The Effects of Periodical Cicada Emergence on Ant Foraging Behaviors

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Periodical cicada emergences produce variety of noticeable, short-lived effects on their ecosystem, however their effects on ants are poorly understood. To quantify the foraging response of ants to periodical cicada emergences, the nutritional preferences and foraging rates of five ant communities in Lake County were measured during the 2024 periodical cicada emergence. Carbohydrates were significantly preferred over lipids, protein, salt, and water. Additionally, foraging rates were found to be significantly higher in the weeks after the periodical cicada emergence than during the emergence. Conclusions as to the extent of the impact of periodic cicada emergences will require subsequent summers of sampling, though data suggests predator satiation and nutritional compensatory behaviors were observed.

Literature Review

Pulse Ecology

Overview of Resource Pulses

A resource pulse is defined as a temporary availability of a resource which occurs relatively rarely within the ecosystem, or a brief period of abundance followed by a longer period of scarcity (Yang et al. 2010; Ostfeld & Keesing 2007). These pulses must have a comparatively greater magnitude of resource availability than non-pulse periods (Ostfeld & Keesing 2007). The effects of resource pulses can be localized to the area of the pulse, but still produce significant changes in the flow of energy, predation and herbivory, and can vary in their duration depending on the conditions of the pulse (Ostfeld & Keesing 2007). Resource pulses can be differentiated according to their duration and regularity, and the spatial scale over which they have an effect. When it comes to duration, pulses vary in how long the resources are present and accessible to consumers: resources may exist for a short time well within their consumers' lifespans before being consumed, or they may be able to persist beyond the initial pulse, such as in the case of some desert-dwelling seed crops that are dropped synchronously and can exist for years before being consumed or germinating (Ostfeld & Keesing 2007). Pulse regularity may vary as well, from being seasonal events to being governed by conditions that do not occur with any regularity and thus being unpredictable, especially on timescales of shorter-lived organisms (Ostfeld & Keesing 2007). Those that occur regularly may be cyclical on timescales too great for some consumers' lifespans and for these organisms the pulses may as well be randomly occurring, multiple generations may pass without ever encountering a resource pulse and learning to respond to it (Ostfeld & Keesing 2007). Lifespans of arthropods, small mammals or birds may be shorter than the intervals between resource pulses that can occur in their environments, such as periodical cicada emergences. Other resource pulses may be random and irregular: conditions that influence the pulses do not occur seasonally or annually, such as rainfall in otherwise arid environments (Chesson et al. 2004).

Effects of Resource Pulses

Resource pulses are categorized as a temporary abundance of a given resource, creating a wave of responses in the short- and long-term after the resource becomes available (Holt 2008). Resource pulses vary in their regularity and predictability with respect to other organisms affected by the pulses, and provide direct bottom-up controls and indirect top-down controls on the energy flowing within ecosystems (Ostfeld & Keesing 2007). The abundance of a new food resource will directly affect the organisms that use this resource, and the response of these organisms will have indirect impacts on other trophic levels through their increased abundance for predators. In other words, the decrease in predation pressure for organisms that would otherwise be eaten in non-resource pulse years. That predation pressure is released when consumers primarily exploit the resources from the pulse (McCary et al. 2021). Organisms may be specialized to exploit resource pulses, with their populations following that resource abundance very closely, booming and crashing along with the resource, such as weevils that feed on acorns from masting events (Ostfeld & Keesing 2007). Other organisms are generalists and will take advantage of this novel resource by adapting their feeding habits, such as birds consuming Magicicada instead of caterpillars (Getman-Pickering et al. 2023) or bears and foxes exhibiting more digging behaviors and changing foraging ranges to access Lyristes cicadas (Tomita 2021). Pulses can lead to an abundance of consumers exploiting them, in turn supporting a temporary boom in the population of consumers at higher trophic levels (Ostfeld & Keesing 2007). Terrestrial resource pulses may also provide nutrients that enrich the populations of plants, fungi, and bacteria through the decomposition of the resource and consumption by detritivores (Yang et al. 2006; Yang et al. 2008; Menninger et al. 2008). Nutrient resource pulses in marine ecosystems can support blooms of plankton, which in turn can drastically increase the productivity of the system. Marine food webs in polar waters are supported in part by resource pulses caused by seasonal upwelling of nitrates (NO_3-) (Varela & Harrison 1999), which contribute to highly productive systems that support highly concentrated populations of organisms such as fish, pinnipeds, and cetaceans (Beltran et al. 2021).

Insects whose life stages are synchronized, and whose populations occur in sufficient numbers can act as a resource pulse if they enter an ecosystem synchronously: cicadas are one such example. The periodical cicadas can emerge in localized areas leading to a high density of biomass available to consumers (Yang 2004). Their periodicity can vary, from the 4-year cycles in Chremistica ribhoi of northeastern India to the 13-17 year cycles of periodical cicadas in Northeastern North America (Hajong & Yaakop 2013; Getman-Pickering et al. 2023). These periodical cicadas synchronize their emergence from the soil where they spend the first 12 or 16 summers of their lives burrowed in, and the adults will persist for approximately a month, calling for mates, feeding, and laying eggs before dying (Ito et al. 2014). There may be up to several hundred cicadas emerging from a single square meter of soil, across areas as large as 105 km^2 (Yang 2004). This density of individuals means periodical cicadas can function as a resource pulse. The synchronicity and density of their emergence sets them apart from other co-occurring cicada species, in that their abundance will be far greater in synchronized broods than they will be for annual cicadas, whose life cycles are staggered such that they emerge every year, in lower densities than periodicals (Chiavacci et al. 2014). Annual cicada emergence densities can be closer to 18,000-26,000 cicadas per acre rather than the 1-2 million estimates for periodical cicadas (Dybas & Lloyd 1966). The pulse of resources is far greater for periodical cicada emergences than for annual cicadas, and thus likely has a far greater impact.

In terms of periodical cicadas' effects on their communities as a resource pulse, one documented response to their abundance is the decrease in predation by avians on other insects (Getman-Pickering et al. 2023). Insectivorous birds that would otherwise feed on seasonal caterpillars, had a temporary dietary change wherein they would decrease their caterpillar predation as they fed more on the abundant cicadas instead (Getman-Pickering et al. 2023). This left more caterpillars uneaten and able to feed on plants which otherwise would have been left unconsumed during a non-emergence year (Getman-Pickering et al. 2023). Indeed, the abundance of caterpillars coincided with a greater level of herbivory on white oak trees than in non-cicada years, as a likely indirect result of the periodical cicadas' emergence (Getman-Pickering et al. 2023). Avians are not the only predators of periodical cicadas, small mammals are also known to eat the insects (Krohne et al. 1991), and detritivores will consume the carcasses that accumulate over the course of the emergence (Yang 2005) which can lead to nutritional enrichment of soil ecosystems (Setlälä et al. 2022). A study performed in 2016 found that soil-dwelling arthropods and

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*This author wrote this paper as a senior thesis under the direction of Dr. Sean Menke nematodes increased in abundance in plots treated with added periodical cicada carcasses, with nematode community composition increasing in diversity compared to nontreated plots (Setälä et al. 2022). This increase in diversity and abundance suggests the productivity of soil increases during cicada emergences, enriching fungal and bacterial-based soil food webs (Setälä et al. 2022). Thus, periodical cicada can provide additional nutritional input to their environment; plant-available N in the form of NH_4+ and NO_3- and P in the form of PO_4- been observed to be more abundant in soil enriched with periodical cicada carcasses (Setlälä et al. 2022).

