

Chemical Communication in Giant Pandas

Experimentation and Application

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Introduction

“How would I ever understand pandas? They moved from odor to odor, the air filled with important messages where I detected nothing” (Schaller, 1993, page 99).

In their seminal work on giant pandas in the wild Schaller and colleagues (1985) brought to the fore chemical communication as a fundamental aspect of the panda's behavioral ecology. Without knowledge of this chemical communication system we cannot understand how pandas locate and choose mates, regulate their use of space, and assess potential competitors; moreover, responses to conspecific odors might determine whether pandas use certain habitat that appears otherwise suitable. Despite the long-recognized importance of scent for pandas (see also Kleiman 1983; Morris & Morris 1966), until recently little effort has been made to address this poorly understood aspect of giant panda biology. Giant pandas are solitary by nature, rarely meeting face-to-face as they traverse their home ranges through dense bamboo forests. Indeed, they appear to make great effort to avoid encountering one another throughout most of the year. Yet, pandas will seek out conspecific odors, and have established a system that maximizes the communicatory potential of scent deposition. Several neighboring pandas with overlapping home ranges will utilize specific sites, called scent stations,

where they deposit scent and investigate odors left behind by previous visitors. These stations can be likened to “community bulletin boards” wherein messages are left at prominent locations where others are likely to find them. Pandas possess a specialized anogenital gland that secretes a waxy substance comprised largely of short-chain fatty acids and aromatic compounds (see Hagey & MacDonald, Box 7.1). They also utilize urine as a chemical signal. Pandas adopt four distinct postures to deposit scent at varying heights above the ground (Kleiman 1983). As with bulletin boards used by people, messages accumulate over time, making for a potentially confusing array of signals, new and old. Surely, pandas must possess sophisticated assessment abilities to extract information from these scent stations. But what exactly does a visitor to one of these scent stations learn about other pandas? In recent years we have undertaken a series of systematic investigations aimed at unraveling the mysteries of chemical communication in this species (e.g., Swaisgood et al. 1999, 2000, 2002).

An obvious starting point for such studies is to develop hypotheses regarding what sorts of information pandas would need to signal and extract from conspecific scent. First and foremost, perhaps, is the need to determine the “message” afforded by the scent. Important components of the message might include classification of the signaler in terms of species, sex, age and so forth (reviews in Brown 1979; Macdonald 1985). Clearly, pandas need to discern whether the signal emanated from a same-sexed individual (representing a potential competitor) or member of the opposite sex (representing a potential mating partner). Of course, male pandas must do more than identify females, but also determine the female’s reproductive condition, that is, is she or will she soon be fertile? If males experience temporal changes in sexual motivation

and reproductive ability, females may need to make similar distinctions between reproductively active and inactive males (as is seen in elephants: Schulte & Rasmussen 1999), a possibility supported by observations of a seasonal change in testicular size, ejaculate volume, sperm quality, as well as behavior (Kleiman 1983; Platz et al. 1983). These functions would be greatly enhanced if pandas could also distinguish the age of the signaler, providing information regarding whether the signaler has reached adulthood. Having attained reproductive maturity, adults are capable of breeding, but might also pose a greater risk by virtue of their larger body size and motivation to defend resources. Following the same line of reasoning, pandas might need to make further assessments regarding the competitive ability or territorial/dominance status of the signaler. Such information might be important not only for avoiding risky encounters with high status individuals, but also provide valuable information about mate quality (cf. Hurst 1993; Rich & Hurst 1999).

Even after assessing these and other components of the chemical message, the panda will need to extract additional information to make this signaling system truly useful and efficient. As with community bulletin boards, it is also important to determine which individual left the signal (“identity”), as well as the amount of time that has transpired since the mark was deposited (“date”). Consider the following scenario that underscores the need for multifunctional chemical signals. An adult male is searching for potential mates and comes across a scent station. He discovers an anogenital mark left by an adult female three days in advance of her fertile period. He recognizes the scent as belonging to a female whose core home range lies on the next ridge

immediately south of the station. The male also ascertains that the female left the mark two days ago, thus making further pursuit worthwhile.

Scent plays a prominent role in the regulation of reproduction in numerous mammalian species, for example, in the attainment of puberty, mate choice, mate location, priming sexual motivation, and reducing aggression (Vandenbergh 1983; Doty 1986; Bronson 1989; Johnston 1990; Hurst & Rich 1999). Knowledge of this important aspect of giant panda behavioral biology could substantially enhance our ability to manage the wild population for conservation purposes and facilitate efforts to breed pandas in captivity, which has proven to be an elusive goal. Take the case of the cheetah (*Acinonyx jubatus*) for comparative purposes. Captive reproduction of this species at the San Diego Zoo floundered until efforts were made to provide potential breeding pairs with opportunities for olfactory communication prior to staging the breeding introduction (Lindburg 1999). Similarly, efforts to reintroduce captive mammals to the wild may be seriously compromised by ignorance of the animal's use of scent for territory settlement, establishing social relationships, and courting and mating. It is therefore incumbent upon us to learn as much about chemical communication in this species as possible, and to seek avenues for its application to conservation measures.

Methods

For detailed descriptions of housing, husbandry and experimental methods, see Swaisgood et al. (1999, 2000, 2002) and White et al. (2002, 2003). These studies are relatively unique in giant panda research in that they utilized relatively large samples

sizes (range = 11-28), and often included individuals of all age-sex categories. Earlier studies do not include subadult subjects because of inadequate sample size, but thanks to recent breeding success at Wolong, later studies have been able to incorporate younger animals. To test responsiveness to odor stimuli, we utilized two distinct experimental designs. In the first we presented pandas with two odors simultaneously, and recorded their behavioral responses to each. This method, often called a “preference test,” has the advantage of controlling for temporal variation in motivation in that the panda’s “mood” is the same when it interacts with each of the two scent stimuli. Thus, this test is most sensitive at detecting a preference between two scent types. In the second design we presented two different scent stimuli at two different times, separated by at least 24 hours to minimize carry-over effects from exposure to the previous scent. This design, while less sensitive, has the advantage of allowing the experimenter to attribute subsequent behavior to the exposure to one or the other of the scent stimuli. For example, in the simultaneous exposure design, if the panda moves off and vocalizes and scent marks, one cannot ascertain which scent may have caused these behaviors. We used three different protocols to expose pandas to scent: (1) placement of scent on wood blocks and presentation of the scent in the subject’s home pen; (2) direct placement of the scent onto the walls or ground in the enclosure of the subject’s home pen; (3) relocation of the subject into the pen of another individual (pen swapping), which exposes the subject to all the odors left by the inhabitant of the pen. In all cases except for pen swapping, anogenital gland secretions or urine were collected fresh from naturally deposited scents from known individuals and were either presented to subjects immediately or frozen at –20 C for later use.

