



Biological rhythms and task allocation in ant colonies

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Task allocation in ant colonies, mediated by social interactions, regulates which individuals perform which task and when they are active, in response to the current situation. Many tasks are performed in a daily temporal pattern. An ant's biological clock depends on the patterns of gene expression that are regulated using a negative feedback loop which is synchronized to the earth's rotation by external cues. An individual's biological clock can shift in response to social cues, and this plasticity contributes to task switching. Daily rhythms in individual ant behavior combine via interactions within and across task groups to adjust the collective behavior of colonies. Further work is needed to elucidate how the social cues, which lead to task switching, influence the molecular mechanisms that generate clock outputs associated with each task and to investigate the evolution of temporal patterns in task allocation in relation to ecological factors.

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Introduction

In social insect colonies, workers perform most of the colony's tasks. This is organized without any central control. Task allocation is the process that determines which individual performs which task and which individuals are actively performing each task at a given moment [1,2]. Task allocation allows the colony to adjust to changing conditions outside the nest, such as weather and food availability, and inside it, such as the amount of brood and demand for nest maintenance [3].

Task allocation arises from interactions among workers and their surroundings. A worker's location in the nest

influences which other workers it is likely to encounter [4–6]. A common pattern in ants and honeybees is that younger workers care for the brood inside the nest, while older ones leave the nest to forage. Both location inside the nest and the worker's age tend to be associated with the task an ant performs [7–9].

The daily temporal pattern of tasks performed by a colony, which depends on the circadian clocks of individual ants, influences which individuals interact and where they interact. The circadian or near 24-hour rhythms in physiology and behavior allow organisms to adapt to the predictable environmental fluctuations that are caused by the earth's rotation around its axis [10–13].

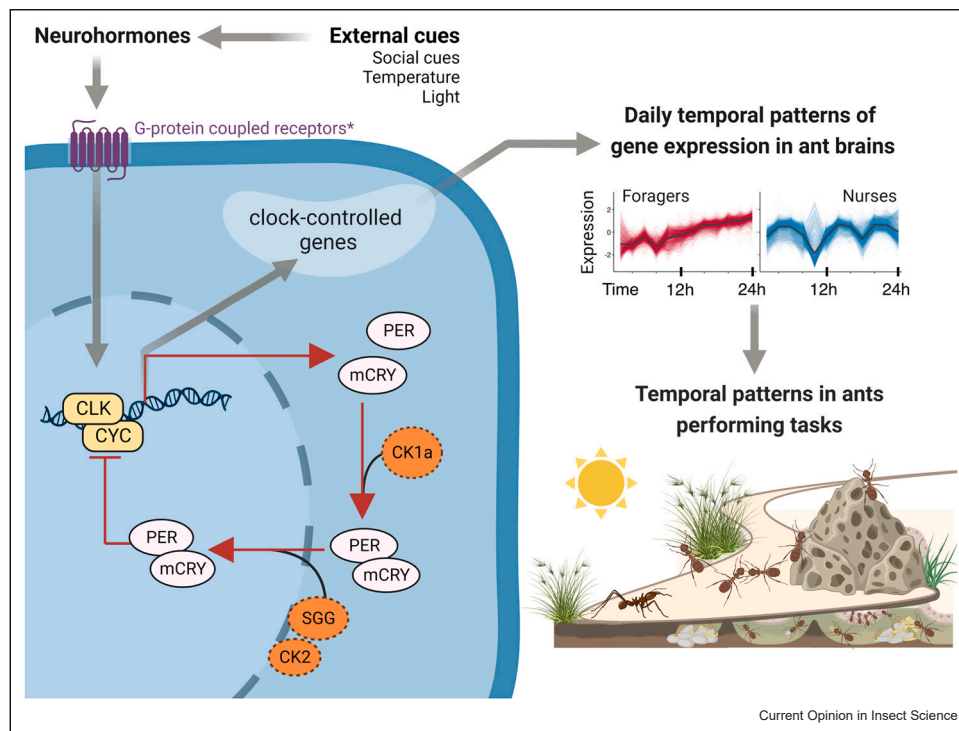
The circadian clock is the molecular machinery that produces these daily rhythms and is found in animals from insects to mammals (reviewed in [14,15]; Figure 1). Circadian entrainment is the synchronization of the phase and periodicity of this internal machinery, driving physiological and behavioral rhythms, to external cues that show predictable 24-hour oscillations. An organism's clock can synchronize to rhythms in biotic cues such as food availability, and abiotic cues, such as light and temperature.

