



## Giant panda scent-marking strategies in the wild: role of season, sex and marking surface

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Scent marking entails significant energetic and opportunity costs that demand efficiency. Signal detection theory offers a theoretical framework that generates testable hypotheses regarding where animals should place scent signals in the environment in a way that maximizes their probability of detection by target receivers while minimizing costs of production and distribution. Solitary and reliant on chemical communication, the giant panda, *Ailuropoda melanoleuca*, offers an interesting model to test these ideas. We studied scent-marking patterns in wild giant pandas in the Foping Nature Reserve by surveying areas containing a high density of scent posts. Pandas did not deploy scent marks randomly in this environment, but targeted trees with specific characteristics that promoted signal persistence, range and/or likelihood of detection. Variables affecting selection of scent-marking sites included bark roughness, presence of moss on the tree trunk, tree diameter and distance to the trail. That pandas should be efficient with their use of chemosignals comes as no surprise, as mounting evidence is suggesting that many aspects of giant panda life history are constrained by their energetically poor diet. We also found seasonal and sex differences in marking patterns, indicating a role for scent marking in reproduction and competition. Males scent-marked throughout the year, whereas females scent-marked predominantly during the mating season, suggesting functional differences in scent marking between the sexes.

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Signalling behaviour serves many functions, but it comes at a cost. The benefits of reproductive coordination, mate selection, competition and social cohesion, among others, must be weighed against the cost of producing and distributing signals (Bradbury & Vehrenkamp 1998; Smith & Harper 2003; Searcy & Nowich 2005). Signal costs include time, energy and missed opportunities to engage in other behaviours that may affect fitness, such as foraging or mate searching ('opportunity costs'). Scent marks are a primary means of communication among many mammalian species, particularly solitary species. However, individuals do not have an unlimited supply of these chemosignals and cannot afford to allocate sufficient time and energy to saturate their entire home range (Gosling 1986; Brashares & Arcese 1999). In addition to deployment costs, some kinds of chemosignals can be energetically

expensive to produce. As waste products, urine and faeces often do not entail additional energetic costs, but specialized secretions can be costly. Spotted hyaenas, *Crocuta crocuta*, may deposit 40% of their body weight annually in lipid-rich scent marks (Gorman 1990) and in laboratory mice, *Mus musculus*, competitive scent marking can reduce growth rate and body size (Gosling et al. 2000). Animals must therefore deploy them strategically to maximize signal detection and function (Gosling 1986; Alberts 1992; Gosling & Roberts 2001a, b).

One mechanism for maximizing signal efficiency is strategic selection of scent mark sites that affect signal detection distance, signal detection probability or signal persistence (Alberts 1992). The physical properties of the marking substrate, such as surface area, porosity and chemical charge, can affect signal range, retention and persistence; however, this aspect of marking behaviour is little studied (Regnier & Goodwin 1977; Alberts 1992). Grizzly bears, *Ursus arctos*, for example, preferentially mark Pacific silver fir, *Abies amabilis*, trees, which have abundant sap, which probably adheres to scent mark chemicals and slows their release (Lloyd 1978). Selectivity for marking sites in other species (Kleiman

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1966; Bowyer et al. 1994; Oehler et al. 1995; Massei & Bowyer 1999; Barja 2009) may also be governed by properties that influence signal range and persistence.

Economic and functional considerations should also influence the temporal pattern of scent marking. Since chemosignals can be costly, animals should also choose when to deploy signals for maximum effect while minimizing costs. Thus, seasonal patterns of marking can also provide insight into motivation and function of scent marking. When chemosignalling primarily serves a reproductive advertisement function, scent marking should be confined largely to the mating season. Many species increase scent-marking frequency (Macdonald 1980; Gese & Ruff 1997; Sillero-Zubiri & Macdonald 1998) or respond more strongly to scent marks during the mating season (Ferkin et al. 1995, 1997; White et al. 2004; Muller & Manser 2008). Signals that serve other functions such as range marking are deposited across seasons (Gorman 1990; Molteno et al. 1998). Similarly, the cost/benefit ratio of chemosignalling may also vary with sex and may interact with season. Sex differences in marking behaviour (Macdonald 1980; Heymann 1998; Smith & Gordon 2002; Begg et al. 2003; Rosell et al. 2006; Muller & Manser 2008) and response to scent marks (Macdonald 1985; Swaisgood et al. 2002; Arnold et al. 2011) are common, and are often interpreted in light of functions relating to mate attraction and intrasexual competition.