What Have we Learned About Giant Panda Olfactory Communication?

Descriptions of Responses to Conspecific Odors

These studies have provided clear evidence of the overriding importance of conspecific odors to giant pandas, as evidenced by the dramatic and often prolonged investigation of experimentally placed scent. For example, during the “pen-swapping” experiment, pandas increased chemosensory investigation (sniffing), flehmen, and licking of scent stimuli approximately 10-fold above baseline levels (Swaisgood et al. 2000). Prior to these studies, neither the flehmen response nor the presence of a vomeronasal organ had been described for the species. Flehmen in pandas is somewhat more subtle than other mammalian species. It is, however, easily recognized by deep inhalation (as evidenced by rapid expansion of the thoracic cavity), an abrupt upward movement of the head, and a slight upward curl of the upper lip, exposing the teeth. This position is only held for a second or two, and lacks the stereotyped appearance seen in ungulates and felids. It is often accompanied by prolific drooling. We have only observed this behavior when pandas are exposed to relatively novel conspecific odors, a rare occurrence at most captive facilities, and difficult to observe in the wild. We were also unable to find any reference to the presence of a vomeronasal organ (VNO) in the giant panda, but we suspected its existence because flehmen functions to deliver socially significant airborne chemicals to the VNO (Hart 1983). Subsequent investigation of the palate of the pandas residing at the San Diego Zoo confirmed the presence of incisive papillae, strongly suggestive of a VNO (D. Janssen, pers. Comm.). Although flehmen is observed most frequently during males’ investigation of female odors, it is also seen in response to other odors and by other individuals, suggesting that it serves important

functions beyond the traditional assessment of female reproductive condition (Estes 1972). Licking of scent stimuli appears to be primarily a male behavior that may aid in the delivery of less volatile chemical constituents to the VNO or be important for gustatory analysis.

Other responses to conspecific scent include scent marking, countermarking over the experimental scent, scent rubbing (rubbing the pelage—especially the back, shoulders and nape—over the scent), foot-scraping (dragging the hindclaws backward, creating claw marks on the substrate), vocalization, and avoidance. These responses occurred less frequently and only occasionally were sufficiently common to merit analysis.

Identification of Sex and Reproductive Condition

Outside the mating season many solitary species avoid or respond aggressively or fearfully to conspecifics. These species must overcome these tendencies during the female's fertile period if successful mating is to occur. Scent often plays a critical role in this process, most prominently in discerning the sex of a conspecific. Male mice, for example, will attack females doused with male urine and mount males scented with female urine (Dixson & Mackintosh 1971; Connor 1972). Female odors can also enhance male copulatory performance (Goodwin et al. 1979; Johnston 1990). Similarly, male odors are often important for activation of female sexual arousal (Floody et al. 1977; Johnston 1990). In addition, the ability of male mammals to assess female reproductive condition via chemical cues is undoubtedly important for reproductive success. Yet only a few species have been tested for this ability and in several instances tests failed to provide evidence of discrimination. These shortcomings led

Taylor and Dewsbury (1990) to conclude that the common assumption that males can discriminate female reproductive condition on the basis of chemical cues is unwarranted. This ability should be of utmost importance, as it is nearly a prerequisite for effective inter-sexual communication during the mating season. A male should be able to discern reproductive condition via chemical cues so that once he has detected a female's odor, he can determine whether it is profitable to pursue her for reproductive purposes at that time. Exposure to estrous female odors may, therefore, instigate mate searching and prime males for sexual behavior (see Rasmussen et al. 1997).

Sex recognition was readily evident among male pandas in one of our experiments using the pen-swapping protocol, in which subjects are exposed to all odors produced by the enclosure occupants (Swaisgood et al. 2000). Males strongly preferred female odors over male odors, investigating, licking, scent marking and bleating more in response to female than male odors. Subsequent experiments have provided confirmatory results in different experimental settings (White 2001), suggesting that this preference is robust. Males also bleated more after investigating estrous than nonestrous female odors. These findings demonstrate that males can indeed tell the difference between male versus female and estrous versus nonestrous female odors. Because bleats are related to sexual motivation (Kleiman & Peters 1990), this study suggests that female odors, especially estrous female odors, promote sexual arousal in males. We suggest that in nature bleating in response to female odors alerts the female to the male's presence, signals affiliative intent and promotes association for mating purposes. Estrous females apparently adopt a similar strategy, as suggested by the higher rate of bleating and chirping in response to male compared with female odors.

Male odors had a dramatically different effect on males, most notably in the complete absence of any bleat vocalizations, and high frequency of foot-scraping, a behavior most often observed during intra-male aggressive interactions. Thus, in contrast to female odors, male odors appear to promote aggressive motivation in other male pandas.

The finding that although we measured several behavioral variables, male pandas only discriminated estrous from nonestrous female scent on the basis of vocalizations was surprising (Swaisgood et al. 2000). We therefore conducted a second study using simultaneous presentations in the hope of obtaining more robust evidence for this ability (Swaisgood et al. 2002). We presented eight male and 10 female pandas with urine from estrous and nonestrous females. Males but not females spent significantly more time investigating estrous than nonestrous female urine. Males also investigated, displayed flehmen and licked female urine in general (estrous and nonestrous samples combined) more than did females. Positive findings for estrous status discrimination by males but not females provides more compelling evidence that male preference for estrous female urine is part of a reproductive strategy, and not just the result of an arbitrary preference. For example, estrous females may produce stronger odors that were investigated more because of their greater olfactory valence, not their salience for reproduction. If true, however, pandas of both sexes should prefer estrous female odors.

The prevalence of flehmen by males during chemosensory investigation of female odors in both studies, coupled with the elevated rate of flehmen to estrous female urine in the second study, indicate an important role for the VNO in the

assessment of female reproductive condition. Because flehmen facilitates transport of nonvolatile chemicals to the VNO, flehmen is believed to be a good behavioral index of VNO utilization (Hart 1983). VNO analysis has been implicated for estrus discrimination and activation of sexual arousal in other mammalian species (Estes 1972; Hart 1983; Beauchamp et al. 1983; Johnston 1990). In addition, in both studies male pandas licked female odors more often than did females, suggesting that direct contact with female odors may be important for estrus discrimination, as has been shown for other species (Johnston 1990; Rivard & Klemm, 1990). Although licking may be important for gustatory analysis, it is perhaps more plausible that it functions to deliver less volatile chemical constituents to the VNO (Ladewig & Hart 1982).

