Global Ecology and Conservation 71 (2026) e04425

Contents lists available at ScienceDirect

Global Ecology and Conservation

journal homepage: www.elsevier.com/locate/gecco

Original research article

Integrating burrow surveys, termite abundance and fecal analysis to reveal seasonal foraging shifts in the Chinese pangolin

Nick Ching-Min Sun [a], Wen-Jun Lin [b], Hou-Feng Li [b], Chun-I Chiu [c], Hsiang Ling Chen [d,*]

[a] Institute of Wildlife Conservation, National Pingtung University of Science and Technology, Taiwan
[b] Department of Entomology, National Chung Hsing University, No.145, Xingda Rd., Taichung, 402, Taiwan
[c] Department of Entomology and Plant Pathology, Chiang Mai University, Thailand
[d] Department of Forestry, National Chung Hsing University, No.145, Xingda Rd., Taichung, 402, Taiwan

ARTICLE INFO

Keywords:
Alternative prey
Caste composition
Foraging ecology
Myrmecophagy
Odontotermes formosanus
Pangolin
Taiwan

ABSTRACT

Seasonal fluctuations in food availability can shape foraging behavior in dietary specialists like the Chinese pangolin (*Manis pentadactyla*), which relies almost exclusively on ants and termites. Although seasonal shifts in diet have been reported, how prey availability relates to foraging effort remains unclear. We integrated seasonal surveys of pangolin burrows, termite abundance, and fecal composition in Taiwan to explore potential associations between prey dynamics and foraging behavior. We recorded 82 newly excavated burrows and surveyed termite abundance near known burrow sites during 2020–2021. We analyzed 132 fecal samples collected during 2010–2016, focusing on caste ratios of *Odontotermes formosanus,* a key prey species of the Chinese pangolin in Taiwan, to infer foraging depth as major workers forage at the surface and minor workers remain underground. Although both burrowing activity and termite abundance fluctuated seasonally, their peaks did not coincide. Burrow excavation was lowest in summer, whereas *O. formosanus* abundance peaked in summer and fall. Fecal samples contained more major workers in summer and more minor workers in winter and spring, suggesting seasonal shifts in the depth of foraging. These patterns provide preliminary support for the hypothesis that seasonal variation in pangolin burrowing activity reflect changes in prey accessibility or alternative prey use, rather than prey abundance alone. However, differences in the spatial and temporal coverage of the datasets preclude direct inference of causal relationships. Synchronous, multi-method studies at comparable spatial scales are needed to test these relationships and improve understanding of seasonal foraging ecology in this endangered specialist.

1. Introduction

Access to sufficient and high-quality food resources is fundamental to animal survival, reproduction, and population persistence (Boutin, 1990; Martin, 1987; Nielsen et al., 2010). Food availability influences energetic intake and can shape species' spatial distributions, behavioral strategies, and reproductive cycles (Charnov, 1976; White, 2008). In environments where food abundance fluctuates seasonally, animals are expected to adjust their foraging behavior to maximize energy intake, a strategy consistent with

* Corresponding author.
E-mail address: hsiangling@dragon.nchu.edu.tw (H.L. Chen).

https://doi.org/10.1016/j.gecco.2026.e04425
Received 27 October 2025; Received in revised form 10 September 2026; Accepted 13 September 2026
Available online 15 September 2026
2351-9894/© 2026 The Author(s). Published by Elsevier B.V. This is an open access article under the CC BY-NC license (http://creativecommons.org/licenses/by-nc/4.0/).

predictions from optimal foraging theory (Krebs and Davies, 1993; Stephens and Krebs, 1986). Such behavioral flexibility is especially critical for dietary specialists, whose limited diet breadth makes them more vulnerable to temporal resource scarcity (Pietersen et al., 2016; Redford and Dorea, 1984).

Myrmecophagy, or dietary specialization on ants and termites, is a foraging strategy shared by over 200 mammalian species worldwide (Redford, 1987). While some species such as armadillos consume both ants and termites (Anacleto, 2007), others are obligate myrmecophages, such as aardvark (*Orycteropus afer*), Chinese pangolin (*Manis pentadactyla*), and numbat (*Myrmecobius fasciatus*), deriving over 90% of their diet from ants and termites (Redford, 1987; Sun et al., 2019a). Myrmecophagous mammals are often characterized by convergent morphological adaptations, such as elongated tongues, strong forelimbs, and edentulous jaws, which enhance their ability to access these patchily distributed, often subterranean prey (Gaudin et al., 2016, 2009; Kingdon, 1997; McNab, 1984). As important regulators of insect populations, myrmecophagous mammals play key ecological roles, underscoring the importance of understanding their foraging ecology and dietary dynamics (Chao et al., 2020; Rodrigues et al., 2020).

Pangolins (Pholidota: Manidae) are highly specialized myrmecophagous mammals that feed almost exclusively on ants and termites. All four Asian species including the Chinese pangolin, Sunda pangolin (*M. javanica*), Indian pangolin (*M. crassicaudata*), and Philippine pangolin (*M. culionensis*) are listed as Endangered or Critically Endangered due to habitat loss and illegal poaching (Challender et al., 2019, 2014). Among these, the Chinese pangolin is distributed across subtropical and tropical Asia, including Taiwan (Corlett, 2007; Wu et al., 2019b), where it inhabits diverse environments such as secondary forests, bamboo stands, and farm lands (Chao, 1989; Chen et al., 2025; Sun et al., 2019b).

In Taiwan, the Chinese pangolin's diet is composed primarily of ants and termites, and a total of 4 species of termites (belonging to 2 families and 4 genera) and 58 species of ants (from 5 families and 25 genera) were identified in feces (Sun et al., 2025a). Understanding the seasonal variation in foraging activity and dietary composition of Chinese pangolins is important for their conservation. Field studies indicate that Chinese pangolins exhibit distinct reproductive phases, including mating, pregnancy, and birthing, that appear to correspond with seasonal changes in food availability (Sun et al., 2024, 2021a, 2018). Seasonal dietary analysis based on feces samples has shown that termite consumption by Chinese pangolins was higher in winter and spring, while ant consumption increases in summer, but the seasonal change in ant consumption was not as significant as that of termites (Sun et al., 2025a). These dietary shifts appear to correspond with reproductive phases (e.g., mating or lactation during winter/spring), suggesting that termites may be the main source of nutrients during the breeding season of pangolins (Sun, 2020). In contrast, captive Chinese pangolins, which lack exposure to seasonal food variation, do not exhibit consistent reproductive rhythms (Sun et al., 2024). Therefore, the seasonal dynamics and distribution of termites may be important factors affecting pangolin behavior and reproductive cycles (Sun, 2020).

The Chinese pangolin is a fossorial specie that excavates burrows for both shelter and foraging (Wu et al., 2019b). Survey of burrow has become a major tool to investigate pangolin habitat use and activity, especially for ground-dwelling species like the Indian and Chinese pangolins (Chen et al., 2025; Dhami et al., 2023; Karawita et al., 2018; Sabin et al., 2024; Tamang et al., 2022). Because pangolins typically excavate burrows to access termites (Fang and Wang, 1980; Heath, 1992), seasonal variation in burrowing activity may provide an indirect indicator of subterranean foraging effort. Previous studies report a higher frequency of new burrows in winter (Fan, 2005; Lin, 2011), suggesting that pangolins may increase foraging effort for termite during the period, which is consistent with increased termite consumption in winter based on fecal samples (Sun et al., 2025a).

One potential explanation for the seasonal variation of diet lies in the relative seasonal availability of prey on the ground surface. Despite the perennial nature of underground colonies of termites, their foraging activity on the ground could be seasonality and affected by the climate conditions. For example, *Microtermes subhyalinus* and *Macrotermes bellicosus* present high foraging activity in rainy season (Korb and Linsenmair, 2001; Mora et al., 1996). On the other hand, in Taiwan, *O. formosanus* are more active in dry and cold season (Chiu et al., 2018). Given that pangolins depend significantly on their highly developed olfactory system to locate food (Imam et al., 2018, 2017; Mohapatra and Panda, 2014), increased activity of prey on the ground surface may influence their feeding behavior. Many termites build the underground tunnels to connect the underground chamber and ground surface. For instance, *O. formosanus* uses an underground tunnel network to connect foraging area on the ground and multiple nest chambers underground (Tsai et al., 1965). Increased activity of termite on the ground may enhance pangolin's chance to find the nest of termite underground though the tunnel, and therefore promote burrowing activity. However, studies examining seasonal variation in termite abundance and its relationship with pangolin burrowing activity are still scarce. Thus, how seasonal changes in food resources influence foraging activity remains poorly understood. Although foraging activity of termite is known to vary seasonally, systematic data on seasonal changes in termite abundance within pangolin foraging areas are lacking. In Yangmingshan National Park, Taiwan, the presence of pangolin burrows was not associated with higher termite abundance (Chen et al., 2025). However, the number of sites and intensity of termite survey in that study was limited, making it difficult to inform temporal dynamics of termite abundance with pangolin burrowing activity. Moreover, few studies have conducted continuous, seasonal burrow monitoring throughout the year, which constrains our ability to detect seasonal patterns in burrowing activity.

