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SHORT NOTE

Diel Patterns Hold Promise as an Ecological Trait for Ants

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Abstract

Ecological traits have flourished in insect-based studies, resulting in a substantial and growing list of measurable traits. One trait that will likely become more attractive as data quality and curation improve are the diel patterns of insect activities. Diel patterns in ants can help better understand vital ecological processes such as competition and invasion biology. Because diel activity has the potential to be an informative trait in ants, we assessed the diel designations of foraging ants across the literature to quantify and assess the variation and sampling extent of this particular trait. We collected diel designations from 104 peer-reviewed scientific articles and quantified these data across important and documented ecological traits. We found that a disproportionate amount of solitary foraging ants were primarily diurnal foragers relative to ants that cooperatively forage. Our data show that diel patterns in foraging vary widely within and across ant genera. Importantly, we highlight the undersampling of this crucial ecological trait, which currently limits its utility. Our efforts highlight the importance of assessing an ecologically important trait's landscape of reported data.

Introduction

Ecological traits are measurable phenotypic characteristics that quantify an organism's fitness or impact on its local environment (McGill et al., 2006). Diel patterns of insect activity are important ecological traits that are likely to become more informative as data collection and quality improve. However, this potential is currently undercut by under-sampling, the need for standardized definitions of diel classes, and mistaken assumptions about plasticity and seasonal changes in diel activity. Once our understanding of diel patterns is better developed, this trait can be applied to assess biodiversity by incorporating crucial life and natural history information, such as the timing of essential insect activities like foraging or reproductive events. These events are increasingly under human interference through habitat destruction and modification (Grubisic et al., 2018; Weiner et al., 2014).

Trait-based ecological research on insects has flourished, and researchers continue to add to the list of ecological traits and databases (Bartomeus et al., 2013; Homburg et al., 2014; Twardochleb et al., 2021). Unfortunately, our knowledge of the patterns and ecological correlates of diel patterns remains limited. This trait shows tremendous variation in insects as it can be conserved in whole clades (e.g., Lepidoptera (Kawahara et al., 2018)) or widely variable in others (e.g., Coleoptera (Lövei & Sunderland, 1996; Ottesen, 1985; Pearson, 1988)). Furthermore, variation can exist based on the activity (i.e., reproduction, foraging, etc.), as reproduction may be limited to specific seasons. In contrast, foraging can occur

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when abiotic or biotic conditions are agreeable. The first step to developing a framework to study diel patterns better is to understand, quantify, and assess this trait within a well-studied taxon, which is the study's objective. Here, we quantify and summarize diel patterns of ant foraging activity (Hymenoptera: Formicidae), an easily identifiable activity outside a colony's nest.

Ants are an excellent insect group for evaluating diel activity patterns. First, they are functionally diverse, spanning a wide variety of dietary, foraging, and nesting niches, resulting in a wide variation in the timing of various activities (Hölldobler & Wilson, 1990). Second, their ecological traits are relatively well-studied relative to other insect groups (Gibb et al., 2022; Ohyama et al., 2023), with some traits linked to temporal activity, such as thermal tolerance, which has been extensively studied in the context of climate change (Parr & Bishop, 2022; Roeder et al., 2021). Additionally, research on gene expressions based on circadian rhythms of specific species, like *Camponotus floridanus* (Das & de Bekker, 2022) or *Solenopsis invicta* (Lei et al., 2019) has also been investigated. These qualities offer a large clade of insects with diverse ecologies and interactions that can be studied in the context of traits.

However, despite various studies on the temporal dimension of ant activity, our understanding of their diel activity in the context of their ecology remains relatively poor at larger taxonomic scales. Here, we offer the most complete dataset concerning the various diel designations assigned to ant foraging activity. This dataset allows for examining the range and coverage of existing data before determining how best to develop and add to it. This study aims to be descriptive and exploratory to provide observations for future physiological, evolutionary, and ecological hypotheses. Considering this, our study is guided by three objectives. (1) Summarizing the extent of existing records on diel patterns of ant foraging. (2) Determining how this trait may vary across different genera and their ecologies. (3) Using emerging patterns observed here to inform future research.

