suppressed the estrous behavior of giant pandas in captivity and that the elasticity of their estrous behavior was great. Therefore, providing larger activity spaces to giant pandas in captivity will enable them to fully express their behaviors, especially estrous behavior.

Key Words: Giant panda (*Ailuropoda melanoleuca*), activity space, behavioral elasticity, behavioral rigidity, estrous behavior

Introduction

Conservation of giant pandas relies on both in situ and ex situ strategies. A natural reserve network for preserving the habitat of giant pandas has been established in China. At the same time, propagation of giant pandas is conducted in breeding centers and zoos. Several recent publications report an increase in natural mating and reproduction in captive pandas (Zhang et al., 1994, 1996, 2004; Swaisgood et al., 2003); however, it remains difficult to breed giant pandas in captivity (Hu, 1988; Schaller, 1993; Lindburg et al., 1997; Peng et al., 2001a, 2001b; Peng et al., 2006). Thus, determining how to enhance the mating success of giant pandas in captivity is the most important problem to be solved in order to establish a self-sustaining giant panda population in captivity. To that end, it is necessary to study the factors that affect the estrous behavior of giant pandas.

Over the past 20 years, research and conservation biology has become more important to zoos since it became clear that zoos are the places for the long-term management of many endangered species, rather than places for the short-term exhibition of exotic species (Hardy and Krackow, 1995; Wilson et al., 2003). Most of the research on giant pandas that is carried out in zoos is applied research (Masui et al., 1989; Chen et al., 1994; Mainka and Zhang, 1994; Zhang et al., 1994; Dierenfeld et al., 1995; Zhang et al., 1996; Maple et al., 1997; Ding et al., 1998; Wilson et al., 2003).

Modern zoos have been rearing pandas in captivity since 1936 (Hu, 1997). *Ex situ* conservation becomes an

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important way to preserve endangered species (Seal, 1988). An endangered species can be preserved in captivity for a long time, but *ex situ* conservation requires knowledge of the relationship between an animal's behaviors and elements of captivity, such as activity space. As researchers began to notice the effect of the captive environment on wildlife in captivity, the impact of captivity on wildlife became a topic of interest and study (Carlstead, 1996; Maple et al., 1997; Jiang, 1999, 2000; Wilson et al., 2003). The amount of space available (space size) for breeding wildlife in captivity is limited in many places throughout the world. Giant pandas are confined in dull and dank pens that are no more than 12 m^2 in most Chinese zoos, and daily activity spaces for those pandas are limited (Figure). Some zoos and breeding centers provide large playgrounds (> 200 m^2) for giant pandas, but 2-3 pandas share the same playground on alternate days. Thus, a giant panda goes out to the playground once every 2-3 days. Yet, the home range of a giant panda in the wild is very large: for a female giant panda, about 4-5 km^2; for a male giant panda, about 6-7 km^2 (Schaller et al., 1985; Hu, 1990).

Hu et al. (1985) observed and studied the estrous and mating behaviors of giant pandas in the field, and Ye (1984) and Gao et al. (1994) reported the sex behavior and contact modes of giant pandas in captivity during their estrous period. We observed mate choosing behavior of male and female giant pandas during their mating period (Peng et al., 2006). Several other studies of behavior and reproduction of captive giant pandas have also been reported (Kleiman et al., 1979; Kleiman, 1983, 1985; Liu et al., 1998), but most scholars have focused on the relationship between physiology and estrous behavior of the female giant panda by monitoring the estrous cycle and receptivity of the female panda according to the profiles of sex hormones in urine and blood (Bonney et al., 1982; Hodges et al., 1984; Zeng et al., 1984, 1990, 1994; Li et al., 1993; Chaudhuri et al., 1988; Lindburg et al., 2001; Snyder et al., 2004). Several good papers reported the effects of enclosure conditions on estrous behavior of captive giant pandas (Maple et al., 1997; Swaisgood et al., 2001; Wilson et al., 2003; Liu et al., 2003); however, the relationship between activity space and estrous behavior of giant pandas needs further study. In this report, we describe the results of 4 years of exploring whether the size of available activity space affects the estrous behavior of giant pandas.