In Taiwan, *O. formosanus* accounts for approximately 85% of the total termite biomass consumed by Chinese pangolin, while termite taxa comprised nearly half of the total prey biomass. Furthermore, pangolins consume fewer termites in summer than in other seasons (Sun et al., 2025a; Wu et al., 2005), suggesting that this species may be a key factor in feeding ecology of pangolin (Sun et al., 2025b; Wu et al., 2019b). Another dietary study on Chinese pangolins in Guangdong Province, China, revealed similar results. The prey of Chinese pangolins primarily consisted of termites and ants, exhibiting seasonal variations in prey composition. Specifically, fungus-growing termites (Odontotermes) constituted the primary dietary component during the dry season, whereas the ant genera Carebara and Pheidole were the major food components during the wet season (Ma et al., 2024). *O. formosanus* is the only member of the Macrotermitinae subfamily in Taiwan and is widely distributed in subtropical forests (Chiu et al., 2010; Lin et al., 2024). This fungus-growing species nests underground but constructs mud tubes that extend above ground onto tree trunks, logs, and leaf litter

(Chiu et al., 2018). As fungus-growing termites, the caste structure of *O. formosanus* is behaviorally segregated: major workers forage and construct mud tubes above ground, while minor workers remain in subterranean chambers and nests for feeding and nursing (Badertscher et al., 1983; deOliveira et al., 2021; McMahan et al., 1984; Wang et al., 2009). These caste-specific roles provide a potential opportunity to infer foraging depth from pangolin fecal samples. For instance, the high prevalence of underground-residing minor workers in fecal samples suggests that pangolins engage in underground foraging and raiding of nests by digging burrows. Conversely, a higher proportion of major workers may suggest more surface-level foraging. Therefore, caste composition of *O. formosanus* in pangolins' feces may provide a useful proxy for assessing seasonal changes in burrowing activity. In particular, if the proportion of minor workers increases in feces during seasons of high burrowing activity, this would support a link between foraging depth and subterranean prey intake.

In this study, we aim to assess how seasonal variation in termite abundance on the ground surface and top soil associated to the burrowing activity and diet of the Chinese pangolin. We combine year-round seasonal surveys of burrow and termite with seasonal fecal analyses to address the following questions: (1) How does burrowing activity of pangolin and termite abundance on the ground surface and top soil vary among seasons? (2) How do seasonal changes in burrow activity of pangolin associate with temporal variation of termite abundance on the ground surface and top soil? (3) How does the seasonal variation in diet, especially termite consumption and caste ratios, correspond with seasonal changes in burrow activity? By linking burrowing behavior, prey availability, and diet, we provide a more complete understanding of how temporal variation in food resources shapes the foraging strategies of a dietary specialist. Such insights are critical for developing seasonally informed monitoring and conservation strategies for this endangered species.

2. Materials and methods

2.1. Study area

Survey of pangolin's burrowing activity and termite abundance were conducted in the Huisun Experimental Forest Station Nantou, central Taiwan (24°04′26″ N, 121°01′56.5″ E). The forest station, managed by the Experimental Forest Management Office of National Chung Hsing University, covers a total area of 7477 ha, with an elevation range of 450–2419 m. The terrain is highly diverse, supporting subtropical, warm temperate, and temperate forest ecosystems along an altitudinal gradient. The average annual temperature is 21.0°C, with seasonal variations ranging from 22 to 30°C in summer and 15–25°C in winter (Cheng et al., 2024). The area receives an average annual rainfall of 2676 mm, with a rainy season spanning from April to September (Chen et al., 2023). The forest composition includes 70% natural forest, 20% plantations, and 10% bamboo groves. The main plantation species are *Taiwania cryptomerioides*, *Chamaecyparis formosensis*, and *Calocedrus formosana* (Lin, 2003)

2.2. Survey of burrow

Burrow surveys were conducted across six routes in Huisun Experimental Forest Station, Nantou, central Taiwan, from February 2020 to February 2021. The number of foraging burrows excavated by pangolins is greater than that of resting burrows. For example, in eastern Taiwan, the burrow density without distinguishing between functions (e.g., resting or feeding) was 110.8 burrows per hectare, whereas only 137 resting burrows were found across100 hectares (Sun et al., 2025b). Based on this disparity, it is likely that

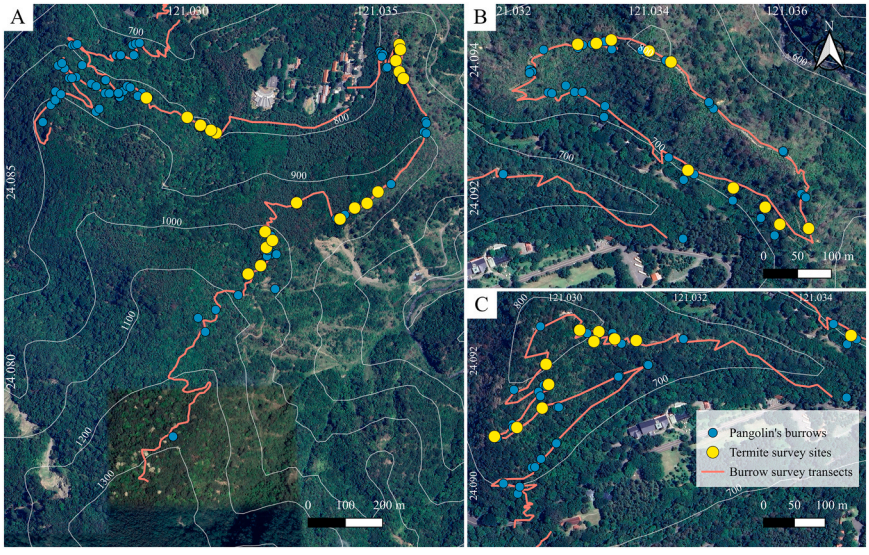


Fig. 1. Locations of the survey routes, burrows of the Chinese pangolin and termite survey sites in Huisun Forest Station, Taiwan.

many of the burrows recorded in the field represent foraging burrows. Therefore, seasonal changes in burrow numbers may provide a rough proxy for changes in pangolin foraging effort targeting subterranean prey.

In February 2020, we established six survey routes totaling approximately 14 km in the study area (Fig. 1). To investigate seasonal variation in pangolin burrowing activity, we first surveyed all existing burrows in late February 2020. We defined seasons as following: spring (March – May), summer (June – August), fall (September – November), and winter (December – February). Subsequent surveys occurred at the end of each season: late May, August, November, and February 2021, to record new burrows created since the previous survey. Each newly recorded burrow represented one that had been created or detected since the previous survey. For example, burrows recorded in late May were those excavated between early March and late May (spring season). Surveys were conducted during daylight hours (8:00 AM to 6:00 PM), with observers walking at a steady pace of approximately 1 km per hour. We searched within 5 m on either side of the survey routes for pangolin burrows. Burrows were identified based on external characteristics such as entrance shape, diameter, depth, surrounding soil mound, and presence of footprints or claw marks (Supplementary S1). Chinese pangolin burrows are generally over 10 centimeters in diameter (Sun et al., 2025b). Burrows with entrance diameters smaller than 9 cm, which were likely created by other species such as the Formosan ferret-badger (*Melogale subaurantiaca*) and the Formosan wild boar (*Sus scrofa taivanus*) were excluded. Each burrow was marked and georeferenced to prevent duplicate counts. We measured the entrance diameter and the maximum depth reachable using a flexible steel tape, following established method (Fan, 2005; Tsai et al., 2004). We used a chi-square test to compare number of burrows among seasons. The effect size (Cohen's w) was categorized as negligible ($<$ 0.05), small (0.05–0.15), moderate (0.15–0.5), and strong ($>$ 0.5) based on Cohen's (1988) guidelines.

2.3. Seasonal variation of termite abundance

The termite dataset was collected at Huisun Experimental Forest Station, Nantou, central Taiwan, from 2021 to 2022, following the burrow surveys conducted from 2020 to 2021. Thus, the termite and burrow datasets were collected at the same general study area but were not fully synchronous in time. The termite surveys were conducted near previously identified pangolin burrows and were used to characterize seasonal variation in termites active on the ground surface and topsoil.