Chemical communication figures prominently in the reproductive and competitive lives of giant pandas, *Ailuropoda melanoleuca* (reviewed in Schaller et al. 1985; Swaisgood et al. 2004). Solitary by nature, pandas communicate without direct contact by leaving and investigating scent marks left in areas used communally by pandas, typically on ridges. Unlike other ursids, pandas possess an anal gland that secretes a waxy substance used for marking. Pandas also use urine for marking purposes, but, unlike most carnivores (Macdonald 1980), do not appear to use faeces for communication.

Field studies of panda chemical communication are limited and remain largely descriptive (Schaller et al. 1985; Pan et al. 2001; Liu et al. 2005). Captive studies have provided clear confirmation that both urine and anogenital gland secretions (AGS) are used as signals, conveying individual identity, sex, reproductive condition, age and competitive status (Swaisgood et al. 1999, 2000, 2002; White et al. 2002, 2003, 2004; Hagey & Macdonald 2003; Yan et al. 2004; Zhang et al. 2008). To date, most research on panda chemosignals has focused on the receiver response or chemical composition, but less is known about spatial and temporal patterning and scent site selection.

Based on what is known about giant panda scent marking and theoretical considerations, we tested the following general hypotheses by investigating scent-marking patterns in wild giant pandas. (1) Giant panda choice of marking surfaces and location will differ according to the physical properties of the pandas' chemosignals and their mechanism of deposition. (2) Scent-marking patterns will vary seasonally, peaking during the mating season, as has been shown for captive pandas (Swaisgood et al. 2000; Lindburg et al. 2001). (3) Patterns of seasonal variation will vary with sex, reflecting functional differences in scent marking between the sexes. Giant pandas are among the most difficult species to study, spending most of their lives in a sea of impenetrable bamboo out of view of the researchers endeavouring to understand their ecology. Fortunately, pandas leave more visible signs in their environment, such as scent-marking posts, allowing researchers to piece together certain aspects of their ecology. Here, we quantified several aspects of giant panda scent-marking behaviour, as inferred through these signs, in an effort to understand how pandas use these marks for communication and how the selection of marking sites conforms to predictions from signal design theory.

## METHODS

### *Study Site and Data Collection*

The study was conducted from October 2007 to October 2008 in Foping National Nature Reserve (33.832–33.845°N, 107.840–107.855°E) in the Qinling Mountains in Shaanxi, China. Established primarily for the preservation of giant pandas, the reserve covers an area of 293 km<sup>2</sup> and elevation ranges from 980 to 2904 m above sea level.

Because giant panda scent marks are found primarily on ridges (Schaller et al. 1985; Y. Nie, unpublished data), we established transects along ridges in the core area of this reserve, near the Sanguanmiao research station. We located and monitored all the main ridges with prior evidence of giant panda marking in this study area covering 20 km<sup>2</sup>. It is impossible to know with certainty how many pandas frequented these scent stations, but preliminary data from a molecular census using faecal DNA indicates that approximately 13–15 individuals live in this area (Y. Hu, unpublished data). Transect length was determined by natural topography (i.e. length of the ridge) and width was 3 m. To establish a transect, we recorded the location and several characteristics of all trees greater than 5 cm diameter at breast height (DBH) within 1.5 m (approximately one panda body length) to either side of the trail (Table 1), labelling them 'available' trees. We have not detected marking on trees less than 5 cm DBH and so we excluded them from analysis. We monitored each of these available trees along transects at 1-week intervals and trees were classified as marked if certain criteria were met. AGS marks were determined by evidence of bark being flaked off and the presence of a thick, waxy substance on the bark. Urine marks were determined by slight discoloration (darkening) of the bark and an obvious, strong musky odour; this odour is so distinctive to the experienced nose that fresh urine marks could be easily detected even when not clearly visible. To distinguish scent marks deposited at different times, we used a clean knife to cut a small piece of the bark in the middle of the marking area so that we could identify whether a new AGS scent mark was deposited during the interval between 2 monitoring days. AGS marks are dark and removal of the surface of a small piece of bark reveals the lighter bark underneath. Darkening of this removed area on subsequent visits reveals that another scent mark has been deposited (countermarking). The musky odour of urine marks was no longer detectable after approximately 5 days, allowing us to determine whether the same site was marked repeatedly. From these observations, we classified each individual tree in the survey as marked or unmarked. As it is unlikely that we detected all marks, our data are likely to underestimate true marking rates.

