Mate choice in giant panda (*Ailuropoda melanoleuca*)

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ABSTRACT. Giant pandas are difficult to breed in captivity due to low oestrus and mating rate, high cub mortality and diseases. Thus, improving the mating success of giant pandas in captivity is an important conservation issue. After observations on eleven female and three male giant pandas from Beijing Zoo, Lanzhou Zoo, Chengdu Zoo and Giant Panda Breeding Center during their mating season in 2000~2001, we found that mate choice plays an important role in mating success. Both male and female pandas actively chose their mates. Successful copulation only occurred in those males and females that both showed high frequencies of courting behaviour towards the opposite sex. Of those cases that only a male or female showed one-sided high or low frequency of courting behaviour in the keeper-arranged panda pairs in random order, no copulation was observed. Only three out of twenty-four paired pandas successfully copulated. All three impregnated female pandas in this study bore cubs. This indicated that mating choice was one of the important factors resulting in unsuccessful copulation and failure to reproduce. We recommend that attention be paid to the mate choice in giant panda when breeding pandas in pens are paired for reproduction in the future.

KEY WORDS: giant panda (*Ailuropoda melanoleuca*), mate choice, natural mating, courting frequency, survival fitness

INTRODUCTION

It is difficult to breed the giant panda in captivity due to their low reproduction rate, high cub mortality rate and diseases (Hu, 1988; Peng et al., 2001a; b). Up to September 1, 1997, 454 giant pandas had been maintained in captivity in the world. Among them were 152 males, 210 females, and 92 of unknown sex (cubs that died before their sex was identified) (Xie & Gipps, 1997). However, only 34 (12 males, 22 females) of those pandas ever produced offspring by natural mating or artificial insemination (Xie & Gipps, 1997; Huang et al., 1999). Currently, there are only six adult male giant pandas kept in captivity, five wild born and one born in captivity that can naturally copulate with adult female pandas (Lindburg et al., 1997; Huang et al., 1999). Moreover, to date only one adult male and six females born in captivity have successfully produced offspring (Xie & Gipps, 1997). How to improve the mating success of giant pandas in captivity, especially of male pandas, is an important conservation issue. We therefore needed to study the reproductive biology, and especially the reproductive behaviour of pandas, because the main reason for failed reproduction in pens is the Jack of successful courting and copulation. So, we studied the courting behaviour and mating success of the arranged pairing in giant pandas from Beijing Zoo, Lanzhou Zoo, Chengdu Zoo and Chengdu Giant Panda Breeding Center during their mating season in 2000~2001.

MATERIALS AND METHODS

We observed the courting frequencies of eleven adult females and three adult males. All observed giant pandas were healthy and 10 of 14 had mated naturally in a previous breeding season (Table 1). In order to increase the genetic variability of giant pandas in captivity and avoid inbreeding, two adult female pandas (Stud# 403 and 421) from Beijing Zoo and one female panda (Stud# 407) from Lanzhou Zoo were transported to Chengdu Zoo, and two adult male pandas (Stud# 369 and 345) from Beijing Zoo were transported to Chengdu at the end of February in 2000 and 2001. Male and female panda were paired by the keepers according to studbook, origin and birth location to avoid inbreeding only when both were observed to present courting or rutting behaviour during their mating season. Twenty-four groups were paired in the study, identified as A, B, …, W, X (Table 2). We scanned each paired group as soon as they were paired every morning from 8:00 am to 11:00 am at 10-minute intervals from March 1st to April 30th in their brief breeding season in 2000-2001 and recorded the courting frequency of a male towards a female or a female towards a male.

TABLE 1

Reproductive records of the giant panda in the study.

