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Application of Behavioral Knowledge to Conservation in the Giant Panda

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Over the past several years we have developed a research program to increase knowledge of giant panda behavioral biology to facilitate efforts to reproduce giant pandas in captivity, particularly at the Wolong Breeding Center in Sichuan, China. Studies of estrus and reproductive behavior have enabled us to better pinpoint the timing of the fertile period and evaluate problems when a pair's behavior diverges from the norm. Experiments with chemosignals demonstrate that pandas possess a sophisticated chemical communication system, extracting information about the signaler's sex, reproductive status, age, social status, and individual identity, as well as the age of the chemosignal. The effects of scent on sexual motivation have important applications for captive breeding. Given the proper behavioral environment, most pandas now mate naturally at Wolong. Following observations documenting several behavioral problems, we developed an environmental enrichment program to reduce abnormal behaviors, encourage behavioral diversity, and promote well being. Females are monitored closely for signs of pregnancy and we are evaluating behavioral and morphological indices to distinguish pregnancy from pseudopregnancy. Identification of pregnant females is important because they are managed differently than nonpregnant females. In cases of maternal abandonment of cubs, we have developed a method to train the mother to accept her cubs. The result of such behavioral research, coupled with efforts by other disciplines and basic husbandry changes, is a dramatic increase in the number of natural matings, pregnancies, births and cub survivorship.

The highly endangered giant panda may be the most popular animal in the world. What other animal draws such huge crowds and the constant scrutiny of the global media? Given such popularity, it is surprising how slow scientists have been to take up the cause and devote their time and energies to understanding their biology and behavior. Despite some early efforts (e.g., Chaudhuri et al., 1988; Kleiman, 1983; Pan & Lü, 1993; Schaller et al., 1985), many aspects of panda

Many have contributed substantially to the development of this research and management program and/or data collection. Among the Wolong staff, major contributors include Wei Rongping, Li Dasheng, Hu Damin, Wu Dafu, Huang Yan, and Han Hongyin. Collaborators and assistants from the Zoological Society of San Diego include Angela White, Megan Owen, Suzanne Hall, Valerie Hare, Laura McGeehan and Staci Wong. Many others too numerous to mention provided invaluable support and assistance. Correspondence concerning this article should be addressed to R. R. Swaisgood, Center for Reproduction of Endangered Species, Zoological Society of San Diego, P. O. Box 120551, San Diego, CA 92112, U.S.A. (rsweisgood@sandiegozoo.org).

biology remain a mystery. Before the late 1990s, most published accounts of captive pandas were based on one or two individuals. The success of captive breeding programs depends in part on the acquisition of such knowledge and its application to the species' management in captivity.

In recent years there has been a surge of research on the giant panda—almost all in captivity—by several institutions, including Zoo Atlanta, Chengdu Giant Panda Breeding Base, National Zoological Park, Wolong Breeding Center, and the San Diego Zoo. These research projects cover a diverse array of topics, including nutrition, veterinary care, endocrinology, reproductive biology, genetics, and behavior. As a result, new insights into giant Panda biology, as well as conservation breakthroughs, are on the horizon. The purpose of this paper is to describe a part of this research effort, namely the behavioral research program at the Wolong Breeding Center in Sichuan, China.

Rigorous behavioral studies of captive animals in zoo settings have been notably rare, and for good reason. Zoo-based studies are notorious for their small sample sizes and consequent lack of statistical rigor, often because zoos generally maintain a single breeding pair or small group, following the "Noah's Ark" approach. Moreover, goals of husbandry and management, as well as public exhibition, almost inevitably run counter to research needs. These obstacles tend to be magnified for endangered species held at zoos. With endangered species comprised of a small number of founders, it is crucial to obtain breeding and genetic representation from all founders quickly so that genetic heterozygosity is maintained (Ralls & Ballou, 1986). At this stage experimental manipulation that might compromise well being or reproduction in some individuals, even if the ultimate goal is to better understand processes that promote well being and reproduction, is justly ruled out. For monoestrous species such as the giant panda, where the opportunity to obtain reproduction comes but once a year, this problem is further exacerbated. Also, the effects of any scientifically-guided, long-term change is almost certain to be confounded by other changes, such as diet, veterinary care, and husbandry practices, rendering determination of cause and effect difficult.

Behavioral researchers are beginning to find a way over--or often around--these obstacles. In an exemplary study, although still with relatively small sample sizes, Wielebnowski and colleagues (Wielebnowski et al., 2002) were able to manipulate housing for female cheetahs, with predicted detrimental effects on stress and reproduction. Female cheetahs housed socially with other females showed behavioral signs of elevated stress and ovarian cyclicity was suppressed compared with those housed singly. This study was possible because (1) the cheetah population is not critically low and (2) social housing was already widespread, and thus research activities would not negatively impact current practices, and could improve them. Such "deprivation" studies are, however, frequently not feasible. Instead, a combination of educated guesswork and compromised scientific investigations proceed hand-in-hand toward an optimal management strategy. Consider the ideal study design to determine the environmental requirements for the development of normal behavior, absent stereotypies and other behavioral problems. It would involve the systematic manipulation of rearing environment, with some animals kept in small, barren cages, and other experimental groups reared in various enriched environments. Clearly, this design would not be ideal for animal well

being and reproduction in an endangered species. Add to that the almost certain need for animal transfer between institutions for genetic management, and opportunities for such lofty experimental goals vanish.

One way around these obstacles is for researchers to capitalize on "accidental" experiments, for example, studying animals that are housed in different environments. Although a reasonable alternative, often animals are moved around from one enclosure to another, so, developmentally speaking, their behavioral phenotype is the consequence of multiple enclosures and husbandry regimes. An example of accidental experiments from our own work comes from studies of stress. To determine if noise affected indices of stress in two giant pandas, we recorded amplitude levels daily to see if days characterized by loud noise were associated with behavioral and hormonal measures of stress (Owen et al., in press). While neither experimentally ideal nor statistically generalizable to the species as a whole, this study did provide insight into the behavioral biology of stress, and aided in management of these two animals. Another strategy is to manipulate some variable that will not harm the animal or reproduction, but may be correlated with reproductive success or otherwise provide insight into reproduction. For example, with giant pandas an ideal experiment to determine the role of scent in reproduction would be to deprive some pairs of any olfactory exchange and evaluate whether aggression levels were higher and mating behavior less successful. Both ethical and conservation issues make such a manipulation impractical. Thus, our strategy has been to look at other effects of conspecific odors on sexual and aggressive motivation. For example, do pandas show increased sexual motivation (as evidenced, for example, by vocalizations) when exposed to certain odors? Such studies led to increased understanding of the effect of odors on motivational processes in support of reproduction, and suggested improved management strategies for captive breeding (Swaisgood et al., in press).