Chinese pangolins rely on olfaction to search for food on the ground surface, and the depth of foraging burrow can even exceed 1 m (Trageser et al., 2017). The termite active on the ground surface could serves as an indicator of the presence and relative activity of termite colonies accessible to pangolins. To investigate seasonal variation in termite activity and relative abundance on the ground surface and top soil. We selected 40 burrows of pangolin marked in 2020 survey and established termite sampling sites in 2021 (Fig. 1). We assume that the seasonal trends observed in sampling plots broadly represent patterns across the Huisun Forest Station and are consistent between years. The distance between adjacent termite sampling sites was at least 20 m (Fig. 1). At each site, we established a 2 m $\times$ 5 m plot within 10 m of a marked burrow, located approximately 1 m from and parallel to the pangolin burrow survey routes. Seasonal surveys (spring, summer, fall, and winter) were conducted from 2021 to 2022. The surveys were conducted in the mid to end of the season. Locations of survey plot for each site were shifted each season to minimize microhabitat variation while maintaining proximity (Fig. 2).

The survey method was adapted from Chen et al. (2025). Each 2 m $\times$ 5 m plot was subdivided into ten 1 m^2 subplots (Fig. 2). After clearing ground vegetation, termites were searched for and collected from each 1 m^2 subplot. Because termites typically inhabit the top 0–15 cm of soil (Abe and Matsumoto, 1979), searches included litter, topsoil (to a depth of 10 cm), snags, and decaying logs. For each subplot, termite was searched with a small shovel (total length: 36 cm; blade width: 7.6 cm; blade depth: 11 cm, made of stainless steel) for 2 min per person. The presence or absence of termites was recorded for each 1 m^2 subplot. The number of subplots in which termites were detected was used as an index of termite abundance. For example, if termites were found in 5 out of 10 subplots, the termite abundance at that site was recorded as 5. This method enabled to standardized termite relative abundance based on spatial coverage. Moreover, this method allowed us to survey termites across termite functional groups in the ground surface and top soil.

Termites found in each subplot were collected with an insect aspirator and preserved in 95% alcohol. Specimens were deposited in the Termite Collection of National Chung Hsing University. Species identification followed the morphological keys provided by Li (2010) and Wu et al. (2019). Species identification primarily relied on the soldier caste. Whereas only worker castes were collected, making species-level identification infeasible for *Sinocapritermes mushae*, and *Pericapritermes nitobei*, both soil-feeding termites with overlapping ecological niches, differ functionally from other termite species in Taiwan (Eggleton et al., 1997). Because the worker castes of *S. mushae* and *P. nitobei* are morphologically indistinguishable, they were treated as a single group in our analysis. Similarly, the worker castes of *Reticulitermes* spp. exhibit highly similar morphology and possible hybridization (Wu et al., 2019a). Therefore, individuals from this genus were identified only to the genus level.

We use Kruskal-Wallis test to evaluate whether the termite activity was seasonal, and infer the season that had the highest abundance on the ground surface. The effect size was calculated as eta-squared (η^2). The post-hoc pairwise comparisons were

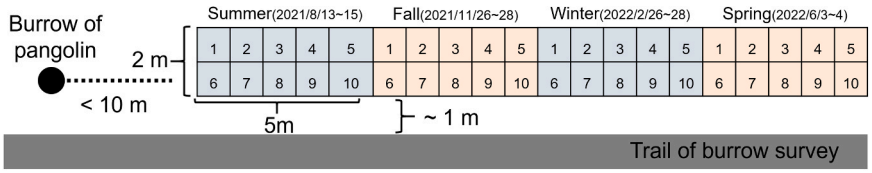


Fig. 2. Schematic diagram of termite survey sample site and relative position with burrow and transect.

conducted using Dunn's tests with Bonferroni correction to identify specific differences between seasons.

2.4. Pangolin fecal sample collection, processing, and analysis

The fecal dataset was collected in the southern Coastal Mountain Range of Taitung, eastern Taiwan, from December 2010 to September 2016, and therefore differed from the burrow and termite dataset in both location and sampling period.

To understand whether caste composition of *O. formosanus* in fecal samples of pangolin can serve as an indicator to estimate the frequency of foraging activity. We surveyed the caste ratio of *O. formosanus* between nest and ground wood from two types of environments during 2018–2020. Supplementary S2 presents the mandible characteristics of different castes of *O. formosanus*. Supplementary S3 presents the method of caste ratio investigation. According to the results of caste ratio investigation in the environments (Supplementary S4), we propose that the caste composition of *O. formosanus* in fecal samples of pangolin could serve as an indicator to estimate the frequency of foraging activity that targets subterranean termite by burrowing.

The fecal samples of pangolins collected from the southern Coastal Mountain Range in Taitung, Taiwan (22°54′38.6″ N, 121°11′13.6″ E) between December 2010 and September 2016, were used for the analysis. The area where the feces were collected spans approximately 1000 ha, with elevations ranging from 100 to 700 m. Samples were collected from 35 radio-tracked and 20 untracked wild Chinese pangolins. After capture, pangolins were held at the Pingtung Rescue Center for Endangered Wild Animals, Pingtung, Taiwan for 1–2 days to collect fecal samples prior to release at their original capture sites (see (Sun et al., 2019b) for ethical guidelines, housing, and sampling procedures). A total of 132 fecal samples were collected, numbered, weighed and stored at −20°C refrigerators for further analysis.

Although fecal samples were collected from a different site than the burrow and termite surveys, we integrated these historically available datasets as an exploratory approach. Previous studies suggest some broad-scale dietary consistency. For example, *O. formosanus* is a widely distributed species in Taiwan, and its colony and swarming cycle show consistent variations across the Taiwan (Chiu et al., 2010, 2018; Lin et al., 2024). In addition, according to Chi (2020), an analysis of 35 Chinese pangolin fecal samples collected from wildlife rescue centers across Taiwan identified 3 termite species and 45 ant species. The study found no significant differences in the composition and occurrence frequency of major prey species between western and eastern Taiwan. For example, the primary prey of Chinese pangolins includes the termites *O. formosanus* and *Nasutitermes parvonasutus* (Termitidae), as well as ants such as *Pheidole* spp., *Carebara* spp., and *Crematogawster* spp. (Myrmicinae), and *Polyrhachis* spp. and *Camponotus* spp. (Formicinae). Nevertheless, we acknowledge that assuming identical ecological conditions across these distinct regions is tenuous due to the Central Mountain Range barrier and the 4–10 year temporal gap. Therefore, the integration of these datasets is intended to formulate suggestive hypotheses regarding seasonal foraging behavior rather than to provide definitive correlative evidence.

Each fecal sample was oven-dried, and a 10 g subsample was used for diet analysis. Fecal filtering procedures were applied to separate the prey items and debris (Sun et al., 2020). The filtered prey items were then subsequently macro-photographed and digitized (See (Sun et al., 2020) for the fecal sample filtering method, prey species identification, and quantification). Recovery rates were applied to account for digestion bias: 65% for ant head capsules and 35% for termite mandibles (Sun, 2020). Supplementary S2 illustrates the mandible characteristics used to distinguish between the various castes of *O. formosanus* recovered from the fecal samples. The number of prey individuals adjusted with recovery rates was subsequently converted to the quantity of 10 g of dry feces.

To determine variation of caste ratio for *O. formosanus* in the fecal samples, the number of individual castes, i.e. major worker, minor worker, and soldier, was calculated and then represented by average percentages monthly. We performed the Kruskal-Wallis ANOVA test to examine variations amongst average percentages for the major worker, minor worker, soldier and alate of *O. formosanus* over the four different seasons as defined earlier. To assess the magnitude of the differences between groups, the effect size for the Kruskal-Wallis test was calculated as eta-squared (η^2). The resulting values were interpreted based on the benchmarks proposed by Cohen (1988). In this study, the effect size of eta-squared (η^2) was interpreted based on the following thresholds: $\eta^2 \geq 0.01$ indicates a small effect, $\eta^2 \geq 0.06$ represents a medium effect, and $\eta^2 \geq 0.14$ denotes a large effect.

The average of caste ratio of *O. formosanus* that collected from foraging tubes and underground nest chambers were used as the baseline for comparing the caste ratios in the fecal samples. We performed a chi-square test to compare monthly differences in the proportions of minor workers, major workers, and soldiers between termites collected from the field and those detected in fecal samples. The level of significance was set to $\alpha = 0.05$. The effect size (Cohen's w) was categorized as negligible (< 0.05), small (0.05–0.15), moderate (0.15–0.5), and strong (> 0.5) based on Cohen's (1988) guidelines.

