

Behavioural changes associated with oestrus in the Giant panda

Ailuropoda melanoleuca

with comments on female proceptive behaviour

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The Giant panda *Ailuropoda melanoleuca* has been the subject of many scientific and popular treatises since the first Chinese writings of the seventh century AD. More recent publications have continued to review both facts and fancy concerning the life history and behaviour of this species (Morris & Morris, 1966; Collins & Page, 1973; Davis, 1973; Perry, 1973; Sheldon, 1975). Yet we remain largely ignorant of some of the most essential aspects of Giant panda behaviour, except at a descriptive level. The most thorough treatment of reproduction in *A. melanoleuca* has been published by the Peking Zoo (Anon, 1974). Reported behavioural changes associated with oestrus and breeding between March and May include greater activity in both sexes, decreased food consumption, especially by the ♀, increased urination by the ♂, and the occurrence of a 'bleat' vocalisation in both sexes (Morris & Morris, 1966; Anon, 1974). As oestrus approaches, the vaginal orifice becomes red and swollen and the ♀ may rub the genital region with the paw or on objects. Descriptions of copulation suggest that it is short and that the ♂ may be in a half-seated position behind the ♀ (Anon, 1974).

This report documents some aspects of the development of socio-sexual behaviour in a pair of Giant pandas at the National Zoological Park, Washington. Data are presented on behavioural changes in the ♂ and ♀ associated with the breeding season and oestrus. Of most importance,

however, we will report on the predominance of ♀ 'proceptive' behaviour (Beach, 1976), which suggests that the ♀ Giant panda has an extremely active role in initiating and controlling the interactions of the pair prior to mating. The importance of ♀ activities in influencing the time and occurrence of copulation until recently has generally been ignored (Doty, 1974; Beach, 1976).

METHODS

A ♂ 'Hsing-Hsing' and a ♀ 'Ling-Ling' Giant panda were received in April 1972 as a gift from the People's Republic of China. They were one and one-and-a-half years old respectively. Housing has been described in detail by Melun (1975) and management techniques and acclimatisation by Collins & Page (1973). The pair are housed separately during most of the year, although they can and do interact through galvanised steel mesh partitions. Introductions have been conducted only prior to and during oestrus.

The data presented in this paper are derived from three main sources. Since November 1972, usually at six-month intervals, nocturnal watches have been conducted, using trained volunteer observers from the Friends of the National Zoo (FONZ). A watch typically runs from 1600 to 0700 hours the following morning for seven consecutive days. The following behaviours are recorded on a checklist: eating, resting or

sleeping, playing, walking or pacing, scent-marking, elimination and grooming. Preliminary results from these watches and further details on the data recording techniques may be found in Kleiman (1974). Data are expressed as the average number of minutes per hour for long duration activities, and the frequency per hour for discrete behaviour patterns like scent-marking.

To monitor the onset of oestrus, both detailed keeper records and daily morning observations (between 0900–1100 hours) of one hour's duration have been used. The hour-long watches have been conducted by trained FONZ volunteers and the senior author, using a checksheet divided into one-minute segments. Activities such as eating, resting and walking were checked if they occurred within a minute. Thus, the results are expressed as the average number of minute blocks per hour during which the activity occurred. Behaviour patterns of short duration are expressed as average frequencies per hour. Although the bleat vocalisation (Morris & Morris, 1966) is a discrete behaviour pattern, it is emitted so continuously by both sexes around oestrus that data on bleating are presented as though it were a continuous activity.

The pandas have usually been introduced only shortly before and during the ♀'s receptive period, following the recommendations of Chinese zoologists (Anon, 1974). Such encounters are conducted between 0600–1000 hours and again from 1600–2000 hours. Encounter length depends on the behaviour of the pair, but some have continued for as long as three hours. During encounters behavioural interactions have been filmed using a videotape recorder, and observations are dictated continuously into a tape recorder.

