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Non-galliform birds' attraction to soil mounds outside Chinese pangolin burrows

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Abstract

The Chinese pangolin (*Manis pentadactyla*) is typically conserved as a flagship species, but its ecological functions, particularly its interactions with birds, remain underexplored. This study used infrared camera traps to investigate the ecological interactions between the Chinese pangolin and bird species in the Junzifeng National Nature Reserve in southern China. To test the hypothesis that the soil mounds created by the burrowing activity of the Chinese pangolin might be highly attractive to birds, infrared cameras were installed at both fresh pangolin burrows and random detection sites. The study analyzed differences in bird species diversity, activity rhythms between the Chinese pangolin and birds, and foraging behavior patterns of birds on the soil mounds. Results revealed higher bird species diversity and biodiversity indices in the experimental group compared to the control group, particularly among non-galliform birds. The Chinese pangolin exhibited nocturnal activity, while birds were active during the day, indicating temporal segregation. Among the observed bird species, none exhibited burrow-entry behavior, but nine demonstrated foraging behavior, with a significantly higher foraging ratio among non-galliform birds. This study provides the first evidence that non-galliform birds are attracted to soil mounds created by Chinese pangolin burrows, suggesting the pangolin's potential role as a keystone species in the local ecosystem. Further research is necessary to explore the mechanisms underlying this attraction.

Keywords

Aves – geophagy – *Manis pentadactyla* – microclimate – soil ingestion

Introduction

The conservation and ecological function of the Chinese Pangolin (*Manis pentadactyla*) are currently hot topics in the field of biodiversity conservation (Emogor et al., 2023). Due to illegal hunting (Nash et al., 2016; Huang et al., 2021) and habitat loss (Zhang et al., 2021), the population of the Chinese Pangolin has declined sharply (Challender et al., 2015; Bashyal et al., 2021; Zhang et al., 2021). In 2014, this species was listed as Critically Endangered (CR) by the International Union for Conservation of Nature (IUCN) (Challender et al., 2019), included in Appendix I of CITES in 2017, and classified as a Class I National Key Protected Wild Animal in China in 2020 (Yang et al., 2018; Cen et al., 2022). As a predator of ants, the Chinese Pangolin plays a crucial role in controlling the population of termites and performs an essential function in the ecosystem (Wu et al., 2023). However, researchers have mainly focused on the Chinese Pangolin from the perspective of it being a flagship species, with relatively less research on its ecological functions, particularly in relation to other animals, such as mammals, birds, amphibians, and reptiles.

The Chinese Pangolin is a typical fossorial animal that relies on digging burrows for foraging and selects some burrows for habitation, reproduction, and rearing of young (Sun, 2022). On average, a Chinese Pangolin can excavate about 70 burrows per year, which can serve as sites for other animals to forage, reside, take refuge, and reproduce, such as rats and mice (Muridae), Eurasian Badger (*Meles meles*), Yellow-bellied Weasel (*Mustela kathiah*), and King Cobra (*Ophiophagus hannah*), playing a positive role in maintaining biodiversity (Wu et al., 2023). During the process of excavating burrows, Chinese Pangolin transport underground soil to the entrance, accumulating it into mounds, thereby creating additional space and exposing soil surfaces, which increases habitat heterogeneity (Sun, 2022). Pangolins can be considered keystone species, as other ecosystem engineers, because they have an important role in recruiting biodiversity and facilitating interspecific interactions (Sun et al., 2025). Research has shown that burrows are utilized as thermal refuges by other species, however, there is a lack of in-depth study on the function of the soil mounds outside the burrows, hindering a comprehensive understanding of the ecological function of the Chinese Pangolin.

To better explore the status and function of the Chinese Pangolin as a keystone species in the ecosystem, we investigated the relationship between the Chinese Pangolin and birds. Birds often ingest a large amount of gravel to aid in the digestion of food (Diamond et al., 1999; Brightsmith et al., 2018; Downs et al., 2019), and the soil mounds excavated by the Chinese Pangolin provide an abundance of fresh gravel. We hypothesized that the soil mounds resulting from the construction of burrows might be attractive to birds because they could represent potential resources (i.e., gravel used by birds for digestion, or directly providing a source of food items like excavated invertebrates), and we predicted that the mounds would attract birds using them to find food or gravel. Here we compare species photos and video data captured by infrared cameras placed near Chinese Pangolin

burrows with those from randomly placed infrared cameras to verify whether the fresh soil mounds outside the burrows of the Chinese Pangolin have a significant attraction to birds.