Additionally, to provide regional context on seasonal ant availability for the fecal sampling area, supplementary pitfall trap data collected at the same site in Taitung (2013–2014) within the study area of the pangolins from which fecal samples were obtained are referenced in the Discussion, with further detailed description provided in Supplementary S6 and S7.

3. Results

3.1. Seasonal variation of burrowing activity

From February 2020 to February 2021, we recorded a total of 290 burrows of Chinese pangolin along the survey routes in the study area (Fig. 1). During the initial survey in February 2020, we identified 208 existing burrows. In the subsequent seasonal surveys, we recorded 82 newly excavated burrows: 27 in May 2020 (spring), 8 in August (summer), 27 in November (fall), and 20 in February 2021 (winter). The number of new burrows were significantly different across seasons ($X^2 = 11.756$, df = 3, p-value = 0.008, Cohen's ω = 0.38). Post-hoc comparisons based on adjusted standardized residuals with a Bonferroni correction indicated that the number of

burrows observed in summer was lower than expected ($z = -3.19$, $p_{adj} < 0.05$). In contrast, the number of burrows in spring, fall, and winter did not differ from the expected distribution. The mean diameter of burrow entrance was 18.78 cm (SE: 0.34), and the mean depth was 42.05 cm (SE: 1.37). The widest burrow measured 55 cm in diameter and approximately 33 cm in depth, while the deepest burrow reached a measurable depth of 130 cm, followed by another at 120 cm. While the presence of termite remains at some entrances supports feeding activity, this evidence was not consistent across all burrows. However, Sun et al. (2025b) reported most resting burrows (66.7%) had a depth of 100–250 cm, and no depth less than 50 cm was recorded. Therefore, most of the burrows we surveyed were likely to represent foraging burrows rather than resting burrows. However, the number of burrows should still be regarded as an indirect indicator of foraging activity. It is also important to note that not all burrows may be linked to termite foraging; some could be excavated for ant predation, which this study could not directly verify.

3.2. Seasonal variation of termite abundance

In total, six termite species from five genera and two families were collected in Huisun Forest Station, including *O. formosanus*, *N. parvonasus*, *Sinocapritermes mushae*, *Pericapritermes nitobei*, *Reticulitermes flaviceps*, and *Reticulitermes leptomandibulus* (Table 1). Across all four seasonal surveys, a total of 1600 subplots were examined. Combining data from all seasons, *O. formosanus* and the soil-feeding termites (*S. mushae* and *P. nitobei*) were the most dominant termite taxa in Huisun Forest Station. Specifically, *O. formosanus* in 70 subplots, soil-feeding termites were recorded in 72, *Reticulitermes* spp. in 55, and *N. parvonasus* in 36 subplots. Although overall termite abundance showed no significant seasonal variation (Kruskal–Wallis test: $X^2 = 3.037$, $p = 0.386$, $\eta^2 < 0.001$), the abundance of *O. formosanus* exhibited significant seasonal variation ($X^2 = 8.147$, $p < 0.05$, $\eta^2 = 0.03$), and the significant difference was found between spring and fall ($p_{adj} < 0.05$). The other species groups showed no significant seasonal variation: soil-feeding termites ($X^2 = 1.2762$, $p = 0.735$, $\eta^2 = 0$), *Reticulitermes* spp. ($X^2 = 0.956$, $p = 0.812$, $\eta^2 = 0$), and *N. parvonasus* ($X^2 = 0.289$, $p = 0.962$, $\eta^2 = 0$). The η^2 of soil-feeding termites, *Reticulitermes* spp. and *N. parvonasus* were negative and were interpreted as 0.

3.3. Seasonal variation of caste ratio of O. formosanus

The caste ratio of *O. formosanus* in the fecal samples showed clear seasonal variations. The ratio of major workers was significantly higher (Kruskal–Wallis test: $X^2 = 22.57$, $p < 0.001$) from June to August (summer), while the ratio of minor workers was significantly lower ($X^2 = 24.87$, $p < 0.001$) during the same period. For soldiers, the number was significantly lower from June to November (summer and fall) ($X^2 = 27.40$, $p < 0.001$) (Fig. 3A, B and C). In all cases, large effect sizes were observed ($\eta^2 = 0.153$, 0.171, and 0.191 for major workers, minor workers, and soldiers, respectively), indicating substantial seasonal variations in the caste proportions found within the pangolin fecal samples.

The Chi-square analysis revealed that the deviation of caste proportions of *O. formosanus* in fecal samples from field availability varied by month and caste, with several months exhibiting moderate effect sizes (Cohen's $w > 0.15$) (Supplementary S5) (Fig. 3). For major workers, moderate associations were observed in January ($w = 0.169$) and throughout the period from July to October, with the highest effect size occurring in July ($w = 0.423$) (Fig. 3A). In contrast, minor workers showed a more prolonged period of moderate deviation, spanning from May to November, as well as in January, with effect sizes peaking in August ($w = 0.406$) (Fig. 3B). Conversely, soldiers consistently displayed negligible to small effect sizes ($w \leq 0.073$) across all months (Fig. 3C), indicating that their proportions in fecal samples remained relatively consistent with field distributions compared to the worker castes.

4. Discussion

We found that both burrowing activity of Chinese pangolin and the abundance of *O. formosanus* on the ground surface and top soil varied seasonally. However, the temporal pattern of newly excavated burrows did not correspond with overall trends of abundance of *O. formosanus*. During the study period, we recorded 82 newly excavated burrows, of which only 8 were observed in summer. The remaining 75 were distributed relatively evenly across spring, fall, and winter. This seasonal pattern is consistent with previous studies that report increased burrow numbers in winter and spring (Fan, 2005; Wu et al., 2004). In contrast, the abundance of all termites in the ground surface and top soil showed no significant seasonal variation. However, species-specific differences were observed. *O. formosanus*, key dietary components of the Chinese pangolin in Taiwan (Liang, 2017; Sun et al., 2025a), were more abundant in the ground surface and top soil in summer and fall. Nevertheless, burrowing activity of Chinese pangolin was lowest during this season, suggesting that the seasonal abundance of termites in the ground surface and top soil does not directly drive underground foraging effort of pangolin. One possible explanation for the low summer burrow count is reduced detectability due to heavy rainfall. The rainy

Table 1
Number of cells of termite presence in each survey across four seasons in Huisun Forest.

Taxa	Spring	Summer	Fall	Winter
Odontotermes formosanus	7	20	29	14
Nasutitermes parvonasutus	8	8	9	11
Soil-feeding termites	15	22	22	13
Reticulitermes spp.	19	8	11	17
Total	46	54	65	53

