

Scent communication behavior by giant pandas

Jin Hou^a, Vanessa Hull^b, Thomas Connor^c, Hongbo Yang^a, Jie Gao^a,
Faqin Zhao^a, Yushan Liao^a, Shiyu Chen^a, Jinyan Huang^d, Yichao Zeng^e,
Shiqiang Zhou^d, Xiaoping Zhou^d, Jindong Zhang^{a,*}

^a Key Laboratory of Southwest China Wildlife Resources Conservation (Ministry of Education), China West Normal University, Nanchong, Sichuan Province, 637002, China

^b Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, FL, 32611, USA

^c Department of Environmental Science, Policy and Management, University of California, Berkeley, CA, 94720, USA

^d China Conservation and Research Center for the Giant Panda (CCRCGP), Wolong Nature Reserve, Sichuan Province, 623006, China

^e Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ, 85721, USA

ARTICLE INFO

Article history:

Received 3 August 2020

Received in revised form 20 December 2020

Accepted 20 December 2020

Keywords:

Giant panda (*Ailuropoda melanoleuca*)

Scent communication

Scent marking

ABSTRACT

Behavioral strategies used in scent communication can reflect the adaptive capacity of animals. Signal detection theory and the principle of least effort posit that scent marking must be efficient and energy maximizing. The giant panda (*Ailuropoda melanoleuca*) is a solitary species that relies heavily on scent communication. There have been few studies on scent communication of wild pandas due to their elusive nature. To deepen the understanding of scent communication in this vulnerable species, we analyze a novel dataset obtained from integrating transect surveys on scent marked trees with infrared camera trapping of wild giant pandas performing scent marking and scent investigation behaviors. We found that pandas selected large coniferous trees for scent marking relative to what was available. Of the scent marked trees, trees that were more frequently marked than others were those of preferred species, high elevation, at topographical aspects conducive for odor transmission, with larger surrounding trees, and at gentle slopes. There were three peaks in the frequency of scent communication throughout the year in October, December, and March, the third period overlapping with the mating season. Scent communication occurred mainly during daytime hours, peaking at dusk (18:00–20:00). Frequency of anogenital gland secretion (AGS) markings were significantly greater than urine markings during the mating season but not during other times of year, which may reflect their stronger capacity to convey estrus state of females during mating season. The findings enrich the understanding of giant panda scent communication, and more broadly emphasize the importance of considering scent communication for conservation efforts such as corridor design for this vulnerable species.

© 2020 The Author(s). Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

1. Introduction

Scent communication exists widely across mammals and is regarded as one of the main communication channels between individuals. This communication approach plays an important role in reproductive coordination, intrasexual competition, mate selection, and social cohesion (Wilson, 1963; Thiessen, 1976; Johansson, 2007). Scent communication can generally be

* Corresponding author.

E-mail address: Zhangjd224@163.com (J. Zhang).

divided into two categories, namely direct signaling and indirect signaling. Direct signals are released only when individuals encounter each other. Signal receivers can assess information of the signaler (e.g. fighting ability) through secretions (e.g. Iberian rock lizard, *Lacerta monticola*, Martin and Lopez, 2007). Indirect signals are often placed on sites where conspecific individuals are most likely to be present, but not in the immediate presence of signal receivers at the time of signal placement (Gosling and Roberts, 2001; Briscoe et al., 2002; Parker and Margaret, 2010; Vogt et al., 2014). For solitary species, indirect signaling is a dominant form of communication among individuals, because they rarely meet directly (Johnson, 1973; Nie et al., 2012). Scent marking (generally by urine, feces and glandular secretions) is the primary means of indirect signaling among many solitary species (Rajagopal et al., 2010; Vogt et al., 2014).

The principle of least effort posits that animals achieve their goals in a manner that minimizes energy cost (Hull, 1943). However, the creation and maintenance of scent marks can expend extra energy on top of routine energy costs allocated for maintaining basic needs for individual survival through behaviors like resting and foraging (Gosling and Roberts, 2001). For the sake of parsimonious energy expenditure, individuals often do not to allocate energy to mark their ranges exhaustively and choose to only mark core ranges (usually in the centers of territories) with abundant resources (Gosling and Roberts, 2001). Furthermore, signal detection theory also indicates that the range, rate of spread, and persistence of signals are important for a scent communication system to function effectively (Bossert and Wilson 1963; Albers, 1992). Animals are known to fulfill these requirements behaviorally, for example, by regulating the amount of time spent on scent marking, time intervals between mark replenishment, and by selecting environmental factors that maximize information transmission (Albers, 1992; Nie et al., 2012).

The giant panda (*Ailuropoda melanoleuca*) is a largely solitary mammal species. Currently, this species has been confined to isolated patches of mountainous habitats in southwestern China due to human activities and climate change (Li et al., 2015; Zhang et al., 2017; Wei et al., 2018). Individuals have been shown to have limited direct contact with one another, except for a few days during their mating season (Hu et al., 1985). Conspecific communication among giant pandas depends heavily on chemical signals, and pandas can discriminate reproductive status (Swaigood et al., 2000; 2002), individual identity (including sex (Hagey and MacDonald, 2003) and age (Yuan et al., 2004)). Unlike other ursids, pandas leave urine and anogenital gland secretions (AGS) more frequently, rather than feces, as communication signals (Hu et al., 1985; Pan et al., 2001). Presumably, urine is less energetically costly, as it is a metabolic by-product, while AGS is metabolically more costly as it requires extra allocation of energy to physiological pathways specialized for olfactory communication (Nie et al., 2012).

Much of what is known about scent communication behavior in giant pandas has been acquired from studies conducted in captivity (e.g. (Swaigood et al., 1999; Zhou et al., 2005)). This is likely due to the secretive nature of wild pandas which makes it difficult to obtain detailed descriptions of their scent-marking behavior patterns (Nie et al., 2012). The exceptions include detailed maps and descriptive analyses constructed on the distribution of scent marking posts in early giant panda research on wild pandas in Wolong Nature Reserve (Schaller et al., 1985), Qingling (Fu et al., 1997) and Wanglang Nature Reserve (Liu et al., 2005). The similar studies were also conducted in Wolong Nature Reserve and Changqing Nature Reserve several years ago, which revealed the characteristics of scent marking trees (e.g. tree species, distribution, features of bark) (Shi et al., 2012; Wang et al., 2012). Other recent studies characterized the selection of trees used as scent marking posts relative to other available trees nearby (Nie et al., 2012) and the impact of ecological context on scent marking behavior (Zhou et al., 2019b). We know from these studies that pandas prefer to engage in scent marking along ridgelines due to high frequency traffic by conspecifics and on large coniferous trees with rougher bark due to potentially higher signal transmission (Schaller et al., 1985; Nie et al., 2012). Both the characteristics of scent marking trees (e.g. distribution, roughness of bark) and habitat features (e.g. moss status, canopy density) influence scent marking behavior (Fu et al., 1997; Liu et al., 2005; Shi et al., 2012; Wang et al., 2012; Nie et al., 2012; Zhou et al., 2019b).

One gap in the literature is that there has never been a study conducted to systematically examine the real-time scent communication behavior of wild giant pandas. We fill this gap in the current study by integrating a transect investigation and an infrared camera trapping study conducted at wild giant panda scent marking sites to study patterns of scent communication behavior over a one-year period. The study allows us to ask new questions to inform a growing understanding of a complex scent communication system in this elusive species, including selection of trees and how the frequency, duration, and type of scent communication varies across time of day and season. The study has implications for enhancing our understanding of adaptive capacity in this species, particularly related to the principle of least effort and signal detection theory. In addition, this work informs conservation efforts for this vulnerable species, such as corridor design as a means of alleviating habitat fragmentation effects.