Methods

Data were collected from 104 published papers focused on diel foraging activities of ants through querying Google Scholar and Web of Science with the combination of terms: "diel", "ant", "temporal", "activity", and "diurnal/nocturnal/crepuscular". We specifically looked for field-based studies or studies that identified and applied diel designations from field-based studies. Laboratory research was not included in this search as this paper focused on the daily patterns of ants in their natural environment. Furthermore, we only acknowledged diel designation where designations were made from authors' observations or determined through diurnal and nocturnal sampling (i.e., sampling done solely in one diel designation did not count). Publications spanned ecological surveys, species observations, meta-analyses, reviews, and experimental ecological studies. We acknowledge that this search is not exhaustive, and there are likely natural history studies that have been missed. We collected species identities and their designated diel activity pattern from these studies. To update species identities, we used AntCat.org, an online resource that records and updates changes to ant taxonomy. We categorized species as diurnal (D, active foraging during the day), nocturnal (N, active foraging during the night), or cathemeral (C, active foraging both day and night). Only some studies (14) delineated crepuscular designations and differed in their definition of crepuscular. Therefore, crepuscular designated species were omitted from this study. We used traits other ant trait studies have frequently used to explore links between diel activities and genus-level ecological traits. More specifically, we used diet, foraging style, nesting niche, presence of sting, and presence of polymorphism from the supplementary materials of Greer et al. (2022). Data were grouped by these diel patterns and trait types to calculate relative proportions. It is essential to recognize the sampling biases that are inherent in the compiled data. While the ecological surveys from our literature search sampled both day and night, other diel designations from non-survey papers can suffer from the potential of missed detections.

We used chi-squared tests to statistically assess the association between the ecological traits against diel designations. We ran five tests for five different ecological traits with an alpha cutoff at 0.05. Results under the alpha value indicate a statistically significant association between the two categorical variables.

Results

Our dataset spanned 755 species by study observations (including the same species but in different studies/locations) from 104 global studies (526 species spanning 113 genera). The studies covered ~90 degrees of latitude, mainly from Brazil and the United States. Diurnal ants comprised 44.6% of the entire dataset, while nocturnal and cathemeral comprised 29.4% and 26%, respectively. Polymorphic ants had relatively even proportions of diurnal and nocturnal foragers, but monomorphic ones had nearly double the proportion (49.1 % to 23.9%).

The top three observed species assuming taxonomic certainty were: *Camponotus atriceps* (9 times), *C. sericeiventris* (7), and *Dinomyrmex gigas* (6). The top three observed genera were: *Camponotus* (129 Observations), *Pheidole* (59), and *Crematogaster* (36) (Fig 1). In addition, species that were designated all three different diel classes across different studies were: *Camponotus atriceps* (9 studies, D: 11.1%, N: 77.8%, C: 11.1%), *Camponotus lespesii* (3 studies), *Ectatomma tuberculatum* (3 studies), *Myrmecocystus mimicus* (3 studies), *Pachycondyla harpax* (3 studies), *Pheidole pallidula* (5 studies, D: 20%, N: 40%, C: 40%), *Technomyrmex albipes* (4 studies, D: 25%, N: 50%, C: 25%), *and Veromessor pergandei* (4 studies, D: 25%, N: 25%, C: 50%).