Taken together, these two studies indicate that males can readily discriminate female reproductive condition on the basis of chemical cues, and that urine contains chemical constituents that change across the estrus cycle. These findings are consistent with the hypothesis that female urine, and perhaps other scents such as anogenital gland secretions, serve a reproductive advertisement function. Male odors probably also affect female reproductive strategies, as suggested by (1) higher rates of sexually motivated vocalizations in response to male than female odors (Swaisgood, et al. 2000), (2) female chemosensory preference for adult male over adult female urine (White 2001), (3) greater responsivity to male urine by females just prior to their fertile period (White et al. 2003.), (4) female preference for odors from reproductively mature males over odors from immature males (White et al. 2003), and (5) female preference for male odors plausibly indicating high competitive status (White et al. 2002).

These results suggest a clear role in the application of chemical communication for captive breeding programs. Indeed, “communication breakdown” is considered to be a primary determinant of reproductive failure in many captive-held species, especially those that are generally solitary (Lindburg 1999). Managers of captive pandas have struggled for years to overcome apparent behavioral deficits that hinder successful mating (He et al. 1994; Lindburg et al. 1997). The most frequently cited reasons for reproductive failure are excessive and sometimes injurious aggression, lack of sexual interest, or fear and avoidance of the opposite sex. Our experiments have shown that conspecific scent is important for recognition of sex and female reproductive condition, and that exposure to these scents may enhance sexual motivation and mitigate aggressive tendencies. In nature pandas would undoubtedly encounter such scents prior to direct contact with potential mates, and scent may play an important role in reducing the tendency to avoid or aggressively confront opposite-sexed conspecifics, while priming sexual motivation. A captive breeding program that incorporated such considerations should, therefore, achieve greater success.

Because of the highly endangered status of the panda, researchers are justly reluctant to deprive animals of opportunities that may promote mating success; it is therefore impractical to compare experimental groups given access to conspecific odors with control groups given no such exposure, a necessary procedure to adequately test the hypothesis that scent exposure and reproductive success are related. However, the breeding program at the Wolong breeding center provides compelling evidence consistent with this hypothesis. In recent years scent exposure has figured prominently in the behavioral management program (Swaisgood et al. 2000, In Press; Zhang et al.

In Revision). At the onset of behavioral estrus, the female is brought to an enclosure adjacent to a potential mating partner, and over the next several days the male and female are given frequent opportunities to investigate each other's odors. This is achieved by swapping the male and female into one another's enclosures. Concomitant with the development of this strategy, Wolong has begun to achieve ever-increasing success, and now about 90% of estrous females mate naturally each year (Swaisgood et al. In Press; Zhang et al. In Revision), a success rate unequaled by any other facility. Although other aspects of the management program also have changed during these years, the staff believe that this policy made a major contribution, in part because of the obvious and immediate effect that scent has on behavioral indicators of sexual motivation.

Our experiments do not provide a precise "recipe" for optimal scent exposure methods. However, it is worth noting that the experiment in which we presented a small amount of a single type of scent (i.e., female urine) did not promote behavioral indicators of sexual motivation to the same degree achieved by the pen-swapping method. Pen swapping exposes the panda to a whole suite of odors that saturate the environment, and it seems probable that such exposure to a complex gestalt of odors will greatly enhance the efficacy of its effects on sexual motivation, as has been found for some rodent species (Johnston 1990). In addition, if our hypothesis of VNO involvement in assessment of sexual odors is correct, simply allowing pandas to smell one another through cage bars between adjoining pens may not provide sufficient stimulation (Swaisgood et al. 2002). Thus, it may behoove managers at captive

breeding facilities to allow pandas direct access to one another's scent prior to mating introductions.

Assessment of Signaler Age and Competitive Ability

In another series of investigations we examined the role that chemical cues play in assessment of reproductive maturity and competitive ability (e. g., dominance, territorial status: White, et al. 2002, 2003). Although it is debatable exactly where pandas lie on the territorial continuum, they appear to be somewhat intolerant of intruders into core areas, and some aggression appears to be governed by spatial considerations. Escalated fights in pandas can have severe consequences, and pandas appear to make an effort to avoid direct encounters. Undoubtedly, confrontations with adults or high status individuals carry higher risks than those with subadults or low status individuals. Therefore, selection should favor individuals that adopt strategies for assessing maturity and fighting ability, and use this information to avoid risky encounters with individuals of high competitive status. Perhaps most useful in this regard is the extraction of information from chemical signals, as this allows the animal to make assessments without risking direct confrontation. Previous research with mice has shown that social odors may contain chemical cues related to signaler age (Brown and Macdonald 1985; Ma et al. 1999), and that discrimination of such odors may structure competitive interactions (Hurst 1989). Similarly, mice possess surprisingly sophisticated chemosensory assessment strategies for identifying individuals of high competitive status, and males use this information in decisions regarding avoidance, submission or challenging the chemical signaler (Gosling et al. 1996a, b; Drickamer 1997; Hurst 1990, 1993), while females base their mate preferences on this same information (Johnston et

al. 1997a; Rich & Hurst 1998, 1999; Hurst & Rich 1999). It also seems plausible that chemical signals might play an important role in governing reproductive behavior in the giant panda, especially given the brief 1-3 day female fertile period. With several female ranges overlapping a given male's range, it is important that the male identify which females should be monitored prior to the onset of the mating season, allowing him to concentrate his efforts on reproductively mature females. Similarly, females might use chemical cues to identify potential mates and assess male quality as it relates to age, dominance, and territory ownership.

In the first study, 25 pandas of all age-sex categories were presented with scent stimuli (male urine, male scent mark, female urine) collected from adults and subadults (White et al. 2003). The results clearly show that pandas from all age-sex categories prefer to investigate adult odors more than subadult conspecific odors of all three types, suggesting that this assessment task is fundamental to many giant panda social functions. The investigatory preference for odors from mature same-sexed individuals documented in this study may serve to gather information about the identity and status of competitors in the area (*sensu* Hurst 1989). Preferences for odors from adult opposite-sexed individuals might relate to identification of potential mates, but the possibility of competitive interactions between males and females should not be discounted. Given the high rate of inter-sexual aggression seen in captivity (Lindburg et al. 1997; Zhang, et al. In Revision) perhaps a consequence of misidentification of estrous females—it seems possible that aggressive competition between males and females occurs in wild pandas outside of the mating season. However, adult females showed no overt investigatory preferences between adult and subadult female urine,

suggesting that adult females have no need to assess the age of a same-sexed potential competitor. As these tests were conducted during the mating season, it is possible that such competition is important during other times of the year, for example, when pregnant females are competing for den sites for giving birth.