To explore sex differences in scent-marking patterns, we collected hair samples for sex determination analysis if fresh hairs were deposited on the scent tree when the panda deposited scent by AGS. We categorized these samples according to reproductive season (mating: February–April; nonmating: all other months).

**Table 1**  
Tree characteristics measured

Main variables	Definition and description
Degree of roughness	Divided into four categories: roughest (Re): crevice depth (>7 mm), crevice width (>14 mm); rough (R): crevice depth (4–7 mm), crevice width (10–14 mm); medium (M): crevice depth (<4 mm), crevice width (<10 mm); smooth (S): no crevice
Moss status	Two categories: moss free and moss covered
DBH (cm)	Diameter of tree at breast height
SDT (cm)	Straight-line distance from the tree to the trail centre (midpoint of transect)

Sometimes giant pandas deposit scent marks on several trees when they pass through a trail. Thus, to avoid sampling repeatedly, hair samples were randomly collected only once on a single transect on each investigation day. We removed the hairs on all monitored trees using tweezers, ensuring that all sampled hairs had been deposited within the past week. Total DNA was extracted from hair using the method of proteinase K digestion in a PCR-compatible buffer (Allen et al. 1998). Giant panda-specific Y-linked sexing marker (ZX1, 210 bp) was used to determine the sex of each hair sample in combination with an X/Y-linked amplification control (ZFX/ZFY, 130 bp; Zhan 2006). Three PCR reactions were simultaneously performed for each DNA extract and PCR products were electrophoresed in a 2% agarose gel (for details see Hu et al. 2010). A hair sample was identified as male if at least two reactions showed two bands of different lengths and as female if only one band (130 bp) occurred. Blood DNA of a male and a female giant panda from zoos was used as positive controls, and a reaction without DNA as a negative control.