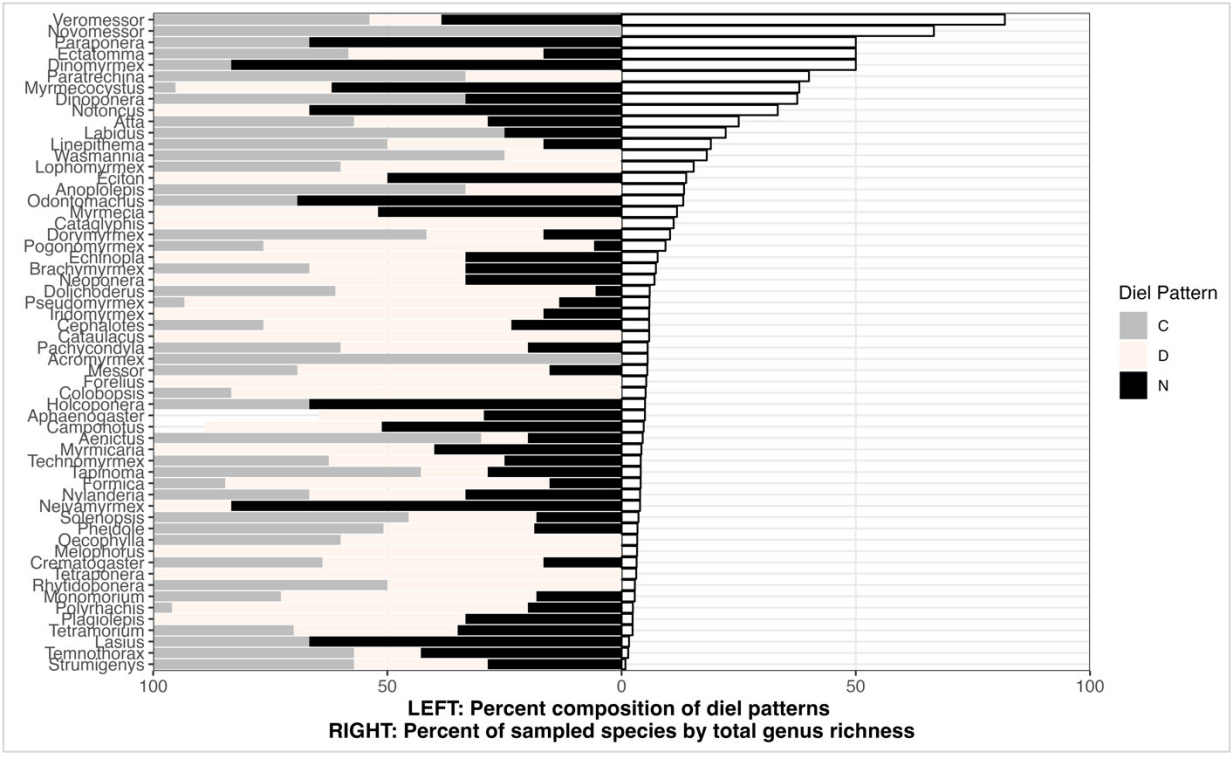

Fig 1. Figure showing the variation in diel classes in genera with three or more observed species. The right panel shows the observed proportion of species relative to the species richness of each genus. The left panel shows the composition in relative proportions across three diel designations (D- Diurnal, N- Nocturnal, C- Cathemeral).

Comparisons of diel foraging activity across natural history traits reveal a range of variations. The chi-squared tests showed significant associations between diel designations and all ecological traits (Traits (Chi-square value): diet (83.02), foraging style (61.82), nesting niche (57.09), polymorphism (51.78); all $P < 0.05$) except for the presence or absence of a sting (Chi-square: 0.005, $P = 0.94$). Across dietary categories, omnivorous and herbivorous classes showed uneven distributions in proportions of diel patterns as both groups had high proportions of diurnal foragers (46.9% and 41.4%, respectively) relative to their lowest proportion class (See Table 1). For nesting niches, arboreal nesters had the highest proportion of diurnal foraging ants (61.2%) and the lowest proportion of nocturnal foragers (14.7%) relative to ground and mixed nesting ants. The most significant difference between diel classes came from foraging styles, in that solitary foragers were primarily made up of ants classified as diurnal (64.7%), with fewer nocturnal designations (11.8%). Contrastingly, cooperative foragers showed low variation among all diel classes (Table 1).

Discussion

Here, to our knowledge, we present the first dataset that synthesizes diel patterns of ant foraging across the literature. The most apparent pattern from this data was that solitary forager ants tended to have a higher proportion of diurnal foragers. In contrast, cooperative foragers showed a more even distribution of proportions. Solitary foraging could be more efficient under higher light intensity conditions, allowing the total utility of vision. This could be explained because navigational efficiency in ants correlates tightly with light intensity (Narendra et al., 2013). Alternatively, eye size and its components based on ommatidia positioning and number can impact the navigational ability of some species (Palavalli-Nettimi & Narendra, 2018) and, subsequently, their foraging behavior, with smaller species possessing smaller eyes being more likely to forage cooperatively. Cooperative foraging is also likely advantageous when navigation during less favorable photoperiod conditions may result in a reliance on chemical trail-making and/or tandem running. These would be interesting future research avenues, considering that diel patterns can correlate with sympatric species or abiotic conditions (Klotz, 1984). For example, foraging styles and diel patterns help explain the co-existence of ants relying on similar resources within an ecological community.