Spatial Scale of Resource Pulses

Periodical Cicada emergences have effects over a relatively large area, with broods being relatively localized to areas wherein previous emergences have occurred. Their range of emergences can be measured in hectares, affecting large regions through their emergence (Williams et al. 1993). The input of food and nutrients thus affects organisms across a vast area. These patches are not evenly distributed, however, and they follow the fragmentation of North American forest habitats, contributing to an uneven distribution of cicadas over the regions in which they occur (Yang 2004). Cicadas in a given area that are synchronized are classified as broods, with cicadas of the same brood emerging on the same 13- or 17-year cycles(Cooley et al. 2009). These broods' spatial ranges can range across hundreds of square miles, and within these regions, there can be further variation in the concentration of emerging cicadas (Cooley et al. 2009). One of the largest broods, Brood XIV, for example, ranges across the states of Kentucky, Tennessee, Pennsylvania, Maryland, and Massachusetts, and thus ecosystems across these regions can all experience the effects of the cicada resource pulses (Cooley et al. 2011).

Predator Satiation Effects

The number of cicadas emerging at once during an emergence can lead to an overwhelming amount of food: the density of the broods has been estimated to be around 133,000 nymphs in an acre (Dybas & Davis 1962), to several million (Cooley et al. 2004). Cicada population density increases independent of predation. However, predation rates have been observed to plateau before the cicada emergence reaches its maximum population, which could be explained by the effect of predator satiation hypothesis (Karban 1982). Predator satiation occurs when the frequency of predation of a prey organism does not increase as the density of the prey increases, which means their appetite for this prey is fully met and these predators cannot or will not consume any more of that prey (Williams et al. 1993). The proportion of the cicada population that is preyed upon has been observed to decrease at the peak of the cicada emergence as well, further supporting this hypothesis (Williams et al. 1993). Around the initiation of the emergence, a greater proportion of the cicada population will be eaten by predators than during the peak of the emergence when the greatest number of cicadas will be above ground and active (Williams et al. 1993). During the peak of the emergence, predation rates do not increase in proportion to the number of cicadas present, suggesting they cannot consume any more cicadas (Karban 1982). Predators that consume cicadas may even primarily consume cicadas during an emergence, eschewing other food sources in favor of the abundant ephemera (Getman-Pickering et al. 2023).

Ant Roles in Ecosystems

Overview

Ants are ubiquitous arthropods in terrestrial ecosystems, with over 15,700 named species and more still yet to be described (Schultheiss et al. 2021). They are found on all continents with the exception of Antarctica, and range from temperate to tropical environments, being most abundant and diverse in the tropics, but still significant in non-tropical ecosystems (Schultheiss et al. 2021). With their foraging, nestbuilding, and insect-tending behaviors, ants serve as highly influential organisms within their habitats. Ant nestbuilding, foraging, and scavenging behaviors contribute to the nutrient cycling of their environment, returning nutrients to soil and facilitating nutrient reintegration (Finér et al. 2013), as well as aerating and transporting the soil (Schultheiss et al. 2021). This nutrient cycling service means more nutrients are available for uptake by other organisms in the ants' ecosystem. Many ants will include carrion in their diets, participating in detritivorous food web, and thus aiding further in nutrient cycling within their ecosystems (Fellers & Fellers982). They can also participate in mutualistic interactions by protecting Hemipterans that feed on plant material and receive sugar-rich honeydew (Ivens 2015). Furthermore, ants can engage in mutualisms with plants themselves through seed dispersal as ants transport elaiosome-bearing seeds to their nests and discard the seeds (Karnish 2024). Their foraging behaviors are subject to the influence of environmental factors such as temperature and humidity, as well as the nutrition and availability of food in their environment (Bezděčková et al. 2024; Schafer et al. 2006; Dusstour & Simpson 2009). For ant communities that share ranges with periodical cicadas in the Northeastern and Midwestern United States, little is understood about their response to the resource pulse provided by the cicadas' emergence. It could be expected there could be a behavioral response to the change in food availability and nutritional balance with the influx of cicada prey and carrion. Periodical cicadas might present a novel food source for ants, both as live prey and as carrion, and their large numbers may lead to a predator satiation effect among ants.

Nutrient Cycling

The foraging and nest-building behaviors of ant colonies mean that ants participate in the nutrient cycling of organic matter in their environments. Nest-building leads to the accumulation of nutrients in the soil around the nest through larvae, ant bodies, food, and waste (Finér e. al 2012). This leads to ant nests concentrating the cycling of nutrients and can present a hotspot of nutrients that can be exploited by plants (Finér et al. 2012), (Fischer et al. 2003). The refuse piles that ant nests produce provide nutrients for plants that live in or around the nests which can be highly beneficial for these plants, especially in areas of low nutrient availability (Farji-Brener & Werenkraut 2017). Ant nests can serve as islands of fertility, supporting more plants in and around them than in soil without ant nests (Farji-Brener & Werenkraut 2017). Their presence can contribute to increased plant species richness within their ecosystems and can be integral to the plant community survival in desert biomes that may have limited water or nutrients available to plants (Farji-Brener & Werenkraut 2017). Additionally, ant nests provide habitats for other microfauna and can host distinct microclimates with different temperatures and moisture levels from the soil outside their nests. (Laakso & Setälä 1998). The excavation of nests contributes to an increase in soil invertebrate diversity, such as earthworms, nematodes and microbial colonies, some of which are specialized for the environmental conditions of ant nests (Laakso & Setälä 1998). Micro- and macroinvertebrates's roles in soil are not fully quantified, but their roles as decomposers, soil aerators, and microbial predators mean that they are highly important for the exchange of nutrients between macro- and microfaunal communities, and for the nutrient and oxygen availability within soil (Briones 2014).

Ants as Predators

Ants are highly efficient predators and can exert top-down controls within their ecosystem on the organisms they prey upon (Wills et al. 2019). For example, through a common garden experiment in Midwestern United States grasslands, it was found that predation rates decreased when ant populations were suppressed through ant-targeting poisons (Wills et al. 2019). Ants are predators of the larvae and eggs of many larger insect species, controlling and limiting the populations of these insects through their activity (López & Potter 2000). These larvae can include agricultural pests such as cutworms (Noctuidae) and Japanese beetles (Popillia japonica) (López & Potter 2000). Thus, their consumption of small prey means that ants can play an integral role in influencing the abundances of other arthropods within their ecosystem through top-down control. In their absence, a release of this control on their prey can come, which may lead to changes in their population sizes (Wills et al. 2019). Ants' eusociality additionally enables them to subdue prey larger than themselves with the aid of nestmates, extending their top-down predation effects to a diverse group of other arthropods (Cerdá & Dejean 2011).

Ants as Scavangers

The detritivorous diets of many ant species, including those represented in the Lake County ant communities, mean that ants play a role in the decomposition of organic matter. They have been found to be some of the dominant scavenging arthropods when experimentally supplied with insect carcasses, as they would be the first to locate and utilize these resources (Faller 1982). Ants are considered to scavenge readily, upon decaying prey both small and large, and the majority of ants will exhibit this behavior as part of their foraging behaviors (Holway & Cameron 2021). Their scavenging behavior is expected to be a key factor in how ants interact with cicada pulses, as the carcasses of the abundant cicadas will provide another source of carrion in the landscape of decaying matter that ants may utilize when foraging. For example, in previous scavenging rate studies in the context of cicada emergence, ants were found to respond with greater activity within one week of carcasses being available to them (Yang 2006). This suggests ants are affected by the presence of cicadas when scavenging, though whether their scavenging rates of other carrion is affected is yet to be determined.