2. Materials and methods

2.1. Study area

The study was conducted in Wolong National Nature Reserve (102°52'–103°24'E, 30°45'–31°25'N) in the Qionglai mountains in Sichuan province, China. Established in 1963, the reserve was set up primarily for conserving giant pandas and forest ecosystems. Wolong Nature Reserve is a flagship protected area covering an area of 2000 km². Its elevation ranges from 1150 to 6250 m (Liu et al., 1999; Zhang et al., 2017). From the lowest to the high elevations, vegetation types range from evergreen broad-leaved forest, evergreen-deciduous broad-leaved mixed forest, deciduous broad-leaved forest, coniferous broad-leaved mixed forest, to subalpine coniferous forest (Hu, 1985; Hou et al., 2018). According to the most recent national

census, more than 100 giant pandas inhabit this reserve (Sichuan Forestry Department, 2015). Our study site was located in the Sanchagou valley of Wolong Nature Reserve (2700–3000 m in elevation). Surrounded by several mountains, a stream flows throughout this valley that is frequently visited by pandas. We chose Sanchagou region as our study site because past research revealed that it has a high panda occurrence (Zhang et al., 2015, 2017; Hull et al., 2016), and DNA evidence also showed that there were feces from 22 individuals in this area (Huang et al., 2015).

2.2. Field data collection

Four transects were established along three ridges and one valley in a core area covering 2 km² in the study region. Transects had a width of 2 m and a cumulative length of 8.7 km. For all trees found in the transects that were greater than 5 cm in diameter at breast height (DBH), we recorded their species, height, DBH, and presence or absence of scent marks. Scent marks were apparent due to the discoloration of areas of bark that had been marked, in addition to the presence of occasional claw markings. After scent marking, the color of bark was altered (i.e. it became a darker brown after being marked with AGS and a greener shade after being marked with urine). In accordance with past studies, the age of scent marks was estimated by degree of color variation, namely the longer the time elapsed, the darker the color (Fu et al., 1997; Shi et al., 2012; Nie et al., 2012; Zhou et al., 2019a,b). For each tree with scent marks, we established a 20 m × 20 m quadrat centering the tree and measured the following: (1) Qualitative description of the roughness of the tree (i.e. rough or smooth); (2) DBH and height of the tree; (3) Angle between animal path and the tree; (4) Canopy coverage and average DBH of trees in the quadrat; (5) Location and topography of the quadrat (including longitude, latitude, elevation, slope, aspect and terrain) (Table 1).

2.3. Camera trapping

We installed 30 infrared camera traps (Ltl Acorn ltl6210 ATM, Shenzhen, China) in front of scent marked trees along the aforementioned transects in the Sanchagou area to record scent marking behaviors. Regarding which scent marked trees were included in the camera monitoring sample, we preferentially chose to put cameras in front of trees that had more marks and those that were at a minimum of 200 m flat distance and 50 m elevational difference from all other cameras. This design allowed the cameras to be relatively evenly distributed across the study region. Cameras collected data from August 2018 to September 2019. The distance between a tree and a trap was about 3 m, with the trap placed 0.5 m–1 m above the ground. We recorded the location of each trap location using a global positioning system (GPS) receiver. Cameras were set to operate 24 h a day, with shooting mode set to photo and video (1 photograph followed by 30 s of video). We screened the data and selected those images and videos depicting giant pandas. We recorded data type (photograph or video), date and time of shooting, season, temperature (recorded by temperature sensor in the infrared camera and automatically displayed on each captured photo), type of marker (urine versus AGS, judged by whether tail rubbing against the tree was recorded), time spent investigating, time spent scent marking, type of marking posture (four distinct postures: the leg cock, squat, quadrupedal and handstand (Fig. 1)), and number of panda individuals recorded. Seasons were defined according to previous research in Wolong Nature Reserve as Spring (April–June), Summer–Autumn (July–October), and Winter (November–March), while the mating season was defined as occurring from March to May (Schaller et al., 1985). Postures were named and categorized based on past ethograms done on captive pandas (Kleiman, 1983). The data from infrared cameras was collected about every two months and stored on an external hard drive and behaviors were later scored. One shot recorded one video only. In this way, we avoided double counting in subsequent analysis of the data.

2.4. Observation and definition of behavior

All of the behavior data were observed and scored from the videos between January and March 2020 by two observers. We used a continuous recording approach to record duration and the number of scent communication behaviors. To improve the

Table 1
Main variables measured in the transects and quadrats established in Sanchagou, Wolong Nature Reserve, China.

Variables	Definition (measuring method)
DBH (cm)	Diameter of tree at breast height, included three types: (1) any tree having a DBH more than 5 cm and located on transects; (2) the scent marking trees; (3) the average DBH of trees in the 20 m × 20 m quadrat centering the scent marking tree
Roughness	Divided into two categories: (1) rough: presence of crevices on the surface of bark; (2) smooth: no crevices
Height of tree (m)	The height of tree from the base to the top, included two types: (1) any tree having a DBH more than 5 cm and located on transects; (2) the scent marking trees
Angle between animal path and tree	The angle between animal path and scent-marking tree
Canopy coverage	The canopy coverage of all trees in each quadrat
Position information	The longitude, latitude and elevation of scent marking tree
Slope	Slope at the scent marking tree
Aspect	Aspect of the slope at the scent marking tree
Terrain	Terrain of the area around the scent marking tree



Fig. 1. The four postures of scent marking. (a) The leg cock: a rear approach with a hindlimb and tail raised to trunk; (b) squat: giant panda squats down and rubs a horizontal surface with the anogenital region; (c) quadrupedal: giant panda backs up to trunk with tail raised and rubs the anogenital region against the trunk; and (d) the handstand: initially follows a leg cock posture, but hindlimbs are kept off the ground, with the forelimbs propped against the ground.

accuracy of behavioral recording, the two observers were trained by repeatedly watching the same series of videos before beginning the actual recording procedure. Reliability analysis using correlation analysis was conducted to ensure the consistency of recorded behavior by the two observers (Liu et al., 2002, 2005). Classifications of behaviors that were not easily distinguishable or clearly defined were modified, and the standards of observation and recording were clarified as needed until an agreed upon observation method was determined. There was a small fraction of videos (less than 10) containing unfinished behavior, which made it difficult to record accurate information. We deleted those data to avoid biased analysis. The main types of behaviors recorded included walking, investigating a scent mark, and scent marking (Table 2).

2.5. Data analysis

Data analysis pertained to three main topics: (1) characterizing trees and their surrounding habitats used for scent marking and (2) characterizing the main factors that determine giant panda's selection of scent marking trees and (3) characterizing the nature and timing of scent communication behaviors performed. With respect to the first part, we summarized the species of trees chosen for marking and the average habitat conditions at the scent-marked sites. We also compared the characteristics of marked trees and available trees using the Vanderploeg & Scavia index (Vanderploeg and Scavia, 1979).

With respect to the second part, we performed two sets of multiple linear regression (MLR) models to determine the key attributes of trees that might affect giant panda scent marking. The models were constructed as follows:

$$Y = a + b_1X_1 + b_2X_2 + b_3X_3 + \dots + b_iX_i$$

where, Y = response variable (either the number of scent marks or total duration of time spent marking), a = intercept, b = regression coefficient, X = independent variables (roughness of bark, species of scent marking tree, DBH, height of scent marking tree, angle to road, canopy coverage, average DBH, average height, slope, slope aspect, slope position, elevation, distance to water, vegetation type).