Other patterns of interest can be observed in the near doubling in the proportion of nocturnal relative to diurnal species for monomorphic species. In contrast, polymorphic species exhibit more even proportions across the diel classes. Polymorphism is often considered a measure of social complexity in ants (Anderson & McShea, 2001). Under this premise, one could predict that polymorphic colonies would have higher capacities to forage across a broad range of diel periods. However, this has yet to be fully investigated and would be an interesting avenue for future research.

Table 1. Table showing the relative proportions of diurnal, nocturnal, and diurnal/nocturnal foraging ants based on natural history traits of diet, nesting strata, foraging style, sting presence/absence, and polymorphism presence/absence.

Diet				
Diel Type	*Predators*	*Omnivores*	*Herbivores*	*Species x Study total by diel type*
Diurnal	35.1 %	46.9 %	41.4 %	333
Nocturnal	34.2 %	29 %	24.3 %	219
Cathemeral	30.7 %	24.2 %	34.3 %	195
Nesting				
Diel Type	*Arboreal*	*Ground*	*Mixed*	*Species x Study total by diel type*
Diurnal	61.2 %	44.3 %	38.9 %	335
Nocturnal	14.7 %	28.2 %	36.0 %	220
Cathemeral	24.1 %	27.6 %	25.1 %	195
Foraging Style				
Diel Type	*Cooperative*	*Solitary*		*Species x Study total by diel type*
Diurnal	39.6 %	64.7 %		283
Nocturnal	31.1 %	11.8 %		189
Cathemeral	29.3 %	23.5 %		189
Sting				
Diel Type	*Present*	*Absent*		*Species x Study total by diel type*
Diurnal	41.9 %	46.2 %		216
Nocturnal	29.7 %	28.7 %		333
Cathemeral	28.5 %	25.1 %		195
Morphism				
Diel Type	*Monomorphic*	*Polymorphic*		*Species x Study total by diel type*
Diurnal	49.1 %	39.2 %		336
Nocturnal	23.9 %	36.2 %		220
Cathemeral	27.0 %	24.6 %		195

The lack of pattern between diel cycles and other traits (e.g. presence of a sting) may be due to inconsistent sampling methods across studies, the taxonomic scale of our ecological trait data, or the absence of a "true" pattern. Firstly, our dataset suggests that the available data on diel patterns skews heavily towards well-studied, surface foraging, and often relatively larger genera (e.g., *Camponotus*, *Pheidole*), likely because larger ants are visually conspicuous and more accessible to monitor in different lighting conditions. We also note that almost all genera have been classified in multiple diel classes with few exceptions; genera with more than three species include *Formica, Forelius, Lasius*, and *Cataulacus* (all diurnal). The designation of exclusive diurnality or nocturnality may prove false with additional data, as our samples only represent a small proportion of the total richness of those genera. Finally, throughout the literature, we observed a need for more standardization in the nocturnal, crepuscular, and diurnal definitions. Many studies omitted the crepuscular label, and most studies differed in their temporal definition of these diel classes. We recommend the implementation of some level of standardization to improve sampling consistency, which can provide better comparability between studies. Secondly, the ecological trait correlates of these diel classes are generalized at the genus level, and these trait designations can be arbitrary and sometimes not fully representative of especially large genera. This course resolution and low number of observations per genera can lead to difficulty assessing patterns. Finally, given that ant foraging activity is a complex behavior influenced by an interaction of physiology, local abiotic conditions, and gene expression (Roeder et al., 2022; Das & de Bekker, 2022), the selected ecological traits may play only a minor role in influencing the timing of foraging.

In insect ecological research, diel patterns are becoming a trait of interest, with relevance to global concerns, such as widespread light pollution that accompanies urbanization and the declines in wide-ranging groups of insects (Firebaugh & Haynes, 2019; Grubisic et al., 2018; Sánchez-Bayo & Wyckhuys, 2019; Wagner et al., 2021). Here, we show the current documented state of how variable this trait can be, especially in association with respective natural history traits, for a well-studied insect group. We encourage other similar efforts to document the state of available information for this trait to identify potential issues that may be taxon-specific and provide the initial steps for progress in cataloging this aspect of life history.

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Authors' Contributions

LO: conceptualization, data curation, validation, formal analysis, methodology, investigation, project administration, writing-original draft, visualization.
DBB: writing-review & editing.
AL: writing-review & editing.

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