Name	Stud #	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 oestrus every year after sexual maturation, but never successfully copulated with a female. His semen is artificially collected every year.
Ji Ni	403	Female	11/4/1993	Captive born	Beijing Zoo	Had her first oestrus last year, naturally mated but not pregnant. Had her second oestrus this year.
Niu Niu	421	Female	9/5/1995	Captive born	Beijing Zoo	Had her first oestrus last year, naturally mated but not pregnant. Had her second oestrus 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 twins) by natural mating or artificial insemination.
Bing Bing	314	Female	8/6/1986	Captive born	Chengdu-Breeding 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 oestrus due to poor health. However, Li Li had her first oestrus 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 oestrus this year.
Shu Lan	407	Female	8/31/1994	Captive born	Lanzhou Zoo	Had her first oestrus this year.

Courting behaviour in the study was defined as one or all of the following behaviours: (1) a panda approached a sexual partner forwardly, and presented estrous or rutting behaviours, such as shaking head, urinating/defecating, rubbing anogenital area etc.; (2) he or she bleated "Mie, Mie", stared at the partner, sniffed the urine, faeces and the scent mark left by the partner; (3) a panda tried to scratch the partner in order to attract his or her attention. A female was paired with a male if she firstly showed no signs of aggression towards the male partner, then she perhaps raised her hindquarters, erected her tail and showed the anogenital region to the male as he courted her, and she finally accepted his mounting. While the male mounted the female inserted his penis and thrust, both pandas bleated during the copulation, and the female vocalized quavery moans as the male ejaculated. If the male's penis entered the female panda's vagina and we later heard the high chirp cries of the female, we recorded the mating as a successful copulation.

If the pandas were paired and they started to bite and attack each other, or if the male or female showed little courting towards the other, or if they seldom approached each other in the pen and never copulated, the keeper finally separated the two pandas. Then, we recorded the pairing as a failed copulation.

We recorded the duration of the copulation, as well as mating success or failure during their copulation. Subsequently, we monitored whether the female pandas became pregnant and gave birth. We used the Mann-Whitney U test to check the difference between the courting behaviours of the male and female panda for each paired group separately. Kruskal-Wallis H tests were used to check the difference in mating and courting frequencies among the groups over all paired experiments.

TABLE 2

Observations (every 10-minute period during their pairing) on courting frequency and mating success in pandas paired by their keepers in random order according to Studbook and birth location to avoid inbreeding.

Group	Male Stud #	Female Stud #	Courting/10 min.		Date of mating (mm/dd/yy)	Copulation duration (min)	Parturition	Kruskal-Wallis H Test
			Male	Female				
A	287	314	0.48 ± 0.08^{h}	0.48 ± 0.08^{h}	3/11~13/00	2±1(2)	2 cubs	*
B	287	278	0.58 ± 0.10^{h}	0.56 ± 0.08^{h}	3/25~28/00	8±2(3)	1 cub	*
C	287	403	0.49 ± 0.09^{h}	0.17 ± 0.05^{l}	4/12~14/00	0	0	
D	287	421	0.48 ± 0.09^{h}	0.07 ± 0.05^{l}	4/10~12/00	0	0	
E	369	297	0.44 ± 0.07^{h}	0.09 ± 0.03^{l}	3/30~4/2/00	0	0	
F	369	407	0.18 ± 0.05^{l}	0.59 ± 0.09^{h}	4/06~08/00	0	0	
G	369	401	0.17 ± 0.04^{l}	0.17 ± 0.04^{l}	4/19~21/00	0	0	
H	345	408	0.14 ± 0.05^{l}	0.16 ± 0.04^{l}	4/12~14/00	0	0	
I	345	425	0.06 ± 0.03^{l}	0.04 ± 0.04^{l}	4/16~18/00	0	0	
J	345	387	0.04 ± 0.03^{l}	0.06 ± 0.03^{l}	4/06~08/00	0	0	
K	369	320	0.64 ± 0.10^{h}	0.58 ± 0.10^{h}	3/27~29/00	4±1(3)	2 cubs	*
L	345	320	0.19 ± 0.04^{l}	0.16 ± 0.05^{l}	4/01~03/00	0	0	
M	369	297	0.55 ± 0.11^{h}	0.12 ± 0.03^{l}	3/21~23/01	0	0	
N	345	297	0.48 ± 0.11^{h}	0.19 ± 0.06^{l}	3/25~28/01	0	0	
O	369	401	0.19 ± 0.04^{l}	0.21 ± 0.05^{l}	4/11~13/01	0	0	
P	345	408	0.21 ± 0.09^{l}	0.19 ± 0.06^{l}	4/16~18/01	0	0	
Q	369	408	0.12 ± 0.03^{l}	0.08 ± 0.04^{l}	4/20~22/01	0	0	
R	345	387	0.14 ± 0.04^{l}	0.18 ± 0.06^{l}	3/16~18/01	0	0	
S	287	403	0.36 ± 0.08^{h}	0.11 ± 0.04^{l}	3/29~4/2/01	0	0	
T	287	421	0.35 ± 0.09^{h}	0.09 ± 0.04^{l}	4/08~10/01	0	0	
U	287	407	0.27 ± 0.08^{l}	0.19 ± 0.06^{l}	4/17~20/01	0	0	
V	369	407	0.19 ± 0.07^{l}	0.52 ± 0.14^{h}	4/23~25/01	0	0	
W	369	425	0.06 ± 0.03^{l}	0.04 ± 0.04^{l}	4/26~28/01	0	0	
X	345	425	0.16 ± 0.03^{l}	0.25 ± 0.03^{l}	4/22~24/01	0	0	
						Copulation rate: 12.5%	Parturition rate: 100%	