The data presented here on behaviour during encounters are from the videotape recordings collected during oestrous periods between 1974–1977. A detailed analysis of the relative time spent 'on top' by the ♂ and ♀ will be given. The measurement 'on top' refers to the situation where one individual has its paws or other body parts on top of the partner. It may include standing over the partner and true mounting by the ♂, but also situations where one animal is sitting upright, but draped over the partner who is either sitting or lying on the side or back. This behaviour is often accompanied by gentle (or even hard)

biting directed towards the partner's limbs, black shoulder markings, ears, cheeks and rump. The percentage of time on top for each animal was calculated by dividing its time on top by the 'total time' from first physical contact to the end of a tape segment.

RESULTS

A. GIANT PANDA BEHAVIOUR

Captive Giant pandas display many behaviour patterns common to other carnivores, but with some unique characteristics. In this section, we will briefly describe their social behaviour and communication.

Olfactory communication: Giant pandas scent-mark with urine and secretions from the anogenital region, using a variety of postures. Squatting and rubbing the perineum on a surface is common to both sexes. On a vertical surface, a leg lift may be used to permit anogenital contact and rubbing. The ♂ often urinates and/or rubs the perineum in the leg-lift posture while the ♀ generally only rubs the anogenital region. The ♂ occasionally urinates in a 'handstand' position where both hind limbs are raised off the substrate; as a juvenile he would urinate and rub the anogenital region in a handstand. Both sexes sniff marking sites extensively, and there is a noticeable build-up of secretions and discoloration at preferred locales.

Defaecation may or may not have a marking function. There is a tendency for the pandas to defaecate at a limited number of sites. Defaecation is often accomplished while lying on the venter above the ground (e.g. on a platform or rock pile) so that the faeces drop below the animal.

There are two related behaviours which may have both a grooming and scent-marking function. The Giant pandas will rub various parts of the body, but especially the nape, cheeks, shoulders and rump, on walls or other vertical surfaces and on the ground. Nape, cheek and shoulder rubbing on the mesh partition is common during interactions when the animals are separated. Rubbing of the nape and shoulders also occurs on sites which have been scent-marked with urine and secretions from the anogenital region. Body rubbing in soil or on grass is typically done while lying on the back, and resembles the rolling and writhing of dogs. Sod or clumps of grass and soil

as well as objects with strong odours may be picked up in the paws and rubbed vigorously over the body.

Vocalisation: The most conspicuous Giant panda vocalisation is the bleat (Morris & Morris, 1966), which is common in both sexes at the ♀'s oestrus. The ♀ also produces a 'chirp', a high-pitched, short, frequency-modulated sound, during the major period of receptivity. A low-pitched 'growl' and 'bark' occur during agonistic interactions and a 'squeal' when an animal is hurt or frightened. The bleat and chirp may intergrade with a 'whine' during bouts of near continuous vocalising when the ♀ is receptive (Kleiman, in prep.).

Visual communication: Somersaults and rolls onto the side or back occur as invitations to play (Wilson & Kleiman, 1974) or to signify non-aggressive intentions. At close contact, paw swats, pounces or body thrusts towards the partner act as threats. Piloerection as a threat has not been seen, but may not be easily distinguished owing to the short dense fur of the Giant panda. In general, the Giant panda does not have conspicuous body postures to indicate motivational tendencies such as aggression, fear, and threat. Moreover, the face and ears are less mobile than in carnivores such as canids, probably on account of the massive skull and jaws—an adaptation for feeding on bamboo. Thus, facial expressions seem relatively unimportant in visual communication.

Tactile communication: During encounters, both before and during oestrus, physical contact is common. Most body contact outside of the ♀'s receptive period includes gentle biting of the partner on cheeks, nape, black shoulder markings, limbs and tail, which is initiated by the ♀. The bites may include rapid open-mouthed jabs or a firm grip with vigorous head shaking. Pawing or swatting at the ♂ and pouncing from an upright position are common, as is pushing the ♂ onto the back or side using the massive head and forequarters. Mutual upright postures with paw swatting and an increase in the intensity and vigour of biting (jabbing) may signify an escalation of the interaction which can lead to fighting. Conflicts in our Giant pandas have