Despite these constraints, it is clear that sound science can be conducted with captive endangered species, and that such science, although sometimes falling short of ideal, can play an instrumental role in development of improved captive breeding techniques. Clearly, such constraints and opportunities arise in giant panda conservation. In almost direct proportion to its appeal, the giant panda is notorious for its reluctance to breed in captivity. In 1996 at the IUCN Captive Breeding Specialist Group meeting in Chengdu, China, Chinese researchers estimated that only 39% of captive female pandas had produced offspring and as many as 80% failed to display normal behavioral estrus. In 1996 only six living males in captivity had ever mated naturally (Lindburg, Huang, & Huang, 1998), and the population was not self-sustaining. In the past six years, however, there has been a steady increase in the number of births and surviving cubs, predominantly at Wolong and the Chengdu Breeding Base. At Wolong the captive population has tripled from about 25 to more than 70 individuals in the past seven years. Wolong's success has hinged to a large degree on the implementation of a highly successful natural mating program. This program owes much of its success to behavioral management strategies based on knowledge or assumptions about what is important for pandas in the wild, coupled with detailed scientific studies to determine the behavioral needs and abilities of pandas, and how these map onto well being and reproduction.

Here we present for the first time a summary of these various research activities, providing a synthesis of previously published work and an update that includes unpublished efforts. These research activities have provided insight into many aspects of the behavioral biology of giant pandas, yielding knowledge we have applied to captive breeding efforts and hopefully—in the not-too-distant future—to conservation in the wild. While no specific applications to wild populations have been made to date, we have taken advantage of the presence of these captive animals to learn a great deal about panda biology, much of which should prove to be relevant to wild pandas as well.

Behavioral Ecology in the Wild

Relatively little is known about the giant panda's behavior in the wild. What is known is based on two long-term field studies in the Wolong Nature Reserve (Schaller et al., 1985) and Qinling mountains (Lü, Pan, Zhu, Wang, & Wang, 2000; Pan & Lü, 1993). The giant panda lives a solitary existence, devoting most of its time to consumption of its primary food source, bamboo. Bamboo makes up about 99% of the panda's diet, yet the panda's digestive tract is inefficient at assimilating protein from this food source. As a result, pandas spend about 55% of their time eating bamboo, 43% resting, and only 2% of their time is devoted to remaining activities (Schaller et al., 1985). Both males and females occupy home ranges that overlap extensively with conspecifics of both sexes, with some evidence of core areas that are mutually exclusive intrasexually. Throughout most of the year pandas encounter one another infrequently, avoiding direct contact with or responding aggressively to conspecifics. Although animals in some populations appear somewhat more social, this asocial temperament is expressed in both intra- and intersexual encounters. Outside the mating season, pandas vocalize infrequently. Long-distance acoustic communication is limited to male "song medleys" heard during the mating season. By contrast, pandas capitalize on opportunities for chemical communication (Schaller et al., 1985). In areas of range overlap, pandas create traditional sites used to deposit urine and scent from a specialized anogenital gland. These communal scent marking stations, consisting of several large conifers in a prominent location, are visited by a number of pandas from the neighboring community. Pandas also mark on isolated communal posts along the network of trails utilized by several pandas.

Females experience a single estrus each spring and males show seasonal rut-like behavioral and physiological changes (Kleiman, 1983; Platz et al., 1983). The fertile period lasts 1-3 days. Several males may locate isolated females in estrus and vie for mating opportunities; the female is known to mate with more than one male on some occasions (Schaller et al., 1985). Following fertilization of the egg, the development of the embryo is arrested and uterine implantation delayed for a period of several weeks to months (Monfort et al., 1989). Accordingly, the gestation period ranges from less than three months to approximately six months (Zhu et al., 2001). At birth the infant panda is the most altricial of all eutherian mammals and the mother expends a great deal of effort on the care of her young. The cub remains in a den for the first 15 weeks of life, and is weaned and separated from the mother at 18-24 months of age.

Overview of Methods

The subjects for the ongoing studies described here are housed at the Wolong breeding center in the Wolong Nature Reserve in Sichuan, China. Sample sizes vary ($N > 20$ for most studies) and have increased with the recruitment of new individuals into the population brought about by increasing birth rates. Between 1996 and 2002 the population increased from 25 to more than 70 individuals (though a few have been transferred to other facilities). Following their natural inclination for solitary living (Schaller et al., 1985), all adult individuals are housed individually, whereas cubs younger than three are generally housed socially. All animals have visual, acoustic, olfactory and limited tactile access to one or two pandas residing in adjoining enclosures. Enclosure size varies, but most pandas are housed in indoor-outdoor pens measuring approximately 12 x 8 m. Wild pandas live on the mountain slopes above the center, thus the captive pandas are exposed to the same climatic factors as their wild-living counterparts.

We have used a variety of methods to study the behavior of pandas. A cornerstone of our methodology has been formal behavioral observations (Martin & Bateson, 1993). We have developed an ethogram of more than 100 operationally defined behaviors. The ethogram describes specific behaviors belonging to functionally distinct categories: Abnormal/stereotypic behaviors, exploration, play and enrichment-directed behaviors, behaviors related to olfactory communication, vocalizations, estrus-related behaviors, social interactions, parturition, mother-infant behaviors, and miscellaneous individual behaviors, as well as location, substrate, and social distances. Observation sessions range from 45 min to 2 h. Behavior frequencies are calculated from all-occurrence sampling of some behaviors. At the end of each one-minute interval, an instantaneous sample is taken, and these data are used to calculate the percent time spent engaged in various activities. We also use one-zero sampling, recording whether or not a behavior occurred during the preceding one-minute interval. This measure is used for behaviors that occur too quickly to record every instance, such as vocalizations and elements of play. These behavioral measures can be compared statistically with other animals, other times of the day or year, during different stages of the reproductive cycle, across different husbandry and enclosure conditions, in response to different stimuli, and so forth.