A second factor that may be correlated with risk and/or mate quality is competitive ability or status. Competitive ability could be conveyed through inherent chemical properties of the scent and/or through the pattern or frequency of scent marking (review in Hurst & Rich 1999), as well as deposition posture. For example, since larger animals can deposit scent higher than smaller ones, the height of a scent mark may afford reliable information regarding the signaler's body size, a known determinant of competitive ability (Huntingford & Turner 1987). If assessors begin to use the height of scent deposition as a cue of competitive ability, fitness benefits should accrue to signalers that exaggerate this cue by using postures to place scents even higher. This selective advantage offers one explanation for the curious use of the handstand posture in several mammalian species (Rasa 1973; Macdonald 1979, 1985; Kleiman 1983). Subsequent selection on the assessor may favor skeptical assessment of these exaggerated cues, as such bluffing will not remain an evolutionary stable strategy (see Krebs & Dawkins 1984). However, the maximum height of scent deposition in the handstand posture may still correlate with body size. Moreover, the use of such postures may be co-opted to advertise competitive status, such as territory ownership or dominance. Such a shift from advertisement of competitive ability to aggressive motivation has been proposed for vocal communication (Morton 1977).

It is well known that pandas use four different postures to deposit scents at varying heights, but the functions of these postures remain unknown. Reverse and leg cock postures, in which the panda backs into a vertical surface to deposit scent, have been seen in both males and females. Squats, where scent is deposited on the ground, are seen in all individuals, but mostly in subadults and females. Handstands have only been observed in adult males and usually only as a urine mark. Advertisement of competitive status (via selection to exaggerate apparent body size) may offer the most plausible explanation for the efforts that males go to when depositing urine in this handstand position. Indeed, males are less likely to use the handstand position when “trespassing” on another panda’s home area, perhaps to avoid assertion of dominance in an area that they do not normally occupy (Swaisgood et al. 2000).

In the second study we examined the effect of the height of the chemical signal on behavioral responsiveness (White et al. 2002). Adult male scent mark was placed at 0 m and 0.5 m to mimic squat and reverse/legcock postures frequently employed by adult males. Adult male urine was placed at 0 m and 1 m, reflecting the common placement of urine by males in either the squat or handstand position. Females usually scent mark in either the squat or reverse positions, and thus we placed female scent mark at 0 m and 0.5 m. Females infrequently urinate in any posture other than the squat posture and therefore female urine was not used in this experiment. The results demonstrated that the height of scent stimuli had a pronounced and highly significant effect on several measures of behavioral responsiveness. For example, males and females of all ages spent more time investigating scent stimuli placed high than those placed low, regardless of whether the scent was male scent mark, male urine, or female

scent mark. Thus, pandas may perceive conspecific odors placed high on vertical surfaces as indicating the presence of a more “important” animal, and therefore invest more time in memorizing the scent in order to recognize it again in the future. As hypothesized earlier, one reason for this perceived importance might be the relationship between height of scent mark deposition and competitive ability. Also consistent with this hypothesis is the finding that pandas showed a significant tendency to subsequently avoid the area where male urine was deposited at a height mimicking the handstand, presumably governed by the perceiver’s attempts to avoid confrontation with a high status male (cf. Gosling et al. 1996a, b; Hurst 1990, 1993). This aversive effect of high male urine was most pronounced in subadult males, who are arguably most at risk of injurious aggression from adult males of high competitive status. Females also showed a tendency to avoid male urine placed to mimic the handstand posture, which on the surface appears inconsistent with the hypothesis that females might mate preferentially with these males. However, because these females were not in estrus at the time of testing, it is possible that they would avoid high status males until the fertile period draws near. In sum, the conclusion most readily drawn from these results is that scent mark postures function in part to convey some aspects of competitive ability and/or status. Other hypotheses for the use of elevated postures, such as detection distance, and signaling sex or age status, are not supported by the evidence (see White et al. 2002).

Mother-Infant Recognition

Scent plays an important role in the mother-infant relationship in a number of species (Leon 1983), and it would be surprising if this were not true for the olfactorily-oriented

panda. We therefore have begun several investigations into the use of scent in mother-infant interactions in this species. Caretakers routinely wean the cub from the mother at about six months of age at the Wolong facility. One or two days after weaning, females were presented with the odor of their cub and the odor of a strange cub. In general, pandas prefer to investigate novel more than familiar conspecific odors (Swaisgood et al. 1999). However, we hypothesized that a female that had recently been separated from her cub might actively prefer the odor of her cub to the odor of a strange cub. Our results were consistent with this hypothesis in that females spent significantly more time sniffing their own cub's odor in comparison with the odor from a strange cub of the same age and sex. Interestingly, females also engaged in significantly more investigation of the environment after detecting their own cub's odor, perhaps because the odor stimulated further searching for the cub's whereabouts. The fact that mothers are capable of recognizing their cub via odors may have implications for management. For example, it may be important to provision a new mother with her cub's odors if the cub is removed for a period of hand-rearing, a strategy we have successfully employed (Zhang et al. 2000). Also, it might be possible to encourage a female to adopt a surrogate cub rejected by their biological mothers if the cub is first covered with the scent of her own cub. [Although females rarely rear two offspring from birth, females will provide care for two older cubs simultaneously; in addition, two cubs may be swapped back and forth between the nursery and the mother every few days (personal observations). Thus, it is probably possible to encourage a panda mother to rear a second unrelated offspring along side her own.