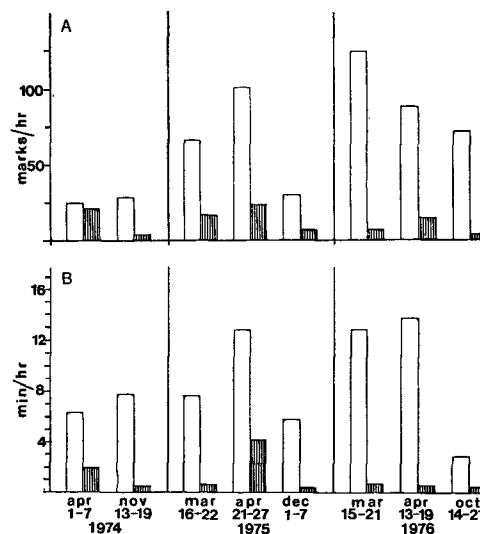


Fig. 1. Average frequency of Giant panda *Ailuropoda melanoleuca* scent-marking (A) and pacing (B) during spring and autumn week-long nocturnal watches (1800-0600 hours) between 1974-1976. ♂ = white bars; ♀ = shaded bars.

usually been initiated by the ♂ after a long period of ♀-initiated contact, and are accompanied by piercing squeals and withdrawal by the ♀ and growls with biting by the ♂. Although such interactions appear extremely serious because of the loud vocalisations and vigorous rapid movements of the animals, no serious wounds have resulted except for a sprained forepaw in the ♀. It is difficult to predict with certainty the onset of such an interaction, although reduced passivity on the part of the ♂ may be a cue.

B. SEASONAL BEHAVIOUR CHANGES

Activity patterns and food consumption change with the seasons. As the annual period of reproduction approaches, both ♂ and ♀ exhibit increased activity. It appears likely that the ♂ has an annual rut since behaviour changes in the ♂ may precede those in the ♀.

Figure 1 presents the average hourly scent-marking and pacing frequencies for seven nights between 1800-0600 hours in the ♂ and ♀ Giant panda in 1974, 1975 and 1976. The data illustrate that ♂ scent-marking frequencies have increased each year as he has approached sexual maturity, and have been higher in the spring than in the

ACTIVITY	1973	1974	1975	1976	1977
Decreased food consumption	13 May	18 Apr	19 Apr	29 Mar	3 Apr
Walking backwards	20 May	15 Apr	24 Apr	23 Mar	10 Apr
Increased ♀ scent-marking	?	3 Apr	23 Apr	30 Mar	5 Apr
♂ 'bleating'	?	3 Apr	?	4 Apr	9 Apr
♀ 'bleating'	18 May	10 Apr	21 Apr	4 Apr	9 Apr
♀ 'chirping'	?	15 Apr	25 Apr	?	11 Apr
Persistent ♀ anogenital rubbing (masturbation)	24 May	22 Apr	24 Apr	9 Apr	14 Apr
Increased pair interaction	26 May	15 Apr	21 Apr	10 Apr	15 Apr
Encounters					
begin	26 May	19 Apr	26 Apr	17 Apr	11 Apr
end	27 May	25 Apr	4 May	19 Apr	18 Apr
First ♀ lordosis	26 May	20 Apr	26 Apr	—	15 Apr
Peak receptivity	26–27 May	20–22 Apr	30 Apr–4 May	10–14 Apr	16–18 Apr

Table 1. Annual oestrus of 'Ling-Ling', ♀ Giant panda *Ailuropoda melanoleuca* at the National Zoological Park, Washington. Dates given are usually the first observations of a noticeable change in the frequency of a particular behaviour pattern or activity. (Variability in dates of first observations of activities reflects, to some degree, variation in the intensity of observations in any given year.)

autumn. It is interesting that ♂ marking frequencies were extremely high during the first two nocturnal watches in November 1972 and April 1973 (Kleiman, 1974), at a time when the pandas were housed at night in adjacent cages; their indoor cages are now separated by a corridor.