Before building the models, we performed a logarithmic transformation of the response variables to ensure that they were normally distributed. We used the variance inflation factor (VIF) to filter out independent variables that showed severe multicollinearity. Independent variables with variance inflation factors greater than 5 were excluded (Fisher et al., 2018). We conducted stepwise regression and evaluated model performance of models with different independent variables included using Akaike Information Criteria (AIC) (Burnham et al., 2002; Bartoń, 2018). Data were analyzed in R (version 4.0.0) using the packages "car" and "MASS" (Fisher et al., 2018).

With respect to the third main section of the analysis regarding characterizing scent communication behaviors from camera trap data, we first calculated the proportion of behaviors by type (i.e., scent investigation, urine marking, AGS marking). We then calculated the proportion of scent markings and summarized the characteristics of the four marking postures (i.e., proportion, occurrence season, duration of time and type of marker for each posture, and the frequency in mating and non-mating season). We also calculated the duration of time spent on each type of behavior and the duration of time between successive scent investigations by individuals. We calculated monthly relative abundance index (MRAI) for each behavior (total number of captures within each month divided by total number of captures throughout the year). We

Table 2

The main behaviors of giant panda captured by infrared cameras.

Behavior variables	Definition
Walking	panda individual just passes by the scent marking tree without investigation and scent marking behavior
Investigating a scent mark	panda individual approaches the scent marking tree and sniffs or licks the scent mark
Scent marking	panda individual deposits the AGS/urine on the bark of scent marking tree

also calculated hourly relative abundance index (HRAI) for each behavior (total number of captures within each time-period divided by the total number of captures throughout the year) and each ecological season (total number of captures within each ecological season divided by the total number of captures throughout the year) (Liu et al., 2013). Additionally, we summarized descriptive statistics on temperature during scent marking across seasons. We used a two-sample *t*-test to compare temperatures associated with AGS and urine marking and also to compare the time interval of investigation in mating and non-mating seasons. We compared the frequency of use of AGS and urine marking in each ecological season and between mating and non-mating seasons with a chi-square test.

3. Results

3.1. Selection of trees for scent-marking

We counted 531 trees along the transects, 42 of which were scent-marked trees. The most common marked tree species was Faxon fir (*Abies faxoniana* Rehd. et Wils.), which accounted for about 60% of the total number of marked trees, followed by the Chinese Hemlock (*Tsuga chinensis* (Franch.) Pritz.) accounting for 14.3% of the total number of marked trees (Table 3). Generally, the marked trees are more commonly located on ridges (mean distribution ratio of marked trees on ridge is 19.7% and non-ridge is 11.4%), where the main forest type was coniferous forests (54.8%), canopy coverage of trees was 0.45 ± 0.19 , the dominant tree species was Faxon Fir (49.9%), the average height of shrub was 3.2 ± 0.6 m and coverage was $38\% \pm 14\%$ (Table 3).

Four of the five most widely distributed trees were selected by giant pandas for marking relative to what was available, especially the Mountain glory Rhododendron (*Rhododendron oreodoxa* Franch.) (Table 4). Only Chinese Hemlock was selected randomly as a scent marked tree (Table 4). Giant pandas also preferred to mark the trees with greater than 50 cm DBH (Table 4). Giant pandas also more commonly chose the trees with heights of more than 5 m as scent marking trees (Table 4).

Factors significantly predicting the number of scent marks on the scent marked trees in all of the top 5 MLR models were roughness, average height of trees in environment, aspect, slope, tree species, and elevation (Table 5). The average height of nearby trees and elevation both positively contributed to explaining the number of scent marks, while roughness, slope and aspect were negatively correlated with the number of scent marks. Giant pandas had higher frequencies of scent-marking four species - Pratt Caudate Maple (*Acer caudatum* wall var. *prattii* Rehd.), Taibai Bluegray Maple (*Acer caesium* Wall. ex Brandis subsp. *giraldii* (Pax) E. Murr.), Tetracentron (*Tetracentron sinense* Oliv.), and Faxon Fir (*Abies faxoniana* Rehd. et Wils.) than other trees.

The 4 best models for predicting total duration of scent marking by giant pandas had roughness of trunk texture, aspect, average height, tree species, DBH, and elevation (Table 6). Elevation, DBH and average height of trees in environment were positively correlated with the total time marking, while the roughness of trunk texture and aspect were negatively correlated with total time marking.

3.2. Scent communication behavior

We collected a total of 798 records of giant pandas in the camera traps. These included 394 instances (49.4%) of behaviors related to scent communication (i.e. scent investigation, scent-marking, or both) and 404 records of other behaviors not related to scent communication. Of the 394 instances of interest, 208 were videos and 186 were photos. Of the 208 videos, 83 contained scent investigation only, 56 contained scent marking only, and 69 contained both scent investigation and scent marking. There were slightly more total AGS markings recorded (54%) as opposed to urine markings (46%). Leg cock (42%) and

Table 3
Characteristics of tree species detected on the transects.

Tree species	Tree count (percentage (%))	Marked tree count (percentage (%))	Mean DBH (cm) \pm SE	Mean height (m) \pm SE	Trunk texture
Faxon Fir (<i>Abies faxoniana</i> Rehd. et Wils.)	265 (49.9)	25 (59.5)	48.1 \pm 25.4	16.1 \pm 4.8	Rough
Himalaya Birch (<i>Betula utilis</i> D. Don)	95 (17.9)	3 (7.1)	26.6 \pm 15.1	11.5 \pm 2.5	Rough
Chinese Hemlock (<i>Tsuga chinensis</i> (Franch.)Pritz.)	42 (7.9)	6 (14.3)	51.5 \pm 32.7	13.0 \pm 3.5	Rough
Mountain glory Rhododendron (<i>Rhododendron oreodoxa</i> Franch.)	37 (7)	0 (0)	15.2 \pm 8.0	6.5 \pm 3.4	Rough
Pratt Caudate Maple (<i>Acer caudatum</i> wall var. <i>prattii</i> Rehd.)	32 (6)	2 (4.8)	19.3 \pm 11.3	8.0 \pm 2.6	Smooth
Other	60 (11.3)	6 (14.3)	32.0 \pm 24.7	11.4 \pm 5.9	
Total	531 (100)	42 (100)			

Table 4

Selection of ecological factors by giant pandas as determined by the Vanderploeg and Scavia index.

Factors	Category	Resource selection coefficient	Resource selection index	Preference
Tree species	Faxon Fir	0.041	−0.205	NP
	Himalaya Birch	0.014	−0.638	NP
	Chinese Hemlock	0.062	−0.001	AR
	Mountain glory Rhododendron	0	−1	DS
	Pratt Caudate Maple	0.027	−0.392	NP
DBH of trees (cm)	5 < x ≤ 25	0.094	−0.359	NP
	25 < x ≤ 50	0.149	−0.147	NP
	50 < x ≤ 75	0.346	0.268	P
	75 < x ≤ 100	0.141	−0.172	NP
	>100	0.270	0.149	P
Height of trees (m)	0 < x ≤ 5	0.000	−1.000	DS
	5 < x ≤ 10	0.027	−0.762	NP
	10 < x ≤ 15	0.033	−0.718	NP
	15 < x ≤ 20	0.056	−0.563	NP
	20 < x ≤ 25	0.088	−0.388	NP
	>25	0.541	0.460	P

DS: Don't select; NP: Not preferred; AR: Almost Random selection; P: Preferred.

Table 5

Top 5 models predicting number of giant panda scent marks on scent marked trees.

Model construction	K	AIC	ΔAIC
Species of tree, slope, average height, aspect, elevation	6	−24.6	0
Roughness, species of tree, slope, average height, aspect, elevation	7	−23.3	1.3
Roughness, species of tree, slope, average height, aspect, elevation, canopy density	8	−21.7	2.9
Roughness, species of tree, slope, average height, aspect, elevation, canopy density, angle to road	9	−20.4	4.2
Roughness, species of tree, slope, average height, aspect, elevation, canopy density, angle to road, DBH	10	−18.7	5.9

Table 6

Top 4 models predicting total duration of scent marking by pandas on scent marked trees.