Interspecies Symbiotic Interactions

Ants participate in a variety of mutualisms, particularly in ones that affect plants: ants feed at nectaries, transport seeds to feed on elaiosomes and tend herbivorous insects for food. A source of carbohydrates for many ant species is the honeydew produced by herbivorous insects that feed on plant phloem: Hemipterans that produce this honeydew can often be seen tended by ants, being guarded from predation, or even moved to new locations to forage (Ivens 2015). This means that ants will have an indirect interaction with plants by way of the herbivorous insects they protect and interact with. The species that display this behavior frequently belong to the subfamilies Dolichoderinae, Formicinae, and Myrmicinae, whose ranges can overlap with that of periodical cicadas (Ivens 2015). Ants can access the nectar produced by flowers and extrafloral nectaries when interacting with plants, which can lead to some pollination occurring as the ants access carbohydrates from the nectar they consume (Fagundes et al. 2015). Ants that harvest and consume seeds form relationships with the seedbearing plants they feed on: protein and lipid-rich elaiosome structures on the seeds can mimic the smell of rotting prey, and this incites foragers to return these seeds to their nests, often bringing the seeds with them, dispersing them further than the plant could unaided. Plants that produce elaiosome-bearing seeds benefit from having highly nutritious elaiosomes, as these seeds are more likely to be taken back to the nest or moved away from their parent plant when the foragers bring this highly valuable food source to their colony (Fischer et al. 2008). Nutrition of these elaiosomes are good sources of amino acids and simple sugars that are easily digestible by the colony members (Fischer et al. 2008). Elaiosomes produce chemicals that simulate the scent of decaying insects, which further appeals to foraging ants that consume these food resources (Fischer et al. 2008). These relationships, while not directly related to the predatory and detritivorous interactions ants may have with periodical cicadas, do describe the primary carbohydrate sources for ant foragers, which is a key part of their nutritional regulation. It is from these nectar and honeydew sources that ants would likely seek out additional carbohydrates when balancing their nutritional intake. Additionally, these interactions demonstrate other impactful roles ants have within their ecosystem.

Ant Foraging Strategies

Seasonal and Temperature Effects on Foraging

Factors that affect ant foraging include the nutrient requirements of the colony, as well as the environmental conditions to which the colony is exposed. Foraging activity is often restricted to specific temperature ranges within the ant foragers critical thermal maximums and minimums (Jayatilaka et al. 2011). Yearly, ant communities tend to increase their foraging activity in summer months, as colonies grow and require more nutrients (Bezděčková et al. 2024). As colonies begin to grow, with populations of larvae increasing within the nest, colonies will require a greater ratio of protein to carbohydrates than when the colony is more fully established and increasing at a slower rate later in the active season, wherein the carbohydrate requirements increase (Bezděčková et al. 2024).

Optimal foraging conditions can vary across different ant species, even within the same community. Species with a greater tolerance for high temperatures will have greater foraging presence at these temperatures than those with lower thermal tolerance maximums (Stuble et al. 2013). These thermal tolerances can lead to niche partitioning within ant communities, reducing competition by decreasing the overlap between optimal foraging temperatures of different species (Lessard et al. 2009). Warm temperatures tend to encourage foraging and other activities, as these allow ants to move faster due to their ectothermic body temperature regulation (Tizón et al. 2014). Most ants will be active within the range of 10 – 40 ˚C, except for some species that are specialized for hot, arid conditions (Tizón et al. 2014). Late spring to early fall, with their relatively warm temperatures thus increase ant foraging activity, especially in temperate regions where activity may slow or stop altogether in the cold of winter, early spring, and late fall (Win et al. 2018).

There is evidence of niche partitioning via thermal tolerances for ant species: ants will forage at different times during the day, with temperature as a contributing factor involved with that behavioral partitioning (Jayatilaka et al. 2011). For example, the diurnal Myrmica croslandi foraging starts at higher soil temperatures than the nocturnal Myrmica pyriformis, with M. croslandi exhibiting experimental thermal limits greater than M. pyriformis (Jayatilaka et al. 2011). Ant species that are more behaviorally dominant within their community are more likely to be active at a narrower range of temperatures than subordinate species that cannot compete as successfully with the more dominant species (Fellers 1989). Subordinate species may be active at wider ranges of environmental conditions, advantageous for reducing the chance of encountering more dominant species and engaging in interspecific competition or conflict, which can be harmful to the individuals involved (Fellers 1989).

Search Behavior and Foraging Success

Foraging success can depend on the behavioral and physical traits of the ants involved, especially when in competition with other species in their community. For instance, the size of an ant's legs, and the directionality of the paths they take to forage are factors in the way that they approach foraging (Pearce-Duvet et al. 2011). Ants that possess long legs in comparison to their body length are able to discover food sources more quickly, by moving more efficiently to allow them to travel farther (Pearce-Duvet et al. 2011). Species that travel more linearly will be able to run across more new food sources (Pearce-Duvet et al. 2011). In contrast, smaller species and those that do not have these linear search paths will be less likely to encounter novel food sources (Pearce-Duvet et al. 2011). The rate of successful foragers returning to the nest may be a factor in encouraging more foragers to be sent out of the nest. For example, in desert-dwelling Pogonomyrmex, the rate of foragers returning to their nest with food was correlated with the stimulation of foragers still in the nest to leave (Schafer et al. 2006). This suggests a mechanism for a proportional foraging response to the amount of food available in the environment (Schafer et al. 2006). When a forager returns after locating a food source, they can enable recruitment through laying pheromone trails as they hunt down food and subsequent foragers are then able to follow that trail to the food source (Lixiang et al. 2014). A positive feedback loop can occur, wherein more heavily-traveled pheromone trails will be supplemented with pheromones by the additional foragers, enticing more foragers to recruit to that food source (Lixiang et al. 2014). Ants can additionally perform tandem-running to show new foragers to a novel food source, where the ant that originally found the food leads another to the food's location (Franklin & Franks 2012). This allows ants to more quickly disseminate information through their colony (Franklin & Franks 2012).

Interspecies Competition While Foraging

There are three distinct roles of ants when it comes to interspecies foraging competition: opportunistic foragers, extirpators, and insinuators. Ants that are opportunistic are the first to arrive to food sources but are usually unable to defend it from competitors for very long and are timid around other ant species (Lach et al. 2010). Extirpator ants, on the other hand, do not find food sources first but are able to force other ants from the resource via aggressive recruitment (Lach et al. 2010). Finally, insinuating ants avoid the recruiting and aggressive extirpators via their small size and limited recruitment to baits. (Lach et al. 2010). This can be described as the "discovery-dominance tradeoff", wherein ants that are adapted to efficiently discover food have an inversely proportional ability to defend that food, and ants that are highly successful at defending food sources from others are less successful in locating new food sources (Fellers 1989). Some environmental factors may additionally affect the amount of competitive behaviors beyond the different competitive roles ants may fill in their environment. Ants can exhibit reduced competitive interactions when encountering abundant resources when compared with more limited resources, suggesting the magnitude of competitive interactions may be responsive to the availability of resources such as extrafloral nectaries (Fagundes et al. 2016).

Nutritional Requirements of Ants

Nutrient Prioritization and Regulation

Ants primarily require carbohydrates in their diet as adults as a source of energy to fuel their activity, with additional protein requirements to enable to growth of larval members of the colony (Dusstour & Simpson 2009). Ants will also consume lipids as well and will feed on salt baits when salt is a limiting resource in their environment (Renyard et al. 2024), though these are not as prominent in their diets as protein and carbohydrate macronutrients are (Reynard et al. 2024). Salts are an essential nutrient to ensure metabolic function, and ants must maintain a baseline level of the nutrient in their bodies (Kaspari et al. 2020). Lipids are also important for the growth of ants, and larvae supplied with lipid-rich diets can grow larger than those without (Bottcher & Oliveira 2014). Epigenetic and environmental factors may influence the eventual adult size of the larvae as well as their caste within the colony (Trible & Kronauer 2017), but lipids remain an important nutrient for supporting the growth of these larvae.

