

Signal detection theory applied to giant pandas: Do pandas go out of their way to make sure their scent marks are found?

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Abstract

The purpose of inter-animal communication is to allow signals released by the animal to be perceived by others. Scent marking, with its characteristics of specificity and delay, is thought to be the primary mode of communication in giant pandas (*Ailuropoda melanoleuca*). The “signal detection theory” predicts that animals choose the substrate and location of their scent marks so that the signals released are transmitted more widely and remain longer. As an energetically marginal species, the cost of generating and marking chemical signals is costly for pandas, so they are predicted to make trade-offs in scent marking. However, existing studies do not account for the selective preferences of pandas for marking, as they are only explained by the density of marks at a certain location. Our study wanted to investigate whether the marking behavior of pandas is indeed consistent with signal detection theory. For the first time, we propose to use fecal counts to reflect the intensity of habitat use by pandas, combined with mark counts to determine the selective preference for marking. Our findings show that the scent marking behavior of pandas is consistent with signal detection theory, and that they go out of their way to ensure that their marks are detected. The results of the study will help us to further develop the conservation of pandas and their habitats.

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Abstract

The purpose of inter-animal communication is to allow signals released by the animal to be perceived by others. Scent marking, with its characteristics of specificity and delay, is thought to be the primary mode of communication in giant pandas (*Ailuropoda melanoleuca*). The "signal detection theory" predicts that animals choose the substrate and location of their scent marks so that the signals released are transmitted more widely and remain longer. As an energetically marginal species, the cost of generating and marking chemical signals is costly for pandas, so they are predicted to make trade-offs in scent marking. However, existing studies do not account for the selective preferences of pandas for marking, as they are only explained by the density of marks at a certain location. Our study wanted to investigate whether the marking behavior of pandas is indeed consistent with signal detection theory. For the first time, we propose to use fecal counts to reflect the intensity of habitat use by pandas, combined with mark counts to determine the selective preference for marking. Our findings show that the scent marking behavior of pandas is consistent with signal detection theory, and that they go out of their way to ensure that their marks are detected. The results of the study will help us to further develop the conservation of pandas and their habitats.

Keywords

chemical communication, conservation implication, giant panda, scent marking, signal detection theory

1 INTRODUCTION

Animal communication refers to the process by which an individual sends signals to other individuals and the individual receiving the signals responds to them. Chemical communication with characteristics such as specificity and delay is considered to be one of the main modes of communication in most mammals (Brown & Macdonald, 1985), as it is independent of light, can propagate even in dark conditions, and can still propagate when the signal releaser is away from the chemical signal (Wyatt, 2014). Scent marking, the deposition of signals by individuals on objects in the environment, is a common form of chemical signal in mammals (Gosling & Roberts, 2001). The main vehicle for transmitting information in mammalian chemical communication is the chemical pheromone, which includes many complex information, such as individual identity characteristics, sex, age, reproductive status, social status and kinship (Brennan & Kendrick, 2006; Ferrero & Liberles, 2010; Johansson & Jones, 2007; Jojola et al., 2012; Kean et al., 2011).

"Signal detection theory" predicts that animals select scent-labeled signal deposit substrates, resulting in a wider range and longer retention of the released signal (Alberts, 1992). A growing number of studies have demonstrated that this choice of signal deposit substrate is more widespread in mammalian chemotaxis than we thought, such as the spotted hyena (*Crocuta crocuta*) (Gorman, 1990) and the African wild dog (*Lycaon pictus*) (Claase et al., 2022), which use urine and feces, among other substances, for chemical communication. However, we also need to be aware that both the chemical signal generation and the marking process are very energy-consuming (Gosling et al., 2000); and that after scent marking, the animal needs to be visited periodically to observe and update the signal markers in order to maintain the continued validity of the signal, a process that also requires a significant investment of time and energy (Clapham et al., 2014; Roberts & Gosling, 2001). The economic constraints associated with travel and time costs of chemical signals deployment across an animal's entire home range preclude rangewide scent signal saturation, forcing animals to be more strategic about selecting scent deposition sites.

Giant pandas (*Ailuropoda melanoleuca*) are typically solitary mammals that rarely come into direct contact with other individuals except for the rutting season when they form gatherings (Nie et al., 2012a; Schaller, 1985), and coupled with their long-term life in dense bamboo forests, which has led to a relative degradation

of vision (Wei et al., 2015), information exchange between individuals in the wild relies mainly on olfaction and hearing (Hu et al., 1985). Auditory communication refers to communication between individuals through acoustic signals and generally occurs during the mating aggregation period in the breeding season (Charlton et al., 2009) or during casual contact between individuals in the non-breeding season. Scent marker-based chemical communication thus becomes a major mode of communication for wild giant pandas (Swaigood et al., 1999; Wei et al., 2015). Giant pandas communicate chemically mainly by tagging anogenital gland secretion (AGS) and urine to transmit individual information, using the chemicals stored therein for inter-individual signal exchange (Hu et al., 1985).