In a second experiment, cubs were presented with odors either from the mother or from a strange adult female. Odors were placed on a burlap sack stuffed with straw in order to provide the opportunity for the cub to express comfort-seeking behavior. Odor presentations were sequential rather than simultaneous. Cubs spent significantly more time sniffing the odor of their mother in comparison with the odor of a strange female. Other responses suggested that the mother's odors produced a calming effect on the generally agitated recently weaned cubs. Although the cub left the sack more frequently to engage in environmental investigation (presumably searching for the mother), the cub also returned to the sack more often, and spent more time resting quietly in contact with the sack. In contrast, when given a strange female's odor, cubs appeared much more agitated, as demonstrated by their greater number of escape attempts, distress vocalizations and bipedal postures. Because these signs of agitation did not differ substantively from the cub's behavior with no scented sack present, it does not appear that the sack with the strange odor increased the cub's distress. These results suggest a role for maternal odors in the mitigation of stress for a few days during the potentially traumatic transitional period following the rather abrupt weaning experienced by most captive panda cubs. In nature, olfaction probably plays a significant role in mother-cub recognition; because the mother and cub may be separated for hours or days (Lü et al. 1994; Zhu et al. 2001), such recognition should prevent misidentification upon reunion.

Discrimination of Individual Chemical Signatures

In addition to these and other "messages" afforded by giant panda scents, it is important for pandas to be able to recognize the identity of the signaler through individually

distinctive chemical signatures. Indeed, many of the above functions require as a prerequisite the ability to discriminate individual differences in conspecific odors (Halpin 1986; Swaisgood, et al. 1999). For example, mothers cannot reliably recognize their own cub's odor unless it contains a unique chemical profile differentiating it from other cubs' odors. Competitor assessment strategies might also be greatly enhanced by discrimination of individual odors: an individual that recognizes the scent of a high status individual may benefit if it can subsequently match that odor to the odor of an individual encountered in the environment (cf. Gosling 1982). This ability allows the individual to avoid potentially injurious escalation with a superior competitor without engaging in more direct probing of the individual's fighting ability and/or motivation. Adaptive female mate choice may also depend on the ability match scent found in the environment with potential mates. For example, they may prefer to mate with males whose scent is encountered most frequently in the environment because the predominance of a particular male's scent is a reliable cue of his ability to exclude rival males (Tang-Martinez et al. 1993; Hurst & Rich 1999). Individual discrimination is so important in some species that there is evidence that odors have become evolutionarily specialized to signal individual identity (e.g. Johnston et al. 1993).

As early as 1966 Morris and Morris suggested that scent marking in pandas served as a 'method of stamping the individual's identity on to its territory,' yet this basic ability was never tested. To determine if individual discrimination is indeed important in giant panda chemical communication, we conducted experiments using 20 adult pandas at the Wolong breeding center (Swaisgood et al. 1999). For pragmatic reasons, we used female urine and male anogenital gland secretions as odor stimuli. Using an

“habituation-discrimination” paradigm (see Halpin 1986), we exposed each subject to the scent of “panda A” repeatedly for five days, and the pandas’ response to this scent gradually diminished. On the sixth day we presented the subject with both the scent of panda A and another panda (“B”). The pandas showed a clear preference for the novel scent from panda B over the habituated scent from panda A, as evidenced by the amount of time spent investigating the two scents. Thus, panda A must *smell different* from panda B, implying that pandas produce individually distinct chemical profiles. Pandas readily discriminated between individuals on the basis of male anogenital gland secretions, but the preference for novel female urine did not quite attain statistical significance, suggesting that male odors or anogenital gland secretions from either sex (most probably the latter) contain more individually distinctive chemical cues. We suggest that anogenital gland secretions are perhaps specialized for this function.

Persistence of Odors through Time and Assessment of the Relative Age of Odors

Chemical signals are unique in that they persist in the environment long after the signaler has left, but eventually even these long-lasting signals will fade (Wilson & Bossert 1963). This temporal persistence allows relatively solitary species to communicate in absentia, greatly enhancing the efficiency of the chemical communication system. In order to understand chemical communication in the giant panda, we must determine how long these chemical signals remain biologically active. Are scent marks ephemeral chemical signals or can pandas detect them days or months later? In 1998 we conducted an experiment designed to test how long giant panda scent marks remain biologically active. We collected male anogenital gland secretions on wood blocks and aged them for approximately 120 days before

presenting them to 16 adult pandas. Although aged indoors, the window was open, and therefore temperature and humidity were comparable to that experienced in the panda's natural environment. Simultaneous presentations of these scent stimuli and identical unscented control blocks were used to assess whether pandas could discriminate between scented and unscented blocks. The results were dramatic: pandas spent only a few seconds investigating control blocks and more than 10 times as much time sniffing scented blocks. It is clear from these results that pandas are able to detect scents that are at least 120 days old under these conditions. At the time of this writing we are conducting a much larger experiment with urine and anogenital gland secretions aged for varying lengths of time outdoors, exposed to sun and rain. Clearly, the persistence of these scents in the environment has ramifications for the functional consequences of chemical communication for the species, as their biologically active period determines how soon another panda must locate the scent for communication to take place. Similarly, knowledge of persistence times will facilitate the use of scent for conservation efforts by providing temporal criteria for their effectiveness.

The ability to assess the relative age of a scent mark also may have important consequences for regulation of giant panda social behavior. As scent marks in the environment age, exposed to sun, air and moisture, they can degrade in fairly predictable ways (Regnier & Goodwin 1977). Volatile constituents are slowly lost, weakening the signal, and the chemical structure of some compounds may be altered. With some mammalian scents lasting more than 100 days (Johnston & Schmidt 1979), an area frequently used for scent marking by many animals may become a confusing and bewildering place unless perceivers possess the ability to determine the age of

scent marks. With the “background noise” of dozens of marks of varying ages, the task of signal detection and interpretation may be rendered difficult. It is just such a challenge that giant pandas confront when visiting communal scent mark stations. The ability to accurately age scents might confer other advantages as well. Patrol intervals of the signaler might be deduced from the amount of time elapsing between bouts of marking in a particular area. How recently a scent has been deposited might also be important because fresh scents might indicate that the signaler is still in the area, enabling the assessor to avoid or challenge the signaler as appropriate. The ability to determine the age of scent might also come into play in the male’s efforts to locate fertile females. For example, one-week old scent from an estrous female informs the male that female has most likely ovulated, rendering further pursuit unprofitable.

In the spring of 1999 we conducted several experiments which show that pandas can indeed tell the difference between scents of different ages. Our experiment with 15 adults and 9 subadults demonstrated that adult pandas can discriminate between fresh vs. 1-day old scent, fresh vs. 3-day old scent, and 1-day vs. 5-day old scent. In all cases, adult pandas spent significantly more time investigating fresher scent marks than older ones. In contrast, subadults, while equally interested in investigating conspecific odors, did not show any tendency to prefer fresh odors over older odors. One interpretation of these findings is that young pandas must learn to discriminate between these odors through repeated exposure to conspecific odor. Alternatively, the ability and/or motivation to discriminate among these odors may be the result of a simple maturational process, perhaps mediated by reproductive hormones. Regardless, this

research highlights the importance of exploring the ontogeny of the chemical communication system in giant pandas.