Ant colonies need to be able to adjust their foraging behavior to ensure they receive the proper ratios of macronutrients to ensure survival and colony growth, and they are capable of regulating this in response to different nutrient availability in their environment by controlling their individual intake of a food resource, and through changing foraging behaviors (Dusstour & Simpson 2009). A key part of this nutritional regulation is the presence of larvae in this colony, as larvae are capable of digesting proteins that adult ants cannot and will regurgitate these proteins as compounds that the adult members of their colony can successfully digest (Dussutour & Simpson 2008, 2009). Excess carbohydrates will be digested by foraging adults, and excess proteins may be digested by larvae to respond to nutritionally imbalanced diets that colonies may encounter or regurgitated by larvae and removed by adult nestmates (Dussutour & Simpson 2008; Dussutour & Simpson 2006). The dynamic between foraging adult ants, and the larvae they feed and received food from can be termed as a "social stomach", with foragers acquiring food and beginning to digest it, and the larvae able to consume and digest proteins and larger prey items (Dussutour & Simpson 2008; Dussutour & Simpson 2006). When there is an overabundance of one macronutrient, ants will adjust their foraging behaviors to address this nutritional imbalance, such as consuming more salt in response to an abundance of insect prey in their diet (Kaspari et al. 2020) or consuming more of a diluted carbohydrate source to receive the proper carbohydrate intake (Dussutour & Simpson 2008). The prioritization of carbohydrates in adult foragers' diets is due to this nutrient being used for energy, essential for any organism's survival, and because protein is less essential for their survival as they no longer are growing and producing more tissue as larve are (Dussutour & Simpson 2009).

Ants Responding to Cicada Resource Pulses

There are gaps within our understanding of ant responses to periodical cicada emergences. The limited study of ant responses to cicada emergences, including periodical cicadas, means little is known about the nutritional needs of ants experiencing these events. Whether they adjust the balance of nutrients in their diets in any way in response to the cicada emergence is not fully known. However it can be inferred that if cicadas change the nutritional intake of the colony due to their abundance, there would be a corresponding behavioral change in the ants foraging to ensure optimal nutritional intake. Regarding foraging, according to available literature, there is evidence cicada emergences can affect detritivore behavior. Across different families of detritivorous arthropods, there were varied responses to periodical cicada abundance in their environment (Yang 2005). Ants were included among the detritivores studied and showed a weak response to cicadas supplied in the experiment (Yang 2005). Regarding other recorded predation and consumption of cicadas by ants, Harvester ants (Pogonomyrmex rugosus) in the Chihuahuan desert, showing an increase of predation upon the annual cicadas within their ecosystem (Whitford & Jackson 2007). While annual cicadas do not emerge with the same abundance as periodical cicadas, they still represent a resource pulse in their ecosystem (Whitford & Jackson 2007). For example, the Pogonomyrmex predation on cicadas could suggest other ant species are also capable of predation upon periodical cicadas and a possible prioritization of this food resource by foragers.

Introduction

The periodical cicadas (Magicicada spp.) of North America emerge every 13 or 17 years, in broods that can number between tens of thousands to two million individuals per hectare (Lloyd & Dybas 1966). At the peak of their emergence, the cicadas present a virtually inexhaustible food source for the rest of their ecosystem, temporarily restructuring the food webs in their communities (Getman-Pickering et al. 2023) and providing a novel food source for small mammals (Krohne et al. 1991) and avians (Getman-Pickering et al. 2023) and enriching detrital food webs as their bodies are decomposed (Setälä et al. 2022). Ants consume carrion and hunt live prey like arthropods, likely being directly affected by the periodical cicadas that will present a novel and abundant food source, though this relationship has not been extensively quantified.

The effect of the periodical cicadas on their ecosystems indicates their role as a resource pulse, an "ephemeral event of resource superabundance" (Yang 2004). Their synchronized emergence and relative inaccessibility after the adults die and nymphs hatch mean that they present a highly abundant resource that is present for a short time before a period of scarcity (Ostfeld & Keesing 2007). Resource pulses' may affect consumers directly via the resources' consumption, (Ostfeld & Keesing 2007), or through indirect effects caused by changes in diet or behavior of the consumers that affect their other interations within the ecosystem. (Getman-Pickering et al. 2023). These effects may be top-down, such as in the release of predation pressure on caterpillars when birds begin to consume cicadas instead (Getman-Pickering et al. 2023), or bottom-up, with decomposing matter from the cicada pulse adding additional nutrients into soil food webs (Setälä et al. 2022).

Due to ant's influential roles within their ecosystems, determining their response to periodical cicada emergences on their foraging behavior will provide a more complete understanding of the effects of the emergence as a resource pulse. Ants are understood to be ecosystem engineers due to their nestbuilding behaviors, which change soil texture, nutrient content, and microbial communities as they excavate soil and move food and waste products through their nests (Cerdá & Dejean 2011). They also prey upon other arthropods and act as scavengers, meaning they not only exert top-down predation pressure on other arthropods in their ecosystem, but also participate in detrital food webs that can contribute to the cycling of nutrients within their environment. The ecological roles ants serve may be affected by the cicada emergence due to the large availability of high-quality food from the cicada bodies: there may be changes in predatory and scavenging relationships between ants and their prey.

As ants are both active predators and scavengers (Makino et al. 2024; Williams et al. 1993), it is likely that ant communities will be directly affected by cicadas that will represent a new source of prey and carrion. However, little has been documented about the effects of this resource pulse on the foraging behavior of ants. What is more understood is that ants can adjust their foraging behaviors in response to the resources available to them while foraging, adjusting ratios of protein and carbohydrates to ensure nutrition is received by the colony for growth and survival (Dussutour & Simpson 2009). Ants tend to require a balanced or slightly carbohydrate-biased diet (Cook et al. 2011) and require an input of protein for the growth of the colony, particularly the development of larvae (Dussutour & Simpson 2006). Larvae within a colony play a key role in the regulation of nutritional intake, as colonies with larvae can regulate their nutritional intake to get a more balanced ratio of carbohydrates and proteins than colonies without larvae (Dussutour & Simpson 2006). Additionally, ants will modulate their foraging to the quality and abundance of food in their environment. Ants recruit other workers to valuable food sources when returning to their nest from successful foraging (Schafer et al. 2006; Dussutour & Simpson 2009). Successful foragers can stimulate ants still in the nest to venture out and forage as well, while unsuccessful foragers will not stimulate this foraging activity, leading to proportional foraging responses to food availability (Schafer et al. 2006). The ability of ants to regulate their foraging rates, and nutritional intake suggests that they will exhibit a response to the resource pulse of periodical cicadas.

This study aims to elucidate the foraging responses of temperate forest and grassland ant communities in Lake County, Illinois, over the course of a periodical cicada emergence. We studied the impact of the periodical cicada emergence through measuring the foraging rates of ants, as well as the nutritional demand of the ant communities. If ants are exposed to the resource pulse conditions of a periodical cicada emergence, we expected to see a greater demand for carbohydrates than other macronutrients given the choice between carbohydrates, lipids, protein, salt, and water. This response was predicted based on the nutrient regulatory behaviors of ants, wherein ants tend to balance the intake of protein and carbohydrates (Dussutour & Simpson 2006). The ant community will be presented with a highly-protein based food source from cicadas and it's expected this intake will elicit a proportional intake of carbohydrates. Additionally, when foraging ants are active during a periodical cicada emergence, we expect to see a

Map 1: Sites of sampling were located in Old School Forest Preserve (42°16'15"N 87°55'23"W), Lake Forest Open Lands' Middlefork Savanna (42°15'27"N 87°52'39"W), Melody Pond (42°14'41"N 87°52'21"W), Captain Daniel Wright Forest Preserve (42°13'17"N 87°55'11"W), and Shooting Star Savanna (42°15'05"N 87°49'39"W). All sites were within Lake County, Illinois

Study Sites

Study site locations were scouted in June of 2023, and were selected on the basis that periodical cicadas were present in the soil at these locations. Melody Pond and Middlefork Savanna are restored prairie and oak savanna respectively, Shooting Star Savanna is restored prairie that borders a wooded glacial ravine, Captain Daniel Wright Forest Preserve and Old School Forest Preserve are deciduous forest.