### Statistical Analysis

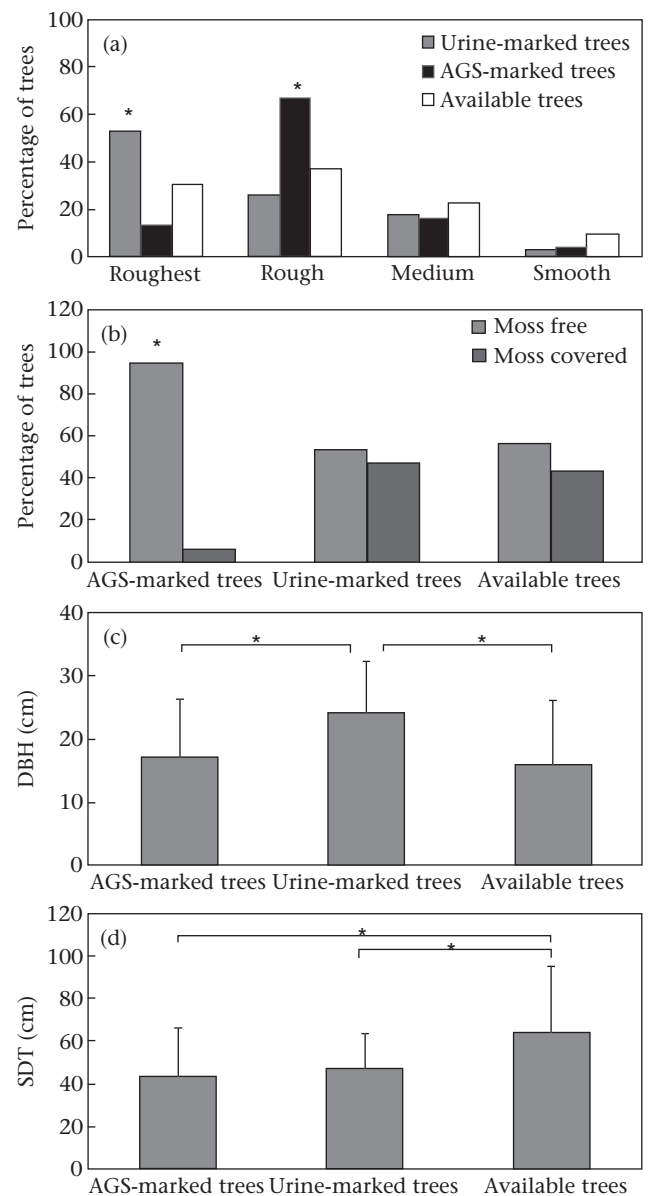
Scent site selection based on bark characteristics was analysed by comparing the proportions of marked trees relative to the available trees with a chi-square test. We used the Mann–Whitney *U* test to determine whether tree DBH and straight-line distance to the trail (Table 1) affected urine and AGS marking preferences. Seasonal scent-marking patterns were analysed using a one-sample Kolmogorov–Smirnov test. Differences were considered significant at  $P < 0.05$  and all tests were two tailed. It is not possible to know the degree to which assumptions of statistical independence were violated in these analyses, as it is impossible to ascribe a mark to a particular individual reliably. Hence, these results should be treated with caution and substantiated in the future using different methodologies.

## RESULTS

The cumulative length of the eight scent transects was 6.9 km with 2186 available trees. We recorded 315 AGS marks on 219 separate trees and 34 urine marks on 34 trees (hereafter, ‘scent trees’); five trees were marked with both AGS and urine scent marks. Of the 219 AGS-marked trees, 123 were marked only once, 73 were marked twice, 13 were marked three times, nine were marked four times and one was marked five times. During the course of the year, we detected panda marks on 11.5% of available trees; 38.3% of these scent trees were re-marked at least once.

### Selection of Scent Trees for Marking

There was a significant difference in the roughness of scent tree bark for AGS-marked and urine-marked trees. Giant pandas preferentially AGS-marked trees with rough bark (chi-square test:  $\chi^2_3 = 75.63$ ,  $P < 0.001$ ), directing 67% of their AGS marks at rough-barked trees, even though these trees only comprised 37% of the available trees along the transect. By contrast, urine-marked trees were more likely to have the roughest bark ( $\chi^2_3 = 8.41$ ,  $P = 0.038$ ; Fig. 1a). Smooth-barked trees were avoided for marking of either type. Pandas AGS-marked moss-free trees 94% of the time, significantly more than expected from their availability ( $\chi^2_1 = 1.17$ ,  $P < 0.001$ ), but urine-marked moss-covered trees randomly with regard to availability ( $\chi^2_1 = 0.17$ ,  $P = 0.681$ ; Fig. 1b). Pandas also showed evidence of selection based on tree DBH and distance to the trail. Urine-marked trees were significantly larger than both available trees (Mann–Whitney *U* test:  $Z = 6.18$ ,  $N_1 = 34$ ,  $N_2 = 2186$ ,  $P < 0.001$ ) and AGS-marked trees ( $Z = 5.36$ ,  $N_1 = 34$ ,  $N_2 = 219$ ,



**Figure 1.** Characteristics of available trees compared with trees marked with urine and anogenital secretions (AGS) as a function of (a) bark roughness, (b) presence of moss, (c) tree diameter at breast height (DBH, mean + SD) and (d) straight-line distance to trail (SDT, mean + SD). \* $P < 0.05$ .