Materials and Methods

We observed the behavior and activity status of 11 adult female and 3 male giant pandas during their non-mating and mating seasons from November 1999 to May 2003. These animals were from the Beijing, Lanzhou, and Chengdu Zoos, and the Chengdu Giant Panda Breeding Center. All the pandas were healthy and their reproductive histories prior to the study are listed in Table 1.

Figure. Giant pandas are confined in dull and dank pens that are no more than 12 m^2 in most Chinese zoos, and daily activity spaces for those pandas are limited.

Table 1. Background information on the giant pandas in the study.

Name	Studbook number	Sex	Birth date (MM/DD/YY)	Origin	Location	Reproduction history before the study
Le Le	320	Female	9/8/1986	Captive born	Beijing Zoo	Gave birth to 7 cubs (3 twins) by natural mating and artificial insemination.
Ying Ying	369	Male	8/15/1991	Captive born	Beijing Zoo	Had a record of natural copulation last year.
You You	345	Male	6/23/1988	Captive born	Beijing Zoo	Has estrus every year after sexual maturation, but never successfully mated with a female. His semen is artificially collected every year.
Ji Ni	403	Female	11/4/1993	Captive born	Beijing Zoo	Had her first estrus last year, naturally mated, but not pregnant. Had her second estrus this year.
Niu Niu	421	Female	9/5/1995	Captive born	Beijing Zoo	Had her first estrus last year, naturally mated, but not pregnant. Had her second estrus this year.
Qing Qing	278	Female	9/9/1984	Captive born	Chengdu Zoo	Gave birth to 8 cubs (2 twins) by natural mating or artificial insemination.
Ha Lan	287	Male	8/1984	Wild born	Chengdu Zoo	Fathered 7 cubs (3 twins) by natural mating or artificial insemination with his semen.
Cheng Cheng	297	Female	9/24/1985	Captive born	Chengdu Breeding Center	Gave birth to 5 cubs (1 set of twins) by natural mating or artificial insemination.
Bing Bing	314	Female	8/6/1986	Captive born	ChengduBreeding Center	Gave birth to 8 cubs (2 twins) by natural mating or artificial insemination.
Li Li	387	Female	9/3/1992	Captive born	Chengdu Breeding Center	Did not have estrus due to poor health. However, Li Li had her first estrus this year.
Er Yatou	401	Female	9/19/1993	Captive born	Chengdu Zoo	Gave birth to 1 set of twins by natural mating and artificial insemination last year.
Mei Mei	408	Female	8/31/1994	Captive born	Chengdu Breeding Center	Gave birth to 1 set of twins by natural mating and artificial insemination last year.
Jiao Zi	425	Female	8/21/1995	Captive born	Chengdu Breeding Center	Had her first estrus this year.
Shu Lan	407	Female	8/31/1994	Captive born	Lanzhou Zoo	Had her first estrus this year.

Non-mating season

During the non-mating seasons, from July to January, we recorded the frequency of behaviors, such as rubbing the anogenital region, bleating, shaking head, sniffing, tail raising, and urinating/defecating, and scan-sampled the activity status, such as movement, feeding, and resting of each panda in their own pens (< 12 m^2) or in a playground (> 200 m^2) at 10 min intervals from 08:00-11:00 on each day during the study period. In order to eliminate the impact of the scents of all the previous pandas on the studied panda, we cleaned up all the feces, urine, and odors in the playground. The playground was left unused to dry in the sun for 3-4 days. During the study period, we only let the studied panda use the playground.

We obtained the numerical frequencies of all behaviors, as well as the activity status that occurred in 10 min; subsequently, we statistically calculated the frequency of each behavior in 10 min, as well as the percent (%) of activity status. These data from pens were regarded as control data and data from playgrounds were regarded as experimental data.

Mating season

Giant pandas are mono-estrous animals that often have an estrous and mate between the end of February and early May. During their mating seasons, we first observed the giant pandas in their own pens (< 12 m^2). We used the same method as in the non-mating seasons to record their frequencies of behaviors and scan-sampled their activity status. These data were regarded as control data. Subsequently, we released the pandas into playgrounds (> 200 m^2). We also scanned-sampled their activity status in the playgrounds and recorded their estrous behavior at 10 min intervals from 0800 to1100.