Model construction	K	AIC	ΔAIC
Roughness, species of tree, DBH, average height, aspect, elevation	7	−19.2	0
Roughness, species of tree, DBH, average height, aspect, elevation, angle to road	8	−18.2	1
Roughness, species of tree, DBH, average height, aspect, elevation, angle to road, canopy density	9	−16.4	2.8
Roughness, species of tree, DBH, average height, aspect, elevation, angle to road, canopy density, slope	10	−14.4	4.8

quadrupedal postures (40%) were used more often than the other two postures of handstand (16%) and squat (2%) (Table 7). The more common leg cock and quadrupedal marking postures were seen across all seasons, but the handstand was only seen in summer-autumn and winter. The least commonly observed posture of the squat was only seen in summer-autumn (Table 7).

The time spent scent marking ranged from 2 to 28 s (mean 8.42 s). The time spent investigating scent marks similarly ranged from 2 to 29 s (mean 11.69 s). The minimum time interval between two consecutive visits for either marking or scent investigation was 30 min and the maximum 236.2 days (mean 37.31 days). The interval between two consecutive visits in mating season was significantly shorter than interval in the non-mating season ($P = 0.001$). The average interval between two scent markings made from urine (52.23 days) was shorter than that from AGS (64.31 days) but the difference was not significant ($P = 0.488$) (Table 8).

The temperature recorded by the camera traps during scent communication behaviors ranged from -12°C to 24°C , with an average of 3.99°C (Table 8). Temperatures in months of most frequent scent communication behaviors (October and March) were relatively cool (averaging 2.35°C and -3°C , respectively). Temperatures during hours of day with most frequent scent communication behaviors (18:00–20:00) were also relatively cool (average of 6.62°C). The temperature at which urine

Table 7

Characteristics of scent marking postures.

Scent marking posture	Proportion (%)	Occurrence season	Mean time spent marking (seconds)	Type of signal and its proportion
Leg cock	42	All seasons	5.7	Urine (76%) and AGS (24%)
Squat	2	Summer-Autumn	13	AGS
Quadrupedal	40	All seasons	11.6	AGS
Handstand	16	Summer-Autumn, Winter	7.9	Urine (95%) and AGS (5%)

markings were performed was significantly cooler than that for AGS markings, which reflects the higher proportion of urine marks performed in colder seasons ($P = 0.015$) (Table 8).

Giant panda scent communication varied across months and seasons. Regarding frequency of scent communication behaviors, there were three peaks throughout the year (i.e., around October, December, and March). March was the highest peak, followed by the lowest level of activity in the summer months (Fig. 2a). This peak in March corresponds to the giant panda mating season and could be attributed to the combined frequencies of both scent investigation and the two scent marking behaviors (Fig. 2a). However, the highest peak of AGS alone occurred in October, earlier than that of urine marking in December (Fig. 2b). The majority of the urine marks were made in winter (69.1%) followed by summer-autumn (26.2%) and spring (4.8%). The same trend could be seen in the AGS markings, but the differences across seasons were less pronounced, with 42.9%, 34.7%, and 22.4% in winter, summer-autumn, and spring, respectively (Fig. 2c). In spring, AGS was used as a marker significantly more often than urine ($P = 0.016$), but urine was used more frequently by giant pandas in winter ($P = 0.012$) (Fig. 2c). There was no significant difference in the frequency of use of the two marking types in summer-autumn ($P = 0.381$) (Fig. 2c). The marking type also varied across mating and non-mating seasons. The frequency of use of AGS signals was significantly greater than urine markings only for the mating season ($P = 0.018$), but not other times of year ($P = 0.396$) (Fig. 2d).

The frequency of four marking postures also varied between mating season and non-mating season. There was little difference in frequency of use of leg cock posture between mating and non-mating season. The frequency of use of quadrupedal posture in mating season was slightly lower than non-mating season. However, only the squat and handstand posture were recorded in non-mating season, and the squat posture was least frequently recorded (Fig. 3a).

With respect to daily patterns, scent communication-related behaviors were more frequent during the daytime than the night (Fig. 3b). The peak in scent communication behaviors occurred at dusk across seasons. Scent marking activity in spring initially increased from 5:00 in the morning, which is earlier than the other two seasons. Springtime scent marking had three apparent peaks (5:00 to 8:00, 11:00 to 14:00, and 17:00 to 19:00). The peak of scent marking in summer-autumn was mainly in the afternoon (15:00 to 16:00) and evening (18:00 to 20:00). The summer-autumn evening peak was the highest peak across the three seasons. In the winter, frequency of scent marking increased from 7:00, then reached the highest peak around 18:00 and then dropped, but increased again from 0:00 to 1:00 at night. Comparing types of markings, AGS had two high peaks at 11:00 and 18:00 and urine marking had one peak at 18:00, while the highest peak of scent investigation was also at 18:00 (Fig. 3d).

4. Discussion

Studies on scent communication behavior reveal key information on the mechanisms of animal communication and adaption to energetic demands. There have been some studies focused on scent marking behavior of giant pandas in the past, which have revealed important factors that influence scent marking behavior (e.g. sex, age, reproductive state, habitat, role of competitors, and season) (Liu et al., 2002; Swaisgood et al., 2002; Tian et al., 2004; Nie et al., 2012; Bian et al., 2013). Because free-ranging pandas are difficult to track and monitor, many of the aforementioned studies were on captive pandas. To our knowledge, there are no systematic studies to monitor and analyze real-time performance of scent communication behavior of wild pandas as we have done here. Previous studies conducted in the field paid more attention to the question of scent marking or no scent marking on available trees. Whereas this study, by linking infrared camera trapping with transect surveys, was able to additionally quantify the intensity of panda use of each scent marking tree, thus revealing some key attributes that affect frequency of scent marking for the first time.

Our results show that in addition to factors mentioned in previous studies (Nie et al., 2012), aspect, elevation, slope and large surrounding trees are also important factors to consider in selection of trees for scent marking. Although our study area was relatively small, based on the topography of the study area, we hypothesize that wind from the valley may have promoted better dissemination of volatile chemicals at particular aspects. Thus, pandas that passed the ridge or went into the valley for foraging or drinking may have been more likely to detect odor information (Alberts, 1992). Higher elevation may also mean closer to the ridge. There are many trails on ridges, making them important pathways for giant pandas to move between the

Table 8
Characteristics of scent communication in giant pandas.