Notes:

(1) Superscript *"h"* denotes *high* frequencies of courting, and superscript *"l"* denotes *low* frequencies of courting.

(2) *h-l* denotes significant differences in courting frequencies between male and female in the same paired group ($P<0.05$; Mann-Whitney U Test).

(3) *h-h* or *l-l* denotes no statistical differences between male and female in the same paired group ($P>0.05$; Mann-Whitney U Test).

(4) Number of matings is shown in the parentheses. "0" indicated the pandas failed to copulate and couldn't become pregnant.

(5) *" * "* denotes significant difference in mating and courting frequencies among the groups over all paired experiments. ($P<0.05$; Kruskal-Wallis H Test).

RESULTS

The courting frequencies of every male or female in each paired group were scanned 216 times. We found a significant difference of courting frequency between males towards females or females towards males ($P<0.05$; Table 2). This indicated that attitudes of males or females to the planned mate could be described as like or dislike. Further, we found that only when both male and female in a paired group showed high frequencies of courting behaviours towards each other did they successfully copulate. When the male and female in a paired group both showed low frequencies of courting behaviours or showed one-sided high or low frequencies of courting behaviours, they failed to copulate.

We noted three types of outcome: First, the male and female panda showed different frequencies of courting behaviour: either the male actively approached and courted the female, but the female ignored him and refused to copulate, or the female actively approached and courted the male but the male declined to mount the female. Second, both male and female showed equal but low frequencies of courting behaviour, they evaded each other and did not copulate. Third, both male and female showed high frequencies of courting behaviour and successfully copulated. Overall the rate of successful copulation was 12.5%. Because the females of all three pairs that successfully copulated became pregnant and bore cubs, the parturition rate was 100%.

Courting frequencies of both males and females in Groups A, B and K were significantly higher than those of other groups (Fig. 1). This indicated that both males and females in Groups A, B and K were interested in each other, and only they mated favourably and successfully. The males and females in other groups were either uninterested in each other, or exhibited one-sided interest only or failed to copulate.