We compared the difference in the frequency of estrous behavior and activity status of the male and female pandas in small pens and in large playgrounds during non-mating and mating seasons with Friedman's two-way ANOVA. If the difference was statistically significant, we then compared the difference between the behaviors in pens and playgrounds with Wilcoxon signed-rank test.

Results

We scanned 1728 times for each behavior and activity status of each of the 14 studied giant pandas during 4 years of study.

Estrous Behavior

For male

Male anogenital rubbing significantly increased from the non-mating season to the mating season (Friedman's two-way ANOVA: $P < 0.05$, Table 2), regardless of available space, but was statistically significantly higher in the playground (larger space) than in the pen (small space) during both the non-mating and mating seasons (Wilcoxon signed-rank test: $P < 0.05$, Table 2), and the difference during the mating season was statistically great (Wilcoxon signed-rank test: $P < 0.01$, Table 2).

Table 2. Male Giant Pandas: Significant differences in behavior as well as activity status between confinement in pens and in playgrounds during non-mating and mating seasons.

		Non-mating Season		Mating Season		Friedman two-way ANOVA
		Pen (< 12 m^2)	Playground (> 200 m^2)	Pen (< 12 m^2)	Playground (> 200 m^2)	
Behavior (times/10 min)	Rubbing anogenital	0.44 ± 0.18	0.68 ± 0.24 *	1.33 ± 0.32	2.12 ± 0.38 * *	★
	Bleating	0.52 ± 0.21	0.88 ± 0.34 *	21.6 ± 3.40	33.2 ± 7.20 * *	★
	Head shaking	0.38 ± 0.15	0.61 ± 0.23 *	12.12 ± 2.0	17.10 ± 2.54 * *	★
	Sniffing	0.73 ± 0.27	1.07 ± 0.41 *	2.12 ± 0.62	4.46 ± 0.96 * *	★
	Urinating/defecating	0.25 ± 0.10	0.38 ± 0.14 *	0.81 ± 0.19	1.58 ± 0.32 * *	★
Activity Status (%)	Movement (%)	22.4 ± 4.1	34.6 ± 5.8 *	51.1 ± 8.8	68.9 ± 9.4 * *	★
	Feeding (%)	28.6 ± 4.5	24.6 ± 3.9 *	18.5 ± 3.8	13.1 ± 2.8 * *	★
	Resting (%)	49.0 ± 8.2	40.8 ± 6.8 *	30.4 ± 5.2	18.0 ± 3.6 * *	★
Wilcoxon signed-rank test		*(P < 0.05)		**(P < 0.01)		

Notes: (1) Data are presented as mean ± standard deviation.
(2) "★" denotes a significant difference between the behavioral frequencies
(times/10 min) as well as activity status (%) of male giant pandas during non-mating and mating seasons (Friedman two-way ANOVA: $P < 0.05$).
(3) "*" or "**" denotes a significant difference between the behavioral frequencies (times/10 min) as well as activity status (%) of male giant pandas in pens and in playgrounds (Wilcoxon signed-rank test: "*": $P < 0.05$; "**": $P < 0.01$).

The same was true for bleating vocalizations, head shaking, sniffing, and urinating/defecating, which increased dramatically from the non-mating season to the mating season (Friedman's two-way ANOVA: $P < 0.05$, Table 2). All these other estrous behaviors occurred at frequencies that were statistically significantly higher in the playground (larger space) than that in the pen (small space), during both the non-mating and mating seasons (Wilcoxon signed-rank test: $P < 0.05$, Table 2), and the difference during mating season was statistically great (Wilcoxon signed-rank test: $P < 0.01$, Table 2).

Thus, all these estrous behaviors could be used as good indicators of reproductive status of male giant pandas during the mating season.

For female

The females hardly ever raised their tails during the non-mating season, but the frequency of tail raising significantly increased during the mating season (Friedman's two-way ANOVA: $P < 0.05$, Table 3).

Moreover, the frequency of female anogenital rubbing, bleating vocalizations, shaking head, sniffing, and urinating/defecating significantly increased from the non-mating season to the mating season (Friedman's two-way ANOVA: $P < 0.05$, Table 3). All these estrous behaviors occurred at frequencies that were statistically significantly higher in the playground (larger space) than that in the pen (small space), during both the non-mating and mating seasons (Wilcoxon signed-rank test: $P < 0.05$, Table 3), and the difference during the mating season was statistically great (Wilcoxon signed-rank test: $P < 0.01$, Table 3).