Female scent-marking frequencies are much lower than those of the ♂, but tend also to increase before oestrus (see Table 1 for dates of ♀ receptivity). Low scent-marking frequencies in April 1976 reflect the fact that the night watches were conducted towards the end of, and after, the ♀'s major receptive period.

Overall activity, as measured by walking or pacing at night, shows the same seasonal changes (see Fig. 1), with the ♂ exhibiting increased activity as he has matured. The unusually low activity of the ♀ in April 1976, like scent-marking, is due to the late scheduling of observations. The data suggest that ♀ scent-marking and activity are more closely correlated with oestrus while the ♂ has a spring rutting period over a broader span of time.

C. REPRODUCTIVE CYCLE

The Giant panda ♀, Ling-Ling, has shown an annual period of heat since 1973, when she was only two-and-a-half years old. The onset of oestrus has always been very conspicuous,

beginning with decreased food consumption, increased scent-marking, backwards walking, and vocalising (bleating). The major impetus for the inception of encounters between the pair has usually been a dramatic increase in anogenital rubbing or masturbation by the ♀ (on objects or with the paw) or an increase in the frequency of interactions at sites where the two animals can see and sniff each other. Table 1 details the onset of Ling-Ling's annual oestrous periods from 1973 to 1977. No strong signs of heat have yet been observed in the autumn although Giant panda ♀♀ are occasionally reported to have an autumn oestrus (Morris & Morris, 1966; Anon, 1974; Brambell, 1978).

Figure 2 presents a more detailed analysis of changes in feeding, scent-marking and bleating before and during oestrus from morning observations conducted in 1976 and 1977. Feeding behaviour decreases in frequency in the ♀ as oestrus approaches. Male feeding activity appears more variable. Scent-marking in the ♀ is common only during the two to three weeks preceding oestrus and drops off rapidly following receptivity. Again, ♂ scent-marking frequencies are more variable. The bleating vocalisation is mainly conspicuous in the week preceding, and during oestrus. The increase in ♂ bleating in 1977 relative to 1976 may reflect the onset of sexual maturity.

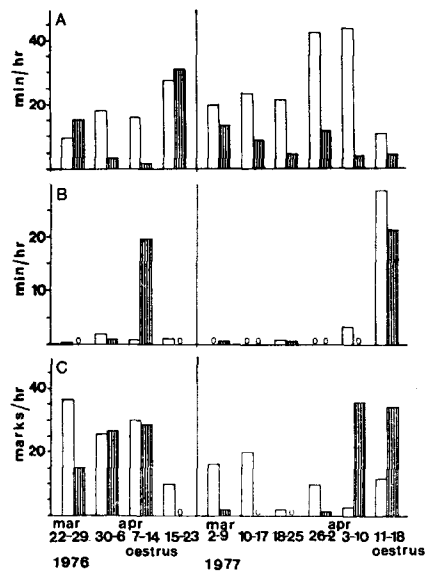


Fig. 2. Average frequency of Giant panda eating (A), vocalising (B), and scent-marking (C) during morning watches before and during oestrus in 1976 and 1977. ♂=white bars; ♀=shaded bars.

D. INTERACTION AT OESTRUS

The major forms of social contact in the Giant panda pair have already been described above. The most conspicuous characteristic of pro-oestrous behaviour has been the control that the ♀ apparently exerts over the interaction. Upon introduction, physical contact between the pair is achieved immediately, and the ♀ begins to 'mount' and bite or jab at the ♂. During such interactions, the ♂ maintains an essentially passive posture, often lying unresisting on the back or side. He may periodically stand and attempt to reverse positions, but rarely stands over the ♀ for long. Separation is usually initiated by the ♀, who sits in a corner, paw swatting and vocalising in response to any ♂ approach, and using a short frequency-modulated vocalisation to indicate her intolerance. After several such attempted approaches, including those accompanied by his lying on the back or side in front of the ♀, the ♂ may leave. Once the first intense post-introduction interactions are terminated, the ♀ may keep the ♂ at a distance simply by vocalising.