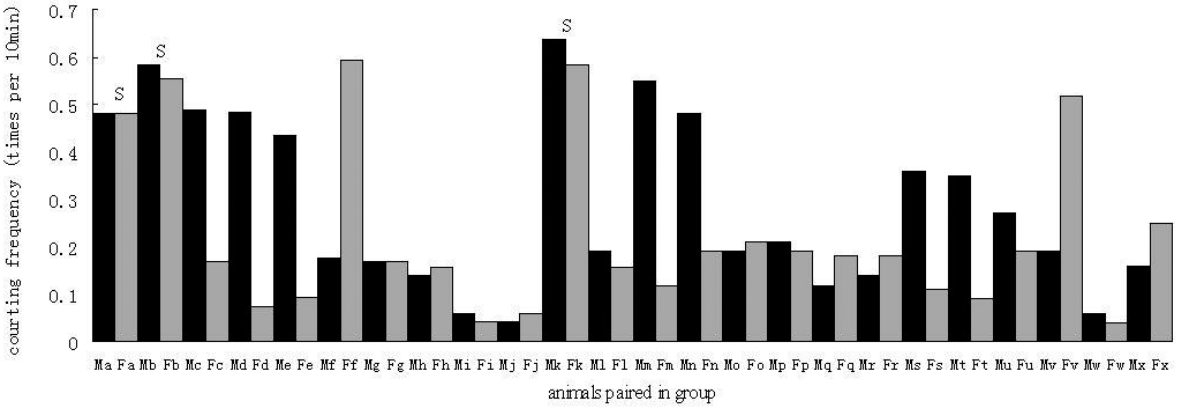

Fig. 1. – Frequencies of active courting of male or female giant pandas during their mating season (times/10min).

Notes:
(1) *"Ma"* (left dark column), *"Fa"* (right grey column) denotes frequencies of active courting of male or female respectively towards the opposite sex in Group A. Likewise, Mb, Fb for Group B, etc.
(2) *"S"* denotes male and female successful copulation and parturition.

DISCUSSION

How to improve the mating and breeding success of giant panda in captivity is a key issue in maintaining the genetic diversity and propagating captive panda populations. Aiming to achieve a high breeding rate in captive panda populations, the rational regime is that the panda keepers in zoos arrange the pairing of the male and female pandas in pens during the breeding season. However, the practice is never assessed even though the pandas in pens have a low mating success.

During the breeding season, giant pandas communicate information about their status of estrous and emotion to each other by olfactory, auditory, visual and touch signs (SCHALLER, 1993; HU, 1988). For example, they transfer the information of their estrous and emotional status to the opposite sex by defecating, urinating, scent-marking, bleating, courting and staring. If they are interested in the the opposite sex, then they will frequently court and show intimate behaviours, which can induce successful copulation. If they are not interested in the partner, they will show less courting behaviour and ignore them. When pandas in zoos were penned together, male or female pandas frequently approached, sniffed and courted their partner. Such courting behaviours pass breeding information and stimulate mating drive in their partners (HU, 1988; MEFFE & CARROLL, 1994; GAO & PU, 1994). When individuals of both sexes show a high frequency of courting behaviour, such a process may ultimately lead to mating.

Giant pandas primarily live solitarily and territorially during the non-breeding season in the field. Males and females seldom contact each other (HU et al., 1985; Hu, 1990a; 1990b). Only during breeding season do the giant pandas start to search for mates frequently. Males may gather and compete for mates. On one occasion, five males chased and mated with a female in turn in the Wolong natural reserve, thus, WANG (1987) thought that female pandas play a passive role in copulation. GAO & PU (1994) also thought the male giant pandas do not choose mates during the breeding season. They thought that mating success depends mainly on the number of healthy, sexually matured males in a population. However, in this study, we found out that male and female giant pandas have diverse behaviour. If only the male panda showed high courting behaviour to a female panda but the female panda had no or little response to the male's courting, then they would not copulate, or vice versa. Giant pandas appear to be selective towards their sexual partners, either male or female pandas refusing to mate with a sexually mature partner when he or she is not interested in courting. Only those, who show high corresponding courting behaviour towards each other will ultimately mate. Coordination between mates is essential for a successful mating (KLEIMAN, 1983). In this study, males or females all chose healthy partners with a mating history, which implies that inter-sexual selection is an important factor in the reproduction of giant panda. Moreover, HU (1990b) observed that one estrous female was actively courting one male but ignored the other males. He thought that not only mate competition but also mate choice occurred in giant pandas.