Thus, all these estrous behaviors can also be used as good indicators of reproductive status of female giant pandas during the mating season. Tail raising is an especially excellent indicator that a female giant panda is in estrous and could be ready to mate.

Activity Status

For male

The movement frequency of the males significantly increased from the non-mating season to the mating season (Friedman two-way ANOVA: $P < 0.05$, Table 2), regardless of available space, but was statistically

Table 3. Female Giant Pandas: Significant differences in behavior as well as activity status between confinement in pens and in playgrounds during non-mating and mating seasons.

		Non-mating Season		Mating Season		Friedman two-way ANOVA
		Pen (< 12 m^2)	Playground (> 200 m^2)	Pen (< 12 m^2)	Playground (> 200 m^2)	
Behavior (times/10 min)	Rubbing anogenital	0.12 ± 0.05	0.20 ± 0.07 *	1.63 ± 0.35	2.68 ± 0.52 * *	★
	Bleating	0.14 ± 0.08	0.23 ± 0.08 *	19.6 ± 2.80	30.21 ± 4.10 * *	★
	Head shaking	0.18 ± 0.09	0.28 ± 0.12 *	10.2 ± 1.87	15.82 ± 2.20 * *	★
	Sniffing	0.32 ± 0.14	0.46 ± 0.18 *	1.82 ± 0.51	3.04 ± 0.72 * *	★
	Tail raising	0	0	0.21 ± 0.04	0.30 ± 0.08 *	★
	Urinating/defecating	0.08 ± 0.03	0.12 ± 0.05 *	0.33 ± 0.06	0.62 ± 0.18 * *	★
Activity Status (%)	Movement (%)	21.1 ± 4.0	35.2 ± 5.6 *	49.2 ± 8.3	68.0 ± 9.3 * *	★
	Feeding (%)	27.8 ± 4.8	23.4 ± 4.2 *	19.3 ± 3.90	12.8 ± 2.8 * *	★
	Resting (%)	52.1 ± 8.9	41.4 ± 6.2 *	31.5 ± 5.3	19.2 ± 3.9 * *	★
Wilcoxon signed-rank test		* (P < 0.05)		* * (P < 0.01)		

Notes: (1) Data are presented as mean ± standard deviation.
(2) "★" denotes a significant difference between the behavioral frequencies (times/10 min) as well as activity status (%) of female giant pandas during non-mating and mating seasons (Friedman two-way ANOVA: $P < 0.05$).
(3) "*" or "**" denotes a significant difference between the behavioral frequencies (times/10 min) as well as activity status (%) of female giant pandas kept in pens and in playgrounds (Wilcoxon signed-rank test: "*": $P < 0.05$; "**": $P < 0.01$).

significant higher in the playground (larger space) than that in the pen (small space), during both the non-mating and mating seasons (Wilcoxon signed-rank test: $P < 0.05$, Table 2), and the difference during the mating season was statistically great (Wilcoxon signed-rank test: $P < 0.01$, Table 2). However, the frequencies of male feeding and resting significantly decreased from the non-mating to the mating season (Friedman's two-way ANOVA: $P < 0.05$, Table 2), regardless of available space, but was statistically significantly lower in the playground (larger space) than that in the pen (small space), during both the non-mating and mating seasons (Wilcoxon signed-rank test: $P < 0.05$, Table 2), and the difference during the mating season was statistically great (Wilcoxon signed-rank test: $P < 0.01$, Table 2).

For female

The movement frequency of the females also significantly increased, whereas the frequencies of feeding and resting significantly decreased from the non-mating to the mating season (Friedman's two-way ANOVA: $P < 0.05$, Table 3), regardless of available space, but the movement was statistically significantly higher, and feeding and resting were statistically significantly lower in the playground (larger space) than that in the pen (small space), during both the non-mating and mating seasons (Wilcoxon signed-rank test: $P < 0.05$, Table 2), and the difference during the mating season was statistically great (Wilcoxon signed-rank test: $P < 0.01$, Table 2).