Social cues are a strong entrainment signal for the circadian clocks of social insects. In honeybees, when newly eclosed workers were presented with social cues, either colony odor or substrate vibrations, and conflicting light-dark cycles, they synchronized their endogenous clocks to the social cues [16,17].

In ants, social contacts are sufficient to synchronize the endogenous clock that drives daily rhythms in the locomotory patterns of workers [18]. In laboratory experiments with the carpenter ant *Camponotus paria*, workers housed in constant darkness were visited by conspecifics kept under oscillating light-dark cycles. The host ants kept in the dark synchronized their circadian clocks to the light-dark cycles experienced only by the visiting ants [18].

The social regulation of the ant's circadian clock is probably mediated by olfactory and mechanosensory pathways that affect neurotransmitter activity. Dopamine, a biogenic amine, functions as a neurohormone and plays a role in synchronizing the insect clock through G-protein coupled receptors or GPCRs (Figure 1 [19]). The same receptor class is linked to the behavioral plasticity that leads ants to switch tasks in response to current colony needs (reviewed in [20]).

Figure 1



Biological clocks of ants and temporal patterns in task allocation. The figure summarizes how biological clocks regulate the temporal pattern of activity in ant colonies. The gray arrows show steps in the process. The red arrows trace the hypothesized TTFL in gene expression. The TTFL is a negative feedback loop involving the protein complex CLK-CYC shown in yellow that activates gene expression of several genes; the protein products of some can repress the activity of CLK-CYC. The repressor proteins PER and mCRY ants are shown in white. The nuclear re-entry of PER and mCRY depends on the activity of kinases, some of which are shown here in orange (CK1a, SGG, CK2). * labels a G-protein coupled receptor, shown in purple, located on the cell membrane; dotted lines represent the nuclear membrane. The figure in the top right shows the daily temporal patterns in the expression of several hundred genes, including period, that show a 24-hour rhythm in the brains of *Camponotus floridanus* foragers (in red), and an 8-hour rhythm in nurses (in blue). The y-axis shows standardized gene expression and the x-axis time, in 2-hour increments, with 0–12 hours as the light phase and 12–24 hours as the dark phase of the day.

Figure 1 summarizes our hypothesis for how the biological clock of ants might regulate the temporal patterns of activity. The cellular clock of ants can be synchronized or entrained by rhythmic, predictable changes in their local environment, including social interactions and abiotic cues. Our knowledge of the molecular underpinnings of the ant clock is limited [21–24] in contrast with our detailed understanding of the molecular biology circadian clocks in two model systems: the fruit fly *Drosophila melanogaster* and the mouse *Mus musculus*. The studies of flies and mice have shown that the cellular clocks of both animals have the same architecture, a negative feedback loop, although some of the proteins that make up the core loop differ among species (reviewed in [14]).

The cellular feedback loop, in the absence of external rhythmic cues, takes nearly 24 hours to complete one cycle. However, the cellular clock can entrain or synchronize the periodicity and phase of its internal rhythm by external cues that repeat every 24 hours, such as day

length and food availability. In flies, the loop includes the heterodimer activator complex CLOCK-CYCLE (CLK-CYC or BMAL1-CLOCK in mammals) that rhythmically binds to the E-box site in the promoter region of several genes [14]. This activates the transcription of those genes, including the repressor gene *period*, as well as several others that regulate daily temporal patterns in physiology and behavior [14] (Figure 1). Once translated, PER heterodimerizes with TIMELESS (CRYPTOCHROME in mammals) and translocates into the nucleus to inhibit the CLK-CYC activator complex, thereby repressing *period* expression [25,26]. This transcription-translation feedback loop (TTFL) is facilitated by kinases; the casein kinases CK1 and CK2, along with the glycogen synthase kinase SHAGGY (SGG), are required for the rhythmic nuclear re-entry of *period* [27] (Figure 1). The daily temporal patterns of *period* expression show 24-hour oscillations in the brains of several animals, including foraging bees [28] and ants [21,22].