Collection of these behavioral data is labor intensive and requires highly trained individuals. These data collection methods are supplemented with simpler, less time-consuming methods that can be used by animal care personnel while carrying out their daily responsibilities. At the end of the day the caretaker provides a quick summary of the behavioral observations he/she made that day. A small number of pertinent behaviors are recorded, and the observer ranks the occurrence of each behavior on a scale from 0 to 3. This method allows important observations that were not observed during formal behavioral observations to be recorded in a systematic and quantitative manner. We use this monitoring system for five management-related research areas: Estrus, male-female interactions during the breeding season, potential pregnancies, indices of stress and well being, and responses to environmental enrichment. We have also developed more systematic record-keeping systems for a variety of important husbandry activities, such as changes to enclosures and potential environmental stressors such as noise; these serve as independent variables in some of our analyses.

Reproductive Behavior

Perhaps most pertinent to the development of a captive breeding program is baseline knowledge of reproductive processes in the species. Toward this goal we conducted a series of studies of reproductive behavior in the giant panda. To document the nature and course of behavioral estrus in females, we made daily observations on all adult female pandas ($N > 20$) throughout the mating season from mid-February to mid-May from 1996 to 2000. These data build on the earlier work of Devra Kleiman with the female residing at the National Zoo (Kleiman, 1983; Kleiman, Karesh, & Chu, 1979). Hormonal data are also available for some of these years, as are data on vulvar color/dilation and vaginal cytology. Together these measures give us a picture of estrus in the panda, and allow us to predict in advance when a female will be entering the fertile period, as well as identify the most likely time when ovulation takes place (Swaigood et al., 2003c). This information is used in deciding when to place pairs together for natural mating or when to conduct artificial insemination.

Some behaviors, such as urinate (at a rate $> 1/h$), scent mark, and water play begin to increase 10 to 20 days before mating, the presumed time of ovulation (Figure 1). Chirping and bleating vocalizations generally commence less than a week before mating. Other behaviors, such as tail up and genital manipulation, occur almost exclusively during the brief mating period. Water play and scent marking decline rapidly at the time of presumed ovulation, and are rarely seen after the first day of mating. For some behaviors the quantitative changes in frequency provides an indication of the timing of ovulation. For example, chirping and bleating vocalizations both peak concurrently with hormonal and morphological indices of ovulation (see also Lindburg, Czekala, & Swaigood, 2001). Scent marking conforms to an interesting pattern that suggests its functional significance (Swaigood, Lindburg, & Zhang, 2002; Swaigood et al., 2000). A few weeks prior to ovulation the female increases her rate of marking, and marks more and more frequently until the day before she mates and presumably ovulates. The female rarely marks during the 1-3 day period in which mating occurs. These observations suggest that females use scent marking in the early stages of estrus to advertise the advent of ovulation and recruit males for mating. By the time the female is ovulating, males are in close proximity and the female switches to communicating primarily through vocalizations.

Another focus of our studies has been the changing form of male-female interactions across the female estrous cycle (Swaigood et al., 2003b). Some males show little interest in the female and do not copulate. Most males will display consistent signs of interest in the female throughout the female's estrous cycle, approaching her frequently, sniffing at her through the cage bars, and bleating (an affiliative vocalization) occasionally. The female's behavior changes more dramatically. Prior to entering estrus, the female almost invariably ignores the male or responds aggressively to him. Upon entering earlier stages of estrus, she approaches the male frequently and displays signs of ambivalence, emitting a combination of affiliative (bleat, chirp) and aggressive vocalizations (moan, bark, growl). With the advent of peak estrus, the female's behavior shifts markedly, and she almost invariably responds to neighboring males with more frequent and more emphatic chirping and bleating, and most often turns to present her hindquarters and adopts

the lordosis posture with tail up. The male displays increasing affiliative and sexual behavior towards the female as she approaches her fertile period. Characterization of this normal course of male-female interaction allows us to identify patterns and evaluate problems when a pair's behavior diverges from this established norm. For example, one female displayed a normal progression of estrous behaviors that were not directed to the male (e.g., scent marking, water play, vocalizations), but typically avoided the male and did not display receptive behaviors or affiliative vocalizations when interacting with the male. In comparison with other females, this female's behavior was aberrant. These observations led us to hypothesize mate incompatibility as the cause of reproductive failure, and when she was allowed to interact with a different male she immediately showed strong receptive behavior and copulated successfully (Zhang, Swaisgood, & Zhang, in press).