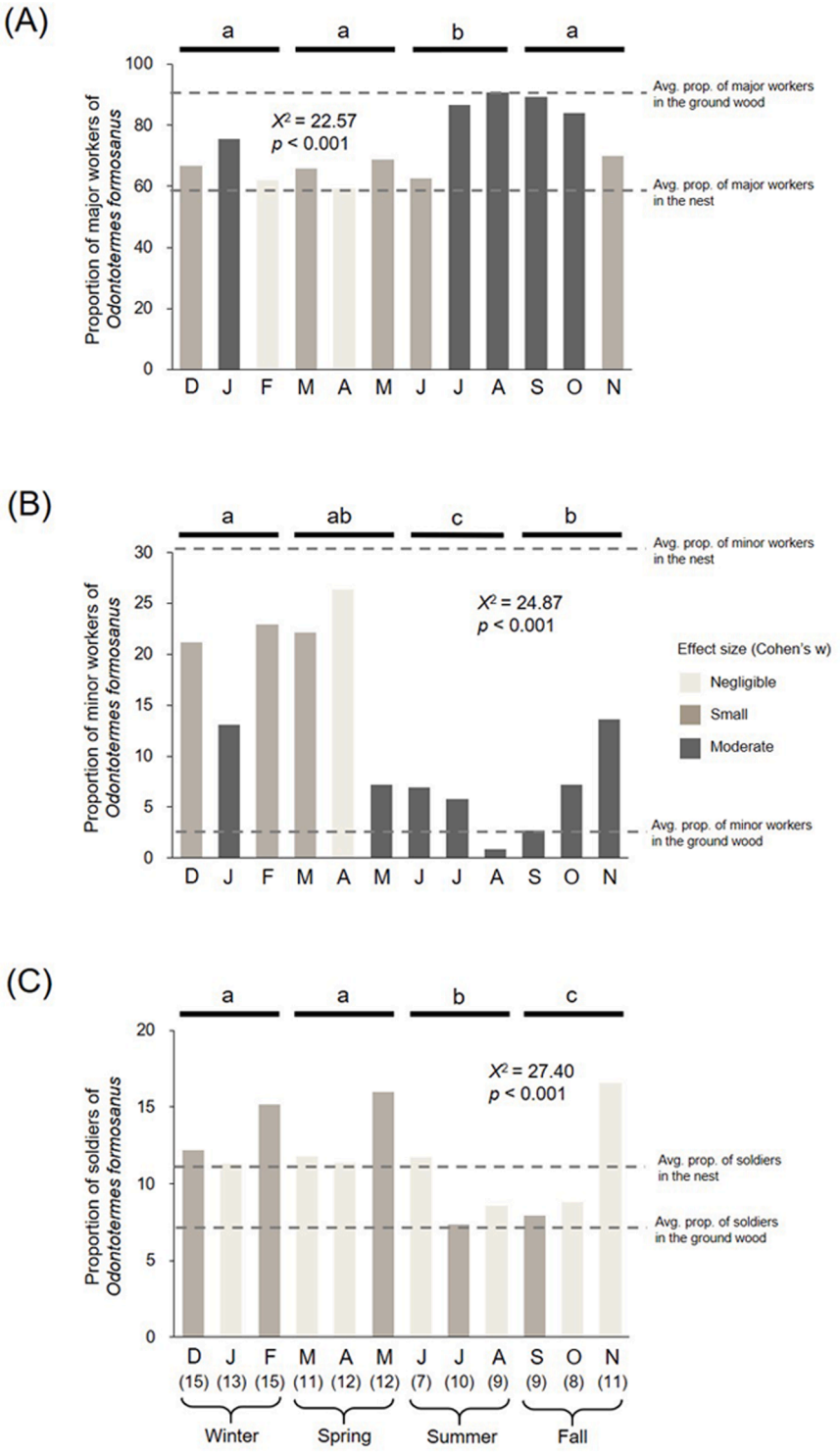


Fig. 3. Analysis of the caste proportion of the fungus-growing termite *Odontotermes formosanus* in fecal samples from the Chinese pangolin (*Manis pentadactyla*). The average percentages of minor workers, major workers, and soldier termites were assessed across four seasons using a Kruskal-Wallis ANOVA test to evaluate variations. Additionally, a chi-square test was performed to compare the ratios of different termite castes collected from the field (Supplementary S4) with those identified in the fecal samples. Sample sizes for the fecal samples are indicated in parentheses. The effect size (Cohen's w) was categorized as negligible (< 0.05), small (0.05–0.15), moderate (0.15–0.5), and strong (> 0.5).

season in Huisun Forest typically spans from April to September (Chen et al., 2023), and heavy rainfall during this period may obscure or wash away visible signs of newly excavated burrow entrances, potentially leading to underestimation of burrowing activity. However, if rainfall were the primary factor, we would also expect reduced burrow counts in May, which was not observed.

Alternatively, the low number of new burrows in summer could indicate higher foraging efficiency. However, seasonal variation in the foraging patterns of Chinese pangolins is unlikely to result from greater efficiency of foraging. If the low number of new burrows in summer is due to less digging needed to locate termite nest underground, we would expect termite consumption and caste ratios in the fecal samples to be similar in summer and other seasons. Instead, the results show that pangolins exhibited less nest-raiding or burrowing during summer, as evidenced by the highest proportion of major workers and the lowest proportion of minor workers during this season (Sun et al., 2025a). In fungus-growing termites, major workers typically serve as foragers, whereas minor workers primarily act as nest-keepers. The ratio of major to minor workers, thus, can differ significantly depending on their activity location. For example, in fungus-growing termites, *O. distans* and *Macrotermes subhyalinus*, a high percentage of individuals collected from ground feeding sites are major workers (94.8% and 88.8%, respectively), while those from queen chambers or nests are predominantly minor workers (95.1% and 56.1%, respectively) (Badertscher et al., 1983; McMahan et al., 1984). In our study, the percentage of major workers exhibited significant variation, with 90.2 $\pm$ 5.1% on the ground and 55.2 $\pm$ 14.8% inside the nest. Similarly, the proportion of minor workers also demonstrated considerable variation, showing 2.6 $\pm$ 1.7% observed on the ground and 32.8 $\pm$ 16.5% within the nest. The seasonal shift in caste ratios suggests that pangolins forage less intensively underground during summer, with relatively more surface feeding. For example, the high proportion of major workers in feces in January, July, August, September, and October implies a decline in nest excavation. In contrast, a greater proportion of minor workers in December, February, March, and April indicates increased nest-raiding behavior. Accordingly, previous studies on the burrowing and dietary habits of Chinese pangolins in mainland China showed that in winter, they consume at least two termite species, including *Macrotermes barneyi*, by raiding nests located up to 2 m beneath the surface; in contrast, they target shallower food resources (15–50 cm) during the summer (Fang and Wang, 1980; Heath, 1992). However, it is important to note that while caste ratios offer insight into the depth or intensity of termite foraging, they do not directly reflect foraging quantity. Previous studies have shown that total termite biomass consumed is lowest in summer (Sun, 2020; Sun et al., 2025a; Wu et al., 2005), despite the higher proportion of *O. formosanus* in fecal samples during this period. Therefore, the proportion of caste ratios of *O. formosanus* in the fecal samples can only be used as an indicator of depth of termite foraging or nest-raiding behavior in pangolins, rather than diet quantity.

Overall, we found that the temporal pattern of Chinese pangolin burrowing activity did not align with the seasonal abundance of termites on the ground and top soil, suggesting that factors beyond termite availability influence foraging behavior. Reduced digging in summer may result from the preference for surface foraging and the presence of alternative prey, particularly ants, on the ground surface. The ants activity likely increases in summer due to higher temperatures and humidity (Kaspari and Weiser, 1999; Levings and Windsor, 1984; Swart et al., 1999), making them more accessible and energetically favorable than deeply burrowed termites. While ants were not systematically surveyed alongside termites in Huisun Forest Station, supplementary ant abundance from pitfall trap surveys collected between 2013 and 2014 in the southern Coastal Mountain Range in Taitung, (Supplementary S6, S7) support this hypothesis. As observed, ant abundance from the pitfall trap surveys exhibited a distinct seasonal pattern, with ant abundance peaking in August and September (Supplementary S6, S7). Studies conducted in low-elevation montane areas in Taiwan also indicate that worker ant abundance positively correlates with temperature. Furthermore, ant species richness exhibits significant seasonal fluctuations, peaking during the warmer months or summer (Chen et al., 2019; Lin et al., 2016). Correspondingly, previous diet analyses show that ants comprise the bulk of pangolin prey during summer, coinciding with a decline in termite consumption (Sun et al., 2025a). In contrast, during fall and winter, ants retreat to deeper soil layers, prompting pangolins to dig more frequently or deeply to reach subterranean prey such as termites (Sun, 2020; Wu et al., 2004). This pattern suggests that termites may function as an alternative prey resource for pangolins when surface-active ants become less accessible. The hypothesis was further supported by the caste composition of *O. formosanus* in fecal samples. The high proportion of major workers in feces in summer and fall suggest that pangolins forage on the ground and excavate the termite nests less frequently.

The alternative prey hypothesis is normally described for generalist predators, stating that when the availability of the primary prey decreases, predators shift to alternative prey, and vice versa (Angelstam et al., 1984; Kjellander and Nordström, 2003; Pöysä et al., 2016). In this case, ants likely serve as the preferred prey during periods of high surface activity, with termites acting as seasonal substitutes. Indeed, the contrasting seasonal activity of ants and *O. formosanus* have been evidenced in Taiwan (Chiu et al., 2018). In detail, ants were more active on the ground surface during the hot and wet seasons and showed a strongly negative correlation to foraging activity of *O. formosanus* (Chiu et al., 2018) which may alternatively enhance seasonal variation in pangolins' dietary intake. Similar seasonal adjustments have been observed in Temminck's pangolins (*Smutsia temminckii*) in the Kalahari, where prey availability declines during dry winters due to reduced grass cover from low rainfall. In response, individuals increased foraging time and shifted their diet toward more energy-rich termites (Panaino et al., 2022).