However, the cost of generating chemical signals is too high for an energetically marginal species like the giant panda, which, unlike other bear species, uses urine and AGS as chemical communication signals rather than feces (Pan et al., 2001). Both urine and feces are metabolic by-products and therefore consume less energy, whereas AGS is produced by specialized glands and has a high fat content (Hagey & Macdonald, 2003), further exacerbating energy expenditure.

Up to the present study, we found that giant pandas have a greater number of scent markers at the ridge and will select the appropriate substrate material depending on the marks (Nie et al., 2012a). However, it is not rigorous to equate the number of markers with selection preference. Because pandas mark more in a certain place may be because they spend more time in that place, but not because they prefer to mark there. We propose, for the first time, that there is a need to demonstrate that giant pandas mark scent more frequently than expected at a given location as an indication of selective preference. The easiest way to do this is to collect feces during the sample line survey and use fecal density to indicate the intensity of use of the site by pandas; since pandas defecate nearly 50 times per day and do not use feces for communication (Nie et al., 2012a), their choice of defecation location is random, depending only on where they are located when they want to defecate, so this method is rigorous.

We have innovated on previous studies by proposing for the first time to use panda feces counts to laterally reflect the intensity of habitat use as a way to assess the selection preferences of giant pandas when scent-marking. This study allows us to investigate whether the scent marking behavior of pandas is consistent with signal detection theory; and whether pandas go out of their way to deposit markers in places where they are most likely to be found. Based on the results of the study, we can protect the habitats that pandas prefer to use with precision and enhance communication among individual pandas and their populations.

2 MATERIALS AND METHODS

2.1 Study sites

We conducted this study in Shaanxi Foping National Nature Reserve (Figure 1), which is located in the Qinling Mountains, with a geographical range between 107°41' and 107deg55' E and 33deg33' and 33deg46' N. The total area is about 293 km² and the elevation range is from 980 to 2904 m. In The Fourth National Survey Report on the Giant Panda, there were about 67 wild pandas in the reserve. There are six conservation stations in the reserve, namely Liangfengya, Sanguanmiao, Xihe, Daguping, Longtanzi and Yueba. Among them, Sanguanmiao and Xihe are the core areas of the reserve, which are rich in flora and fauna. In addition to the giant panda, there are also a wide range of national key protected animals such as the takin (*Budorcas taxicolor*), forest musk deer (*Moschus berezovskii*), leopard (*Panthera pardus*) and so on.

2.2 Field data collection

We established a sample line for the study near Sanguanmiao, the core area of the reserve, where the density of giant pandas is known to be high and where pandas are often scent marked (Nie et al., 2012a). We established six types of sample lines along three types of terrain (Table 1): 12, 7, and 3 each of ridge, valley, and slope samples with animal trails, and 11, 7, and 4 each without animal trails, the former as experimental samples and the latter as control samples, corresponding to roughly equal sample line lengths. Animal trails are identifiable trails traveled by wildlife on repeated trips, evident by worn appearance, compacted soil, and lack of vegetation.

The width of the sample line was 4 m, i.e. 2 m on each side of the road, and within this range we could easily detect marked trees and feces. Data collection methods followed Nie et al., (2012a), but differed (Nie et al., 2012a). Walking along the sample line, the number of giant panda faeces found along the line was recorded, as well as the species and location of all trees with DBH greater than 5 cm and several characteristics that may affect the selectivity of giant panda markers (Table 2), and they were marked as "available trees". For the trees with scent marks, additional characteristics such as mark type and orientation were recorded as "marked trees". Urine marks causing a greener bark with a musky smell, and AGS marks causing the bark to turn brown. To determine if the marked trees were repeatedly marked, we monitored each marked tree on the sample line every other week. The musky smell of the urine marker disappeared after about 5 days, which allowed us to determine if the same area was repeatedly marked. For AGS marking, we cut a small piece of bark in the middle of the marked area, leaving out the lighter colored bark underneath, and monitored it to see if it was again covered with AGS marks to determine if it was repeatedly marked.

For each scent-marked tree, where feasible, we set up a 5*5m sample square centered on them and measured the variables of vegetation density, vegetation coverage, slope and slope aspect (Table 2). After that, a control sample was set up by walking 200m along the sample line and the same indicators were measured for it. Note that if there are marked trees that happen to be located within the control sample, we need to reposition the sample to the nearest area that does not contain the marked trees in order to form a better control.

2.3 Data analysis

We used the Mann-Whitney U test and one-way ANOVA to determine whether the presence or absence of a sample line of animal trails influenced the degree of preference for marking by pandas, based on whether the independent variables conformed to a normal distribution and the chi-squaredness of the variance; for the degree of preference for different terrain we used the Kruskal Wallis test. In addition, we used the Mann-Whitney U test as well as the chi-square test to determine whether individual variables were significantly different between the marker and control samples, and between the marked and control trees. Afterwards, we used Pearson Correlation Analysis to determine the correlation among the variables, and after eliminating the significantly correlated variables, we used stepwise regression to build the best model to determine which variable had the greatest effect on the selection of marking sites by giant pandas. In this study, we determined that the differences were statistically significant at $P < 0.05$ and all tests were two tailed. All data analysis was carried out in IBM SPSS Statistics 27.0.1.