Resource Baits

For each transect, we prepared 100 15 ml centrifuge vials which would be placed in 2 50-m transects for each location's day of sampling. The vials in a transect were placed 1 m apart, and the two transects were laid out approximately 10 m apart. We filled the vials with one of 5 different nutrients: 7 ml of 5% salt (Morton brand sea salt) solution, 20% sugar (Domino brand) solution, extra virgin olive oil, 20% protein (Glutamine solution),or distilled water. Distilled water was used as the solvent for the protein, salt, and sugar vials. After the vials had been filled, half of a cotton ball was inserted into each vial such that it was saturated with the nutrient resource. The transects were laid out around 10 AM and retrieved at 12 PM when one site was sampled in a day, or at 10 AM – 12PM and 1:30 PM – 3:30 PM. Sampling occurred once per week per site, for 10 weeks. The stage of the periodical cicada emergence was documented each day of sampling. Pre-emergence was characterized as the stage when cicadas had not emerged from the soil, and mid-emergence was characterized as the stage when cicadas were emerging from the soil, calling, and reproducing. Post-emergence was the stage when the periodical cicadas' lifespans were complete, and there was mass mortality of the adults. Pre-emergence was a time period of 1 week (within May 21 – May 27 2024), mid-emergence was a time period of 4 weeks (within June 3 – June 27 2024), and post-emergence was a time period of 5 weeks (within July 8 – August 14 2024). For each sample period vials were left uncapped for 2 hours before being picked up and recapped. Vials with ants inside were placed in a freezer for approximately 15 minutes before the ants were transferred to ethanol for future identification.

Foraging Rate Transects

To perform foraging rate sampling, we prepared 15 ceramic tiles, each with 10 dead Drosophila fruit flies set on top. The tiles were placed in 2 transects of 45 m in length with 3 m between individual tiles. Transects were separated by approximately 10 mat each site, and the same transect arrangement was used across all sites. The tiles were observed for 1 hour during a sampling period, which occurred from approximately 10 – 11 am. We used three different measures of foraging activity. 1) We recorded the first timestep an ant was observed on a tile, to estimate the mean (+/- SE) time it takes for ants to discover the foraging baits. 2) We calculated the mean (+/- SE) proportion of flies absent from the foraging tiles at the end of the observation period. 3) We estimated the mean (+/- SE) rate at which flies were removed from bait tiles, after ants discovered the tiles as per the previously described metric. Any ants present on the tiles at time of observation were identified by eye to genus level. No ants were collected, so as not to interfere with their behavior during the observation period. The timestep in which an ant was first observed, and the genus of that ant was recorded for each tile, as well as the total number of observed ants of any genus on all tiles over the course of the observation period. The first observed ant on a tile was considered the discoverer of the resource. Between sampling, the tiles were rinsed and cleaned with water to remove dirt and any residual pheromone trails, and any remaining flies were dumped off the tiles after each observation period was completed. Sampling followed the same schedule as the nutrient vial sampling and was performed simultaneously, though separated from the nutrient transects by a distance of a minimum of 5 meters.

Estimated Cicada Density

A 0.41 m diameter hula hoop was used as a standard area of measurement to estimate the density of cicada carcasses during the periodical cicada emergence from June 18, 2024 to June 27, 2024, with each site being sampled twice over two weeks. The hoops would be thrown at random in the study site, and the number of whole dead cicadas were counted when found within the area of the hula hoop. A minimum of 10 replications were performed at each study site once per week. The area within the hoop was 0.53 m^2, and data was standardized to 1 m^2 during data analysis.

Identification and Categorization of Ants

Ants captured in the resource baits were identified to genus using the online Pictorial Key to the Ant Genera of Illinois arranged by N.C. Wilkins and S. B. Menke. Ants were then identified to species level using A Field Guide to the Ants of New England (Ellison et al. 2012), The Ants of North America (Creighton 1950), The Ants of Ohio (Coovert 2005), and Ants (Formicidae)of The Southern United States (MacGown 2024).

Data Analysis

All ants collected from resource vials and observed in foraging transects were categorized into one of three size classes: large, medium, and small based on their body size relative to each other. Aphaenogaster, Formica, and Camponotus were classified as large ants; Myrmica, Prenolepis, and Crematogaster were classified as medium ants; Tapinoma, Brachymyrmex, and Temnothorax were classified as small ants. Ant foraging at nutrients was analyzed using both incidence and recruitment. Incidence was defined as the presence of one or more ants of a given species in any single vial and, and recruitment presence of three or more ants of the same given species in any single vial. Recruitment data was used for site-based recruitment activity, and for nutrient preference data, as recruitment demonstrates what resources are in high demand by ant colonies. Incidence data was used for analyzing nutrient use by body size as the recruitment dataset had an abundance of zero-values, and using incidence ensured all ant activity across the different size classes was recorded.

A Two-Way ANOVA on sample site and emergence status was used to analyze the recruitment data on all resource types, and all possible pair-wise comparisons were made using Tukey's multiple comparisons procedure. Additionally, a Two-Way ANOVA on nutrient and emergence status was used to analyze the recruitment data from all sites, with the same Tukey's multiple comparisions procedure used for all pair-wise comparisons of this nutrient preference data. Two-Way ANOVA tests were also used to analyze the incidence of ant size classes observed in all nutrient baits and emergence status, combined across all sites with all possible pairwise comparisons made using Tukey's multiple comparisons procedure. Two-Way ANOVAs were also used to analyze the effect of site and emergence status on three measurements of ant foraging for fruit flies; 1) time taken for ants to discover a tile, 2) proportion of flies taken from tiles, and 3) rate at which flies were removed from tiles. Ant foraging patterns by body size was analyzed using Two-Way ANOVAs with Tukey's multiple comparison procedure was used to determine patterns in 1) discovery of tiles, and 2) frequency observed on tiles across size class and emergence status used. The day's air temperature during foraging observation was used to calculate the residual of each of the sampling metrics from temperature, to remove any possible effect temperature may have on the foraging rates of the ants. Additionally, the abundance of dead periodical cicada bodies was analyzed across all field sites using a One-Way ANOVA with Tukey's multiple comparison procedure. All statistical analyses were performed in JMP (Version 17.2).

Results

Nutrient Preference

We found that sugar baits had significantly greater recruitment than all other nutrient types, with a mean (+/- SE) of 4.45 sugar vials recruited per 100 vials, compared to a range of 0.05 – 0.85 mean (+/- SE) vial recruitment for other recruited nutrient vials mid-emergence. There was approximately a 5-fold difference between the recruitment at sugar vials and non-sugar vials. There was a non-significant decrease in the mean (+/- SE) resource vial recruitment post-emergence, with 4.24 sugar vials recruited per 100 vials, and a range of 0 – 0.28 non-sugar resource vials recruited (Fig. 1). [Two-Way Analysis of Variance (ANOVA): $F_{4,249}$=50.9491, P< 0.0001] (Fig. 1). There was no effect of emergence on recruitment to the baits [Two-Way ANOVA: $F_{2,249}$=0.0971, P = 0.90747] or an interaction between emergence and nutrient type [Two-Way ANOVA: $F_{8,249}$= 0.3389, P = 0.95016] (Fig. 1).