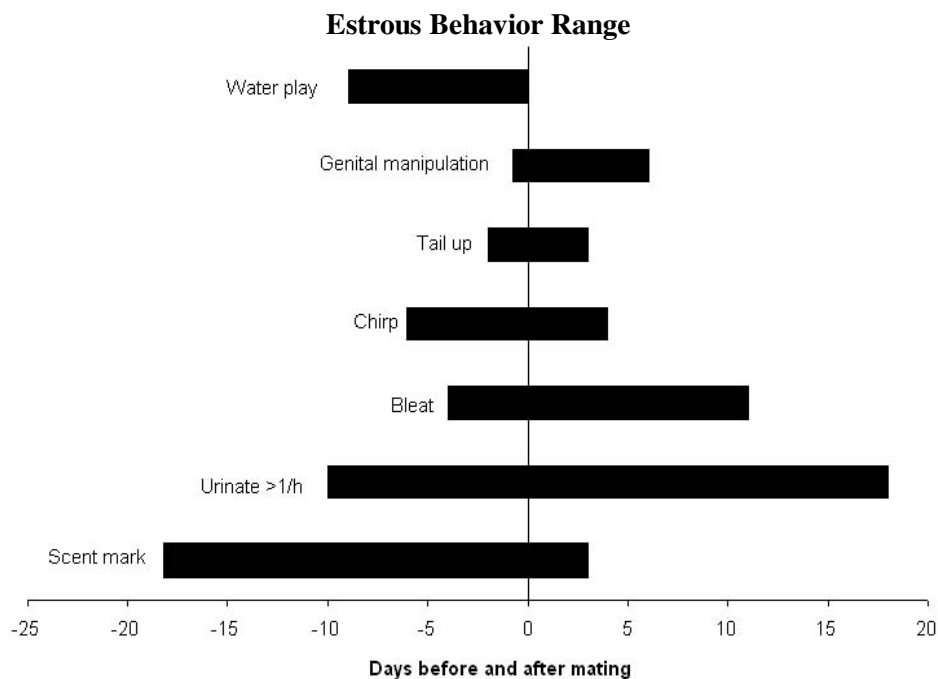


Figure 1. The onset and termination of behaviors seen during estrus. Depicted here is the range of days in which each of these estrus behaviors were observed, with outliers excluded. Data are from 14 females and 27 estrous periods, collected over four years. Day "0" refers to the first day of mating, negative values to days prior to mating, and positive values to days after mating.

More recently these labor-intensive formal behavioral recording protocols have been replaced by a quantitative record-keeping systems that allows keepers and animal management staff to capitalize on important knowledge that they gain from observing animals while going about their normal daily activities (see above). A few behaviors important for assessing reproductive status and mate compatibility, along with husbandry changes related to mating management are recorded. For an example, see Table 1. This protocol is used to monitor behavior during four circumstances: (1) male-female behavior for animals housed in adjacent pens during the period leading up to ovulation (Table 2); (2) male-female behavior when pandas are exposed to the odors of potential mates during pen swapping (see below); (3) male-female behavior during the female's peak estrus, including a quantitative

assessment of behaviors used to judge the pair's compatibility and reasons for attempting or not attempting a mating introduction; (4) male-female behavior during mating introductions, including assessment of the reasons for success or failure to copulate. Husbandry data include a complete record of the location where each animal is housed and the type, level and duration of exposure that the male and female experience prior to mating introductions, as well as the precise manner in which the pair were managed during mating introductions. Behaviors recorded include several indices of social interaction related to indifference, avoidance, affiliation, aggression, sexual motivation, and competence of sexual performance (e.g., mating postures). These indices are defined by measures of proximity-seeking behavior, vocalizations, visual signals, olfactory signals, and other indices of attractiveness, receptiveness and proceptiveness (Table 1).

Table 1

Examples of Interval Scale Used for Studies on the Effects of Mating Management.

Aggressive	Panda responds to other panda's approach, proximity or behavior with aggressive acts 0 = no aggression observed. 1 = mild aggression observed; occasionally footscrapes, huffs, snorts, chomps, honks, barks or moans. 2 = panda usually footscrapes, huffs, snorts, chomps, honks, barks or moans; more than half of interactions are accompanied by barking and moaning (more intense aggressive vocalizations); panda may paw swat or lunge at other panda. 3 = panda almost always barks or moans at other panda, and more intense aggression may be observed (growl, roar, fighting through cage bars); vocalizations should be loud.
Neutral	Panda ignores, shows minimal overt response or simply observes the other panda in response to the approach or behavior of another panda. 0 = panda responds more than 70% of the time when the other panda is less than 1 body length away. 1 = panda responds 30-70% of the time when the other panda is less than 1 body length away. 2 = panda responds only about 10-30% of the time when the other panda is less than 1 body length away. 3 = panda responds < 10% of the time when the other panda is less than 1 body length away.

These methods allow us to address several questions. Which management practices are most reliably associated with successful mating? For example, is there an optimal length of time that males and females should be housed next to each other to promote sexual interest and compatibility? What behaviors can be used to predict whether a particular pair will mate? What factors do managers use in deciding whether to attempt a mating introduction? How many males is a female exposed to before a compatible pair is found? Do males or females have mating preferences, that is, do they *reject* some pandas and choose others? What traits or behaviors are associated with preferred partners? At the time of this writing, this methodology had only been used for part of one mating season. Although these answers must await further analysis, it is clear that while behavioral detail is lost, many other aspects of mating management and behavior are being recorded that were missed by previous formal behavioral observations during prescribed observation sessions. A combination of these methodologies gives us greater understanding of these reproductive processes.

Table 2
An Example Datasheet for Male-female Behavior for Animals Housed in Adjacent Pens.

Female ID	Pen	Neighboring Male ID	Date	% \geq IBL	Female Behavior						Male Behavior						Comments												
					Avoid	Ignore	Shows Int.	Aggressive	Chirp	Bleat	Sexual	Avoid	Ignore	Shows Int.	Aggressive	Chirp		Bleat	Sexual										
Ying Ying	N2	Pan Pan	14 Mar 02	15 %	1	0.5	2	2	1	0.5	0	0	0	1	2	0.5	0	0	1	0	0	0	0	0	0	0	0	0	Ying Ying approaches Pan Pan often, but does not stay long. She usually Shows Interest, but when Pan Pan Shows Interest, she moans and leaves. Pan Pan occasionally moans when she approaches.
Ying Ying	N2	Da Di	14 Mar 02	5%	2	0.5	1	2.5	0.5	0	0	0	0	1	1.5	1.5	0	0	1	1.5	0	0	0	0	0	0	0	0	Da Di frequently running around cage, charging toward Ying Ying, footscraping very often, moaning occasionally. Ying Ying moans and barks very loudly when Da Di charges.
No. 1	N8	Xi Meng	14 Mar 02	25 %	0	0	0	0	3	2.5	3	3	0	0.5	0	0.5	0	0.5	0	3	1.5	0	3	1.5	0	0	0	0	No.1 frequently in lordosis with tail up toward Xi Meng; Xi Meng very excited, trying to get to No. 1, but does not sniff her vaginal area for very long.
No. 1	N8	Xing Xin	14 Mar 02	35 %	0	0	0	0.5	3	3	3	3	0	0	1	0	0	0	0	2	3	0	2	3	0	0	0	0	Xing Xin removed from cage in morning for medical treatment; in the afternoon was recovered and interacting well with No. 1.