3 RESULT

The total length of the 22 experimental lines was 18.02 km and the total length of the 22 control lines was 16.37 km. 152 marked trees were found in the former and 5 in the latter. A total of 790 giant panda faeces were found in the former and 498 in the latter (Table S1).

3.1 Preferred terrain for marking by giant pandas

There was a significant difference in the degree of marking preference between experimental and control lines, with pandas preferring to scent mark on lines with animal trails (Mann-Whitney $U = 33.00, P < 0.001$, Figure 2). The preference for terrain also differed significantly, with giant pandas preferring to scent mark on ridges, followed by valleys, and finally slopes (Kruskal Wallis test, $\chi^2 = 9.74, P = 0.008$, Figure 3). The preferred location for scent marking by giant pandas was ridges with animal trails, while no selection was made for slopes without animal trails (Table S1).

3.2 The tree species preferred by pandas for marking

We counted the species of giant panda marked trees and classified their marking frequency into 3 categories, low frequency (i.e., the species had only 1 to 5 marking records in total), medium frequency (i.e., the species had 6 to 10 marking records in total) and high frequency (i.e., the species had more than 10 marking records in total). There were 16 species of low frequency, 4 species of medium frequency and 3 species of high frequency. The three species with high frequency are Badung oak (*Quercus engleriana*), Yaupon pine

(*Pinus tabulaeformis*), and Huashan pine (*Pinus armandii*) (Table S2). These three trees are all locally dominant species with a wide distribution (Ming et al., 1999).

3.3 Microhabitat differences between marked and control sites

We found a total of 157 scent marked trees in the sample line survey, but due to topography and slope, etc., not every location of the marked trees was suitable for sample squares, so we made a total of 144 marked samples, corresponding to 114 control samples. Compared to the control sample, bamboo density ($U = 5474.00$, $P < 0.001$), bamboo cover ($U = 5905.50$, $P < 0.001$), and slope ($U = 6328.50$, $P < 0.001$) were lower in the marked sample; however, tree density ($U = 4731.00$, $P < 0.001$) and tree cover ($U = 5729.00$, $P < 0.001$) were higher; shrub density ($U = 7523.50$, $P = 0.226$) and shrub cover ($U = 7500.00$, $P = 0.130$) were not significantly different between both (Table S3). In order to detect which variables had the greatest influence on the selection of this sample site by pandas, we performed stepwise logistic regression analysis on the remaining variables after Pearson Correlation Analysis to remove the significantly correlated variables. Finally, only tree density, bamboo density, slope, tree cover and shrub cover entered into the stepwise logistic regression equation. where tree cover was the most explained variable for whether giant pandas chose the location for scent marking or not (Table 3), and giant pandas preferred to scent mark at sites with higher tree cover.

3.4 Microhabitat differences between marked and control trees

Our survey identified 157 marked trees, corresponding to 441 unmarked control trees, with significant differences in bark roughness between both ($\chi^2 = 19.31$, $P < 0.001$); DBH was greater in scent-marked trees compared to control trees, but the difference was not significant ($U = 34473.00$, $P = 0.079$); SDT was significantly shorter in marked trees than control trees ($U = 11791.50$, $P < 0.001$) (Table S4). To detect which variables had the greatest influence on the selection of the tree by pandas, we performed stepwise logistic regression analysis on the remaining variables after Pearson Correlation Analysis to eliminate those that were significantly correlated. Finally, only roughness, DBH and SDT entered into the stepwise logistic regression equation, where roughness was the variable that explained the highest degree of whether pandas selected the tree species for scent marking (Table 4), and pandas preferred scent marking on trees with higher roughness.

3.5 Microhabitat differences between repeatedly and singly marked trees

We found a total of 157 scent marked trees, of which 139 were marked multiple times, accounting for 88.3% of all marked trees, and 18 were marked only once, accounting for 11.7% of all marked trees (Figure S1). One-way ANOVA was performed on the factors that might affect the frequency of marking, and we found no significant differences between roughness ($P = 0.65$), DBH ($P = 0.82$) and SDT ($P = 0.70$) (Table S5).

3.6 Giant panda mark types and orientations

We recorded the type of marks used for scent marking in pandas and the orientation of the marks. The most frequently found marker was the AGS mark, which contained 144 of the 157 scent marked trees, accounting for 91.7% of all marked trees. The least frequent mark was Scratch mark, which contained 4 out of 157 scent marked trees, accounting for 2.5% of all marked trees, and Scratch mark was always accompanied by AGS mark (Figure S2). The most marker orientation is face to trail, which contains 128 out of 157 scent marked trees, accounting for 81.5%, while the least mark orientation is back to trail, with 6 trees, accounting for 3.8%, and multiple directional marks were accompanied with face to trail mark (Figure S3).

4 DISCUSSION

By monitoring a total of 44 sample lines, we found that the scent-marking behavior of giant pandas is indeed consistent with signal detection theory (Alberts, 1992), and that giant pandas do select and modify their marking sites to maximize their signaling function at both micro- and macro-habitat scales. Giant pandas are an energetically marginal species, their diet is bamboo and their nutritional phase is low, which affects aspects of movement, communication and reproduction (Hu et al., 1985; Nie et al., 2012b; Nie et al.,

2015). The selection of marking sites will minimize energy expenditure while increasing the effectiveness of inter-individual communication.