As peak receptivity approaches, the nature of the encounter changes. The ♀ becomes less assertive and allows the ♂ to mount. While he

does so, she will stand quietly and may periodically lift the tail and depress the back. Lordosis is displayed more commonly when the ♂ has the forepaws extended and placed on the centre of the ♀'s back. During peak oestrus, the ♀ may stand for periods of up to several minutes allowing multiple mounts by the ♂. At this point it is the ♂ who is essentially responsible for initiating and terminating physical contact. When the two are separated, the ♀ may approach the ♂, bleating as she does so, and orient her hindquarters towards him prior to making contact. This typically provokes an approach and mount from the ♂. The receptive ♀ may also spontaneously exhibit lordosis with a raised tail, without physical contact or a moult by the ♂.

Figure 3 shows the change in the percentage of time which each partner spent 'on top' during their encounters between 1974-1977 (see Methods). The ♀'s scores are initially high, reflecting her mounting, standing over and biting the ♂. Receptivity is clearly recognised by the reversal in on top time. The data for 1976 reflect encounters that were effected late in the receptive period, with a reversal to pro-oestrous-like behaviour on 18 April.

As of the spring 1978 oestrus, the NZP's Giant pandas had not yet successfully mated. However, changes in the form of the ♂'s mounting suggest a gradual maturation of appropriate sexual behaviour. The 1973 oestrus was short (see Table 1). Neither animal was fully grown, and ♂ mounts were brief and directed to the side, head and hindquarters of the ♀. The ♂ was only two years old at the time. By 1974 the orientation of mounting was mainly towards the hindquarters. During 1974 the ♂'s testes became visible in the inguinal region. Two more elements of appropriate sexual behaviour were added to the repertoire in 1975. During mounts, lateral pelvic movements were commonly observed as the ♂ attempted to contact the ♀'s genital region. Moreover, the ♂ assumed the partially seated copulatory posture with the extended forepaws pressing down on the ♀'s centre back reported by Chinese zoologists (Anon, 1974). Finally, mounting bouts increased in frequency and duration. Encounters were initiated too late in the 1976 receptive period, and copulatory attempts were frustrated in 1977 when the ♀ suffered a sprained forepaw

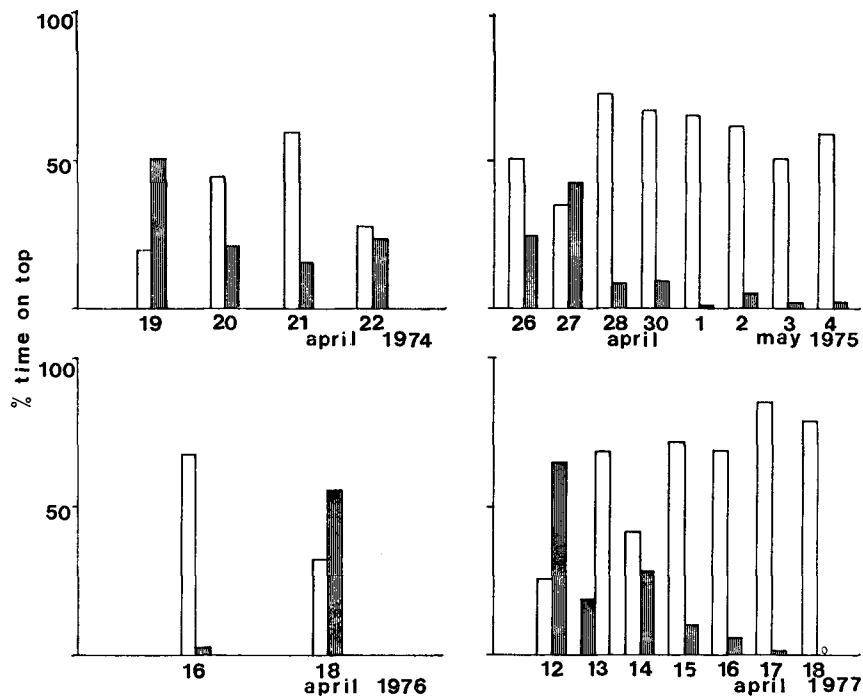


Fig. 3. Percentage of time spent 'on top' by the ♂ and ♀ during oestrous encounters between 1974-1977. ♂ = white bars; ♀ = shaded bars.

during an early oestrous alteration which prevented her from maintaining the lordosis posture while the ♂ was mounted. In 1978 erections of the penis during mounting were observed more frequently than in previous years, suggesting the onset of full sexual maturity.