Note. Frequency and intensity of behaviors are recorded on a scale from 0-3 (see Table 1), at 0.5 unit intervals. "% \leq IBL" refers to the % time spent less than 1 body length from neighboring panda.

Chemical Communication

From the outset of these studies we hypothesized that some sort of communication breakdown in captivity might be partially responsible for reproductive failure. As a solitary species that rarely encounters conspecifics face to face, pandas undoubtedly rely heavily on chemical communication, as suggested by observations in the wild (Schaller et al., 1985). Giant pandas occupy overlapping home ranges and in areas of overlap they establish communal scent mark stations, usually a cluster of trees on a prominent ridge. Here pandas leave scent "messages" and "read messages" left behind by other pandas, similar to the use of community bulletin boards. Pandas use two substances to communicate with conspecifics--urine and secretions from the anogenital gland--which are deposited in four distinct postures. Pandas are quite responsive to conspecific odors, and use three chemo-perception modalities to investigate them: Gustation (lick), olfaction (sniff), and vomeronasal organ reception (as facilitated by flehmen; Swaisgood, Lindburg, & Zhou, 1999). But what information do pandas extract from these signals? In addition to the message, do pandas also leave cues to their individual identity (a chemical signature) and are pandas able to determine how long a scent mark has been left in the environment (i.e., a "date").

We have used several methods to address these questions (Swaisgood et al., in press). One method is to place two scents that differ in some regard (e.g., sex or age of donor) onto wooden boards and present them simultaneously to the subjects. If pandas significantly prefer to investigate one odor more than another, this demonstrates that the scents differ in chemical composition and that pandas can detect these differences. It also shows that discrimination of these differences is important to pandas, and therefore likely has some important function. We also present pandas with only one scent at a time, and compare responses to these sequential presentations, usually separated by 24-48 h. The advantage of this method, while less sensitive to fine discrimination abilities and more likely to be impacted by temporal motivational changes, is that behaviors other than direct investigation (sniff, lick, flehmen) can be attributed to one of the scents. For example, if pandas vocalize, scent mark or avoid the odor stimulus, it is possible to determine which odor causes these responses. For all of these methods, and discrimination studies in general, negative findings are difficult to interpret. These methods rely on intrinsic motivation to express different overt behaviors in response to different odors. Thus, lack of a differential response may be due to either deficient perceptual abilities or lack of motivation. In the future we plan to utilize reinforcement discrimination training paradigms to determine if pandas have perceptual abilities that are not expressed in traditional discrimination tests.

Our findings, as illustrated in Figure 2, demonstrate that a variety of information is extracted from chemosignals, including the sex (Swaisgood et al., 2000; White, 2001), age (White, Swaisgood, & Zhang, 2003), and estrous status (Swaisgood et al., 2002; Swaisgood et al., 2000) of the signaler. Males consistently investigate female more than male odors and show signs of increased sexual motivation after sniffing female odors, especially estrous female odors. By contrast, males display evidence of aggressive motivation after sniffing the odors of other males. Female urine marking peaks just prior to ovulation, suggesting that this chemosignal is used to advertise reproductive condition. In addition, the chemical

constituents of urine must also change because males spend significantly more time investigating estrous than nonestrous female urine in controlled experiments. However, females do not overtly discriminate estrous from nonestrous female urine, strengthening the argument that male interest in female odors is motivated by reproductive concerns rather than as an incidental byproduct of odor valence. By spreading these male attractant odors widely around the environment prior to ovulation, the female probably recruits several male suitors and primes the male's sexual motivation and decreases his aggressiveness toward her. This may decrease risk and facilitate sexual behavior upon encountering the male during the fertile period.

Male odors also play a role in female reproductive behavior. Females spend more time investigating male than female urine. Estrous females bleat and chirp more (a clear sign of heightened libido) after sniffing male but not female odors. In addition, females are most interested in investigating male odors at the time she should be locating and perhaps choosing a suitable mate: females spend significantly more time investigating male urine during the preestrous period than during peak or postestrus. In the future we will examine the role that male odors play in female mate choice. For example, in the threatened pygmy loris we have found that females prefer males whose odors are familiar (Fisher, Swaisgood, & Fitch-Snyder, 2003) and males who regularly countermark the marks of other males (Fisher, Swaisgood, & Fitch-Snyder, in press). The ability of a male to monopolize an area with his own scent or at least ensure that he is the most recent male to visit the area and countermark his competitors' odors may be reliable indicators of his competitive ability (Hurst & Rich, 1999). Because pandas possess a similar mating system to that of lorises, we propose that females may use the same choice criteria. If so, this is fortunate because a female's familiarity with a particular male's odor is easy to manipulate experimentally for conservation purposes. In the past, mating and offspring production has been skewed toward a few males, raising the possibility of scent manipulation to encourage more equitable contributions from different males and improve genetic management of the population.

Chemosignals can also be used in competitor assessment. For example, pandas will upend themselves to deposit urine high up on a tree or other vertical object. This improbable handstand marking posture demanded explanation. Two clues suggested that it served a competitive advertisement signaling function: (1) this posture is used exclusively by adult males and (2) it is seen most frequently after the male's home area has been "invaded," and least frequently when the male is "intruding" on another panda's area (Swaisgood et al., 2000). But does the recipient's response to male urine vary as a function of the height of urine deposition? Many other species use postures to deposit scent above the ground, yet no one had ever addressed this question. To test the effects of signal deposition height, we took an individual urine sample, divided it in two, and experimentally placed the same chemical stimulus 1 m above ground to mimic a handstand and on the ground to mimic the squat posture (White, Swaisgood, & Zhang, 2002). Pandas spent significantly more time investigating these artificial handstand urine marks than the squat marks. After investigation they were more likely to avoid the area; this was especially true of subadult males, who have the most to risk in an encounter with a high status male. We speculate that initially active assessors capitalized on the height of urine deposition to assess competitive ability (higher mark = larger body size) and avoid larger males. Because males appear to emphasize this signal when in their

home area, we propose that subsequent signal evolution has led to the use of the signal by adult males to signal spatially-dependent dominance and/or willingness to escalate in a contest.