Material and methods

Study area

The Fujian Junzifeng National Nature Reserve, located in Mingxi County in the central-western part of Fujian Province, is situated on the eastern slopes of the mid-section of the Wuyi Mountains, with geographic coordinates ranging from 26 °19′03″N to 26 °39′18″N and 116 °47′21″E to 117 °31′22″E. The total area of the reserve is 180.6 km^2. The altitude ranges from approximately 300 to 1,561 meters, with ten peaks exceeding an altitude of 1,000 meters, predominantly consisting of mid-low mountains. The average annual temperature is 18.0 °C, with an annual precipitation of 1,737 mm. The reserve is dedicated to the protection of the mid-subtropical evergreen broad-leaved forest ecosystem. It is rich in flora and fauna resources, with 34 nationally protected plant species including *Ormosia microphylla*, Golden Chicken Fern (*Cibotium barometz*), *Phoebe bournei*, and 78 nationally protected animal species such as Elliot's Pheasant (*Syrmaticus ellioti*), Chinese Pangolin, Asiatic Black Bear (*Ursus thibetanus*), and Mainland Serow (*Capricornis milneedwardsii*) (Huang, 2023).

Infrared camera installation and valid Photo statistics

The infrared cameras were installed in November 2022, with fieldwork spanning from November 2022 to November 2023. The installation sites were divided into burrow detection sites (experimental group) and random detection sites (control group). The burrow detection sites were located near fresh burrows of the Chinese Pangolin (determined by the freshness of the soil at the burrow entrance and the accumulation of fallen leaves). At each fresh burrow, one infrared camera was installed at a suitable location to directly capture the surroundings and interior of the Chinese Pangolin burrows, with a total of 10 devices deployed (Zhang et al., 2023).

Random detection sites were established using a grid method, dividing the reserve into uniform grid squares of 1 km × 1 km (Zhang et al., 2024). Within each square, infrared cameras were installed at appropriate locations, such as animal trails, near water sources, or near foraging traces (Zhu et al., 2017), with a total of 39 infrared cameras installed. A "random number generator" was used to randomly select 10 sites as the control group.

The infrared cameras were installed at a height of approximately 0.5 meters, capturing both photos and videos. Photos were taken consecutively twice, and each video segment was recorded for 15 seconds (Xiao et al., 2019). To ensure the normal operation of the cameras, maintenance, data retrieval, and memory card replacement were performed quarterly. Multiple valid photos of the same species captured by the same camera at the same site within 30 minutes were combined as one independent valid photo (Zhu et al., 2017; Tanwar et al., 2021). Each infrared camera operating normally for 24 hours was counted as one valid camera working day.

Data analysis

Analysis of species diversity differences

In this study, the Wilcoxon method was utilized to analyze the differences in avian species diversity between the experimental and control groups based on independent valid photos (Parsons et al., 2016; Weeks et al., 2022). The species diversity indices used were the Margalef richness index, the Simpson's dominance index, the Shannon-Wiener diversity index and Pielou's evenness index.

Additionally, the same analytical method was employed to compare the significance of differences between the experimental and control groups in the following indices: (1) Number of bird species, total number of bird individuals; (2) Number of non-galliform bird species, proportion of non-galliform bird species, number of non-galliform bird individuals, proportion of non-galliform bird individuals; (3) Number of galliform bird species, proportion of galliform bird species, number of galliform individuals, proportion of galliform individuals. In this study, non-galliform birds, primarily passerines that rarely forage on the ground, and galliform birds, which are predominantly ground dwelling, were distinguished to highlight the significant attraction of pangolin burrow mounds to birds, especially non-galliform birds.

The number of bird species refers to the total count of different bird species at the same site, while the total number of bird individuals refers to the aggregate count of all bird individuals at the same site. Galliformes are those that primarily move on the ground, such as the Silver Pheasant (*Lophura nycthemera*), the Collared Partridge (*Arborophila gingica*), and the Elliot's Pheasant (*S. ellioti*). Non-galliform birds refer to all other birds excluding the Galliformes; in this study, all other birds excluding the Silver Pheasant (*L. nycthemera*), the Collared Partridge (*A. gingica*), and the Elliot's Pheasant (*S. ellioti*) are considered non-galliform birds.