$P < 0.001$ ), whereas AGS-marked trees did not differ from available trees with regard to diameter ( $Z = 0.83$ ,  $N_1 = 219$ ,  $N_2 = 2186$ ,  $P = 0.404$ ; Fig. 1c). Both urine-marked ( $Z = 2.94$ ,  $N_1 = 34$ ,  $N_2 = 2186$ ,  $P = 0.003$ ) and AGS-marked ( $Z = 9.78$ ,  $N_1 = 219$ ,  $N_2 = 2186$ ,  $P < 0.001$ ; Fig. 1d) trees were on average closer to the trail than available trees within the 3 m wide transect width.

### Effects of Season and Sex on Scent-marking Patterns

We recorded no scent marking in July and August when the pandas moved to higher elevations to feed on the shoots of *Fargesia qinlingensis* (Yong et al. 1994; Z. Zhang unpublished data collected during this study). Whether pandas have alternative scent trees in this habitat or deposit scent during these months remains unknown. Data from GPS satellite collars and faecal surveys (Z. Zhang, unpublished) indicate clearly that pandas remained in the vicinity of these

scent ridges, but there was obvious seasonal variation in scent-marking frequency along these ridges (Kolmogorov–Smirnov test:  $Z = 2.12$ ,  $N = 11$ ,  $P < 0.001$ ; Fig. 2). Peak scent-marking frequency occurred in November (10.8 scent marks/km) and February (15.0 scent marks/km).

A total of 28 hair samples were analysed for sex determination. Of these, 19 were male and nine were female. While our data are limited, they suggest a tendency for females to mark scent trees most during the mating season, whereas males also marked outside the mating season (Fig. 3).

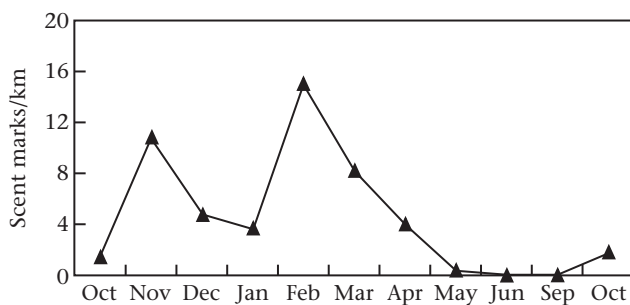
## DISCUSSION

### Selection of Scent-marking Sites

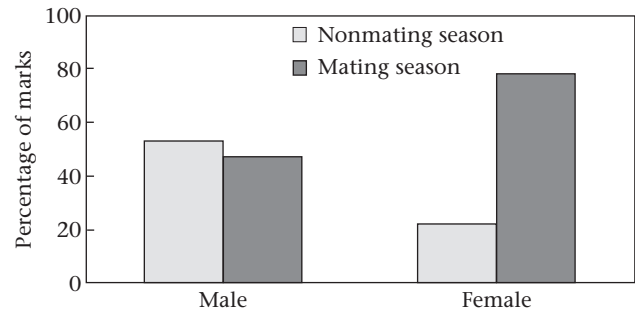
Our findings indicate that giant pandas place scent marks in their environment in a manner that conforms to predictions from signal detection theory (Alberts 1992; Bradbury & Vehrenkamp 1998), particularly those relating to signal range, persistence and likelihood of being detected by conspecifics.

Some features of giant panda scent marks allow us to hypothesize how they should be deployed for efficient, economic communication. AGS are deposited via vigorous rubbing against a surface, contain chemicals with low volatility and are rich in lipids, and are therefore long lasting (Hagey & Macdonald 2003; Swaisgood et al. 2004). Urine is sprayed over vertical surfaces (or deposited directly on the ground), is more volatile, and is short lasting. Consistent with this characteristic, urine does not appear to convey information for individual recognition; range marks conveying individuality are predicted to be long lasting on theoretical grounds (Alberts 1992; Swaisgood et al. 1999). By contrast, short-lived panda urine does convey temporally dynamic information about reproductive status (Swaisgood et al. 2002) and male competitive status (White et al. 2002).