	Minimum	Maximum	Mean	SD
Time spent scent marking	2 s	28 s	8.42 s	5.46 s
Time spent investigating scent mark	2 s	29 s	11.69 s	6.94 s
The interval between consecutive visits	0.01 d	236.2 d	37.3 d	51.87 d
The interval between consecutive visits in mating season	18 min	42 d	10.9 d	5.9 d
The interval between consecutive visits in non-mating season	36 min	289 d	43.9 d	65.7 d
Interval between two scent marks by urine	3.60 d	279.10 d	52.23 d	55.07 d
Interval between two scent marks by AGS	0.27 d	288.82 d	64.31 d	78.95 d
Temperature at time of scent marking	-12 °C	24 °C	3.99 °C	8.10 °C
Temperature at time of scent marking by urine	-12 °C	15 °C	0.31 °C	6.63 °C
Temperature at time of scent marking by AGS	-10 °C	24 °C	3.58 °C	6.83 °C

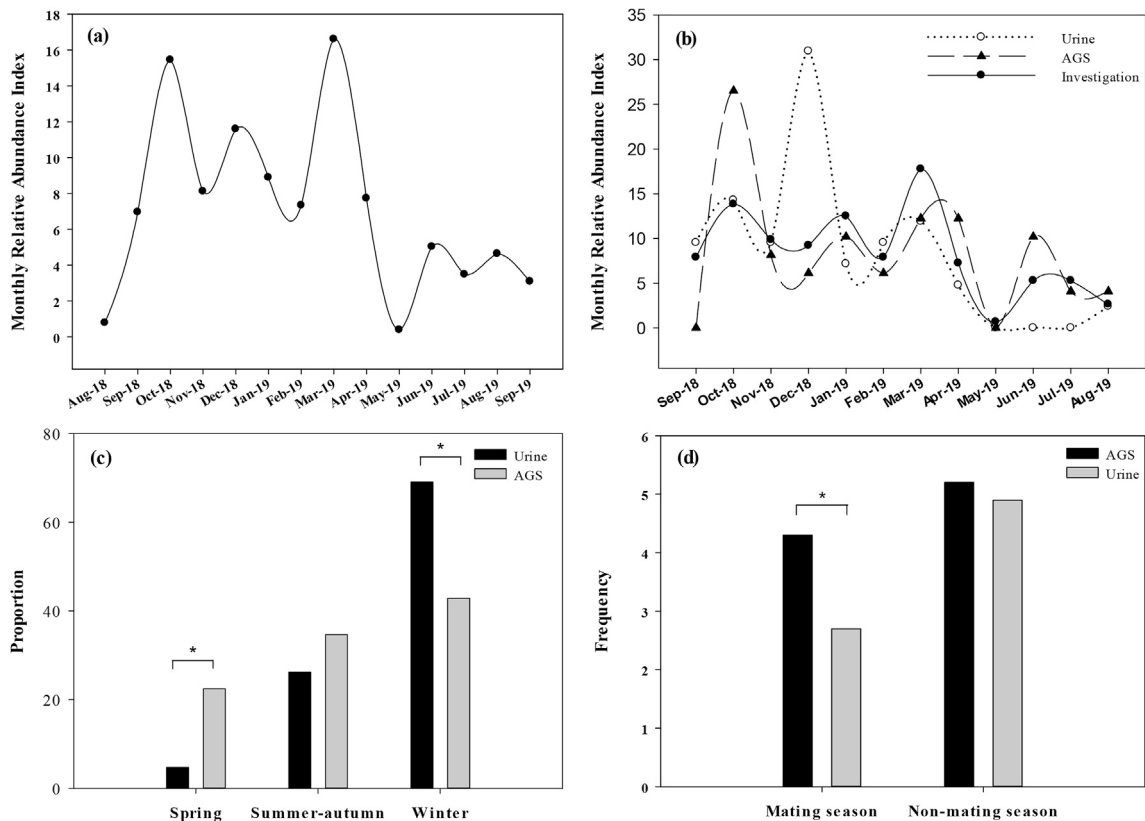


Fig. 2. (a) The monthly relative abundance index (MRAI) of scent communication behaviors across months, (b) the monthly relative abundance index (MRAI) of scent investigation and scent marking using urine or AGS, (c) the proportion of urine and AGS in each season, calculated by dividing number of captures for each signal type in each season divided by total number of captures for that type, and (d) the frequency of scent marking using AGS and urine marking in the mating season and non-mating season. * $P < 0.05$.

mountains (Bai et al., 2020). In addition, the significance of coniferous trees (54.8% of the scent mark trees) and medium canopy coverage (0.45) areas at high elevation are not only consistent with broader habitat selection patterns for giant pandas (Wei et al., 2000; Hull et al., 2014), but also may facilitate the dissemination of odor information due to better air flow, thereby increasing encounter rate by receivers. Gentle slope is not only suitable habitat that giant pandas prefer (Hu, 1985), but also may ensure pandas can accurately accomplish deposition of scent marks with a steady posture. Large surrounding trees with large height or DBH reflects the overall condition of mature forest and abundant resources. For example, abundant bamboos guarantee nutrition source of giant pandas, while dens from trees with a large DBH can provide a place for giant panda to breed and raise their young (Wei et al., 2018).

In addition, the study revealed new information on scent communication behaviors. One finding from our study was that the leg cock and quadrupedal were the most commonly used postures for scent marking. The marker secreted via the leg cock position was mainly urine, while quadrupedal was mainly AGS, a difference likely related to the structure of the panda's body. Lifting one hindlimb brings the body closer to the deposition site and is more conducive to urine spray on the tree trunk. AGS is deposited through rubbing vigorously against a surface of bark, such that stable limb support via quadrupedal posture can ensure completion of this behavior. It makes sense that the handstand was less commonly observed. The handstand (mainly used by male pandas) consumes more energy than the other three positions (Zhou et al., 2005). In addition, that the behavior is believed to be more common in adult males who use this special posture to convey a powerful competitive state by marking higher up on the tree while also increasing signal range (Nie et al., 2012; Sharpe, 2015), whereas subadults investigate odors of high-status individuals more and tend to avoid handstand urine marks (White et al., 2002). The fact that males did not perform handstands in spring was an interesting finding. This posture's role in reproduction is still unclear and worth exploring in the further study. The fact that the squat position was the least frequently recorded may be because the lower mark may minimize the size of the odor field (White et al., 2002; Nie et al., 2012), and fallen leaves, snowfall, and rainfall may also obscure the scent information (Nie et al., 2012; Zhou et al., 2019b), leading it to be less effective as a communication modality.

One surprising finding in our study was that the time spent investigating scents was usually less than 30 s. The mean duration (11.69 s) was lower than that in previous studies on captive pandas (31.6 s) (Zhou et al., 2005). One possible reason

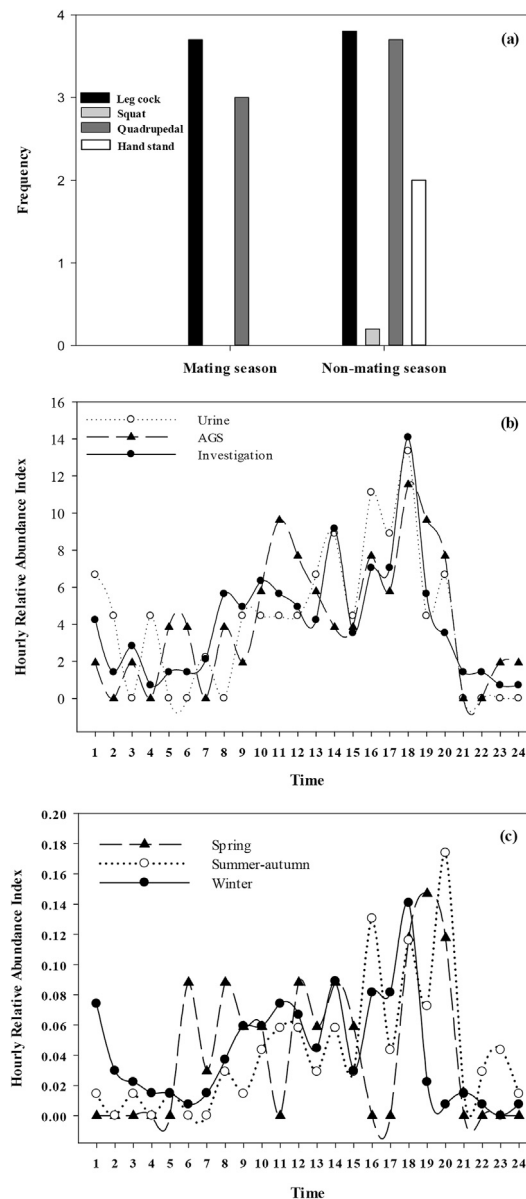


Fig. 3. (a) The frequency of use of four marking postures in mating and non-mating season, (b) the hourly relative abundance index (HRAI) of scent investigation and scent marking using urine or AGS, (c) the hourly relative abundance index (HRAI) of scent communication behaviors across different seasons.

for this difference is that pandas in captivity are often presented with unfamiliar odors. Previous studies demonstrated that giant pandas spend more time investigating unfamiliar odors and gradually decrease investigation time with subsequent presentations of the same individual's odor (Zhou et al., 2005; Liu et al., 2011). There are also differences in the surrounding environmental stimuli between captive and wild settings, in addition to the possible differences in ability to process scent information between captive and wild pandas. The long duration of time (average of 37 days) in between successive visits to scent posts was also interesting to note, as it reinforces past research suggesting a strong salience of panda scent marks.