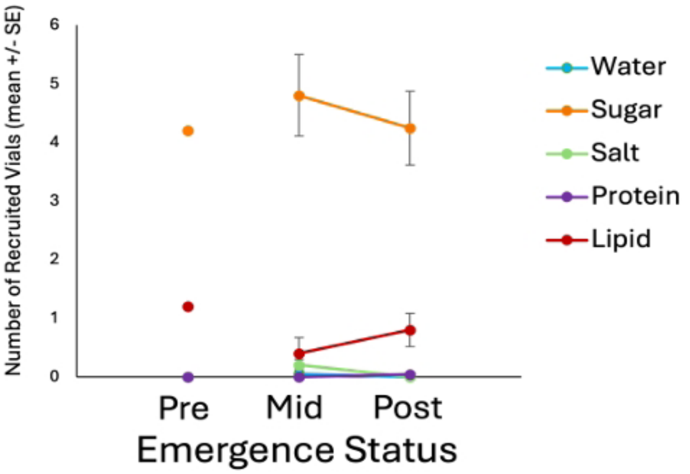


Figure 1: Mean (+/- SE) recruitment to nutrient baits (3 or more ants/bait vial), across all five sample sites for all five nutrients before, during, and after the periodical cicada emergence.

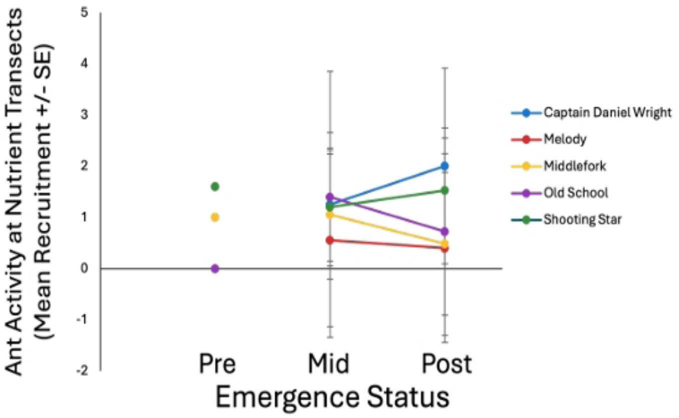


Figure 2: Mean (+/- SE) recruitment of ants (3 or more ants/bait vial) per 100 vial transect at each sample site before, during, and after the periodical cicada emergence.

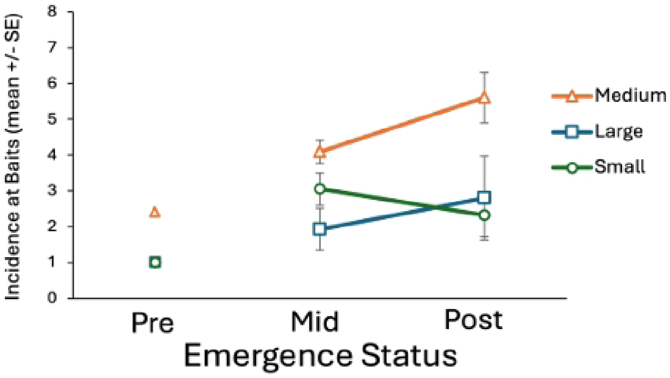


Figure 3: Mean (+/- SE) incidence of ants (1 or more ants/bait vial) within any of the three size classes observed in nutrient baits across all nutrient transects before, during , and after the periodical cicada emergence.

When looking at overall nutrient use, we found that there was a significant effect of site on the mean incidence of ants at all nutrient vials at the sample sites [Two-Way ANOVA: $F_{4,44}$ =6.6938 P = 0.0004] (Fig. 2). Captain Daniel Wright's mean recruitment was found to be 7.2

out of 100 vials, with Shooting Star's mean recruitment at 5.7 out of 100 vials, Old School recruitment at 4.7 out of 100 vials, and Melody Pond mean (+/- SE) recruitment at 3.2 out of 100 vials. Melody Pond showed the least mean (+/-SE) recruitment, with 1.7 out of 100 vials recruited to (Fig. 2). Captain Daniel Wright's mean (+/- SE) recruitment activity was approximately 4.2 times greater than that of Melody Pond, and 1.2 times greater than the recruitment at Shooting Star. We found there was no significant effect of emergence on the mean (+/- SE) incidence of ants at nutrient transects [Two-Way ANOVA: $F_{1,44}$ = 0.1709 P = 0.6819] (Fig. 2). We additionally found no significant interaction between site and emergence [Two-Way ANOVA: $F_{4,44}$ F =2.3005 P = 0.0781] (Fig. 2).

Medium-sized ant incidences were found to be significantly more common in nutrient transects than small and large-bodied ants [Two-Way ANOVA: $F_{2,134}$= 8.4616, P = 0.0035] (Fig. 3). The mean (+/- SE) incidence of medium sized ants was 4.09 incidences per two transects mid emergence, nearly twice the mean (+/- SE) incidence of large ants per transect (1.93) at that same stage of the cicada emergence. The mean (+/- SE) incidence of small ants was approximately 1.5 times that of the large ants, and 0.75 times that of the medium-sized ants, showing a mean (+/- SE) of 3.04 small ant incidences per two transects. There was a non-significant increase in mean (+/- SE) incidence for medium and large ants, with post-emergence with an incidence of 2.8 and 5.6 ants per 100 vials respectively(Fig. 3). Small ants decreased in incidence, post-emergence with a mean (+/- SE) incidence of 2.32 ants per transect (Fig. 3). There was no effect of emergence [Two-Way ANOVA: $F_{1,134}$= 1.5363, P = 0.21742] or interaction between emergence and body size [Two-Way ANOVA: $F_{2,134}$ = 0.8784, P = 0.4179] (Fig. 3).

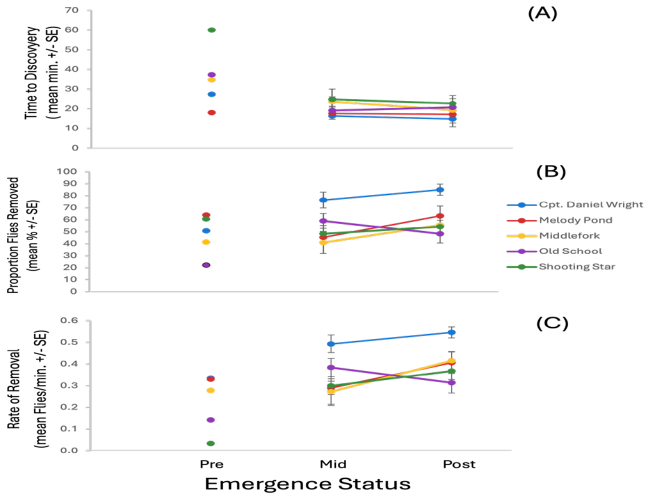
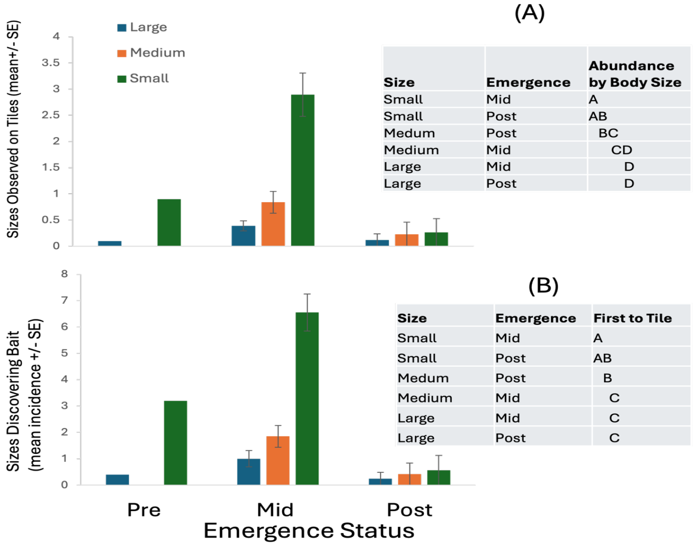


Figure 4: Foraging responses recorded across for each study site. (A) Mean (+/- 1 SE) time in minutes before first ant is recorded at a transect tile (B) Mean (+/- 1 SE) proportion of flies absent from tiles after observation period is ended, calculated as a percentage our of 100. (C) Mean (+/- 1 SE) rate of flies removed from transect tiles in flies/minute, after timestep when first ant is observed on a given tile.