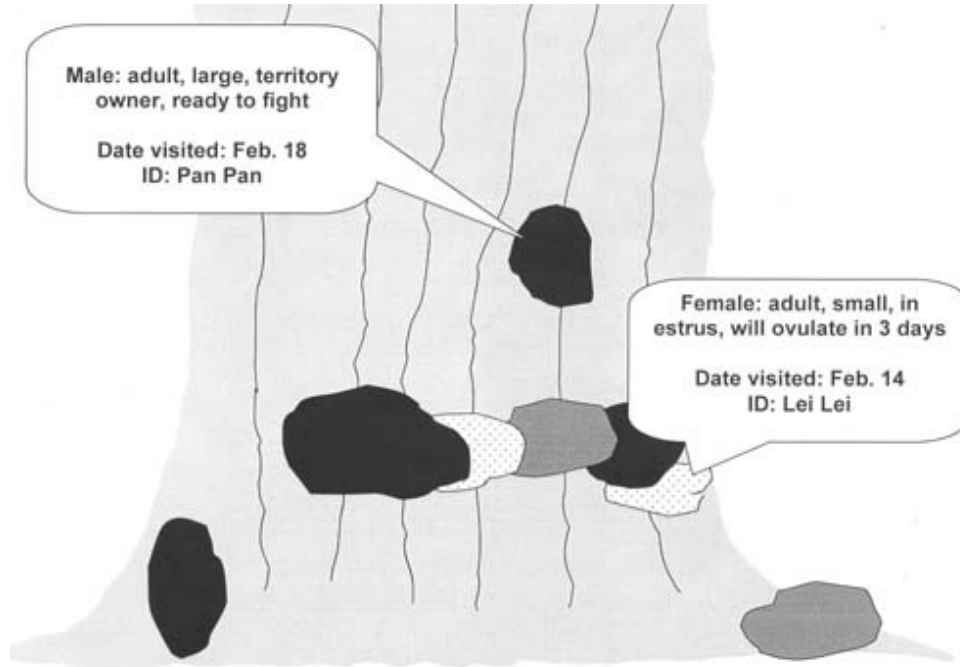


Figure 2. A simple illustration of the types of information that experimentation indicates may be extractable from panda urine and anogenital gland secretions. Note that by the time Pan Pan visits this marking station on February 18, Lei Lei will have already ovulated, rendering further pursuit unprofitable. This assumes that pandas can determine the precise stage of the estrous cycle via scent, which has not yet been demonstrated.

We have found evidence that pandas do leave individually discriminable chemical signatures that may allow pandas to recognize one another solely on the basis of scent (Swaisgood et al., 1999). Pandas are also quite adept at discriminating between scents of various ages, presumably cueing in on changes in odors brought about by chemical degradation and dissipation from exposure to sun, rain and air (Swaisgood et al., in press). In all cases pandas spend more time investigating fresher odors than older odors. These latter two factors provide important supplemental information needed for an efficient communication system. Obviously, a scent mark revealing that the signaler was female and coming into estrus is of little use if the perceiver cannot determine the signaler's identity, and hence know where to search for her. Also, it is of little use if the receiver cannot tell how long ago the signal was left. For example, consider a male encountering a female's mark indicating that she will ovulate in two days. If the mark was deposited five days ago, then the female's fertile period will have passed already.

Taken together, these studies reveal a sophisticated chemical communication system that is an integral part of many facets of the social lives of pandas. They also suggest clear application for the use of scent to encourage mating in captivity, as will be discussed later.

Enrichment and Well Being

Many pandas in captivity display stereotypic behavior, other abnormal behaviors, or signs of stress or poor well being (Lindburg, Swaisgood, Zhang, Narushima, & Zhou, in press; Owen et al., in press; Swaisgood, 1996; Swaisgood et al., 2001; Tepper et al., 2001). Although captive pandas are fed ample bamboo, supplementation with other food reduces the overall time pandas spend feeding in comparison with wild panda activity budgets. This “free time,” coupled with confinement to areas offering little environmental complexity and few behavioral opportunities, has led to signs of suboptimal well being in some cases. To address these problems, we developed an enrichment program at the Wolong Breeding Center (Swaisgood et al., in press; Swaisgood et al., 2001; Swaisgood, Zhang, & Zhang, 2003). Remedial measures taken include increasing the amount of bamboo fed, adding more feeding times throughout the day, increasing the structural complexity of existing enclosures (e.g., climbing structures, digging pits, logs, stumps, rocks), building larger naturalistic enclosures, better crowd control, gentler keeper interactions, and the development of a supplemental enrichment program. We are testing the efficacy of all of these strategies. For example, larger more naturalistic enclosures have greatly reduced or eradicated abnormal behaviors in some cases (Swaisgood, 1996).

As part of the supplemental enrichment program, pandas are given manipulable objects such as burlap sacks stuffed with straw, rock piles, and fresh branches, as well as numerous devices designed to make pandas work for food. When such enrichment is present we have found a significant reduction in time spent in stereotypic behavior and time spent in restless anticipation of feeding, and an increase in behavioral diversity and the amount of time spent active (Swaisgood et al., 2001). In an interesting case of applied and theoretically-motivated research, this study also provided support for the ethological needs model of motivation. This model posits that animals are motivated to *perform* certain behaviors, particularly appetitive behaviors preceding attainment of food or some other important biological resource (Hughes & Duncan, 1988). Animals are reinforced not only by the functional consequences of their behavior, but also by the behaviors used to obtain the resource. In the absence of sufficient opportunity to perform these behaviors, well being suffers and is manifest in the performance of abnormal behavior. If this hypothesis is true, we can make two predictions. (1) The opportunity to perform behavior should reduce the motivation to perform abnormal behavior. To demonstrate that *motivation* is affected, one must not just compare abnormal behavior when enrichment is present versus absent because this shows only that the time occupied with the enrichment item is incompatible with performance of abnormal behavior. If the animal's motivation is affected, it should continue to exhibit less abnormal behavior in the aftermath of an enrichment interaction. (2) Objects that provide no obvious biological reward such as food, but do provide opportunities to perform a greater diversity of behaviors, should also generate these motivational carry-over effects. Our data were consistent with both of these predictions, and we were therefore unable to reject the ethological needs model of motivation.