Our findings suggest that seasonal variation in burrowing activity may be more likely influenced by the accessibility of surface-dwelling ants than by the abundance of termites. Pangolins may reduce their digging effort during summer when ants are plentiful and easier to access, and intensify burrowing when ants become less accessible, relying more heavily on termites. Another explanation for burrow excavation may relate to prey nutritional value. For instance, the relative contribution of termites to the nutritional intake (specifically protein and fat) of pangolins is at its annual minimum during the summer months (Sun, 2020). Furthermore, protein levels in the ants consumed during summer were higher than those in the termites ingested by pangolins (Sun, 2020). This behavioral plasticity allows pangolins to optimize energy intake across fluctuating environmental conditions, a strategy consistent with optimal foraging theory (Stephens and Krebs, 1986). Nonetheless, further research is required to test whether fluctuations in surface prey availability are indeed the primary driver of burrowing effort.

While our study offers insights into the seasonal drivers of pangolin foraging behavior, several methodological limitations affect our interpretations. The surveys of burrow and termite were not conducted simultaneously or at identical locations in the Huisun Forest Station and fecal data were collected independently from the southern Coastal Mountain Range (Taitung) during different years. Although previous studies suggest broadly similar ecological conditions and prey use patterns across regions in Taiwan (Chi, 2020), these assumptions remain uncertain given the spatial separation across the Central Mountain Range. The spatial and temporal heterogeneity introduces potential geographical bias, limiting our ability to make direct correlative inferences between local prey availability and specific foraging behavior. Because these datasets are not perfectly synchronized, developing quantitative mathematical models to validate the correlation between fecal caste ratios and burrowing activity would be statistically unreliable. Therefore, our comparisons remain qualitative. Consequently, our findings should be interpreted as suggestive hypotheses requiring validation through synchronized sampling, rather than definitive evidence. Validating the alternative prey hypothesis warrants a simultaneous assessment of the abundance and availability of both ants and termites in the environment, integrated with long-term burrow monitoring and dietary analyses of pangolins. In addition, Chinese pangolins construct burrows for various purposes, including foraging for termites or ants and seeking shelter (Sun et al., 2021b; Sun et al., 2025; Wu et al., 2019). Differences in habitat and food resource availability across geographical regions likely drive spatio-temporal variations in their burrowing behavior. This study explores the use of dietary composition as a proxy to infer burrowing activities in Chinese pangolins, using Taiwan as a case study. Although our findings identify *O. formosanus* as the primary prey and suggest a correlation between burrowing frequency and the presence of the *O. formosanus* worker caste, several factors remain unaddressed. Specifically, this study did not analyze how the seasonal caste fluctuation of *O. formosanus* within the nest influences the termite castes recovered in pangolin feces. Furthermore, we did not quantify the differential digestibility of various termite castes in fecal samples, which may confound the interpretation of burrowing frequency. Consequently, more detailed experimental designs are required to optimize data interpretation. Future studies should implement multi-method, synchronous monitoring within the same geographic scale to better link prey dynamics with foraging behavior, enabling the development of predictive models and more robust tests of these patterns.

This study provides an integrated understanding of association between seasonal variation in prey availability and the foraging behavior of the Chinese pangolin, a highly specialized and critically endangered species. Our findings carry several important implications for conservation. First, we highlight the need for long-term, seasonally aware monitoring of pangolin activity based on burrow counts. Seasonal variation in burrowing behavior, combined with the influence of rainfall on burrow visibility, means that summer surveys may underestimate actual activity level. Accurate estimates of activity thus require consistent survey timing and consideration of weather-related detection biases. Second, inferences about pangolin diet and burrowing behavior based solely on ant or termite surveys may be misleading. Comprehensive surveys that include both ants and termites, across surface and subterranean environments, are needed to better characterize prey dynamics. While such work is labor-intensive, it is essential for understanding the full spectrum of pangolin foraging ecology and guiding habitat management.

CRediT authorship contribution statement

Nick Ching-Min Sun: Writing – review & editing, Writing – original draft, Visualization, Resources, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Wen-Jun Lin:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation. **Hou-Feng Li:** Writing – review & editing, Supervision, Resources, Project administration, Funding acquisition, Conceptualization. **Chun-I Chiu:** Validation, Methodology, Investigation. **Hsiang Ling Chen:** Writing – review & editing, Writing – original draft, Validation, Supervision, Resources, Project administration, Methodology, Funding acquisition, Formal analysis, Conceptualization.

Ethics Statement

If this manuscript involves research on animals or humans, it is imperative to disclose all approval details. The live-trapping permission was issued by the Forestry and Nature Conservation Agency (permit numbers 0980129850, 0991616024, 1011701139, 1031700176 and 1050143346).

Declaration of Generative AI and AI-assisted technologies in the manuscript preparation process

During the preparation of this work the authors used Chat GPT and Monica to improve language and readability. The R script for statistical analysis in this study were generated with help of ChatGPTo3. After using this tool, the author reviewed and edited the content as needed and take full responsibility for the content of the publication.

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

We would like to thank the Experimental Forest Management Office of National Chung Hsing University for funding support and

assisting with transportation and accommodation during the field surveys. We also thank research assistants and students from the Department of Forestry, National Chung Hsing University, for their help with fieldwork, sample and data processing. We thank Dr. Wei-Ren Liang, Ren-Hau Liu, Guan-Yu Chen, Mu-Hsuan Chen, Ren-Han Liu and Hsiang-Chun Liu for the help of termite survey. We thank Man-Rong Yu, Xiang-Hua Hu, Jia-Hui Lin, and Ya-Wen Leu for their help in collecting pangolin fecal samples.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2026.e04425.

Data availability

Data is provided as Supplementary Material

References

Abe, T., Matsumoto, T., 1979. Studies on the distribution and ecological role of termites in a lowland rain forest of West Malaysia: (3) distribution and abundance of termites in pasoh forest reserve. Jpn. J. Ecol. 29, 337–351.

Anacleto, T.C.S., 2007. Food habits of four armadillo species in the Cerrado area, Mato Grosso, Brazil. Zool. Stud. 46, 529–537.

Angelstam, P., Lindström, E., Widén, P., 1984. Role of predation in short-term population fluctuations of some birds and mammals in Fennoscandia. Oecologia 62, 199–208. https://doi.org/10.1007/BF00379014.

Badertscher, S., Gerber, C., Leuthold, R.H., 1983. Polyethism in food supply and processing in termite colonies of *Macrotermes subhyalinus* (Isoptera). Behav. Ecol. Sociobiol. 12, 115–119. https://doi.org/10.1007/BF00343201.

Boutin, S., 1990. Food supplementation experiments with terrestrial vertebrates: patterns, problems, and the future. Can. J. Zool. 68, 203–220. https://doi.org/10.1139/z90-031.

Challender, D., Wu, S., Kaspal, P., Khatiwada, A., Ghose, A., Ching-Min Sun, N., Mohapatra, R.K., Laxmi Suwal, T., 2019. *Manis pentadactyla* (errata version published in 2020). IUCN Red. List. Threat. Species 2019, 8235 e.T12764A168392151.

Challender, D.W.S., Waterman, C., Baillie, J.E.M., 2014. Scaling up pangolin conservation. IUCN SSC Pangolin Specialist Group Conservation Action Plan, IUCN SSC Pangolin Specialist Group Conservation Action Plan. Zoological Society of London, London, UK.

Chao, J.T., 1989. Studies on the conservation of the Taiwanese Pangolin (*Manis pentadactyla pentadactyla*), General biology and current status. Division of Forest Biology, Taiwan Forestry Research Institute. Council of Agriculture, Executive Yuan, Taiwan.

Chao, J.T., Li, H.F., Lin, C.C., 2020. The role of pangolins in ecosystems. Pangolins Sci. Soc. Conserv. 43–48. https://doi.org/10.1016/B978-0-12-815507-3.00003-4.

Charnov, E.L., 1976. Optimal foraging, the marginal value theorem. Theor. Popul. Biol. 9, 129–136. https://doi.org/10.1016/0040-5809(76)90040-X.

Chen, H.L., Liao, Y.C., Lin, W.J., Li, H.F., 2025. Historic record, current distribution and habitat selection of Chinese pangolin in Yangmingshan National Park, Taiwan. Glob. Ecol. Conserv. 59, e03521. https://doi.org/10.1016/j.gecco.2025.e03521.

Chen, Y.-A., Tseng, Y.-H., Chen, H., Tzeng, H.-Y., 2023. Using autonomous recording units to record the changes of birds after patch cutting in Luanta fir plantation (In Chinese). Q. J. For. Res. 45, 51–70.

Chen, Y.F., Hsu, P.C., Lin, C.C., 2019. Differences of ant community composition in tree, floor and litter among adjacent natural broad-leaved forest and plantations. J. Exp. For. Nat. Taiwan. Univ. 33, 55–64.

Cheng, C.-H., Ho, Y.-L., Wang, W., Tzeng, H.-Y., 2024. Comparison of short-term post-fire vegetation recovery and regeneration in secondary forest and China fir plantation (In Chinese). Q. J. For. Res. 46, 117–146.