The number of non-galliform bird species refers to the total count of non-galliform bird species at the same site. The proportion of non-galliform bird species is the ratio of the number of non-galliform bird species to the total number of bird species at the same site. The number of non-galliform bird individuals refers to the aggregate count of all non-galliform bird individuals at the same site. The proportion of non-galliform bird individuals is the ratio of the number of non-galliform bird individuals to the total number of bird individuals at the same site.

Similarly, the number of galliform bird species refers to the total count of galliform bird species at the same site. The proportion of galliform bird species is the ratio of the number of galliform bird species to the total number of bird species at the same site. The number of galliform bird individuals refers to the aggregate count of all galliform bird individuals at the same site. The proportion of galliform bird individuals is the ratio of the number of galliform bird individuals to the total number of bird individuals at the same site.

Analysis of temporal activity rhythms between the Chinese Pangolin and birds

The infrared cameras in the experimental group captured images of the Chinese Pangolin and birds, as shown in fig. 1. All independent valid photos from the experimental group were selected for analysis.

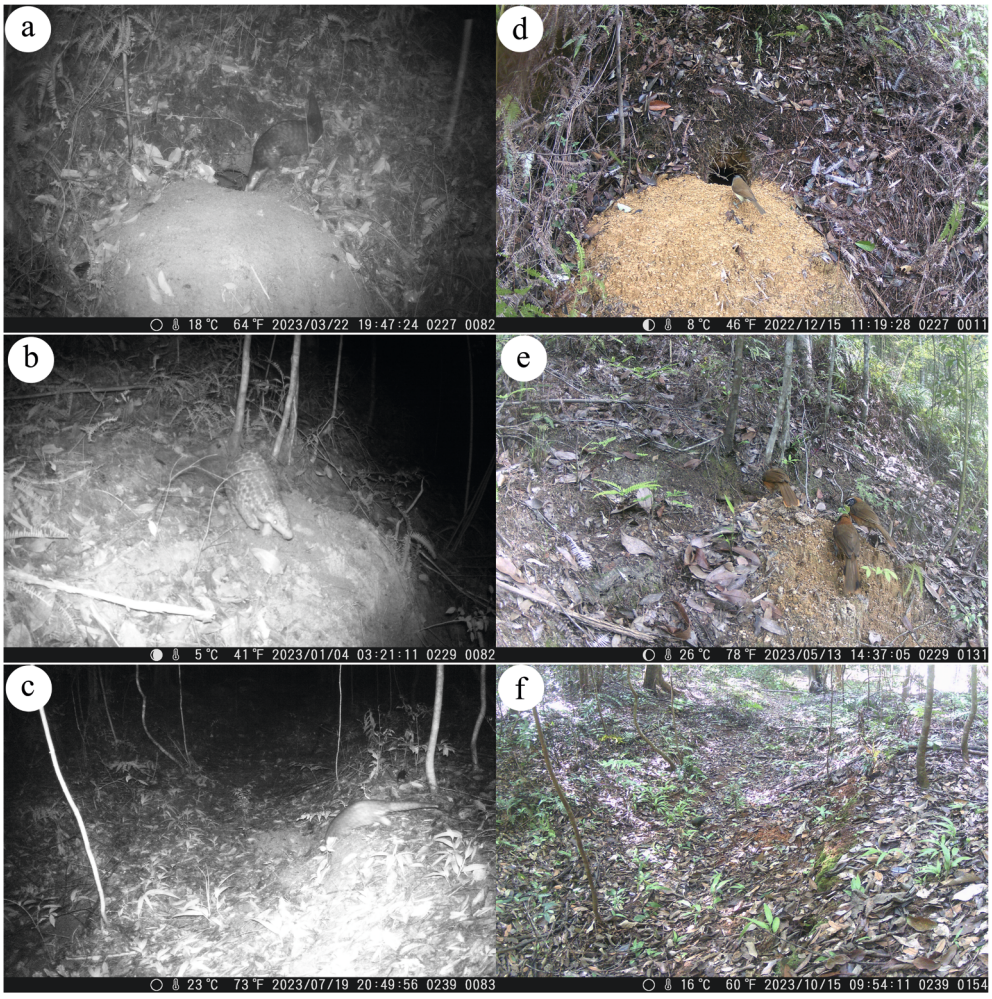


FIGURE 1 Birds outside the burrows of the Chinese Pangolin in the Fujian Junzifeng National Nature Reserve. The parameters below the photo, from left to right, are Ambient Temperature in Celsius, Fahrenheit, Date, Time (24-hour format), Camera Number, and Photo Number. (a) and (d) are the same burrow, with d showing the Grey-headed Parrotbill (*Paradoxornis gularis*) (on the soil mound); (b) and (e) are the same burrow, with e showing the Greater Necklaced Laughingthrush (*Garrulax pectoralis*) (on the soil mound); (c) and (f) are the same burrow, with (f) showing the Grey-capped Emerald Dove (*Chalcophaps indica*) (on the left side of the soil mound). The video data corresponding to panels (a), (b), (c), (d), (e), and (f) are provided in supplementary videos S1a–S1f.

The daily activity rhythms of animals were analyzed using kernel density estimation for data from cameras outside the burrows (Ridout & Linkie, 2009; Rovero et al., 2013), with related analysis and plotting completed using the "overlap" package (Ridout & Linkie, 2009; Meredith & Ridout, 2024). The compareChern function in the *activity* package (Rowcliffe, 2023) was used to analyze differences in daily activity