Our findings show that pandas prefer to scent mark on ridges with animal trails, and we know by the density of faeces on the sample line that this is indeed the area with the highest intensity of use by pandas as well (Table S1). The presence of many animal trails on the ridges also makes them important paths for the movement of giant pandas (Bai et al., 2020). However, we likewise noted that slopes without animal trails as well as ridges had high fecal densities, demonstrating that pandas spend a significant amount of time in these areas, yet the preference index for these areas was significantly lower than the corresponding terrain with animal trails. From this we learn that pandas choose these locations for scent marking not because they happen to be there, but because they really need to choose such terrain to maximize signal propagation efficiency.

The tree species most frequently scent-tagged by giant pandas were Badung oak (*Quercus engleriana*), Yaupon pine (*Pinus tabulaeformis*), and Huashan pine (*Pinus armandii*), which are dominant species with a wide local distribution (Ming et al., 1999). We speculate that they choose dominant species for marking because they take less time and energy to be found. In addition to their wide distribution, their high marking frequency may also be due to the fact that marked trees are well located for signal transmission and over time become scent stations (Hu et al., 1985), and they are often located along animal trails on mountain ridges (Nie et al., 2012a). Marking on these scent stations commonly used by giant pandas would also increase the likelihood of their information being detected by signal receivers. Zhou et al. (2019) have demonstrated that both volatile and non-volatile compounds in AGS marks were not significantly degraded within two weeks, suggesting that pandas visit and update marks frequently (Zhou et al., 2019). Thus depositing marks in better located scent stations would also reduce the energetic cost of returning and updating markers. Future work could increase research on scent stations and explore their microhabitats and conditions such as light that may affect marker persistence and dispersal to increase conservation of habitats where potential scent stations exist.

The roughness and SDT of the marked tree of giant pandas differed significantly from the control tree, similar to the results of previous study (Nie et al., 2012a), where giant pandas generally do not scent mark on smooth trunks, which would reduce the persistence of marking; and the SDT of the marked tree was significantly shorter than that of the control tree because the closer the distance to the animal trail, the more likely it is to be detected by the signal recipient, and because when marking here, giant pandas can travel shorter distances and save energy.

For both marked and control samples, bamboo density, bamboo cover and slope were lower and tree density and cover were higher in the marked sample. Higher bamboo density and cover make it more difficult for giant pandas to walk among bamboo forests, while relatively low bamboo density will allow giant pandas to obtain sufficient nutrition while reducing energy expenditure to traverse bamboo forests (Wei et al., 2015). As for the lower slope of the marked samples, the reason is that the gentle slope is a suitable habitat preferred by pandas (Hu et al., 1985), and the lower slope ensures that pandas complete scent marking in a relatively stable position (Hou et al., 2021), and walking in a gentle slope reduces energy expenditure. The higher tree density and tree cover in the marked sample is mainly due to the fact that the more trees there are, the greater the chance of trees with larger DBH appearing around them, and trees with larger DBH are more likely to form tree dens for giant pandas to breed and nurse their cubs (Wei et al., 2018; Zhang et al., 2011). In addition, the higher the density of arborvitae, the more concealed the habitat is, and thus the less likely to be detected by natural predators (Hu et al., 1985).

We found that the number of marked trees that were reused was much higher than those that were used only once, but did not detect significant differences between the variables of either. We hypothesize that the location of the repeated marked trees may be more prominent and have a wider field of view, where pandas often pass by, which may also increase the chance of other similar species finding the signal. The most used mark type in giant pandas is the AGS marks, which often remain in the natural environment for more than 3 months because of their low volatility (Hagey & Macdonald, 2003; Swaisgood et al., 2004), in order to

better convey individual information. In contrast, urine markers contain more volatile substances than AGS marks and have a shorter retention time in the environment, and are often used to convey the estrus status of individuals (Zhou et al., 2019) and the competitive ability of males (White et al., 2002), among others.

The appearance of scratch mark is always accompanied by AGS mark, so we believe that scratch mark itself does not convey information, but is a by-product left behind when AGS marking is performed. An interesting finding is that some marked trees have only bite mark and are more numerous than those with only urinary mark, which was not found in previous studies, and we predict that its role is also correlated with mark height, and if the mark is higher, it indicates that the individual is larger and more competitive, similar to AGS mark and urinary mark (White et al., 2002), but specific role needs to be further investigated. McGuire et al. found that body size affects the frequency of marking in a study of domestic dogs (*Canis lupus familiaris*) (McGuire & Bemis, 2017). However, in the study of giant pandas, we only know that body size reflects their competitive ability (Nie et al., 2012b), but whether it affects the frequency of marking deserves further investigation.