Active mate choice has been inferred from the observation that individuals visit several prospective mates but choose only one (or a subset) of them and reject the remaining ones (GIBSON & LANGEN, 1996). Most studies report that animals, over a wide taxonomic range, engage in a process of active choice while searching for mates (PARKER, 1983), including insects (MOORE, 1989), crustacea (BACKWELL & PASSMORE, 1996), fish (WARNER, 1995), frogs (RYAN, 1985), birds (GIBSON, 1996; FISKE &

KÅLÅS, 1995; RINTAMÄKI et al., 1995; DALE et al., 1990; PETRIE et al., 1991; BENSCH & HASSELQUIST, 1992; TRAIL & ADAMS, 1989) and mammals (BYERS et al., 1994). In our study, we also found that giant pandas actively choose their mates during their breeding season. Not only the females actively chose the males, but also the males actively chose the females. Finally, only those males and females who showed high frequencies of courting behaviour to each other mated.

Sexual selection has been a major focus of research in evolutionary biology since Darwin noted that mate choice confers an immediate advantage to preferred individuals. The origin of mate preferences remains controversial, and the operation of mate choice as a force independent of natural selection is still disputed (REAL, 1990). Whatever its origin, when certain potential mates are differentially attractive, those characteristics conferring the advantage increase in frequency within the population (REAL, 1990; 1991). Sexual selection depends on differential patterns of mate preference and choice. PARKER (1983) distinguishes three types of mate choice: (1) both sexes are non-discriminating in their choice of mates; (2) one sex is passive and non-discriminating, but the other sex engages in active choice; and (3) both sexes are discriminating and engage in active choice. The first two types are treated by traditional optimal-diet theory, and the third is modelled as an evolutionarily stable strategy (REAL, 1990; 1991). Giant panda may belong to the third type.

When both sexes choose their mates, low quality (less desirable) individuals should be less discriminating (GIBSON & LANGEN, 1996). Pandas in captivity have a limited number of mates to choose from and most pandas declined to copulate with mates they disliked. In our study, only three out of twenty-four paired pandas successfully copulated, the success rate being 12.5%. This indicates that mate choice was one of the important factors in unsuccessful copulation and failure of reproduction. We should pay attention to mate choice in giant panda when we pair breeding pandas in pens in the future. Moreover, only three mated female pandas in this study bore cubs, and all others failed. Generally, female pandas reproduce every 1.5~2.5 years after sexual maturity in the field, meaning that they only produce 6~8 litters throughout their lifetime (HU, 1988; 1990a).

Research and conservation biology have become much more important to zoos ever since it became clear that the zoo is a place for the long-term management of many endangered species rather than just a place for the short-term keeping of exotic exhibits (HARDY & KRACKOW, 1995). Most of the research carried out in zoos has therefore an "applied" focus towards these goals (ZHANG et al., 1996; DING et al., 1998; MASUI et al., 1989; ZHANG et al., 1994; MAINKA & ZHANG, 1994; CHEN et al., 1994; DIERENFELD et al., 1995). We should compare the behaviour of wild and captive pandas to reveal any differences in reproductive behaviour and try to enhance copulation rate in captivity. Unfortunately, this has rarely been done because of the difficulty of work in the wild. Zoos could thus be a useful yet under-used resource for behavioural research. However, only a small number of animals have been bred in captivity, thus small group size leads to small sample size for research. In our study, we only studied 24 groups of paired pandas because of limited availability of animals, and even the number of males was far less than that of females. So, it is necessary to make more male pandas become founders, or else, the shortage of reproductive males will increase the inbreeding probability and decrease the genetic diversity of the captive population.

Captive pandas have been separated into tens of very small populations in the world, some zoos even having only one or two pandas. Furthermore, all captive pandas seldom have the chance to meet and copulate, and around eighty percent of pandas in captivity never reproduced before they died (PENG et al., 2001a; b). So, we advise that all reproductive pandas in captivity should be gathered together to let them have their chances to choose their mates during the breeding season. This is required to ensure successful breeding for the limited number of pandas in captivity.

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