rhythms between the two animal groups and to explore whether there is temporal niche segregation between sympatric species. The Δ1 value was used for both animal groups when the minimum sample size was less than 75, while the Δ4 value was used when the sample size was 75 or more. The 95% confidence intervals for Δ for each animal group were obtained from 1,000 bootstrap samples, with values ranging from 0 (no overlap) to 1 (complete overlap) (Meredith & Ridout, 2014).

Analysis of bird burrow entry and foraging behavior

In the video data collected by the experimental group, videos in which birds could be clearly observed were considered valid videos. The Wilcoxon method was used to compare the significance of differences in foraging proportions between non-galliform birds and galliform birds.

The foraging proportion of birds on soil mounds refers to the ratio of the number of individuals exhibiting foraging behavior on soil mounds to the total number of bird individuals observed at the same site. The foraging proportion of non-galliform birds is equal to the number of non-galliform birds exhibiting foraging behavior at the same site divided by the total number of non-galliform bird individuals observed. Similarly, the foraging proportion of galliform birds is equal to the number of galliform birds exhibiting foraging behavior at the same site divided by the total number of galliform bird individuals observed. In each valid video, the total number of bird individuals refers to the sum of all bird individuals observed. The total number of bird individuals at the same site is the sum of all bird individuals observed in all valid videos at that site. We used the same analytical method to compare the significance of differences in the burrow entry proportion between non-galliform birds and galliform birds. The burrow entry proportion of birds is defined as the ratio of the number of bird individuals exhibiting burrow entry behavior to the total number of bird individuals observed at the same site.

All analyses in the methods section were conducted using R version 4.3.2 (R Core Team, 2023).

Results

The experimental group had 3,560 effective working days. A total of 22 independent valid photos of Chinese Pangolin (data provided in supplementary table S1) and 96 independent valid photos of birds (including 10 species: Silver Pheasant (*L. nycthemera*), Collared Partridge (*A. gingica*), Greater Necklaced Laughingthrush (*Garrulax pectoralis*), Lesser Necklaced Laughingthrush (*Garrulax monileger*), Grey-headed Parrotbill (*Paradoxornis gularis*), Grey-faced Woodpecker (*Picus canus*), Grey-capped Emerald Dove (*Chalcophaps indica*), Grey Treepie (*Dendrocitta formosae*), Grey-cheeked Fulvetta (*Alcippe morrisonia*), and Oriental Turtle-dove (*Streptopelia orientalis*) were captured (data provided in supplementary table S2). The control group had 3,330 effective working days, with no Chinese Pangolin captured but 246 independent valid photos of birds (including 4 species: Silver Pheasant (*L. nycthemera*), Collared Partridge (*A. gingica*), Elliot's Pheasant