Foraging Rates

The time until discovery of fruit fly baits by ants was not significantly affected by emergence status [Two-Way ANOVA: $F_{1,41}$ = 0.7921, P= 0.1094]. or by site [Two-Way ANOVA: $F_{4,41}$ F = 3.2606, P = 0.0237] (Fig 4A). The proportion of flies removed from baits was significantly greater post-emergence than during the cicada emergence across all sites [Two-Way ANOVA: $F_{1,41}$ = 56.549, P = 0.00313], with a significantly greater proportion of flies removed at Captain Daniel Wright compared to other sites [Two-Way ANOVA: $F_{4,41}$ = 6.073, P=0.00079]. The mean (+/- SE) proportion of fly removal at Captain Daniel Wright was 76.5% mid- emergence and 85% post- mergence, with the other sites' removal proportions ranging from 41 – 59% mid-emergence and 48 – 63% post-emergence (Fig. 4B). We found there was no significant interaction between site and emergence status[Two-Way ANOVA: $F_{1,41}$ = 0.3371, P = 0.65032] (Fig. 4B). The rates of fly removal for all sample sites were also greater in post- emergence sample periods than mid-emergence sample periods [Two-Way ANOVA: $F_{1,41}$ = 9.7985, P = 0.0037], with a significant difference between samples from Captain Daniel Wright and all other sites [Two-Way ANOVA: $F_{4,41}$ = 4.7194, P = 0.0042], and no interaction [Two-Way ANOVA: $F_{4,41}$ = 0.3147, P = 0.8660] (Fig 4C). Captain Daniel Wright's mean (+/- SE) removal rate was 0.49 flies/minute mid-emergence and 0.55 flies/minute post-emergence. Fly removal rates at the other 4 sites ranged between 0.27–0.38 flies per minute mid-emergence and 0.31–0.41 flies per minute post-emergence (Fig. 4C). The mean (+/- SE) removal rates at Captain Daniel Wright were approximately 1.8 - 1.3 times faster than the other 4 sample sites both at mid-emergence and post-emergence (Fig. 4C).



Size	Emergence	Abundance by Body Size
Small	Mid	A
Small	Post	AB
Medum	Post	BC
Medium	Mid	CD
Large	Mid	D
Large	Post	D

Size	Emergence	First to Tile
Small	Mid	A
Small	Post	AB
Medum	Post	B
Medium	Mid	C
Large	Mid	C
Large	Post	C

Figure 5: Diversity of foragers at fly bait transects by the three body size categories quantified by the proportion of bait tiles occupied by ants (A) Mean (+/- SE) body size of ants occurring across all transects and sites over the course of the periodical cicada emergence. (B) The mean (+/- SE) body size of the first ants observed on the tiles, and how many ants of each size were observed discovering the tiles, again across the emergence.

Forager Dominance

Body size had a significant effect on the abundance of ants at the foraging baits, with small-bodied ants more common than medium-bodied ants, which were more common than large-bodied ants [Two-Way ANOVA: $F_{2,134}$ 34.2180 P <0.0001] (Fig. 5A). The mean (+/- SE) proportion of tiles in a transect with small-bodied ants was 0.16, or 16%; twice as much as the medium-bodied ants that were present on 0.08 or 8% of tiles (Fig. 5A). Large-bodied ants were present in a proportion of 0.03, or 3% of tiles, less than half of the values we observed for medium-bodied ants, and less than a quarter of the values we observed for small-bodied ants (Fig. 5A). Emergence status had no significant effect on ants' observed body sizes [Two-Way ANOVA: $F_{1,134}$ = 0.0088 P = 0.9256] (Fig. 5A). However, there was a significant interaction between ant body size and emergence status in determining ant occurrence at bait tiles [Two-Way ANOVA: $F_{2, 134}$ = 0.0088, P = 0.00286], with small ants during the mid-emergence being more common than medium ants post-emergence, both of which were more common than large ants during both emergence period (Fig. 5A). Small ants mid-emergence were present on 19.6% of tiles in a transect, and 13.5% of tiles in a transect post-emergence (Fig. 5A). The observations of small ants decreased by 1.5 times. The proportion of medium ants present on tiles mid-emergence was 5.6%, and in post-emergence they were present on 11% of tiles in a transect (Fig. 5A). This was approximately a 4-fold increase across the emergence. Large ants were present on 2.6% of tiles in a transect mid-emergence and 4.0% of tiles post-emergence (Fig. 5A). Post-emergence observations increased by 1.5 times for large-bodied ants. With regard to discovery of bait tiles, body size had a significant effect on the ants discovering the tiles [$F_{2,134}$ = 47.8361 P <0.0001] (Fig. 5B). Small-bodied ants discovered a mean (+/- SE) of 5.6 tiles, medium-bodied ants discovered a mean (+/-SE) of 3.04 tiles, and large-bodied ants discovered a mean (+/-SE) of 1.22 tiles (Fig. 5B). The discovery rate by small-bodied ants was 4.6 times greater than large-bodied ants (Fig. 5B). Emergence status alone had no effect on the discovery of tiles [Two-Way ANOVA: $F_{1,134}$= 0.5947 P = 0.4420](Fig. 5B). Additionally, we observed a significant interaction between the body size of the first ants to encounter the baits and the stage of the periodical cicada emergence [Two-Way ANOVA: $F_{2, 134}$ =8.4244 P = 0.00036] (Fig. 5B). Small ants at mid- and post-emergence timepoints discovered tiles significantly more frequently than medium ants mid-emergence and large-bodied ants at both emergence timepoints (Fig. 5B). Small ants post-emergence and medium ants post-emergence were not significantly distinct from each other, but were significantly more common as the first ants on the tile than medium ants at mid-emergence and large ants at both emergence timepoints [Two-Way ANOVA: $F_{2, 134}$ =8.4244 P = 0.00036] (Fig. 5B). Small-bodied ants discovered a mean (+/-SE) of 6.6 tiles mid-emergence, and 4.9 tiles post-emergence, while medium bodied ants discovered a mean (+/- SE) of 1.9 tiles mid-emergence and 4 tiles post-emergence. Large-bodied ants discovered a mean (+/-SE) of 1 tile mid-emergence and 1.4 tiles post-emergence (Fig. 5B).