Conclusions

From these studies we are beginning to gain meaningful insights into the pervasive role that social odors play in the social lives of giant pandas. Conspecific odors' governing influence appears to run the gamut across all aspects of social behavior, ranging from the mother-cub relationship to reproductive behavior and competition. Pandas possess a suite of sophisticated discriminatory abilities for distinguishing between odors emanating from various categories of conspecifics, and the pattern of response often varies with the sex, age and reproductive condition of the perceiver in ways meaningful to the fulfillment of specific functional endpoints. Although our tests were conducted on captive animals, it seems reasonable that all of these abilities come into play in the regulation of social behavior among wild pandas. One might expect captive animals to lose some of these chemosensory abilities, but it seems highly implausible that these abilities are somehow the artifact of captivity, especially given their important functional implications. Moreover, it is important to point out that it would be virtually impossible to conduct such tests on wild pandas; the researcher would have to monitor an experimentally placed scent for days or weeks before it was discovered, and by that time the response would be confounded by the age of the scent. Nonetheless, it is important to obtain more data on giant panda social dynamics in the wild in order to place these experiments in appropriate context in nature.

Throughout this paper we have also suggested potential applications of these experimental results to management and conservation of the species in the wild and captivity. Ramifications of the results obtained are most readily evident in the use of scent to encourage natural mating in captivity. In addition to a potential role in activating sexual motivation discussed earlier, it might also be possible to use scent to recruit new breeders into the captive population that may well suffer from lack of genetic diversity. For example, we may be able to encourage a female to mate with a particular male that is genetically unrepresented by manipulating the female's mating preference. It has been shown in some rodent species that females will use olfactory cues to mate preferentially with males of high competitive ability (Johnston et al. 1997b; Hurst & Rich 1999). Females may use encounter rate, relative predominance of the male's scent over other males, or prevalence of countermarking on top of other males' scents as an indicator of the male's ability to exclude other males or effectively patrol and maintain his chemical signature as the predominant one in the area. We have recently used this idea to manipulate female mate preference in another threatened species, the pygmy loris (Fisher et al. 2003; unpublished data). We presented six females with a particular male's odor repeatedly for three months, and then provided the female with a choice between the familiar-smelling male and a novel-smelling male. In all six cases the female displayed more sexual interest in the familiar-smelling male. In the case of pandas it might also be important to consider the height of presentation of the male's scent, since this may also be used as a cue of male competitive ability. It is important to point out, however, that conspecific odors can have both suppressive or facilitative

effects on reproduction (Doty 1986; Bronson 1989; Bartos & Rödl 1990; Lindburg 1999), and thus the effects of odors should be studied carefully and used judiciously.

We also envision a day when it might be possible to apply what we have learned in captivity directly toward the conservation of the panda in the wild. For example, one can make a strong case for a role for scent in habitat selection and settlement. There is growing evidence that many species use the presence of conspecifics as a cue to habitat quality, following the rule of thumb that if the area is safe and productive enough to support other members of the species, then it must be a good place to settle (Stamps 1988; Reed & Dobson 1993). This behavioral mechanism raises the possibility of “planting” conspecifics or cues from conspecifics to encourage settlement in unoccupied areas, such as new reserves or “habitat corridors” between islands of habitat. In pandas, where olfaction reigns supreme, it may be possible to place conspecific odors in these areas to encourage pandas to use them, with the caveat that some odors may be aversive rather than attractive. For example, there is the distinct possibility that odors from adult males placed on trees at the level of a handstand urine mark may actually deter pandas from entering the area, especially individuals of low competitive ability. A thorough understanding of how pandas of all age-sex classes respond to various conspecific odors is crucial for the successful application of scent in such conservation measures.

Scent may also provide a useful tool in proposed reintroduction efforts (see Swaisgood et al. 1999). Many reintroductions and translocations fail because the released animal fails to remain at the release site or because of excessive aggression between the reintroducee and resident conspecifics (Yalden 1993; Reading & Clark

1996). It may be possible for researchers to use a reintroducee's own scent to pre-establish a home range by depositing scent throughout the area for several months prior to release. This may have several beneficial consequences for the reintroduction. First, it might encourage the reintroducee to remain in the area where it encounters its own scent, as this may diminish the stress response to the novel environment. Second, it may discourage neighboring pandas from aggressively confronting the released panda. This second effect relies on the applicability to pandas of Gosling's (1982) scent-matching hypothesis for recognizing territory owners. Under this hypothesis animals recognize territory owners by matching the scent that predominates in the environment with the scent of an individual that is encountered in the area. Since only an animal that is occupying and successfully defending an area will deposit its scent frequently in the area, this provides a reliable cue of territory occupation. Territory owners have proven their competitive ability in maintaining the territory and are also more motivated to fight in defense of this resource. Thus, it behooves other animals to recognize such individuals and avoid an escalated contest with them. If pandas use this strategy, it may be possible to "fake" territory ownership prior to the animal's release, thereby mitigating aggressive interactions with neighboring pandas.

We still have much to learn about chemical communication in giant pandas, in particular the role it plays in regulating social dynamics in the wild. Continued research efforts in these areas hold promise for both a deeper understanding of the animal and more informed management of the species in the wild and captivity.

Acknowledgments

We express our sincere gratitude to the State Forestry Administration of China and the Zoological Society of San Diego for their generous support, and the Wolong animal care staff for their assistance. Ronald R. Swaisgood's position was supported by a donation from J. Dallas Clark.

References

- Bartos, L., and P. Rödl. 1990. Effect of a conspecific's urine on reproduction in arctic foxes. In *Chemical Signals in Vertebrates. Vol. 5*, edited by D. W. MacDonald, D. Müller-Schwarze and S. E. Natynczuk. Oxford: Oxford University Press.
- Beauchamp, G. K., G. I. Martin, J. L. Wellington, and C. J. Wysocki. 1983. The accessory olfactory system: role in maintenance of chemoinvestigatory behaviour. In *Chemical Signals in Vertebrates. Vol. 3*, edited by D. Müller-Schwarze and R. M. Silverstein. New York: Plenum.
- Bronson, F. H. 1989. *Mammalian Reproductive Biology*. Chicago: University of Chicago Press.
- Brown, R. E., and D. W. Macdonald, eds. 1985. *Social Odours in Mammals*. Oxford: Clarendon Press.
- Brown, R. E. 1979. Mammalian social odors: a critical review. In *Advances in the Study of Behavior. Vol. 10*, edited by J. S. Rosenblatt, R. A. Hinde, C. Beer and M. C. Busnel. New York: Academic Press.
- Connor, J. 1972. Olfactory control of aggressive and sexual behavior in the mouse (*Mus musculus*). *Psychonomic Sciences* 27:1-3.