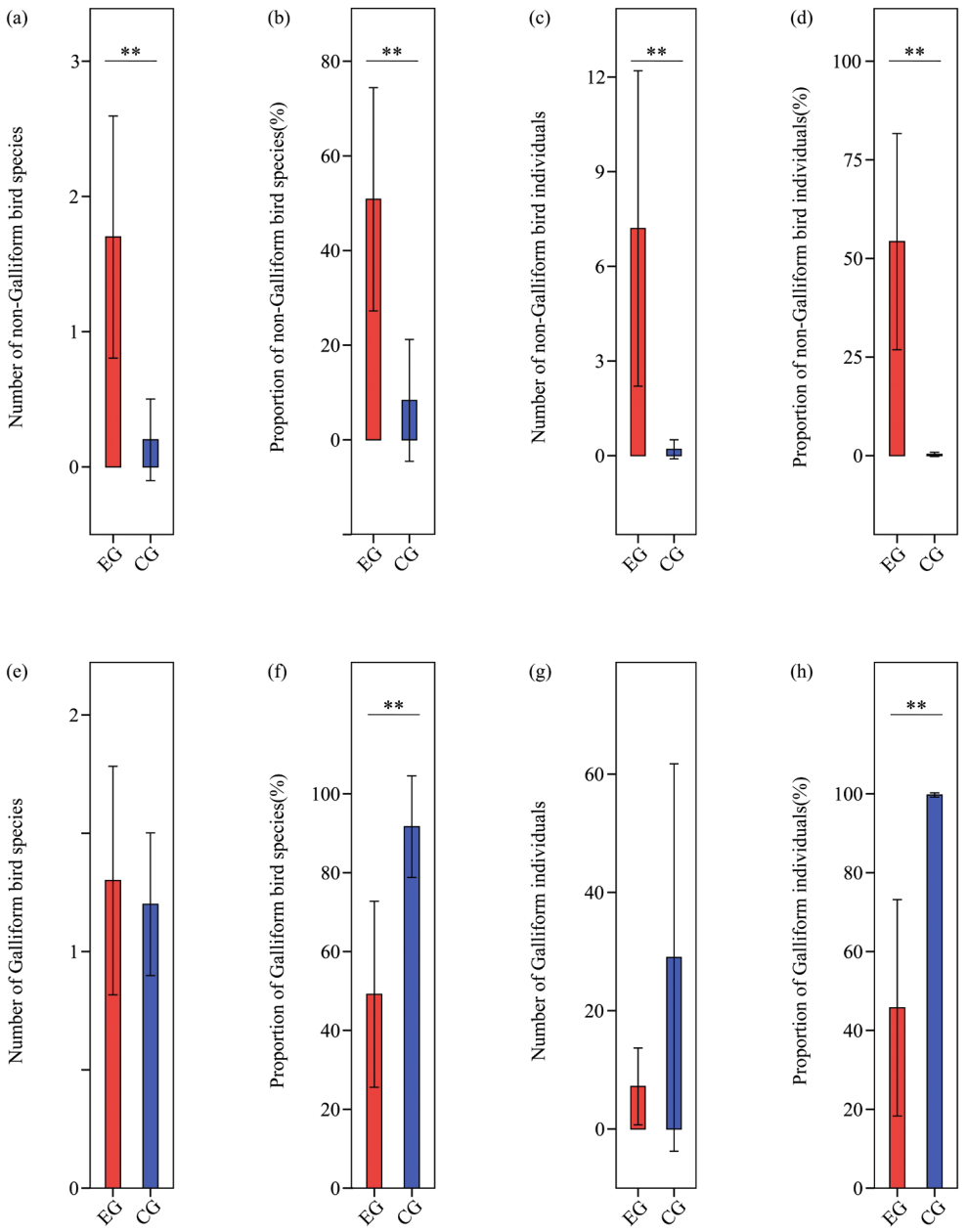


FIGURE 2 Significance of differences in bird species diversity indices between the experimental and control groups. Panels (a) to (d) show the four indices for non-galliform birds, while panels € to (h) show the four indices for galliform birds. EG represents the experimental group, and CG represents the control group. The experimental group consists of data collected by infrared cameras placed near Chinese pangolin burrows, while the control group consists of data collected by infrared cameras randomly placed within the study area, as detailed in Section 1.2. ** indicate a highly significant difference in species diversity indices between EG and CG ($P < 0.01$).

(*S. ellioti*), and Greater Necklaced Laughingthrush (*G. pectoralis*) were obtained (data provided in supplementary table S3).