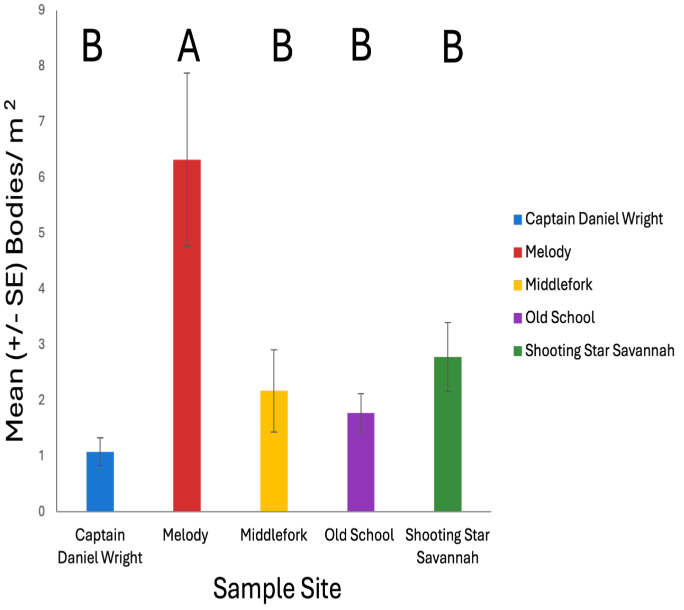


Figure 6: Mean (+/-) density of periodical cicada carcasses per square meter, from all sample sites. Sites not labeled with the same letter are significantly different from each other.

Periodical Cicada Density

There was a significantly higher density of bodies at the Melody Pond site than all others [One-Way ANOVA: $F_{4,102}$= 6.1703 P < 0.0002] (Fig. 6). Melody Pond had a mean (+/-SE) density of 6.32 bodies/ m^2, while the other sites' mean (+/-SE) body density ranged between 2.78 bodies/m^2 at Shooting Star Savannah, and 1.078 bodies/m^2 at Captain Daniel Wright.

Discussion

From the foraging and nutrient requirement data compiled here, it can be understood that under the periodical cicada emergence's resource pulse conditions, ants exhibit a significant preference for carbohydrates over other macronutrients. Additionally, the amount of alternate prey taken by ants during the periodical cicada emergence was significantly lower than the amount of prey taken after the periodical cicada emergence. Coupled with that, the rate at which prey was taken by ants was greater after the emergence. We also found the primary size classes of ants observed locating and lingering on the prey baits were small and medium. These responses are invaluable to characterize the influence periodical cicada emergences have on ant communities; ants' diverse effects on their environment are important to nutrient cycling and plant reproduction, and impact the predation rates of other arthropods, making any change in these functions important to understand when studying the ecology of resource pulses.

To quantify the nutrient requirements of ants, we recorded the recruitment of ants at nutrient baits before, during, and after the 2024 periodical cicada emergence. We set out nutrient transects of carbohydrates, lipids, proteins, salt, and water, and calculated the mean recruitment of ants to each different nutrients and found significantly more recruitment to the carbohydrate baits than to all other resources during and after the periodical cicada emergence. A proportional recruitment to protein was not observed, though ants are understood require relatively equivalent amounts of both nutrient (Dussutour & Simpson 2008; Cook et al. 2011). This response could suggest that carbohydrates were prioritized to balance the intake of other nutrients that could be supplied by predation and scavenging of periodical cicada carcasses. This data is in line with possible compensatory nutritional balancing response to the periodical cicada emergence. Subsequent years of sampling will further determine whether the demand of carbohydrates within the emergence year matches demand for carbohydrates and other nutrients in a non-emergence year. Whether this response is consistent across different seasons cannot be determined from only one summer of sampling, as sampling during non-cicada seasons is necessary to support or reject this. Additionally, we found significantly more ant activity in the nutrient vials laid out at Captain Daniel Wright than all other sites, which could suggest that these ants were not receiving as much nutritional input as other sites. While a One-Way ANOVA found that it was not significantly different from Shooting Star, Middlefork, and Old School sites, Captain Daniel Wright's mean was still the least of all sites observed. Melody's nutrient vial recruitment was significantly less than other sites tested, and it had a significantly greater density of cicada bodies than all other sites tested, which further lends credence to a possible inverse relationship between cicada abundance and demand for food and nutrients. This could be evidence of a possible satiating effect of the emergence on these ant communities

In addition to nutritional requirements of ants, we intended to quantify foraging activity as ants respond to the periodical cicada emergence. We expected that foraging activity would be decreased on typical food sources, as the periodical cicadas would cause a satiation effect due to their abundance for ant foragers, reflecting other responses of predators during resource pulses. Fruit flies were used to represent non-cicada prey for the foragers to encounter. With regards to foraging rate, there was an increase in foraging rate and proportion of bait removed after the cicada emergence, compared to removal of baits during the periodical cicada emergence. This further suggests foragers could be experiencing satiation by cicada prey during the emergence: foragers may be locating cicadas and receiving much of their nutrition from them instead of the flies. This phenomenon has been observed in other organisms affected by resource pulses, such as birds reducing their predation on caterpillars (Getman-Pickering et al. 2023), or the reduction in seed predation during oak masting events (Szymkowiak et al. 2024). The time it took for ants to discover fly baits was not affected by the emergence, suggesting the number of foragers present in the environment was not affected directly by the emergence, which is contrary to proportional responses to food availability that have been observed elsewhere (Lixiang et al. 2014). Ants found on foraging transects were most commonly small-bodied, and these also tended to be the first ants to locate the tiles. The presence of an interaction between body size and emergence mean that it is not possible to definitely determine which factor is driving the ants' responses observed in this study. Some possible interpretations of these observed data are that small ants likely fill the opportunistic foraging role, as they are able to locate resources before other ants, though their abundance across tiles over whole observation periods suggests they are not being driven off the tiles by extirpators, which would be an expected interspecific competitive dynamic (Fellers 1989). We did not record a significant effect of emergence alone on the responses of ants, though the proportion of small-bodied ants was smaller post-emergence than mid-emergence, while medium- and large-bodied ants showed an inverse response. It is possible that large and medium ants may be utilizing the fruit fly bait tiles more in the absence of periodical cicadas, and beginning to dominate the tiles. This pattern could suggest a change in the body size of dominant foraging ants could occur in response to resource pulses, with more dominant ants exerting less competitive pressure on more subordinate ants for non-pulsed resources.

The abundance of cicada resources may make prey more difficult to completely control during the periodical cicada emergence, and lead to less interspecific competitive pressure between ant body size classes. Such a dynamic of dominant ants defending limited resources more successfully than more abundant ones occurs in ant communities utilizing plants' nectaries and the honeydew of tended hemipterans (Fagundes et al. 2016). More competitively dominant ant species can more successfully exclude other species from limited resources, in this case, hemipterans that are less abundant than extrafloral nectaries (Fagundes et al. 2016). However, with more abundant nectaries, it is more difficult to completely exclude other ants from them. It is possible this behavioral stratification could occur in response to the periodical cicada emergence wherein the abundance of cicadas in the environment means behaviorally dominant ants cannot exclude other ants from the fruit fly resource, due to the abundance of other food resources presented by the cicadas. The presence of interaction terms means further observations in non-cicada years are required to fully characterize the competitive dynamics of ants at the foraging baits, a similar conclusion to the nutrient requirement data.

Based on one season of sampling, we found that the emergence of periodical cicada (Magicicada spp.) did have significant impacts on the foraging and nutrient-seeking behaviors of ant communities in Lake County, Illinois. We found some evidence supporting predator satiation effects on ants, and possible changes in interspecific competitive dynamics and nutritional requirements of ants, all in response to the periodical cicada emergence. This lays the groundwork for future study of ant responses to periodical cicada emergences which is relatively understudied at present. However, there is still more work to be done, to build more robust datasets, as one season of sampling has only limited replication and analytical power. Additional years of sampling can offer data for non-cicada year behaviors, with multiple year replication allowing for separation from any lingering effects of the periodical cicada emergence that may not have been tested for in this study. There is much to still understand about the effects of periodical cicada resource pulses on ant communities, and the data compiled here will inform future investigations and build up the body of literature on ant-specific responses to resource pulses.

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