The circadian clocks of ants are similar to those of *Drosophila* in their location in the brain, and in the patterns of neuronal innervation that the clock uses to receive input and drive rhythmic behavior [29]. However, the circadian clocks of social insects and fruit flies differ. Unlike *Drosophila*, ants and honeybees do not possess the clock gene *timeless* that makes up the negative arm of the feedback loop. Instead, ants and honeybees have a mammalian-like *cryptochrome* (mCRY) gene (Figure 1; [22,30]).

Individuals vary in the phase, amplitude, and period length with which clock-controlled processes oscillate. Workers within a colony of the carpenter ant, *C. rufipes* vary greatly in the periodicity with which their movement-rest or locomotory patterns oscillate, including ultradian (period < 20 hours), circadian (between 20 hours and 28 hours), and to a lesser degree infradian (> 28 hours) oscillations [31]. The individual variation and within-individual plasticity in the phase of the clock are well studied in humans. For example, the phase or preferred timing of sleep-wake cycles is a clock-controlled process that varies widely across individuals but shows consistent changes with age; teenagers wake up relatively late in the day, and elderly people relatively early.

Here we outline past research, summarized in Table 1, that examines how the plasticity of the ant clock is linked to task allocation. We consider the following topics:

- Circadian rhythm and environmental cues in brood care inside the nest.
- Circadian rhythms in tasks outside the nest.
- Plasticity of daily rhythms in foraging.
- Molecular links between the plasticity of the circadian clock and task allocation.

Circadian rhythm and environmental cues in brood care inside the nest

The temporal patterns produced by an ant's biological clock change in response to social cues. In the ant *Diacamma* sp. (putative species *indicum*), isolated nurses show circadian rhythms in locomotion [55]. However, *Diacamma* nurses kept with larvae and eggs, though not those kept with pupae, showed a weaker circadian rhythm in locomotion; the strength of circadian rhythm was measured as the power of fitting a circadian waveform onto the movement patterns of the ants. In a group setting, the presence of circadian locomotion in a

Table 1

Studies in ants exploring the links between biological rhythms and task allocation.

Topic explored	Ant species studied	Where?	Reference
The circadian rhythm and environmental cues in brood care	<i>Camponotus mus</i> , <i>C. rufipes</i>	Lab	[32-34]
	<i>Pogonomyrmex salinus</i>	Lab, Field	[35]
	<i>Solenopsis invicta</i>	Field	[36]
Daily rhythms in tasks outside the nest	<i>Linepithema humile</i>	Field	[37]
	<i>Formica subclucida</i> , <i>F. fossiceps</i> , <i>F. sanguinea subnuda</i>	Lab	[38]
	<i>Atta cephalotes</i>	Field	[39]
	<i>Acromyrmex lobicornis</i> , <i>A. striatus</i>	Field	[40]
	<i>Pogonomyrmex barbatus</i> , <i>P. californicus</i>	Field	[41]
	<i>P. rugosus</i> , <i>P. desertorum</i> , <i>P. maricopa</i>		
	<i>Pogonomyrmex montanus</i> , <i>P. subnitidus</i> , <i>P. rugosus</i>	Field	[42]
	<i>Solenopsis invicta</i>	Lab	[43]
	<i>Camponotus floridanus</i>	Lab	[23.]
	<i>Camponotus rufipes</i>	Lab	[31]
	<i>Diacamma</i> sp.	Field	[44]
	<i>Dinoponera quadriceps</i>	Field	[45,46]
	<i>Monomorium orientale</i>	Lab	[47]
<i>Myrmica punctiventris</i> , <i>M. emeryana</i> , <i>Prenolopis impairs</i> , <i>Formica subsericea</i> , <i>Aphaenogaster rudis</i> , <i>Tapinoma sessile</i> , <i>Lasius alienus</i> , <i>Camponotus ferrugineus</i> , <i>Leptothorax curvispinosus</i>	Field	[48]	
The plasticity of daily rhythms in foraging	<i>Pogonomyrmex occidentalis</i>	Field	[49,50]
	<i>Pogonomyrmex barbatus</i>	Field	[51]
	<i>Pogonomyrmex californicus</i> , <i>P. rugosus</i> , <i>Veromessor pergandei</i>	Field	[52]
	<i>Dinoponera quadriceps</i>	Field	[45]
	<i>Formica pratensis</i> , <i>F. polyctena</i>	Field	[53]
Molecular links between the plasticity of the circadian clock and task allocation	<i>Pogonomyrmex occidentalis</i>	Lab	[21]
	<i>Solenopsis invicta</i>	Lab	[43]
	<i>Pogonomyrmex barbatus</i>	Lab	[24]
	<i>Camponotus floridanus</i>	Lab	[23]
	<i>Temnothorax longispinosus</i>	Lab	[54]