Other attributes of captive environments may compromise animal well being. For example at the San Diego Zoo, we found that high levels of ambient noise

typical of a zoo setting can be associated with elevated indices of stress, as determined by endocrine and behavioral measures (Owen et al., in press). In a more systematic follow-up study, we created a new monitoring system designed to capitalize on the casual observations of animal care staff made throughout the day as they perform routine husbandry responsibilities (Swaisgood et al., 2003a). These keepers spend a great deal of time observing the animals, and are a wellspring of information and understanding of the animals. The goal is to provide a way for keepers to record their observations in a quantitative way that allows the evaluation of environmental influences on stress and well being. Toward this end, we created and precisely defined a list of specific environmental changes (e.g., enclosure modifications, changes in feeding schedules, large crowds, noise, etc.) that may affect well being, accompanied by a list of behaviors that pandas may exhibit when disturbed (e.g., retreat, hide, pace, vocalize). Guidelines are provided on how to rank the severity of these disturbances and behaviors and estimate the amount of time devoted to these behaviors. In addition, corticoids—known physiological indicators of stress—are being evaluated via radioimmunoassay of daily urine samples collected from the pandas. Feedback from these studies should provide insights into how management practices and disturbances affect giant pandas, and allow managers to adapt their practices to maximize panda well being in captivity.

Pregnancy and Mother-Infant Behavior

Another important element of captive-breeding programs is management of potentially pregnant females. Because pandas often experience a “pseudopregnancy” that is virtually indistinguishable from true pregnancy by hormonal, morphological and behavioral measures, it is often difficult to know which females are pregnant. It is important to determine pregnancy status so that proper management actions can be taken, such as efforts to reduce stress and provide an appropriate environment for parturition. Toward this end, we have developed a detailed monitoring system. Each day animal caretakers record the incidence of several potential signs of pregnancy, and rate them on a scale from 0 to 3. These data have confirmed our initial impression that pseudopregnancy is a close mimic of pregnancy, but we were able to discern a few signs that are more pronounced in pregnant females as parturition approaches (unpublished data). The best signs that give fairly early warning are depressed appetite and swelling of the mammary glands. Other signs such as vulvar swelling, vulvar licking, urination and restlessness only begin to differ between pregnant and pseudopregnant females a day or two before parturition.

Adequate maternal care is a prerequisite to any successful captive-breeding program. In many species the survival rate of mother-reared infants is higher than that for hand-reared infants (Baker, Baker, & Thompson, 1996), a pattern which is certainly true for giant pandas. Mother-reared offspring display more competent social, sexual and parental behavior as adults (Baker et al., 1996), and make better candidates for reintroduction to the wild. For the past several years we have conducted detailed observations of mother-infant interactions during the period from birth to weaning (e.g., Zhang et al., 2000). By observing the interactions between the mother and infant closely, we began to understand what sorts of activities a good panda mother engages in, and how these behaviors change as the cub devel-

ops. At birth the cub is completely helpless and weighs a mere 100 g. The mother must provide for all the needs of their extremely undeveloped offspring: nutrition, thermoregulation, comfort, and elimination of waste.

The nature of this relationship changes as the cub ages, and the mother is gradually freed from the need for strict vigilance as the cub becomes less fragile and more self-sufficient. When the cub is young, the mother invariably exercises caution when attempting to pick it up lest she injure it. For example, she always picks up the cub using her mouth rather than her paw. The mouth affords more precise movements in grasping the infant than does the comparatively clumsy paw, equipped with only a small “pseudthumb.” As the cub grows larger and less fragile, the mother begins to use her paw, often reaching out to retrieve it by dragging it along the ground. During the cub’s first month of life, the mother maintains contact with the cub nearly 100% of the time—primarily resting on her ventrum—but as the cub’s pelage grows in, the mother spends progressively less time in contact with her cub. Initially, the infant is almost always covered by the mother’s paw, arm or head, and is rarely exposed to the air for more than a few seconds. If the infant is exposed, it vocalizes and the mother adjusts her position to provide warmth and comfort. As the infant ages, the mother covers the infant less, and allows it to be exposed to the air more often.

The infant’s increasing self-sufficiency is best illustrated by the dramatic reduction in vocalization rate in about the third month of life, close to the end of den life. At the same time the mother’s perception of the urgency of her cub’s needs apparently diminishes, as suggested in the pattern of reduced responsiveness to the cub’s vocalizations. A quick response to a neonate’s cries literally may be a matter of life and death, whereas older cubs’ needs can be postponed safely. Mothers also play an important role in the stimulation of urination and defecation, which young cubs are incapable of without vigorous licking of the anogenital area by the mother. The cub’s ability to eliminate waste unaided increases with age, and the mother shows a corresponding reduction in the time devoted to this activity. The mother also spends a considerable amount of time licking the cub’s fur to keep it clean, an activity that doesn’t begin to decline until the cub is approximately seven months of age, perhaps because maternal licking also functions in the maintenance of the social bond. Olfaction also undoubtedly plays a role in recognition and maintenance of the bond. Mothers prefer the odors of their own cub to those of strange cubs, and maternal odors appear to have a calming effect on recently weaned cubs (Swaisgood et al., in press).

Our observations highlight the importance of the mother-infant relationship for the survival and well being of the cub. Not only do they help us understand the interactive dynamics between mother and cub, but they also address several management concerns. For example, observations of maternal licking to stimulate waste elimination and keep the cub clean can be used as a model for caregiving for cubs that must be hand-reared. Although these observations leave open the question of the long-term developmental effects of precocial weaning, they do illustrate a pattern of progressively reduced dependence on the mother. Cubs at Wolong are routinely weaned at about six months of age, compared with approximately 18-24 months in the wild. Our observations indicate an initial stress response when cubs are removed from the mother, but their behavior quickly recovers to relatively normal levels, and they develop new relationships with peers in the nursery. They

frequently engage in social play with their pen-mates, and this social interaction is probably an important substitution for the interaction they would have had with the mother (cf. Mason, 1979). Although social play is common, they also begin to express their solitary disposition by showing an apparent reluctance to interact with pen-mates at times, and by climbing trees where they rest alone.