Differences in species diversity between experimental and control groups

The experimental group showed significantly higher indices of bird species richness, Simpson's dominance index, Shannon-Wiener diversity index, and Pielou's evenness index compared to the control group ($P < 0.05$). The number of bird species in the experimental group was significantly higher than in the control group ($P < 0.01$), while there was no significant difference in the total number of bird individuals between the two groups ($P > 0.05$).

More non-galliform birds (both in terms of different species and individuals) visited the experimental sites compared to controls ($P < 0.01$) and that for galliform birds the opposite was true (i.e. fewer galliform birds visited the experimental sites,

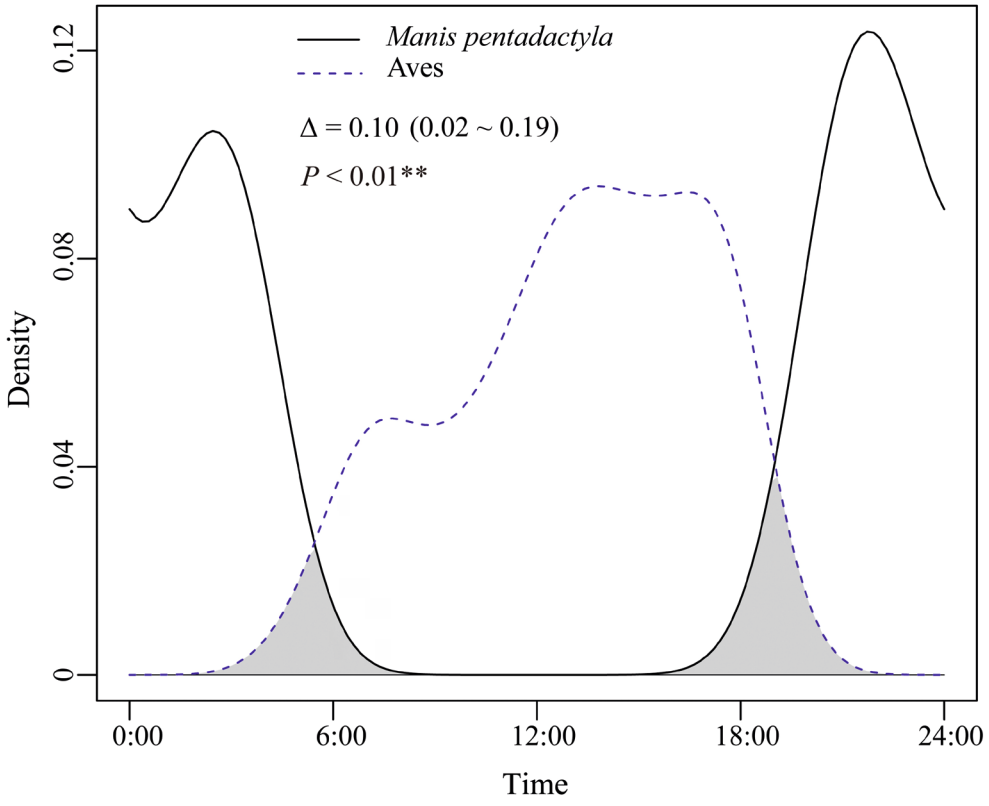


FIGURE 3 Overlap of daily activity between the Chinese pangolin and birds. "Density" refers to the kernel density estimation for data from cameras outside the burrows, as detailed in Section 1.3.2. "Time" refers to the activity rhythm times of the Chinese pangolin and birds, with specific data provided in Table S6 of Appendix 1. "Aves" includes 10 bird species, as described in the results section 2. The overlap (Δ value and 95% confidence intervals) and significance of differences are reflected in the legend, with ** indicating a highly significant difference in daily activity overlap between the Chinese pangolin and birds.

$P < 0.01$), as shown in fig. 2 (data provided in supplementary tables S4 and S5).

Differences in temporal activity rhythms between the chinese pangolin and birds

The Chinese Pangolin exhibited strictly nocturnal activity, with activity recorded from 19:31 to 4:12, and two activity peaks occurring around 22:00 and 3:00. The birds captured in the photos were only active during the day, from 05:00 to 19:04, with no distinct activity peaks, but increased activity from 12:00 to 17:00 (fig. 3 and data provided in supplementary table S6). The daily activity rhythms of Chinese Pangolin and birds showed highly significant temporal differentiation ($\Delta = 0.10$, 95% CI: 0.02–0.19, $P < 0.01$).