In our study, pandas selected marking surfaces that should maximize signal strength and retard evaporation. By urine marking on the roughest surfaces, pandas may accomplish several objectives with functional significance. First, signals should be placed high on theoretical and practical grounds. Placing urine on the roughest surfaces may ensure that it is captured by the crevices to prevent it running down the trunk, leaving a larger quantity of chemosignal available at nose level of potential receivers. Keeping the mark higher on the tree trunk may also serve to maximize the size of the odour field, thereby increasing signal range and encounter rate by receivers (Wilson & Bossert 1963; Alberts 1992). For male pandas, placement of urine high on vertical surfaces, using a handstand posture, conveys competitive status (Swaisgood et al. 2000; White et al. 2002), suggesting a second disadvantage to allowing urine to



**Figure 2.** Seasonal dynamics of scent-marking frequency quantified as scent-marking events/km per month; AGS and urine marking were combined for analysis. Pandas migrate to higher elevations outside our study area from July to August and so data for these months are not included.



**Figure 3.** Seasonal sex differences in scent marking.

run down to the base of a tree. Second, a rough surface may also increase the surface area over which the scent is deposited, increasing evaporation and signal range more economically than producing and depositing greater quantities of scent (Alberts, 1992). Rough surfaces may also be resistant to rainfall, which might wash away marks, particularly urine. Foping Nature Reserve and all areas of the pandas' range experience very high rainfall, so it would be surprising if panda scent signalling were not shaped by this climatic variable (see Alberts 1992).

These observations may also explain why pandas preferentially marked rough surfaces with AGS, to increase surface area and signal range and to retard loss of signal from rainfall. Why pandas selectively marked the 'roughest' trees with urine and only 'rough' trees with AGS is more difficult to explain, but plausibly the roughest bark is needed to prevent the urine from escaping the signalling platform, that is, running down the tree trunk. The importance of maximizing the amount of urine on the tree may also be seen in the finding that pandas preferentially urine-marked larger trees, compared with those marked with AGS or available in the vicinity. Aiming urine backwards and hitting the target is probably no easy task, particularly when doing a handstand, so selection of larger trees for urine marks probably maximizes the amount of urine that reaches the target.

Based on this line of reasoning we also hypothesized that pandas may preferentially urine-mark moss-covered trees, but our results were inconsistent with this hypothesis. We reasoned that moss, like rough bark, might capture more urine and increase evaporative surface area, but pandas urine-marked moss-covered trees at rates coincident with their availability along the trail transect. By contrast, pandas rarely AGS-marked mossy tree trunks. One plausible explanation is that the moss covers the bark's sap, which has been proposed to bind to scent chemicals and increase signal fade-out time (Alberts 1992). Signal persistence is likely to be more important for panda AGS than urine marks. Pandas respond to conspecific urine aged up to about 2 weeks, but remain responsive to AGS aged for more than 3 months probably because AGS conveys individual identity and is used for range marks, while urine is used to signal more ephemeral messages relating to reproductive status (Swaisgood et al. 2004). If moss shortens the life expectancy of AGS marks, this may explain why pandas appear to avoid marking moss with these secretions.

Of course, there are alternative explanations for our results that do not require adherence to signal detection theory. One might try to construct hypotheses based on physical comfort or discomfort of marking surfaces, or suggest that pandas are just scratching an itch. Such explanations have been offered for marking by other ursid species (reviewed in Green & Mattson 2003), but bear marking differs from panda marking. Bears rub their pelage on trees, and sometimes scratch them with their claws, but do not mark them with a specialized gland (Burst & Pelton 1983; Green & Mattson



2003). Pandas, by contrast, mark with a specialized anogenital gland that no doubt evolved for communication purposes. Urine marking by pandas does not typically involve contact with the marking substrate and so comfort hypotheses do not apply.

For signalling effort to be efficient it is not enough to place marks on surfaces that enhance signal range and persistence; it is also important to place them where receivers will find them. This may be why pandas seem prone to mark along ridge trails, using them as communal marking stations for communication (Schaller et al. 1985). But once pandas reach these areas, they still need to select trees for marking that are most likely to be encountered by conspecifics passing through. In our study, pandas marked trees closer to the trail than expected by chance. An alternative, and perhaps more parsimonious, explanation is that marking trailside trees is merely a by-product of convenience.