Previous studies found a seasonal pattern of scent marking (Nie et al., 2012). Pandas in our study area also showed similar pattern of scent marking, peaking at October and also just before mating activity during spring mating season. We also found that the type of scent marking varied significantly with season, as the frequency of urine marking increased from summer-autumn to winter. Future work should examine the relative roles of temperature and food resource availability in explaining this pattern. Temperature affects the diffusion rate of gas molecules that in turn impacts the possibility of a scents being detected (Alberts, 1992; Cai et al., 2014). It is interesting to consider whether pandas deposit urine as a marker in winter and AGS in summer due to a difference in temperature-related volatility or whether limited food resources in winter make it advantageous for pandas to adopt urine marking as a lower cost (metabolic by-product) marker compared to AGS.

Unlike other ursids, pandas have a specialized gland to perform AGS. Past studies have posited that urine, due to its lower salience and higher volatility, may play a more important role in timely information transfer relating to reproductive status (Swaigood et al., 2002; Nie et al., 2012). However, recent analysis of gas chromatography in the form of mass spectrometry suggests that AGS may be important because several chemical constituents in AGS are present only during mating season (Zhou et al., 2019a). Our results showing more frequent use of AGS during mating season support this line of thinking. AGS may be particularly more important for female signals that relay information on estrus state to males (Schaller, 1985; Nie et al., 2012).

While we found the highest peak of overall scent communication behaviors during the mating season, in line with past studies (Nie et al., 2012), it is important to emphasize that when separating out scent investigation from scent marking, we detected stronger peaks of AGS and urine marking from October to December. This finding emphasizes that giant pandas may prepare for mating long in advance and that scent communication is important year-round for pandas. For female pandas, scent marking in the mating season may advertise their reproductive status and increase the chance of detection by male pandas (Swaigood et al., 2002; Nie et al., 2012). For male pandas, they may also seek to transfer their competitive advantages and assess intrasexual competitors far ahead of the mating season (Swaigood et al., 2002; Nie et al., 2012).

The diurnal rhythm of scent marking that we documented in this study is another point worthy of discussion. Past research demonstrates that pandas are regularly active throughout the day and night and experience three activity peaks over a 24-h period that alternate with periods of rest (Hu, 1985; Zhang et al., 2015). One might expect that scent marking would follow this general pattern. Our results however, were inconsistent with this expectation because scent marking did not occur at night. We also found that scent communication activity peaks shifted earlier as the seasons progressed from spring to winter, coinciding with a decline of light intensity from spring to winter that has been documented in previous studies (Zhang, 2012; Zhang et al., 2015). It is worth exploring in further studies whether light availability affects the diurnal rhythm of scent marking of wild pandas. Another potential factor to consider is that availability of high energy foods for pandas is lower in winter. Pandas may extend their activity time until later in the evening to compensate for this and scent communication may in turn follow this general pattern (Dierenfeld et al., 1982; Zhang et al., 2015, 2017; Hou et al., 2018).

Our results have implications for panda conservation in the future. As one of the major threats to the species, habitat fragmentation disconnects neighboring panda populations, which obstructs gene flow. A promising approach to ease this threat may be to promote scent communication between fragmented populations. Previous studies on other species have shown that corridors are effective for connecting isolated habitats (Spackman and Hughes, 1995; Rosenberg et al., 1997; Khazan and Emily, 2014). Corridors have also been a point of discussion in the panda literature (Li et al., 2010; Wang et al., 2014; Kang and Li, 2016). In addition to traditional factors considered in the planning and design of corridors (Bond, 2003), we suggest that scent communication can also be considered for giant pandas. Our findings demonstrating the importance of scent communication across the entire year (and not just the mating season) further illustrate this idea. To increase the possibility of being used by giant pandas, the corridor should be located on a major ridge that connects the two habitats or in a resource-rich valley in medium canopy coverage and facing a slope direction conducive to odor transmission to ensure that giant pandas can use this area as a scent marking station. Selection of tree species in the corridor should conform to the main type of scent marking tree found in the same region.

We encourage expansion of more giant panda scent communication studies in the wild in the future. More research can be done for example on customizing corridor design. One topic that would be meaningful to pursue would be to tie scent marking behaviors to individual pandas. New technology such as individual identification of panda images based on deep learning show promise for facilitating this work (Hou et al., 2020).

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The authors wish to thank Y. Hong, L. Li, Z. Mao, F. Zhao and Y. Liao from China West Normal university for assistance with data collection. We thank Dr. Lai Jiangshan for his guidance on the data analysis. We appreciated W. Yang and H. Yang's help in conducting field work for this project. This study was financially supported by the following sources of funding: the Second Tibetan Plateau Scientific Expedition and Research Program (STEP) (#2019QZKK0402), the National Natural Science Foundation of China (#42071279; 41571517), research innovation team funding project of China West Normal University (#CXTD2018-9), the Key Laboratory of Southwest China Wildlife Resources Conservation (China West Normal University), Ministry of Education, China (#XNYB19-1), 2020 College students' innovative entrepreneurial training plan program of China West Normal University (S202010638084X, S202010638087) and the fund of China West Normal University (#17E073; #17E074).