- Dixson, A. K., and J. H. Mackintosh. 1971. Effects of female urine upon the social behaviour of adult male mice. *Animal Behaviour* 19:138-140.
- Doty, R. L. 1986. Odor-guided behavior in mammals. *Experientia* 42:257-271.
- Drickamer, L. C. 1997. Responses to odors of dominant and subordinate house mice (*Mus domesticus*) in live traps and responses to odors in live traps by dominant and subordinate males. *Journal of Chemical Ecology* 23:2493-2506.
- Estes, R. D. 1972. The role of the vomeronasal organ in mammalian reproduction. *Mammalia* 36:315-341.
- Fisher, H. S., R. R. Swaisgood, and H. Fitch-Snyder. 2003. Countermarking by male pygmy lorises (*Nycticebus pygmaeus*): do females use odor cues to select mates with high competitive ability? *Behavioral Ecology and Sociobiology* 53:123-130.
- Floody, O. R., D. W. Pfaff, and C. D. Lewis. 1977. Communication among hamsters by high-frequency acoustic signals II. Determinants of calling by females and males. *Journal of Comparative and Physiological Psychology* 91:807-819.
- Gosling, L. M. 1982. A reassessment of the function of scent marking in territories. *Zeitschrift für Tierpsychologie* 60:89-118.
- Gosling, L. M., N. W. Atkinson, S. A. Collins, R. J. Roberts, and R. L. Walters. 1996a. Avoidance of scent-marked areas depends on the intruder's body size. *Behav* 133: 491-502.
- Gosling, L. M., N. W. Atkinson, S. Dunn, and S. A. Collins. 1996b. The response of subordinate male mice to scent mark varies in relation to their own competitive ability. *Anim Behav* 52: 1185-1191.

- Halpin, Z. T. 1986. Individual odors among mammals: origins and functions. *Adv. Study Behav.* 16:39-70.
- Hart, B. L. 1983. Flehmen behavior and vomeronasal organ function. In *Chemical Signals in Vertebrates. Vol. 3*, edited by D. Müller-Schwarze and R. M. Silverstein. New York: Plenum.
- He, T., K. Zhang, H. Zhang, R. Wei, C. Tang, G. Zhang, and M. Cheng. 1994. Training male giant pandas for natural mating. In *Proceedings of the International Symposium on the Protection of the Giant Panda (Ailuropoda melanoleuca)*, edited by A. Zhang and G. He. Chengdu. China: Chengdu Foundation of Giant Panda Breeding.
- Huntingford, F., and A. Turner. 1987. *Animal Conflict*. London: Chapman & Hall.
- Hurst, J. L. 1989. The complex network of olfactory communication in populations of wild house mice *Mus domesticus* Rutt: urine marking and investigation within family groups. *Animal Behaviour* 37:705-725.
- Hurst, J. L. 1990. Urine marking in populations of wild house mice *Mus domesticus* Rutt. I. Communication between males. *Animal Behaviour* 40:209-222.
- Hurst, J. L., and T. J. Rich. 1999. Scent marks as competitive signals of mate quality. In *Advances in Chemical Communication in Vertebrates*, edited by R. E. Johnston, D. Müller-Schwarze and P. Sorensen. New York: Kluwer Academic.
- Hurst, J. L. 1993. The priming effects of urine substrate marks on interactions between male house mice, *Mus musculus domesticus* Schwarz and Schwarz. *Animal Behaviour* 45 (1):55-81.

- Johnston, R. E., E. S. Sorokin, and M. H. Ferkin. 1997. Female voles discriminate males' over-marks and prefer top-scent males. *Animal Behaviour* 54:679-690.
- Johnston, R. E., E. S. Sorokin, and M. H. Ferkin. 1997. Scent counter-marking by male meadow voles: females prefer the top-scent male. *Ethology* 103:443-453.
- Johnston, R. E., A. Derzie, G. Chiang, P. Jernigan, and L. Ho-Chang. 1993. Individual scent signatures in golden hamsters: evidence for specialization of function. *Animal Behaviour* 45:1061-1070.
- Johnston, R. E., and T. Schmidt. 1979. Responses of hamsters to scent marks of different ages. *Behavioral and Neural Biology* 26:64-75.
- Johnston, R. E. 1990. Chemical communication in golden hamsters: from behavior to molecules to neural mechanisms. In *Contemporary Trends in Comparative Psychology*, edited by D. E. Dewsbury. Sunderland, Massachusetts: Sinauer.
- Kleiman, D. G. 1983. Ethology and reproduction of captive giant pandas (*Ailuropoda melanoleuca*). *Zeitschrift für Tierpsychologie* 62:1-46.
- Kleiman, D. G., and G. Peters. 1990. Auditory communication in the giant panda: motivation and function. In *Proceedings of the Second International Symposium on the Giant Panda*, edited by S. Asakura and S. Nakagawa. Tokyo: Tokyo Zoological Park Society.
- Krebs, J. R., and R. Dawkins. 1984. Animal signals: mind-reading and manipulation. In *Behavioural Ecology: An Evolutionary Approach*, edited by J. R. Krebs and N. B. Davies. Sunderland, Massachusetts: Sinauer.
- Ladewig, J., and B. L. Hart. 1982. Flehmen and vomeronasal organ function. In *Olfaction and Endocrine Regulation*, edited by W. Breipohl. London: IRL Press.