Statistics on mark orientation revealed that the most marks were toward the animal path, which is because facing the animal trail also increases the chance of the mark being detected by its own species; for those marks that were backward toward the trail, we predicted possible scent counter-marking behavior, which is one of the main responses taken by animals when they encounter the scent of other competitors of the same species (Johnson, 1973). But before counter-marking they evaluate individuals that are already marked, probably because they are not as competitive as the former and want to mark in a superior position on the marker tree, so they mark on the back (Müller & Manser, 2008). However, the exact reason needs to be confirmed by a large number of future studies.

Footpad scent communication has been found in fellow bear species brown bear (*Ursus arctos*) (Sergiel et al., 2017) and polar bear (*Ursus maritimus*) (Owen et al., 2015), and most bear species have large home ranges and are non-dominant, and releasing scent while walking is a very effective form of intraspecific communication. An interesting question is whether giant pandas use footpad scent similarly for communication? We monitored some sites in this study where giant panda tracks were pitted (Figure S4). Unfortunately, we did not find other pandas observing and sniffing the tracks in our follow-up observations. This may be due to our small sample size or the fact that we did not specifically focus on this direction, and we hope to continue this study in the future to confirm our suspicions.

It has been shown that the frequency of marking in giant pandas (Nie et al., 2012a) and the compound content of AGS marks (Zhou et al., 2019) differ significantly between the sexes. Zhou et al. detected large differences in the composition and content of compounds in AGS marks between captive and wild giant pandas (Zhou et al., 2019), which may also be one of the reasons for the low reproductive ability of captive giant pandas, and future research on scent marks of giant pandas in the field environment should be strengthened to clarify which compounds affect the estrus and reproduction of giant pandas, and applied to captive giant pandas to improve their reproductive success. This is a tremendous step forward for the survival and reproduction of the panda populations.

However, current research on chemical communication has still not kept up with acoustic communication (Wiley, 2006). Due to the construction of Giant Panda National Park, some human facilities will inevitably be built in the living environment of giant pandas in the future. It has been shown that human facilities can affect the scent marking behaviors of domesticated felines (Krofel et al., 2017), and scent marking of pandas should be continuously studied to detect whether the marking behaviors of pandas will be changed due to the influence of human facilities, so that more precise conservation of panda habitats can be carried out. For example, assessing the impact range size of human facilities prior to their construction and then locating them as far away from core giant panda habitat as possible.

5 CONCLUSION

Our findings suggest that pandas prefer to scent-mark ridges with animal trails in order to maximise the probability of their information being found by their companions. We can therefore strengthen the protection

of such habitats as a matter of policy. In addition, we can take these habitats into account when building ecological corridors to maximise communication between pandas. In addition, there are significant differences in scent marking behaviour between captive and wild pandas, so scent marking learning for captive individuals should be enhanced during wild release, habitats with moderate bamboo density and high tree cover should be provided within the release enclosure, and commonly used marked tree species for giant pandas should be planted in them to maximise the survival probability of released individuals in the wild.

AUTHOR CONTRIBUTIONS

Yue Wang: Data curation (equal); formal analysis (equal); writing – original draft (equal). Ronald R. Swaisgood: Writing – review and editing (equal). Wei Wei: Writing – review and editing (equal); resources (equal). Hong Zhou: Writing – review and editing (equal). Feiyun Yuan: Funding acquisition (equal). Mingsheng Hong: Writing – review and editing (equal). Han Han: Supervision (equal); writing – review and editing (equal). Zenjun Zhang: Supervision (equal); writing – review and editing (equal).

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

PERMISSION TO REPRODUCE MATERIALS FROM OTHER SOURCES

None.

DATA AVAILABILITY STATEMENT

Raw dataset is available at the online version.

References

- Alberts, A. C. (1992). Constraints on the design of chemical communication systems in terrestrial vertebrates. *The American Naturalist* , 139 , S62-S89
- 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. *Biological Conservation* , 247 , 108615. <https://doi.org/https://doi.org/10.1016/j.biocon.2020.108615>
- Brennan, P. A., & Kendrick, K. M. (2006). Mammalian social odours: attraction and individual recognition. *Philosophical Transactions of the Royal Society B: Biological Sciences* , 361 (1476), 2061-2078
- Brown, R. E., & Macdonald, D. W. (1985). *Social odours in mammals* : Clarendon Press.
- Charlton, B. D., Huang, Y., & Swaisgood, R. R. (2009). Vocal discrimination of potential mates by female giant pandas (*ailuropoda melanoleuca*). *Biology Letters* , 5 (5), 597-599
- Claase, M. J., Cherry, M. I., Apps, P. J., McNutt, J. W., Hansen, K. W., & Jordan, N. R. (2022). Interpack communication in african wild dogs at long-term shared marking sites. *Animal Behaviour* , 192 , 27-38. <https://doi.org/https://doi.org/10.1016/j.anbehav.2022.07.006>
- Clapham, M., Nevin, O. T., Ramsey, A. D., & Rosell, F. (2014). Scent-marking investment and motor patterns are affected by the age and sex of wild brown bears. *Animal Behaviour* , 94 , 107-116