References

- Alberts, A.C., 1992. Constraints on the design of chemical communication systems in terrestrial vertebrates. *Am. Nat.* 139, S62–S89. <https://doi.org/10.1086/285305>.
- Bai, W., Huang, Q., Zhang, J., Stabach, J., Huang, J., Yang, H., Songer, M., Connor, T., Liu, J., Zhou, S., Zhang, H., Zhou, C., Hull, V., 2020. Microhabitat selection by giant pandas. *Biol. Conserv.* 247 <https://doi.org/10.1016/j.biocon.2020.108615>.
- Bartoń, K., 2018. Multi-Model Inference [WWW Document]. accessed 2.28.19.
- Bian, X.X., Liu, D.Z., Zeng, H., Zhang, G.Q., Wei, R.P., Hou, R., 2013. Exposure to odors of rivals enhances sexual motivation in male giant pandas. *PLoS One* 8 (8), e69889. <https://doi.org/10.1371/journal.pone.0069889>.
- Bond, M., 2003. *Principles of Wildlife Corridor Design, vol. 4. Center for biological diversity.*
- Bossert, W.H., Wilson, E.O., 1963. The analysis of olfactory communication among animals. *J. Theor. Biol.* 5 (3), 443–469. [https://doi.org/10.1016/0022-5193\(63\)90089-4](https://doi.org/10.1016/0022-5193(63)90089-4).
- Briscoe, B.K., Lewis, M.A., Parrish, S.E., 2002. Home range formation in wolves due to scent marking. *Bull. Math. Biol.* 64 (2), 261–284. <https://doi.org/10.1006/bulm.2001.0273>.
- Burnham, K.P., Anderson, D.R., Burnham, K.P., 2002. *Model Selection and Multimodel Inference: a Practical Information-Theoretic Approach*, second ed. Springer Press, New York.
- Cai, Y., Pan, Z., Liu, D., Zheng, G., Tang, S., Connell, L.D., Yao, Y., Zhou, Y., 2014. Effects of pressure and temperature on gas diffusion and flow for primary and enhanced coalbed methane recovery. *Energy Explor. Exploit.* 32 (4), 601–619. <https://doi.org/10.1260/0144-5987.32.4.601>.
- Dierenfeld, E., Hintz, H., Robertson, J., Soest, P., Oftedal, O., 1982. Utilization of bamboo by the giant panda. *J. Nutr.* 112 (4), 636–641. <https://doi.org/10.1093/jn/112.4.636>.
- Fisher, R., Wilson, S.K., Sin, T.M., Lee, A.C., Langlois, T.J., 2018. A simple function for full-subsets multiple regression in ecology with R. *Ecol. Evol.* 8, 6104–6113. <https://doi.org/10.1002/ece3.4134>.
- Fu, D., Wang, H., Qin, D., Pan, W., 1997. Surveys of scent marking and vegetation of mating place of giant panda in Qinling mountain. *CNKI:SUN:SWXT.0.1997-04-013 Chinese Bulletin of Biology* 32 (4), 19–20 (In Chinese).
- Gosling, L.M., Roberts, S.C., 2001. Testing ideas about the function of scent marks in territories from spatial patterns. *Anim. Behav.* 62 (3), F7–F10. <https://doi.org/10.1006/anbe.2001.1802>.
- Hagey, L., MacDonald, E., 2003. Chemical cues identify gender and individuality in giant pandas (*Ailuropoda melanoleuca*). *J. Chem. Ecol.* 29 (6), 1479–1488. <https://doi.org/10.1023/A:1024225806263>.
- Hou, J., Yang, J., Li, Y., Huang, J., Liu, D., Zhang, J., 2018. Spatiotemporal distribution characteristics of mammals investigated using camera trap traps in Wolong Nature Reserve. *J. Nanjing For. Univ. (Nat. Sci. Ed.)* 42 (3), 187–192 (In Chinese).
- Hou, J., He, Y., Yang, H., Connor, T., Gao, J., Wang, Y., Zeng, Y., Zhang, J., Huang, J., Zheng, B., Zhou, S., 2020. Identification of animal individuals using deep learning: a case study of giant panda. *Biol. Conserv.* 242 <https://doi.org/10.1016/j.biocon.2020.108414>.
- Hu, J., Xia, L., Pan, W., Zhu, J., 1985. *Wolong's Giant Panda*. Sichuan Science and Technology Press, Chengdu (In Chinese).
- Huang, J., Li, Y., Du, L., Yang, B., Shen, F., Zhang, H., Zhang, X., Yue, B., 2015. Genome-wide survey and analysis of microsatellites in giant panda (*Ailuropoda melanoleuca*), with a focus on the applications of a novel microsatellite marker system. *BMC Genet.* 16 (1) <https://doi.org/10.1186/s12864-015-1268-z>.
- Hull, C., 1943. *Principles of Behavior*. Appleton Century Crofts, New York.
- Hull, V., Roloff, G., Zhang, J., Liu, W., Zhou, S., Huang, J., Xu, W., Ouyang, Z., Zhang, H., Liu, J., 2014. A synthesis of giant panda habitat selection. *Ursus* 25 (2), 148–162. <https://doi.org/10.2192/URSUS-D-13-00011.1>.
- Hull, V., Zhang, J., Huang, J., Zhou, S., Vina, A., Shortridge, A., Li, R., Liu, D., Xu, W., Ouyang, Z., Zhang, H., Liu, J., 2016. Habitat use and selection by giant pandas. *PLoS One* 11 (9), e0162266. <https://doi.org/10.1371/journal.pone.0162266>.
- Johansson, B.G., Jones, T.M., 2007. The role of chemical communication in mate choice. *Biol. Rev.* 82 (2), 265–289. <https://doi.org/10.1111/j.1469-185X.2007.00009.x>.
- Johnson, R.P., 1973. Scent marking in mammals. *Anim. Behav.* 21, 521–535. [https://doi.org/10.1016/S0003-3472\(73\)80012-0](https://doi.org/10.1016/S0003-3472(73)80012-0).
- Kang, D., Li, J., 2016. Connect the fragmented habitat patches for giant panda. *Environ. Sci. Pollut. Res.* 23 (12), 11507–11508. <https://doi.org/10.1007/s11356-016-6725-y>.
- Khazan, E.S., 2014. Tests of biological corridor efficacy for conservation of a Neotropical giant damselfly. *Biol. Conserv.* 177, 117–125. <https://doi.org/10.1016/j.biocon.2014.06.006>.
- Kleiman, D.G., 1983. Ethology and reproduction of captive giant pandas (*Ailuropoda melanoleuca*). *Z. Tierpsychol.* 62 (1), 1–46. <https://doi.org/10.1111/j.1439-0310.1983.tb02139.x>.
- Li, H., Li, D., Li, T., Qiao, Q., Yang, J., Zhang, H., 2010. Application of least-cost path model to identify a giant panda dispersal corridor network after the Wenchuan earthquake—case study of Wolong Nature Reserve in China. *Ecol. Model.* 221 (6), 944–952. <https://doi.org/10.1016/j.ecolmodel.2009.12.006>.
- Li, R., Xu, M., Wong, M.H.G., Qiu, S., Li, X., Ehrenfeld, D., Li, D., 2015. Climate change threatens giant panda protection in the 21st century. *Biol. Conserv.* 182, 93–101. <https://doi.org/10.1016/j.biocon.2014.11.037>.
- Liu, J., Ouyang, Z., Taylor, W.W., Groop, R., Tan, Y., Zhang, H., 1999. A framework for evaluating the effects of human factors on wildlife habitat: the case of giant pandas. *Conserv. Biol.* 13 (6), 1360–1370. <https://doi.org/10.1046/j.1523-1739.1999.98418.x>.
- Liu, D., Zhang, G., Wei, R., Zhang, H., Fang, J., Sun, R., 2002. Effects of sex and age on the behavior of captive giant pandas (*Ailuropoda melanoleuca*). *Acta Zool. Sin.* 48 (5), 585–590. <https://doi.org/10.3969/j.issn.1674-5507.2002.05.002> (In Chinese).
- Liu, G., Wang, H., Yin, Y., 2005. Giant panda's scent marks and scent mark trees in Wanglang National Nature Reserve, Sichuan. *Biodivers. Sci.* 13 (5), 445–450. <https://doi.org/10.3321/j.issn:1005-0094.2005.05.010> (In Chinese).
- Liu, J., Chen, Y., Guo, L., Gu, B., Liu, H., Hou, A., Liu, X., Liu, D., 2005. Stereotypic behavior in relation to fecal cortisol level in captive giant pandas. *J. Beijing Normal Univ. (Nat. Sci.)* 41 (1), 75–78. <https://doi.org/10.3321/j.issn:0476-0301.2005.01.022> (In Chinese).
- Liu, D., Huang, K., Zhang, J., 2011. Individual recognition and odor in rat-like hamsters: behavioral responses and chemical properties. *Chem. Senses* 36, 799–810. <https://doi.org/10.1093/chemse/bjr055>.
- Liu, X., Wu, P., Songer, M., Cai, Q., He, X., Zhu, Y., Shao, X., 2013. Monitoring wildlife abundance and diversity with infra-red camera traps in Guanyinshan Nature Reserve of Shaanxi Province, China. *Ecol. Indic.* 33 (oct), 121–128. <https://doi.org/10.1016/j.ecolind.2012.09.022>.
- Martin, J., Lopez, P., 2007. Scent may signal fighting ability in male Iberian rock lizards. *Biol. Lett.* 3 (2), 125–127. <https://doi.org/10.1098/rsbl.2006.0589>.
- Nie, Y., Swaisgood, R.R., Zhang, Z., Hu, Y., Ma, Y., Wei, F., 2012. Giant panda scent-marking strategies in the wild: role of season, sex and marking surface. *Anim. Behav.* 84 (1), 39–44. <https://doi.org/10.1016/j.anbehav.2012.03.026>.
- Pan, W., Lu, Z., Zhu, X., Wang, D., Wang, H., Long, Y., Fu, D., Zhou, X., 2001. *A Chance for Lasting Survival*. Peking University Press, Beijing (In Chinese).
- Parker, M., 2010. *Territoriality and scent marking behavior of african wild dogs in northern Botswana. Dissertations & Theses Gradworks.*
- Rajagopal, T., Archunan, G., Geraldine, P., Balasundaram, C., 2010. Assessment of dominance hierarchy through urine scent marking and its chemical constituents in male blackbuck Antelope cervicapra, a critically endangered species. *Behav. Process.* 85 (1), 58–67. <https://doi.org/10.1016/j.beproc.2010.06.007>.
- Rosenberg, D.K., Noon, B.R., Meslow, E.C., 1997. Biological corridors: form, function, and efficacy. *Bioscience* 47 (10), 677–687. <https://doi.org/10.2307/1313208>.
- Schaller, G.B., Hu, J., Pan, W., Zhu, J., 1985. *The Giant Pandas of Wolong*. University of Chicago Press, Chicago.
- Sharpe, L.L., 2015. Handstand scent marking: height matters to dwarf mongooses. *Anim. Behav.* 105 (Jul), 173–179. <https://doi.org/10.1016/j.anbehav.2015.04.019>.