#### *Effects of Season and Sex on Scent-marking Patterns*

Seasonality is a common feature of scent marking, typically following the same temporal pattern as mating behaviour in seasonally breeding species, as the two are closely associated (Brown 1979). Sex differences in marking behaviour also diverge in predictable ways conforming to the different roles for which odours are applied as sex attractants and competitive signals (Brown & Macdonald 1985).

The seasonal patterns of giant panda scent marking (Fig. 2) are readily interpreted with regard to reproductive and competitive activities. The strongest peak in marking occurred in February–March, which is the mating season for pandas in the Foping Nature Reserve where we carried out this research (Pan et al. 2001; Nie et al. 2012a, b). Captive pandas also show increased seasonal marking, peaking just before mating activities during the spring breeding season across several facilities in different hemispheres (Kleiman 1983; Swaisgood et al. 2000; Lindburg et al. 2001). Female marking increases dramatically during oestrus, presumably to advertise reproductive status and maximize signal detection by males, and males are sensitive to urinary chemosignals indicating receptivity (Swaisgood et al. 2000, 2002). Male scent marks, readily investigated and known to affect the behaviour of receivers of both sexes, are used during the mating season for both intramale competition and to facilitate mating with females (Swaisgood et al. 2004). Pandas are also most responsive to olfactory signals during the spring mating season (White et al. 2004). Thus, for pandas, spring is the time when the most effort is allocated to chemical communication in the service of mating activities.

In the present study we observed a second smaller peak in scent marking in November, a period during which a second mating season is sometimes seen. Oestrous events have been observed in the autumn in both captive and wild pandas (Morris & Morris 1981; Yong 1981; Zhang & Wei 2006). We also documented a November mating event at the same study site during the course of this study, corresponding to the period when we saw the second peak in scent marking. Unfortunately, we are not able to determine whether the scent marking peaks seasonally in the absence of these sociosexual interactions or occurs only in response to such activity.

We did find evidence of scent marking at lower levels throughout the year, however, with the exception of the summer months when pandas in Foping migrate to higher elevations outside the study area (Yong et al. 1994). We do not know whether pandas adopt alternative marking sites in summer habitat. Captive pandas, particularly males, also scent-mark at lower levels outside the mating season (R. Swaisgood, unpublished data).

Our admittedly limited data on sex differences in scent marking shed light on this seasonal pattern. Male marks, as evidenced by DNA

sex determination of hair samples found in association with a fresh mark, were found comparatively more commonly outside the mating seasons than were female marks. Thus, it appears that males mark year-round whereas females confine most marking activity to the brief mating season(s). Pandas do not appear to be territorial, in that limited data (Schaller et al. 1985; Yong et al. 1994; Pan et al. 2001) show that inter- and intrasexual ranges overlap considerably. Thus, male marking is not associated with territory demarcation. However, it is likely that male marking outside the mating season does serve as a kind of range mark, conveying home range occupation and competitive status and possibly facilitating future mating activities with females (see also Swaisgood et al. 2004).

#### *Conclusions*

Previous research on chemical communication in captive giant pandas demonstrated that olfactory signals convey a wide range of information (reviewed in Swaisgood et al. 2004). The present study demonstrates that wild giant panda chemical communication is also efficient, with pandas selecting marking surfaces and locations in ways that optimize signal transmission and probability of reception. That giant pandas should be efficient with their use of chemosignals comes as no surprise. Indeed, mounting evidence suggests that many aspects of giant panda life history are constrained by their energetically poor diet (Schaller et al. 1985; Nie et al. 2012a, b). Consequently giant pandas are likely to be particularly sensitive to any energetic costs that chemosignalling entails (Gosling 1986; Alberts 1992; Gosling & Roberts 2001a, b).

Previous research has also shown that trees, particularly old growth, are important ecological resources for pandas and the rightful target of serious conservation efforts (Zhang et al. 2007; Swaisgood et al. 2010, 2011; Zhang et al. 2011). Our study of scent marking reinforces yet another important service that trees provide pandas, a platform for communicating. Solitary for most of the year, pandas rely on efficient chemical communication to come together for mating purposes and to regulate intrasexual competition. Anthropogenic activities that reduce availability or access to these scent trees, particularly large trees with rough bark, may further impair conservation efforts.

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