Chi, M.J., 2020. Drafting of research and conservation action plan for the Formosan pangolin. Biodiversity Research Institute, Ministry of Agriculture. (In Chinese).

Chiu, C.-I., Li, H.-F., Yan, M.-M., 2010. The geographical distribution and the dispersal flight season of *Odontotermes formosanus* (Isoptera: Termitidae) in Taiwan (in Chinese). Formos. Entomol. 202, 193–202.

Chiu, C.I., Yeh, H.T., Li, P.L., Kuo, C.Y., Tsai, M.J., Li, H.F., 2018. Foraging Phenology of the Fungus-Growing Termite *Odontotermes formosanus* (Blattodea: Termitidae). Environ. Entomol. 47, 1509–1516. https://doi.org/10.1093/ee/nvy140.

Cohen, J., 1988. The Effect Size. Statistical Power Analysis for the Behavioral Sciences. Routledge, Abingdon, pp. 77–83.

Corlett, R.T., 2007. The impact of hunting on the mammalian fauna of tropical Asian forests. Biotropica. https://doi.org/10.1111/j.1744-7429.2007.00271.x.

deOliveira, M.H., Viana-Junior, A.B., Nascimento, C.C., Bezerra-Gusmão, M.A., 2021. Worker dimorphism in nasute termites reflects different tasks during food collection. J. Insect Behav. 34, 96–105. https://doi.org/10.1007/s10905-021-09773-1.

Dhami, B., Neupane, B., Devkota, B.P., Maraseni, T., Sadadev, B.M., Bista, S., Adhikari, A., Chhetri, N.B., Panta, M., Stewart, A.B., 2023. Factors affecting the occupancy of Chinese pangolins (*Manis pentadactyla*) suggest a highly specialized ecological niche. Ecosphere 14, e4356. https://doi.org/10.1002/ecs2.4356.

Eggleton, P., Homathevi, R., Jeeva, D., Jones, D.T., Davies, R.G., Maryati, M., 1997. The species richness and composition of termites (Isoptera) in primary and regenerating lowland dipterocarp forest in Sabah, east Malaysia. Ecotropica 3, 119–128.

Fan, C.Y., 2005. Burrow habitat of Formosan pangolins (Manis pentadactyla pentadactyla) at Feitsui Reservoir. M.Sc. Thesis, National Taiwan University, Taipei, Taiwan (In Chinese).

Fang, L.X., Wang, S., 1980. A preliminary survey on the habits of pangoline (In Chinese). Mem. Beijing Nat. Hist. Mus. 1–6.

Gaudin, T.J., Emry, R.J., Morris, J., 2016. Skeletal Anatomy of the North American Pangolin *Patriomanis americana* (Mammalia, Pholidota) from the Latest Eocene of Wyoming (USA). Smithson. Contrib. Paleobiol. 1–102. https://doi.org/10.5479/si.1943-6688.98.

Gaudin, T.J., Emry, R.J., Wible, J.R., 2009. The phylogeny of living and extinct pangolins (mammalia, pholidota) and associated taxa: a morphology based analysis. J. Mamm. Evol. 16, 235–305. https://doi.org/10.1007/s10914-009-9119-9.

Heath, M.E., 1992. Manis pentadactyla. Mamm. Species 3, 1. https://doi.org/10.2307/3504143.

Imam, A., Ajao, M.S., Bhagwandin, A., Ihunwo, A.O., Manger, P.R., 2017. The brain of the tree pangolin (*Manis tricuspis*). I. General appearance of the central nervous system. J. Comp. Neurol. 525, 2571–2582. https://doi.org/10.1002/cne.24222.

Imam, A., Bhagwandin, A., Ajao, M.S., Spocter, M.A., Ihunwo, A.O., Manger, P.R., 2018. The brain of the tree pangolin (*Manis tricuspis*). II. The olfactory system. J. Comp. Neurol. 526, 2548–2569. https://doi.org/10.1002/cne.24510.

Karawita, H., Perera, P., Gunawardane, P., Dayawansa, N., 2018. Habitat preference and den characterization of Indian Pangolin (*Manis crassicaudata*) in a tropical lowland forested landscape of southwest Sri Lanka. PLoS. One 13, e0206082. https://doi.org/10.1371/journal.pone.0206082.

Kaspari, M., Weiser, M.D., 1999. The size-grain hypothesis and interspecific scaling in ants. Funct. Ecol. 13, 530–538. https://doi.org/10.1046/j.1365-2435.1999.00343.x.

Kingdon, J., 1997. The Kingdon field guide to African mammals. The Kingdon field guide to African mammals. Academic Press, London.

Kjellander, P., Nordström, J., 2003. Cyclic voles, prey switching in red fox, and roe deer dynamics - a test of the alternative prey hypothesis. Oikos 101, 338–344. https://doi.org/10.1034/j.1600-0706.2003.11986.x.