Diacamma worker depends on its own age and previous task experience, the age and task experience of the ant it interacts with, and the group size. Fujioka et al. [56] continuously tracked the movement-rest patterns of individual *Diacamma* ants that were housed in groups of up to five ants. Interactions between young, previously brood tending and old, previously foraging workers of *Diacamma* reduced circadian rhythm in patterns of movement and rest in both age groups, but young workers retained their rhythms if interacting only with young workers. In a subsequent study, Fujioka et al. [57] tracked larger groups (88–194 ants) of *Diacamma* ants and found that both young and old workers did not show 24-hour rhythms in locomotion, indicating that colony size influences the temporal patterns of locomotion.

Task performance also shows daily rhythms. In some ant species, nurses regulate the brood's temperature by moving it to higher temperatures during the day and back to lower temperatures later in the day or at night. For example, when laboratory colonies of the carpenter ant *C. mus* [32] are provided with a thermal gradient and oscillating 12:12 hours of light-dark cycles, the nurse workers move brood to around 31°C in the middle of the day (light period), and eight hours later move it back to around 28°C [32]. This daily rhythm of brood translocation in *C. mus* is linked to the development of brain regions in larvae and pupae that are related to sensory processing and learning ability in adult ants [33]. This daily routine of two brood translocations, one at mid-day and another eight hours later, persisted even in constant-light or constant-dark conditions, suggesting that temperature preference in *C. mus* nurses is a clock-controlled process [58]. The brood movement by nurses ceased when the nest surface temperature was adjusted to warmer temperatures by day and cooler temperatures at night, demonstrating that the behavior depends on the circadian rhythms in temperature [34].

Species differ in response to daily rhythms in temperature. Unlike *C. mus*, brood translocation does not occur in *C. rufipes* colonies. However, the nurse ants of *C. rufipes*, like *C. mus*, show a circadian rhythm in thermal sensitivity. The brood movement can be experimentally induced by changing the nest surface temperatures. The temperature thresholds at which nurses move brood changed predictably over a day, at different thresholds for the two species [34]. These differences may be associated with the ecology of each species: *C. rufipes* mostly inhabits sub-tropical and tropical regions, with a narrow range of temperature fluctuations, while *C. mus* is also found in temperate climates that show a broader and harsher range of temperature fluctuations. Field studies, one in the harvester ant *Pogonomyrmex salinus* [35] and the other in the red imported fire ant *Solenopsis invicta* [36], further indicate that the location and timing of brood translocation depend on thermal conditions.

Daily rhythms in outside nest tasks

Ant colonies perform many tasks outside the nest, including foraging, searching and removing refuse. Many studies have demonstrated temporal patterns in exterior tasks (Table 1). Temporal patterns in task performance differ among species that respond to different rhythmic abiotic cues [59]. Species differences in daily foraging patterns can allow species to coexist through temporal partitioning [60]. For example, in an ant community in a temperature woodland, different species partition foraging activity on daily and seasonal scales [48]. Similarly, in a desert habitat, a comparative study of five harvester ant species showed that while in all species, foraging is preceded by a daily peak in midden work and, usually, patrolling [41], all show different temporal patterns in the number of ants actively performing nest maintenance, patrolling, midden work, and foraging outside the nest [41].