Analysis of bird behavior in the experimental groups

A total of 96 valid videos were collected, with a duration of 1,440 seconds. Ten bird species were recorded, none of which exhibited burrow entry behavior. Nine of these bird species exhibited foraging behavior, including the Silver Pheasant (*L. nycthemera*), Collared Partridge (*A. gingica*), Greater Necklaced Laughingthrush (*G. pectoralis*), Lesser Necklaced Laughingthrush (*G. monileger*), Grey-headed Parrotbill (*P. gularis*), Grey-faced Woodpecker (*P. canus*), Grey-capped Emerald Dove (*C. indica*), Grey Treepie (*D. formosae*), and Oriental Turtle-dove (*S. orientalis*), with only the Grey-cheeked Fulvetta (*A. morrisonia*) not exhibiting foraging behavior.

TABLE 1 Proportion of foraging behavior on soil mounds outside Chinese Pangolin burrows by birds (%) (%, percent)

Camera number	Non-galliform birds			Galliform birds		
	Total number of individuals	Number of individuals with foraging behavior	Foraging proportion (%)	Total number of individuals	Number of individuals with foraging behavior	Foraging proportion (%)
222	4	1	25	1	0	0
223	5	4	80	3	0	0
224	17	17	100	7	0	0
225	9	7	78	10	1	10
227	9	7	78	2	0	0
228	21	14	67	2	0	0
229	4	4	100	0	0	0
230	0	0	0	9	5	56
234	0	0	0	7	1	14
239	3	1	33	31	0	0
Total	72	55	76	72	7	10

The foraging proportion of non-galliform birds was significantly higher than that of galliform birds ($P < 0.01$; table 1 and supplementary table S7).

Discussion

This study is the first report on the attraction of soil mounds outside Chinese Pangolin burrows to non-galliform birds. By analyzing the differences in bird diversity between the experimental and control groups, this research verified the effect of attraction of fresh soil mounds outside Chinese Pangolin burrows to birds, especially non-galliform birds, and explored the possibility that the Chinese Pangolin is a keystone species in the local ecosystem. We found that the temporal rhythm significantly differed between birds near the burrows and the Chinese Pangolin in the experimental group data, and that the foraging behavior on soil mounds differed significantly between non-galliform birds and galliform birds in the experimental group data.

Attraction phenomenon of fresh soil mounds outside Chinese Pangolin burrows on non-galliform birds

Although we found no significant difference in the total number of bird individuals between the experimental and control groups, the number of bird species in the experimental group was significantly higher than in the control group. Our results suggest that more birds that do not commonly move on the ground appear on the soil mounds outside fresh burrows of the Chinese Pangolin. For non-galliform birds, all four related indicators in the experimental group were significantly higher than those in the control group, further suggesting that non-galliform birds are less active on the ground yet appear more frequently on soil mounds outside Chinese Pangolin burrows due to the presence of fresh soil. As for Galliformes, we found no significant differences between the experimental and control groups in the number of bird species and the number of individuals, indicating that the fresh soil mounds outside Chinese Pangolin burrows have no apparent attraction to galliform birds.

Most previous infrared camera studies have recorded Galliformes and some mammals, with more records of Silver Pheasant (*L. nycthemera*), Collared Partridge (*A. gingica*), and Greater Necklaced Laughingthrush (*G. pectoralis*) (Lin et al., 2018); fewer records of Oriental Turtle-dove (*S. orientalis*) (Lyu, 2019), Grey-faced Woodpecker (*P. canus*), Lesser Necklaced Laughingthrushe (*G. monileger*), and Grey-cheeked Fulvettas (*A. morrisonia*) (Lyu, 2019), and no records of Grey Treepie (*D. formosae*), Grey-headed Parrotbill (*P. gularis*), and Grey-capped Emerald Dove (*C. indica*). The locations of these data records are around the study area, including the Wuyi Mountains and Daiyun Mountains. Therefore, our study demonstrated the attraction of soil mounds outside fresh burrows of the Chinese Pangolin to bird species that rarely or even seldom move on the ground.