Korb, J., Linsenmair, K.E., 2001. Resource availability and distribution patterns, indicators of competition between Macrotermes bellicosus and other macro-detritivores in the Comoé National Park, Côte d'Ivoire. Afr. J. Ecol. 39, 257–265. https://doi.org/10.1046/j.1365-2028.2001.00312.x.
Krebs, J.R., Davies, N.B., 1993. An introduction to behavioural ecology, 3rd ed. Blackwell Scientific Publications, Oxford.
Levings, S.C., Windsor, D.M., 1984. Litter moisture content as a determinant of litter arthropod distribution and abundance during the dry Season on Barro Colorado Island, Panama. Biotropica 16, 125. https://doi.org/10.2307/2387844.
Li, H.-F., 2010. Identification and collection of termites in Taiwan, 1-2 October 2010. In: Wu, W.J., Li, H.F. (Eds.), Proc. Symp.& Workshop on Termite Biology and Control in Taiwan. Department of Entomology, National Taiwan University, Natio, Taipei, Taiwan, pp. 37–60.
Liang, C.-C., 2017. Termite species composition in soil and feces of Formosan pangolin (*Manis pentadactyla pentadactyla*) at Luanshan, Taitung. M.Sc. Thesis, National Pingtung University of Science and Technology, Pingtung, Taiwan (In Chinese).
Lin, W.P., 2003. A Multi objective Planning System for Forest Resource Management in Taiwan: A Case Study on Hui-Sun Forest Station. University of Hawaii, Honolulu, HI, USA.
Lin, J.S., 2011. Home range and burrow utilization in Formosan pangolin (*Manis pentadactyla pentadactyla*) at Luanshan, Taitung. M.Sc. Thesis, National Pingtung University of Science and Technology, Pingtung, Taiwan (In Chinese).
Lin, S.Y., Giusto, B.D., Bain, A., Chou, L.S., 2016. Variation of ant community structure on Ficus benguetensis. Taiwania 61, 49–57.
Lin, W.J., Chiu, C.I., Li, H.F., 2024. Divergent effects of climatic factors on termite body size: alate versus worker castes. Environ. Entomol. 53, 1157–1168. https://doi.org/10.1093/ee/nvae088.
Ma, M.J., Li, J., Dou, H.L., Wang, K., Yang, J.Z., Wang, J.X., Guo, R.P., Wang, H., Hua, Y., 2024. Diet composition and its seasonal variation for Chinese pangolin based on DNA macrobarcoding technology. Chin. J. Ecol. 43 (3), 1–8.
Martin, T.E., 1987. Food as a limit on breeding birds: a life-history perspective. Annu. Rev. Ecol. Syst. 18, 453–487. https://doi.org/10.1146/annurev.es.18.110187.002321.
McMahan, E.A., Kumar, S., Sen-Sarma, P.K., 1984. Male/Female (Size) Polyethism in Workers of *Odontotermes distans* Holmgren and Holmgren (Isoptera: Termitidae: Macrotermitinae). Ann. Entomol. Soc. Am. 77, 429–434. https://doi.org/10.1093/aesa/77.4.429.
McNab, B.K., 1984. Physiological convergence amongst ant-eating and termite-eating mammals. J. Zool. 203, 485–510. https://doi.org/10.1111/j.1469-7998.1984.tb02345.x.
Mohapatra, R.K., Panda, S., 2014. Behavioural descriptions of Indian pangolins (*Manis crassicaudata*) in captivity. Int. J. Zool. 2014, 795062. https://doi.org/10.1155/2014/795062.
Mora, P., Rouland, C., Renoux, J., 1996. Foraging, nesting and damage caused by Microtermes subhyalinus (Isoptera: Termitidae) in a sugarcane plantation in the Central African Republic. Bull. Entomol. Res. 86, 387–395. https://doi.org/10.1017/s0007485300034970.
Nielsen, S.E., McDermid, G., Stenhouse, G.B., Boyce, M.S., 2010. Dynamic wildlife habitat models: seasonal foods and mortality risk predict occupancy-abundance and habitat selection in grizzly bears. Biol. Conserv. 143, 1623–1634. https://doi.org/10.1016/j.biocon.2010.04.007.
Panaino, W., Parrini, F., Phakoago, M.V., Smith, D., vanDyk, G., Fuller, A., 2022. Do seasonal dietary shifts by Temminck's pangolins compensate for winter resource scarcity in a semi-arid environment? J. Arid. Environ. 197, 104676. https://doi.org/10.1016/j.jaridenv.2021.104676.
Pietersen, D.W., Symes, C.T., Woodborne, S., Mckechnie, A.E., Jansen, R., 2016. Diet and prey selectivity of the specialist myrmecophage, Temminck's ground pangolin. J. Zool. 298, 198–208. https://doi.org/10.1111/JZO.12302.
Pöysä, H., Jalava, K., Paasivaara, A., 2016. Generalist predator, cyclic voles and cavity nests: testing the alternative prey hypothesis. Oecologia 182, 1083–1093. https://doi.org/10.1007/s00442-016-3728-9.
Redford, K.H., 1987. Ants and termites as food. In: Genoways, H.H. (Ed.), Current Mammalogy. Springer, Boston, MA, pp. 349–399. https://doi.org/10.1007/978-1-4757-9909-5_9.
Redford, K.H., Dorea, J.G., 1984. The nutritional value of invertebrates with emphasis on ants and termites as food for mammals. J. Zool. 203, 385–395. https://doi.org/10.1111/j.1469-7998.1984.tb02339.x.
Rodrigues, T.F., Mantellatto, A.M.B., Superina, M., Chiarello, A.G., 2020. Ecosystem services provided by armadillos. Biol. Rev. 95, 1–21. https://doi.org/10.1111/brv.12551.
Sabin, K.C., Regmi, S., Pant, B., Nepali, A., Katuwal, H.B., Sharma, H.P., 2024. Factors influencing Chinese pangolin (*Manis pentadactyla*) burrow selection in the Chandragiri-Champadevi hills of Kathmandu Valley, Nepal. Heliyon 10. https://doi.org/10.1016/j.heliyon.2024.e25774.
Stephens, D.W., Krebs, J.R., 1986. Foraging theory. Princeton University Press.
Sun, C.-M., 2020. Feeding ecology of the Chinese pangolin (Manis pentadactyla) in southeastern Taiwan. Ph.D. Thesis, National Pingtung University of Science and Technology, Pingtung, Taiwan (In Chinese).
Sun, N.C.M., Arora, B., Lin, J.S., Lin, W.C., Chi, M.J., Chen, C.C., Pei, C.J.C., 2019b. Mortality and morbidity in wild Taiwanese pangolin (*Manis pentadactyla pentadactyla*). PLoS. One 14, 1–11. https://doi.org/10.1371/journal.pone.0198230.
Sun, N.C.M., Liang, C.C., Chen, B.Y., Lin, C.C., Pei, K.J.C., Li, H.F., 2019a. Comparison of two faecal analysis techniques to assess Formosan pangolin *Manis pentadactyla pentadactyla* diet. Mammalia 84, 41–49.
Sun, N.C.M., Liang, C.C., Lin, C.C., Pei, K.J.C., Li, H.F., 2025a. Prey composition and seasonal dietary patterns of Chinese pangolins in southeast Taiwan. Glob. Ecol. Conserv. 58, e03444. https://doi.org/10.1016/j.gecco.2025.e03444.
Sun, N.C.M., Lin, J.S., Pei, K.J., 2025b. Characteristics, location, and usage patterns of resting burrows in Chinese pangolins: insights from radio-telemetry tracking. Glob. Ecol. Conserv. 57, e03406. https://doi.org/10.1016/j.gecco.2025.e03406.
Sun, N.C.M., Lo, F.H.Y., Chan, F.T., Lin, K.S., Pei, K.J., 2024. Inconsistent reproductive cycles and postnatal growth between captive and wild Chinese pangolins and its conservation implications. Glob. Ecol. Conserv. 54, e03057. https://doi.org/10.1016/j.gecco.2024.e03057.
Sun, N.C.M., Lo, F.H.Y., Chen, B.Y., Yu, H.Y., Liang, C.C., Lin, C.C., Chin, S.C., Li, H.F., 2020. Digesta retention time and recovery rates of ants and termites in Chinese pangolins (*Manis pentadactyla*). Zoo. Biol. 39, 168–175. https://doi.org/10.1002/zoo.21534.
Sun, N.C.M., Pei, K.J.C., Wu, L.Y., 2021a. Long term monitoring of the reproductive behavior of wild Chinese pangolin (*Manis pentadactyla*). Sci. Rep. 11, 1–9. https://doi.org/10.1038/s41598-021-97618-4.
Sun, N.C.M., Sompud, J., Pei, K.J.C., 2018. Nursing period, behavior development, and growth pattern of a newborn Formosan pangolin (*Manis pentadactyla pentadactyla*) in the wild. Trop. Conserv. Sci. 11. https://doi.org/10.1177/1940082918788450.
Sun, S., Dou, H., Wei, S., Fang, Y., Long, Z., Wang, J., An, F., Xu, J., Xue, T., Qiu, H., Yan, H., Jiang, G., 2021b. A review of the engineering role of burrowing animals: implication of chinese pangolin as an ecosystem engineer. Zool. Res. 3 (3), 1–20.
Swart, J.M., Richardson, P.R.K., Ferguson, J.W.H., 1999. Ecological factors affecting the feeding behaviour of pangolins (Manistemminckii). J. Zool. 247, 281–292. https://doi.org/10.1111/j.1469-7998.1999.tb00992.x.
Tamang, S., Sharma, H.P., Belant, J.L., 2022. Foraging burrow site selection and diet of Chinese pangolins, Chandragiri Municipality, Nepal. Animals 12. https://doi.org/10.3390/ani12192518.
Trageser, S.J., Ghose, A., Faisal, M., Mro, P., Mro, P., Rahman, S.C., 2017. Pangolin distribution and conservation status in Bangladesh. PLoS. ONE 12, e0175450.
Tsai, P.-H., Chen, N.-S., Chen, A.-K., Chen, C.-H., 1965. Architecture and development of the termitarium of *Odontotermes (O.) formosanus Shiraki* (in Chinese). Acta Entomol. Sin. 14, 53–70. https://doi.org/10.16380/J.KCXB.1965.14.1.5370.
Tsai, Y.-L., Yuan, H.-W., Chen, P.-C., Yang, C.-W., 2004. A Preliminary Study on the Wild Habitat of the Taiwanese Pangolin (*Manis pentadactyla pentadactyla*) in the Muzha Mountain Area. In: Research Bulletin of the Experimental Forest, College of Bioresources and Agriculture, 18. National Taiwan University, pp. 29–34.
Wang, Z., Mo, J., Lu, Y., 2009. Biology and ecology of Macrotermes barneyi (Isoptera: Termitidae). Sociobiology 54, 777–785.
White, T.C.R., 2008. The role of food, weather and climate in limiting the abundance of animals. Biol. Rev. 83, 227–248. https://doi.org/10.1111/j.1469-185X.2008.00041.x.
Wu, C.C., Tsai, C.L., Liang, W.R., Takematsu, Y., Li, H.F., 2019a. Identification of subterranean termite genus, Reticulitermes (Blattodea: Rhinotermitidae) in Taiwan. J. Econ. Entomol. 112, 2872–2881. https://doi.org/10.1093/jee/toz183.

Wu, S., Ma, G., Chen, H., Xu, Z., Li, Y., Liu, N., 2004. A preliminary study on burrow ecology of *Manis pentadactyla*. Chin. J. Appl. Ecol. 15, 401–407.
Wu, S., Sun, N.C.M., Zhang, F., Yu, Y., Ades, G., Suwal, T.L., Jiang, Z., 2019b. Chinese pangolin *Manis pentadactyla* (Linnaeus, 1758). In: Pangolins: Science, Society and Conservation. Elsevier, pp. 49–70. https://doi.org/10.1016/B978-0-12-815507-3.00004-6.
Wu, S.B., Liu, N.L., Li, Y., Sun, R., 2005. Observation on food habits and foraging behavior of Chinese pangolin (*Manis pentadactyla*) (in Chinese). Chin. J. Apppl. Environ. Biol. 11, 337–341.