- Ferrero, D. M., & Liberles, S. D. (2010). The secret codes of mammalian scents. *Wiley Interdisciplinary Reviews: Systems Biology and Medicine* ,2 (1), 23-33
- Gorman, M. L. (1990). Scent marking strategies in mammals. *Revue Suisse De Zoologie* , 97 (1), 3-29
- Gosling, L. M., Roberts, S. C., Thornton, E. A., & Andrew, M. J. (2000). Life history costs of olfactory status signalling in mice. *Behavioral Ecology and Sociobiology* , 48 (4), 328-332
- Gosling, L. M., & Roberts, S. C.(2001). Scent-marking by male mammals: cheat-proof signals to competitors and mates, *Advances in the Study of Behavior* pp. 169-217): Elsevier.
- Hagey, L., & Macdonald, E. (2003). Chemical cues identify gender and individuality in giant pandas (ailuropoda melanoleuca). *Journal of Chemical Ecology* , 29 (6), 1479-1488
- Hou, J., Hull, V., Connor, T., Yang, H., Gao, J., Zhao, F., Liao, Y., Chen, S., Huang, J., Zeng, Y., Zhou, S., Zhou, X., & Zhang, J. (2021). Scent communication behavior by giant pandas. *Global Ecology and Conservation* , 25 , e1431. <https://doi.org/https://doi.org/10.1016/j.gecco.2020.e01431>
- Hu, J. C., Schaller, G. B., Pan, W. S., & Zhu, J. (1985). The giant panda of wolong. *Sichuan Science and Technology Press, Chengdu*
- Johansson, B. G., & Jones, T. M. (2007). The role of chemical communication in mate choice. *Biological Reviews* , 82 (2), 265-289
- Johnson, R. P. (1973). Scent marking in mammals. *Animal Behaviour* ,21 (3), 521-535. [https://doi.org/https://doi.org/10.1016/S0003-3472\(73\)80012-0](https://doi.org/https://doi.org/10.1016/S0003-3472(73)80012-0)
- Jojola, S. M., Rosell, F., Warrington, I., Swenson, J. E., & Zedrosser, A. (2012). Subadult brown bears (ursus arctos) discriminate between unfamiliar adult male and female anal gland secretion. *Mammalian Biology* , 77 (5), 363-368
- Kean, E. F., Müller, C. T., & Chadwick, E. A. (2011). Otter scent signals age, sex, and reproductive status. *Chemical Senses* , 36 (6), 555-564
- Krofel, M., Hočevár, L., & Allen, M. L. (2017). Does human infrastructure shape scent marking in a solitary felid? *Mammalian Biology* , 87 , 36-39. <https://doi.org/https://doi.org/10.1016/j.mambio.2017.05.003>
- Mcguire, B., & Bemis, K. E. (2017). Scent marking in shelter dogs: effects of body size. *Applied Animal Behaviour Science* , 186 , 49-55. <https://doi.org/https://doi.org/10.1016/j.applanim.2016.11.001>
- Ming, Y., Yi, R., Gao-Di, D., & Tian-Qi, G. U. (1999). Species diversity of higher plant communities in foping national reserve. *Biodiversity Science* , 7 (4), 263
- Müller, C. A., & Manser, M. B. (2008). Scent-marking and intrasexual competition in a cooperative carnivore with low reproductive skew. *Ethology* , 114 (2), 174-185
- Nie, Y., Speakman, J. R., Wu, Q., Zhang, C., Hu, Y., Xia, M., Yan, L., Hambly, C., Wang, L., & Wei, W. (2015). Exceptionally low daily energy expenditure in the bamboo-eating giant panda. *Science* ,349 (6244), 171-174
- Nie, Y., Swaisgood, R. R., Zhang, Z., Hu, Y., Ma, Y., & Wei, F. (2012a). Giant panda scent-marking strategies in the wild: role of season, sex and marking surface. *Animal Behaviour* , 84 (1), 39-44. <https://doi.org/https://doi.org/10.1016/j.anbehav.2012.03.026>
- Nie, Y., Swaisgood, R. R., Zhang, Z., Liu, X., & Wei, F. (2012b). Reproductive competition and fecal testosterone in wild male giant pandas (ailuropoda melanoleuca). *Behavioral Ecology and Sociobiology* , 66 (5), 721-730
- Owen, M. A., Swaisgood, R. R., Slocomb, C., Amstrup, S. C., Durner, G. M., Simac, K., & Pessier, A. P. (2015). An experimental investigation of chemical communication in the polar bear (vol 295, pg 36,

2015). *Journal of Zoology* , 297 (3), 243

Pan, W., Lu, Z., Zhu, X., Wang, D., Wang, H., Long, Y., Fu, D., & Zhou, X. (2001). A chance for lasting survival. *Beijing University*

Roberts, S. C., & Gosling, L. M.(2001). The economic consequences of advertising scent mark location on territories, *Chemical signals in vertebrates* 9 pp. 11-17): Springer.

Schaller, G. B. (1985). *Giant pandas of wolong* : University of Chicago press.