- Shi, X., Hu, Q., Jin, S., Wang, M., Yang, C., Peng, X., 2012. Preliminary investigation on distributions of giant panda scent mark trees in Wolong national nature reserve sanjiang area. *Sichuan J. Zool.* 31 (5), 704–707 (In Chinese).
- Sichuan Forestry Department, 2015. *The Fourth Survey Report On Giant Panda of Sichuan*. Sichuan science and technology press, Chengdu (In Chinese).
- Spackman, S.C., Hughes, J.W., 1995. Assessment of minimum stream corridor width for biological conservation: species richness and distribution along mid-order streams in Vermont, USA. *Biol. Conserv.* 71 (3), 325–332. [https://doi.org/10.1016/0006-3207\(94\)00055-U](https://doi.org/10.1016/0006-3207(94)00055-U).
- Swaigood, R.R., Lindburg, D.G., Zhou, X., 1999. Giant pandas discriminate individual differences in conspecific scent. *Anim. Behav.* 57 (5), 1045–1053. <https://doi.org/10.1006/anbe.1998.1070>.
- Swaigood, R.R., Lindburg, D.G., Zhang, H., 2002. Discrimination of oestrous status in giant pandas (*Ailuropoda melanoleuca*) via chemical cues in urine. *J. Zool.* 257 (3), 381–386. <https://doi.org/10.1017/S0952836902000985>.Thiessen.
- Tian, H., Wei, R., Zhang, G., Sun, R., Liu, D., 2004. Behavioral Difference of Sub-adult Giant Pandas (*Ailuropoda melanoleuca*) in Traditional and semi-natural enclosures. *Zool. Res.* 25 (2), 137–140. <https://doi.org/10.3321/j.issn:0254-5853.2004.02.009>.
- Vanderploeg, H.A., Scavia, D., 1979. Calculation and use of selectivity coefficients of feeding: zooplankton grazing. *Ecol. Model.* 7, 135–149. [https://doi.org/10.1016/0304-3800\(79\)90004-8](https://doi.org/10.1016/0304-3800(79)90004-8).
- Vogt, K., Zimmermann, F., Kolliker, M., Breitenmoser, U., 2014. Scent-marking behaviour and social dynamics in a wild population of Eurasian lynx *Lynx lynx*. *Behav. Process.* 106 (Jul), 98–106. <https://doi.org/10.1016/j.beproc.2014.04.017>.
- Wang, L., Yan, Y., Yuan, Z., 2012. Survey on the scent mark trees of giant panda. *Shanxi Forestry Science and Technology* 11 (4), 5–7. <https://doi.org/10.3969/j.issn.1001-2117.2012.04.002> (In Chinese).
- Wang, F., McShea, W.J., Wang, D., Li, S., Zhao, Q., Wang, H., Lu, Z., 2014. Evaluating landscape options for corridor restoration between giant panda reserves. *PloS One* 9 (8), e105086. <https://doi.org/10.1371/journal.pone.0105086>.
- Wei, F., Feng, Z., Wang, Z., Hu, J., 2000. Habitat use and separation between the giant panda and the red panda. *J. Mammal.* 81 (2), 448–455.
- Wei, W., Swaigood, R., Dai, Q., Yang, Z., Yuan, S., Owen, M.A., Pilfold, N.W., Yang, X., Gu, X., Zhou, H., Han, H., Zhang, J., Hong, M., Zhang, Z., 2018. Giant panda distributional and habitat-use shifts in a changing landscape. *Conserv. Lett.* 11 (6), e12575 <https://doi.org/10.1111/conl.12575>.
- White, A.M., Swaigood, R.R., Zhang, H., 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 (6), 519–529. <https://doi.org/10.2307/4602087>.
- Wilson, E.O., Bossert, W.H., 1963. Chemical communication among animals. *Recent prog. Horm. Res.* 19, 673–716.
- Zhang, J., 2012. *Activity Patterns and Space Use of the Giant Panda in Relationship to Human and Natural Disturbance*. Ph. D Dissertation. Beijing: Research Center for eco-environmental sciences, Chinese Academy of Sciences (In Chinese).
- Zhang, J., Hull, V., Huang, J., Zhou, S., Xu, W., Yang, H., McConnell, W.J., Li, R., Liu, D., Huang, Y., Ouyang, Z., Zhang, H., Liu, J., 2015. Activity patterns of the giant panda (*Ailuropoda melanoleuca*). *J. Mammal.* 96 (6), 1116–1127. <https://doi.org/10.1093/jmammal/gyv118>.
- Zhang, J., Hull, V., Ouyang, Z., Li, R., Connor, T., Yang, H., Zhang, Z., Silet, B., Zhang, H., Liu, J., 2017. Divergent responses of sympatric species to livestock encroachment at fine spatiotemporal scales. *Biol. Conserv.* 209, 119–129. <https://doi.org/10.1016/j.biocon.2017.02.014>.
- Zhou, X., Wang, P., Zhang, H., Wei, R., Zhang, G., Li, D., Huang, Y., Swaigood, R.R., 2005. *Research on Behavior and Methods of Captive Giant Panda*. Sichuan Science and Technology Press, Chengdu (In Chinese).
- Zhou, W., Nie, Y., Hu, Y., Swaigood, R., Zhang, Y., Liu, D., Wei, F., 2019a. Seasonal and reproductive variation in chemical constituents of scent signals in wild giant pandas. *Sci. China Life Sci.* 62 (5), 648–660. <https://doi.org/10.1007/s11427-018-9388-9>.
- Zhou, W., Nie, Y., Swaigood, R., Li, Y., Liu, D., Wei, F., 2019b. Ecological context influences scent-marking behavior in the giant panda. *J. Zool.* 309 (3) <https://doi.org/10.1111/jzo.12711>.