General Results

In a word, the increase of movement and the decrease of feeding and resting indicated that the males and females spent more time expressing estrous behavior and trying to find a mate during the mating season, and the frequencies of behaviors and movement significantly increased in the larger space. This result indicated that the size of activity space significantly influenced the behaviors and other activities of these pandas, during both the non-mating and mating seasons.

Discussion and Conclusion

The full expression of behavior requires resources, such as energy, time, and space. When energy, time, or living space of an individual animal is limited, some behaviors are still expressed, while others are not. Thus, those behaviors that can still be expressed have high rigidity, but low elasticity (Jiang, 1999). An animal will first use its available metabolic energy to satisfy its survival needs and then its reproductive needs. When the activity space for survival is limited, an animal will ensure its survival needs first, engaging in behaviors such as feeding, elimination, and rest, prior to satisfying reproductive needs. However, such behaviors as estrous and social behavior require more space for their expression. Since an animal will first fulfill its survival needs with available resources and then fulfill reproductive needs, inadequate space may be why giant pandas are difficult to mate in captivity.

Some scholars have observed and reported the estrous and mating behaviors of giant pandas in the wild and in captivity (Ye, 1984; Hu et al., 1985; Gao et al., 1994; Peng et al., 2006); however, to date, the effect of activity space on the behaviors has not been reported. To the best of our knowledge, we report the change in frequency of estrous behavior in different sizes of activity space for the first time.

When the giant pandas were confined in pens, because the activity space was < 12 m^2, estrous behavior was restrained by the available activity space. Once the giant pandas were put into larger activity spaces, such as a playground > 200 m^2, their estrous behaviors were expressed with greater frequency. If the giant pandas were again confined in pens after being in the playgrounds, the frequency of their estrous behaviors were again reduced. This reversibility of estrous behavior in captive giant pandas indicated that activity space affected the expression of estrous behavior in giant pandas in captivity. Thus, providing capacious space for giant pandas in captivity might help to enrich their behaviors, including estrous behavior. Activity space for each giant panda should be > 200 m^2, the larger the better, which will ensure that each panda can perfectly express its behavior; however, most captive pandas are confined in small and dank pens in most zoos, so that their daily activity is limited and the expression of estrous behavior is restrained.

Behavior is a reaction of an animal to its environment. The behaviors of any wildlife species are the result of long-term natural selection and adaptation to special environments (Carlstead, 1996). Animals often cannot fully express the same behaviors in captivity as those in the wild. With the development of the theory and practice of ex situ conservation, people are recognizing the importance of environmental diversity to animals.

Behavioral diversity is a part of biological diversity. Animals raised in captivity usually only express behaviors of high rigidity because they often lack the space to express more flexible behaviors and lack behavioral models. Many behaviors of high elasticity are lost and the behavioral diversity of captive animals declines. For endangered species like the giant panda, we should fully maintain their behavioral diversity when conserving in breeding centers and ensure the development of their individual behavior. Wildlife in natural environments need behavioral flexibility, which may be lost in captivity. When field-release is a goal of captive breeding of the giant pandas, we must be particularly concerned with providing a large enough space, similar to the wild environment, so as to ensure they can fully express their natural behavior and maintain their normal survival ability after they are reintroduced into the wild.

Captive breeding is one of the ways to ex situ conserve endangered species. Even though endangered animals should not be confined and bred in captivity forever (Campbell, 1980), an endangered species can survive in captivity for a long time on the precondition that the biological and behavioral characteristics of the species are comprehensively understood. In general, biologists usually pay more attention to the nutrition and reproduction of captive animals than the full expression of normal behaviors. A successful ex situ conservation project would also require an appreciation for the relationship between the behavior of an individual animal and activity space, so that we can enact correct conservation policy. Now, more and more biologists are paying attention to the behaviors of animals in captivity and are starting to emphasize the importance of space and environmental factors in the expression of the behavior of these animals (Seidensticker and Doherty, 1996). To understand the development of behavior and the behavioral differences between captive pandas and those in the wild, as well as to gradually restore behaviors of high elasticity that have been restrained or lost in captivity, are goals that will enable the giant panda population to survive longer in captivity. Finally, such knowledge and experience will also help to reintroduce captive-bred giant pandas to their natural environment.

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