Significant temporal rhythm differences between birds near burrows and the Chinese Pangolin

We found a significant difference in activity times between birds near burrows and the Chinese Pangolin. Although we

recorded two activity peaks of the Chinese Pangolin, which were significantly different from the data in Lishui County, Jiujiang City, Jiangxi Province (Ta, 2023), we confirmed its strictly nocturnal activity pattern. In contrast, the birds we captured were active during the day, with basically no overlap with pangolin activity. This temporal differentiation, indicates that the Chinese Pangolin and nearby birds occupy different temporal ecological niches in the ecosystem. Our results also suggest that the Chinese Pangolin itself does not attract birds, probably because of the lack of edible matter or other materials on the Chinese Pangolin that could attract birds.

Differences in foraging behavior on soil mounds between non-Galliformes and Galliformes

Firstly, it should be noted that we did not capture any birds entering the burrows of the Chinese Pangolin. In contrast, there is evidence of mammals entering the burrows (own data; Sun, 2022; Wu et al., 2023), indicating that the burrows of the Chinese Pangolin could provide thermal refuges for other animals. However, regarding birds, the Chinese Pangolin seems not to attract birds because of its burrows, and they do not approach the burrows as thermal refuges.

Our results showed that the fresh soil mounds outside the burrows of the Chinese Pangolin were the reason for attracting birds. Statistical analysis showed that the foraging proportion of non-galliform birds was significantly higher than that of galliform birds (table 1). Our results demonstrated a clear attraction effect of fresh soil mounds outside the burrows of the Chinese Pangolin on non-galliform birds.

The reasons for the attraction of birds to these soil mounds might be: (1) Soil mounds cover an area of ferns, reducing the coverage of ferns in the forest, thus increasing the visibility of birds' food, thereby improving foraging efficiency. (2) Soil mounds provide gravel resources for non-galliform birds to help digestion and may therefore be a significant source for geophagy. (3) Soil mounds provide essential trace elements for the growth and development of non-galliform birds. Further research is, however, needed to determine the specific reasons for attraction.

Our research underscores that the Chinese Pangolin is an important keystone species in subtropical forest ecosystems. As an ecosystem engineer, the Chinese Pangolin transforms soil structures and physicochemical properties through its digging behavior, thereby directly affecting the distribution and diversity of various species (Sun et al., 2021, 2025). The function of the Chinese Pangolin in its ecosystem is often considered to mainly control the number of ants, whereas we found that the fresh soil mounds outside its burrows form a significant attraction to birds, especially non-galliform birds. The Chinese Pangolin probably has many ecological functions that are not yet fully understood or documented, and may provide a new perspective for the conservation efficacy of the Chinese Pangolin. By protecting the Chinese Pangolin, the protection of other species and the health of the ecosystem could be indirectly promoted. Future research should explore the specific mechanisms of the attraction of soil mounds outside Chinese Pangolin burrows to individual bird species and their impact on other animal groups.

Conclusion

This study revealed that the soil mounds outside Chinese pangolin burrows significantly attract non-galliform birds. The experimental group exhibited higher bird species richness and biodiversity indices than the control group. Additionally, non-galliform birds showed a significantly higher proportion of foraging behavior on the mounds compared to Galliformes. The temporal segregation between Chinese pangolins and birds confirms their occupation of different temporal niches. The mounds probably provide non-galliform birds with grit resources, reduce fern cover to enhance food visibility, and supply essential trace elements. As an ecosystem engineer, the Chinese pangolin modifies soil structure and physicochemical properties, influencing species distribution and diversity. This study underscores the keystone role of the Chinese pangolin in subtropical forest ecosystems and provides new directions for future research.

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Author contributions

Wei Liu and Fei Yu designed the study; Xiaoxiao Nie, Xuanxuan Liu, Xiaopin Zhu, Yanbin Huang, Haiping Shangguan, Wenhao Zeng, Ning Guo, Mingle Shi, and Yong Zhang performed the experiments; Wei Liu, Xuanxuan Liu, Xiaopin Zhu and Yanping Xie analyzed the data; Wei Liu, Xiaoxiao Nie and Fei Yu wrote the manuscript.

Conflict of interest

The authors have no conflict of interest to declare.

Ethics

All fieldwork was conducted in accordance with the Law of the People's Republic of China on the Protection of Wildlife.

Supplementary material

Supplementary material is available online at:
https://doi.org/10.6084/m9.figshare.28436729

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