DISCUSSION

The data presented here illustrate both the long- and short-term behavioural changes associated with oestrus as well as maturational changes in the behaviour of the NZP Giant panda pair.

Since her first period of heat in May 1973 at two-and-a-half years old, Ling-Ling has had a conspicuous annual spring oestrus in April. There have been no strong signs of reproductive activity in the autumn, although recently the ♀ has exhibited decreased food consumption in September and October. The onset of the spring heat in the ♀ has always been characterised by decreased food consumption, increased pacing, and increased scent-marking, beginning one to two weeks before peak oestrus. Although ♂ activity and scent-marking are higher in the

spring, suggesting a rutting period, the ♂ may be reproductively active throughout the year since there has been no observable seasonal change in testes size. Moreover, the ♂ continues to scent-mark throughout the year. In both ♂ and ♀ bleating is more common near the period of oestrus. Peak receptivity has lasted for two to five days in our ♀.

The display of reproductive activity in the NZP Giant panda pair has been unusual compared to that reported from some other zoos (Brambell, 1978). Ling-Ling first came into oestrus at two-and-a-half years old; the Chinese report that sexual maturity occurs at six to seven years (Anon, 1974). It is unlikely that Ling-Ling could have conceived at this age, since she was not fully grown, but the subsequent annual periods of oestrus have been both obvious and regular in occurrence. By comparison, the Tokyo ♀, who arrived in Japan in October 1972 at four years of age, first showed signs of oestrus in May 1974 (six years old) and then again in July and October 1975, June 1977 and May 1978; on the latter two dates copulation with apparently

successful intromission was seen. In London, strong signs of oestrus in the ♀ were not observed until 1977 when she was five years old. Prior to that, oestrus was thought to have occurred in March and October 1975 and April and December 1976, although the signs were weak (Brambell, 1978). The differences between ♀♀ in the age of puberty may be idiosyncratic, but they may also be due to differences in management, both in terms of housing and of feeding. The Washington pair have the largest enclosure, but are also the most isolated from each other. Both Tokyo and Washington appear to feed more bamboo than London. Furthermore, the London pair were housed together until October 1975 when the ♀ began losing weight (Brambell, 1978). Clearly, it is too early to determine the cause of the variability in the ♀ reproductive cycle, but these housing and feeding procedures must be considered should additional animals be exported from the People's Republic of China. Moreover, a successful conception cannot occur without a sexually mature ♂, and ♂ puberty may also be variable in age of occurrence.

One of the more interesting aspects of Giant panda socio-sexual behaviour is the strength of the ♀'s proceptive behaviour. The initiation and maintenance of interactions by the ♀ during pro-oestrus is very marked and mainly comprises 'physical contact responses' (gentle biting) and 'mounting by the ♀' although not with pelvic movements (Beach, 1976). When closer to peak receptivity, the ♀ exhibits 'solicitational' behaviour, including presentation of the anogenital region to the ♂.

The behaviour of the ♀ during pro-oestrus appears designed first to locate a ♂ (increased activity, scent-marking, bleating) and then physically to stimulate him prior to her receptive period. Such ♀-controlled interactions may also permit the pair to assess each other's reproductive condition without conflict. The elaborate proceptive behaviour of the Giant panda may be necessary for a large and potentially dangerous carnivore which is solitary, but typically has only a short period of oestrus each year. In this respect Giant panda reproductive behaviour appears to differ from that of the large, solitary

felids, where ♀♀ show little proceptive behaviour but are polyoestrous, thus permitting periodic mating attempts. It differs also from the behaviour of the large, social canids which, like *Ailuropoda*, are monoestrous, but where constant ♂/♀ contact results in a higher level of ♂ courtship behaviour than of ♀ proceptive behaviour.

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