Sergiel, A., Naves, J., Kujawski, P., Maślak, R., Serwa, E., Ramos, D., Fernández-Gil, A., Revilla, E., Zwijacz-Kozica, T., & Zieba, F. (2017). Histological, chemical and behavioural evidence of pedal communication in brown bears. *Scientific Reports* , 7 (1), 1-10

Swaigood, R. R., Lindburg, D. G., White, A. M., Hemin, Z., & Xiaoping, Z. (2004). Chemical communication in giant pandas. *Giant pandas: biology and conservation* , 106

Swaigood, R. R., Lindburg, D. G., & Zhou, X. (1999). Giant pandas discriminate individual differences in conspecific scent. *Animal Behaviour* ,57 (5), 1045-1053

Wei, F., Hu, Y., Yan, L., Nie, Y., Wu, Q., & Zhang, Z. (2015). Giant pandas are not an evolutionary cul-de-sac: evidence from multidisciplinary research. *Molecular Biology and Evolution* , 32 (1), 4-12

Wei, F., Swaigood, R., Hu, Y., Nie, Y., Yan, L., Zhang, Z., Qi, D., & Zhu, L. (2015). Progress in the ecology and conservation of giant pandas. *Conservation Biology* , 29 (6), 1497-1507

Wei, W., Nie, Y., Zhang, Z., Hu, Y., Yan, L., Qi, D., Li, X., & Wei, F. (2015). Hunting bamboo: foraging patch selection and utilization by giant pandas and implications for conservation. *Biological Conservation* , 186 , 260-267. <https://doi.org/https://doi.org/10.1016/j.biocon.2015.03.023>

Wei, W., Swaigood, R. R., Dai, Q., Yang, Z. S., Yuan, S. B., Owen, M. A., Pilfold, N. W., Yang, X. Y., Gu, X. D., Zhou, H., Han, H., Zhang, J. D., Hong, M. S., & Zhang, Z. J. (2018). Giant panda distributional and habitat-use shifts in a changing landscape. *Conservation Letters* ,11 (6). <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. *Behavioral Ecology and Sociobiology* , 51 (6), 519-529

Wiley, R. H. (2006). Signal detection and animal communication. *Advances in the Study of Behavior* , 36 , 217-247

Wyatt, T. D. (2014). *Pheromones and animal behavior: chemical signals and signatures* : Cambridge University Press.

Zhang, Z., Swaigood, R. R., Zhang, S., Nordstrom, L. A., Wang, H., Gu, X., Hu, J., & Wei, F. (2011). Old-growth forest is what giant pandas really need. *Biology Letters* , 7 (3), 403-406

Zhou, W., Nie, Y., Hu, Y., Swaigood, R. R., Zhang, Y., Liu, D., & Wei, F. (2019). Seasonal and reproductive variation in chemical constituents of scent signals in wild giant pandas. *Science China Life Sciences* ,62 (5), 648-660

Zhou, W., Nie, Y., Swaigood, R. R., Li, Y., Liu, D., & Wei, F. (2019). Ecological context influences scent-marking behavior in the giant panda. *Journal of Zoology* , 309 (3), 191-199. <https://doi.org/10.1111/jzo.12711>

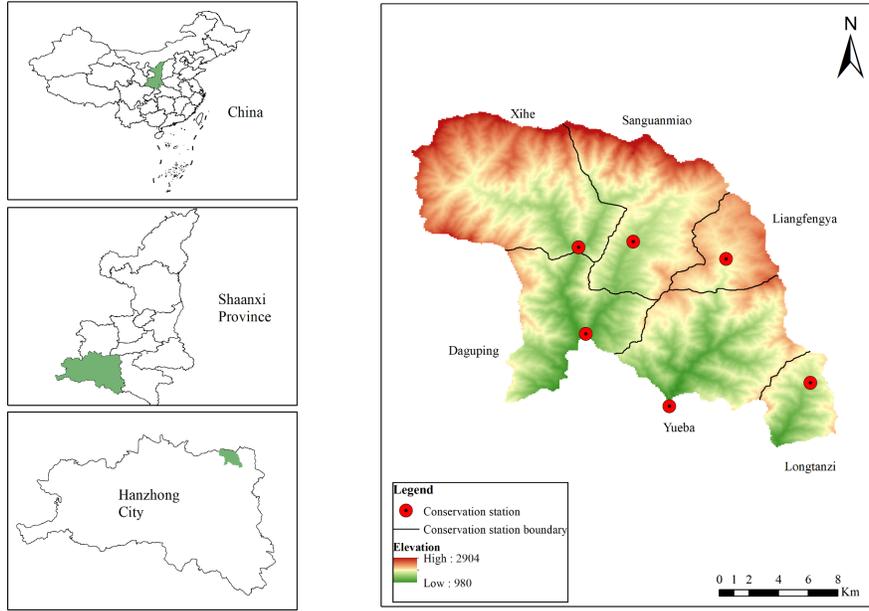


Figure 1 Diagram of the Foping National Nature Reserve.