- Leon, M. 1983. Chemical communication in mother-young interactions. In *Pheromones and Reproduction in Mammals*, edited by J. G. Vandenberg. New York: Academic Press.
- Lindburg, D G. 1999. Zoos as arks: issues in ex situ propagation of endangered wildlife. In *The New Physical Anthropology: Science, Humanism, and Critical Reflection*, edited by S. C. Strum, D. G. Lindburg and D. Hamburg. Upper Saddle River, New Jersey: Prentice Hall.
- Lindburg, D. G., X. Huang, and S. Huang. 1998. Reproductive performance of giant panda males in Chinese zoos. In *Proceedings of the International Symposium on the Protection of the Giant Panda (*Ailuropoda melanoleuca*)*. edited by A. Zhang and G. He. Chengdu, China: Sichuan Publishing House of Science and Technology.
- Lü, Z., W. Pan, and J. Harkness. 1994. Mother-cub relationships in Giant pandas in the Quinling Mountains, China, with comment on rescuing abandoned cubs. *Zoo Biology* 13:567-568.
- Ma, W., D. Wiesler, and M. V. Novotny. 1999. Urinary volatile profiles of the deermouse (*Peromyscus maniculatus*) pertaining to gender and age. *Journal of Chemical Ecology* 25:417-431.
- Macdonald, D. W. 1985. The primates II: a case study of the saddle-back tamarin, *Saguinis fudicollis*. In *Social Odours in Mammals, Vol. 2*, edited by R. E. Brown and D. W. Macdonald. Oxford: Clarendon Press.
- Macdonald, D. W. 1979. Some observations and field experiments on the urine marking behavior of the red fox, *Vulpus vulpus* L. *Zeitschrift für Tierpsychologie* 51:1-22.
- Morris, R., and D. Morris. 1966. *Men and Pandas*. New York: McGraw-Hill.

- Morton, E. S. 1977. On the occurrence and significance of motivation-structural rules in some bird and mammal sounds. *American Naturalist* 111:855-869.
- Platz, C. C., D. E. Wildt, J. G. Howard, and M. Bush. 1983. Electroejaculation and semen analysis and freezing in the giant panda (*Ailuropoda melanoleuca*). *Journal of Reproduction and Fertility* 67:9-12.
- Rasa, A. E. 1973. Marking behaviour and its social significance in the African dwarf mongoose, *Helogale undulata rufula*. *Zeitschrift für Tierpsychologie* 32:293-318.
- Rasmussen, L. E. L. 1997. Purification, identification, concentration and bioactivity of (Z)-7-dodecen-1-yl acetate: sex pheromone of the female Asian elephant, *Elephas maximus*. *Chemical Senses* 22:417-437.
- Reading, R. P., and T. W. Clark. 1996. Carnivore reintroductions: an interdisciplinary examination. In *Carnivore behavior, ecology, and evolution*, edited by J. L. Gittleman. Ithaca: Cornell University Press.
- Rich, T. J., and J. L. Hurst. 1999. The competing countermarks hypothesis: reliable assessment of competitive ability by potential mates. *Animal Behaviour* 58:1027-1037.
- Rich, T. J., and J. L. Hurst. 1998. Scent marks as reliable signals of the competitive ability of mates. *Animal Behaviour* 56 (3):727-735.
- Rivard, G., and W. R. Klemm. 1990. Sample contact required for complete bull response to oestrous pheromone in cattle. In *Chemical Signals in Vertebrates. Vol. 5*, edited by D. W. MacDonald, D. Müller-Schwarze and S. E. Natynczuk. Oxford: Oxford University Press.
- Schaller, G. B. 1993. *The Last Panda*. Chicago: University of Chicago Press.

- Schaller, G. B., J. Hu, W. Pan, and J. Zhu. 1985. *The Giant Pandas of Wolong*. Chicago: University of Chicago Press.
- Schulte, B. A., and L. E. L. Rasmussen. 1999. Signal-receiver interplay in the communication of male condition by Asian elephants. *Animal Behaviour* 57:1265-1274.
- Stamps, J. A. 1988. Conspecific attraction and aggregation in territorial species. *American Naturalist* 131:329-347.
- Swaigood, R. R., D. G. Lindburg, and H. Zhang. 2002. Discrimination of oestrous status in giant pandas via chemical cues in urine. *Journal of Zoology, London* 257:381-386.
- Swaigood, R. R., D. G. Lindburg, and X. Zhou. 1999. Giant pandas discriminate individual differences in conspecific scent. *Animal Behaviour* 57:1045-1053.
- Swaigood, R. R., X. Zhou, G. Zhang, D. G. Lindburg, and H. Zhang. In press. Application of behavioral knowledge to giant panda conservation. *International Journal of Comparative Psychology*.
- Swaigood, R. R., D. G. Lindburg, X. Zhou, and M. A. Owen. 2000. The effects of sex, reproductive condition and context on discrimination of conspecific odours by giant pandas. *Animal Behaviour* 60:227-237.
- Taylor, S. A., and D. A. Dewsbury. 1990. Male preferences for females of different reproductive conditions: a critical review. In *Chemical Signals in Vertebrates. Vol. 5*, edited by D. W. Macdonald, D. Müller-Schwarze and S. E. Natynczuk. Oxford: Oxford University Press.

- Vandenburgh, J. G. 1983. *Pheromones and Reproduction in Mammals*. New York: Academic Press.
- White, A. M. 2001. Chemical communication in giant pandas: the role of marking posture and age of signaler, Masters thesis, San Diego State University, San Diego.
- White, A. M., R. R. Swaisgood, and H. Zhang. 2002. The highs and lows of chemical communication in giant pandas (*Ailuropoda melanoleuca*): effect of scent deposition height on signal discrimination. *Behav Ecol Sociobiol.* 51:519-529.
- White, A. M., R. R. Swaisgood, and H. Zhang. 2003. Chemical communication in giant pandas: the role of signaler and assessor age. *J Zool Lond* 259: 171-178.
- Wilson, E. O., and W. H. Bossert. 1963. Chemical communication among animals. *Recent Progress in Hormone Research* 19:673-716.
- Yalden, D. W. 1993. The problems of reintroducing carnivores. *Symposium of the Zoological Society of London* 65:289-306.
- Zhang, G. Q., R. R. Swaisgood, R. P. Wei, H. M. Zhang, H. Y. Han, D. S. Li, L. F. Wu, A. M. White, and D. G. Lindburg. 2000. A method for encouraging maternal care in the giant panda. *Zoo Biology* 19:53-63.
- Zhang, G., R. R. Swaisgood, and H. Zhang. In Revision. An evaluation of behavioral factors influencing reproductive success and failure in captive giant pandas. *Zoo Biology*.
- Zhu, X., D. G. Lindburg, W. Pan, K. A. Forney, and D. Wang. 2001. The reproductive strategy of giant pandas: infant growth and development and mother-infant relationships. *Journal of Zoology, London* 253:141-155.