This research program has already begun to bear tangible fruits in the management realm (Zhang et al., 2000). We developed a method to facilitate maternal care in a giant panda female that rejected her cub immediately after giving birth. Upon birth the mother appeared fearful of her newborn cub, sniffing it cautiously and jumping back when it vocalized. Following removal of the cub, the female was systematically exposed to a regime of infant-related stimuli. We used a stuffed panda toy as a vehicle to deliver the infant's scent (urine and feces) to the mother, which was accompanied by playbacks of the infant's vocalizations. The female treated the surrogate almost as if it were a real cub; for example, she spent 61% of her time holding the surrogate in positions typical for the species, licked the surrogate to clean off the urine, and responded to playbacks of the cub's croaks, squawks, and cries. She also showed signs of gradual improvement in how she treated the surrogate, encouraging us to begin a process of gradual reintroduction of the cub to her mother. Results also indicate that the female was responsive to both infant vocalizations and urine, but not milk. After a transitional period in which we assisted the female in her efforts to nurse and groom the infant, all maternal caregiving responsibilities were returned to the mother. Over the next three months the pattern of maternal care followed the species-typical course of declining mother-infant contact, grooming, overall interaction time, and responsiveness to the cub's vocalizations. This study marks the first successful reunification of a giant panda mother with an infant separated at birth, and hopefully will serve as a model for similar efforts elsewhere.

These findings suggest that female pandas can be quite flexible in maternal provisioning. In recent years we have capitalized on this flexibility to increase cub survival rate. Panda females usually give birth to singletons or twins, but when twins are born, they virtually always abandon one cub in favor of the other (Schaller et al., 1985). Historically, rejected cubs born in captivity have been hand-reared, and those reared in the nursery from birth inevitably died. However, we have learned that females will readily accept either twin if presented to her individually. This information has led to our current practice of swapping all twins back and forth between the mother and the nursery every few days, so that each cub is half mother reared and half hand reared. This practice is also routinely used at the Chengdu Breeding Base. The survival rate of cubs currently approaches 100% (Table 3).

Conclusions

From this and other research we have learned several lessons that have been applied to the breeding program. This program entails both a general management strategy and scientifically guided efforts to address idiosyncratic causes of and creative solutions to reproductive failure. Behavioral management for reproduction is not just limited to the breeding season. It is important to promote good psychological well being throughout the year and during the crucial developmental years

from birth to adulthood. We believe, but cannot prove, that the efforts made to promote well being discussed above have helped recruit new breeders into the population (Zhang et al., in press). In an interesting case study, three females that were unusually timid and responsive to stressors were targeted for improved husbandry, enrichment and stress reduction, and all three subsequently mated naturally and gave birth for the first time. While opportunities for mate selection do not appear to be essential for most pandas, a few individuals appear quite choosy and efforts to provide alternate partners have encouraged mating in these animals.

Table 3
Cub survival to six Months of Age at Wolong Breeding Center, 1986-2002 (Stillborn Infants Excluded).

Year	Singletons (survived/born)	Twins (survived/born)	Triplets (survived/born)	Total (survived/born)
1986	1/1			1/1
1991		1/2		1/2
1992	1/1	1/2		2/3
1993	2/2			2/2
1994	1/1			1/1
1995	2/2	1/2		3/4
1996		2/4		2/4
1997	2/2	1/6		3/8
1998	3/3	1/2		4/5
1999	1/1	4/4	2/3	7/8
2000	5/5	6/6		11/11
2001		4/4		4/4
2002	2/2	2/2		4/4
Total	20/20	23/34	2/3	45/57

Note. Before 1999 one cub of each twin survived and one died, with the exception of 1997, in which one female rejected both her twins, which later died in the nursery, and another female rejected one twin and the other died of unknown causes at two days of age. In 1999 Wolong began swapping twins so that both cubs were part mother-reared and part hand-reared, and has experienced 94% twin survival since that time. Birth rates were down in 2001 because few females entered estrus, most likely because so many (8) were lactating and caring for infants until the onset of the mating season.

As part of the general management strategy, females are monitored closely for signs of estrus during the mating season. When early signs of estrus are evident, the female is moved to a pen adjacent to a male and the pair is allowed to become familiar with one another through the cage bars. However, access to odors is limited, so the male is occasionally locked in his bedroom and the female is allowed to enter his enclosure and investigate his odors. The same procedure is followed for introducing the male to the female's odors. This strategy clearly increases libido in both the male and female, as suggested in the olfactory tests described earlier. In the past many mating attempts with pandas have failed because of insufficient sexual motivation or excessive aggression. Exposing pandas to one another's odors appears to open the channels of communication and prime the pair for a sexual encounter, a process that may be essential for modulating avoidance and aggressive tendencies in this mostly solitary species.

Throughout the estrous period several behavioral and physiological indices of ovulation are monitored in the female (as discussed earlier). This information is crucial for determining when to attempt a mating introduction or perform artificial

insemination. The male's behavior is also evaluated to determine whether he is sufficiently aroused and unlikely to attack and injure the female, as will often occur if the mating introduction is ill-timed. If the signs are poor for a particular pair, the female is exposed to a different male. In this way nearly every female is allowed the opportunity to mate with a male.

The last few years have witnessed an explosion in the number of natural matings, births and surviving cubs. As a result, the Wolong facility population is expanding rapidly. Nearly all females and 2/3 of the males mate naturally and cub survival rate approaches 100%. We do not attribute all of these changes to behavioral research and management. A number of other factors, such as improved veterinary care, nutrition, and methods of artificial insemination have undoubtedly played a role. As is often the case with the wedding of management and research in the development of captive propagation programs, advancements do not proceed one step at a time, with all factors but one held constant. Fortunately, for panda conservation, these many confounding simultaneous activities have led to the blossoming of captive propagation, but the relative importance of each of these endeavors are difficult to disentangle, at least with regard to offspring production.

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