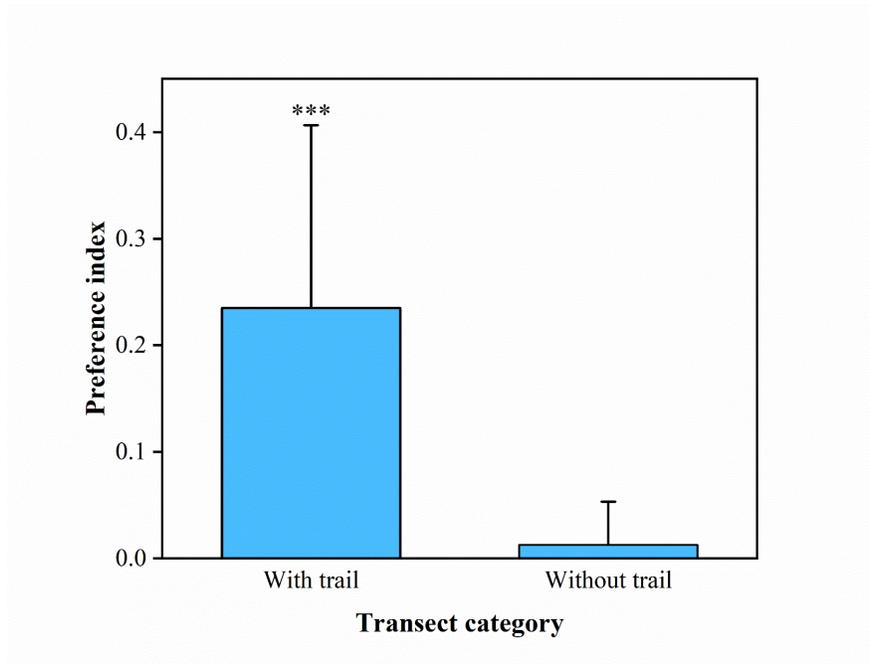


Figure 2 Comparison of marking density on transects between those with trails and without (Mann-Whitney $U = 33.00$, $P < 0.001$)

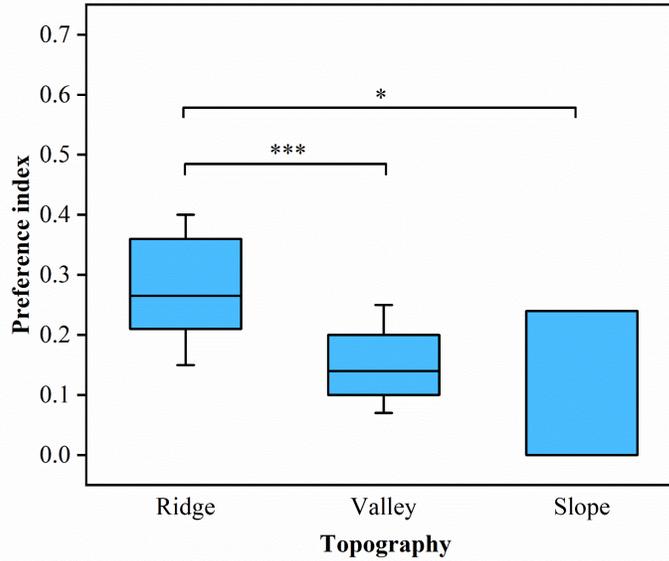


Figure 3 Comparison of Preference index on different topographies which with trails (Kruskal Wallis test, $\chi^2 = 9.74$, $P = 0.008$)

Table 1 Definition of the topography where the transects are located

Topography	Definition
Ridge	Narrow raised area, typically 2-5 meters wide, with steep slopes on either side
Valley	Low and narrow area between two hills, often with a water source
Slope	A surface that is higher at one end or side than at the other; a rising or falling level

Table 2 Main variables to be measured for marked/control trees and sites

Variables	Definition and description
Marking type	Including anogenital gland secretion mark, bite mark, urinary mark and scratch mark.
Marking orientation	Whether the mark is face to, parallel to or back to the trail.
DBH (cm)	Tree trunk diameter at 1.5 m above ground level.
Roughness	Divided into four categories: (1) smooth, (2) relatively smooth, (3) relatively rough and (4) rough.
SDT (cm)	Straight line distance from the tree to the center of the trail.
Topography	Whether the site located in ridge, valley or slope.
Slope	Slope of the mark tree or the tree in the middle of the control sites.
Slope aspect	Aspect of the slope of the mark tree or the tree in the middle of the control sites.
Vegetation density	Including tree density, shrub density and bamboo density in the sites.
Vegetation coverage	Including tree cover, shrub cover and bamboo cover in the sites.

Table 3 Variables entered stepwise logistic regression equation between marked sites and control ones

Variables	Non-Standard regression coefficient	Non-Standard regression coefficient	Standard regression coefficient
	B	SE	Beta
Tree density	0.048	0.018	0.204
Bamboo density	-0.015	0.004	-0.166
Slope	-0.097	0.030	-0.234
Tree cover	0.169	0.027	0.739
Shrub cover	0.085	0.037	0.176

Table 4 Variables entered logistic regression equation between marked trees and unmarked ones

Variables	Non-Standard regression coefficient	Non-Standard regression coefficient	Standard regression coefficient	t
	B	SE	Beta	
Roughness	0.132	0.012	0.673	10.9
DBH (cm)	0.004	0.001	0.156	2.9
SDT (cm)	-0.002	<0.001	-0.407	-7.5