Plasticity of daily rhythms in foraging

Colonies within a species vary in their daily temporal patterns of foraging [48,61]. This variation is associated with genetic diversity among workers in the colony. In the western harvester ant *Pogonomyrmex occidentalis*, colonies that began foraging earlier in the day showed greater genetic diversity among workers [49].

Daily rhythms in foraging outside the nest have been observed in many ant genera [41,37–40,42,43,23,44]. Although most studies have focused on the circadian or near 24-hour rhythms in foraging patterns, co-existing circadian, ultradian (< 20 hours), and infradian (> 28 hours) rhythms have been detected in the foraging activity of two red wood ant species, *Formica pratensis* and *F. polyctena*, studied in the field [53].

The daily temporal pattern of foraging is plastic, shifting in response to changing colony needs. For example, in the red harvester ant *P. barbatus*, the daily temporal pattern of foraging activity changes in response to an increased demand for workers in a different task. These changes vary with colony age, which is linked to colony size and reproductive status [51].

The daily temporal pattern of foraging activity also changes with the season. For example, the colonies of *P. occidentalis* that foraged for a short duration in the spring increased the duration of foraging in August. [50]. Seasonal changes in the foraging activity are probably associated with changes in the rhythmic properties, such as phase, amplitude, or periodicity, of the ants' circadian clock. A common method to assess rhythmic state is to characterize the daily rhythms in the expression of core clock genes, such as *period*. In *P. occidentalis* foragers, *period* expression shows circadian oscillation in both fall and spring, but with a different phase [21]. The expression of the *period* gene

shows a dusk peak in spring and a dawn peak in fall, even when kept without oscillating abiotic cues [21].

Seasonal or circannual rhythms in colony foraging behavior have been observed in other desert harvester ant species [52] as well as in tropical species, *Dinoponera quadricaps* [45]. The harvester ants collect seeds that remain on the ground until collected, so there is no circadian rhythm in food availability. However, the dry conditions in the desert, which set the risk of water loss for foraging ants, show 24-hour fluctuations and seasonal changes. By contrast, *D. quadricaps* engages in solitary foraging and hunts live ground-dwelling organisms [62,63]. The temporal patterns of foraging in *D. quadricaps* might be shaped by the temporal patterns in food availability.

Molecular links between plasticity of the circadian clock and task allocation

Daily temporal fluctuations in gene expression inside an ant's brain depend on its task and the temporal patterns in activity associated with that task. In the fire ant *Solenopsis invicta*, colony foraging over 24 hours was correlated with the expression of *foraging* in forager brains [43]. The *foraging* gene is associated with task allocation in honeybees as well [64], suggesting that the role of *foraging* is probably conserved across eusocial *Hymenoptera*.

Task behavior is associated with genome-wide changes over 24 hours in the transcriptome. For example, foragers and nurses differ in the number and identity of genes whose expression shows daily oscillations in the ant brain. Bulk-mRNA sequencing of *C. floridanus* forager and nurse brains showed that foragers' brains had about three times as many genes that showed a 24-hour rhythm in expression as did nurses' brains [23]. Similarly, in honeybees, the set of genes with circadian rhythms was reduced in nurses relative to foragers [65]. Such differences between task groups in gene expression may be regulated by epigenetic processes [54]. The circadian foraging pattern of *Temnothorax longispinosus* is lost when the workers are fed an inhibitor of histone acetyltransferases [54]. Histone acetylation regulates the opening or closing of chromatin and affects the temporal patterns of gene expression.

The temporal patterns of gene expression in foragers' and nurses' brains show some similarities. For example, in the nocturnal species *C. floridanus*, while half of the 24-hour rhythmic genes in nurses' brains were unique, the other half showed similar 24-hour oscillations in both nurse and forager brains, with no difference in phase or amplitude, and a peak activity during rest.

Intriguingly, these *C. floridanus* genes are involved in glycosylphosphatidylinositol-anchor biosynthesis; the same process regulates sleep in insects, fish, and humans [66].

As ants shift tasks, the rhythmic gene expression can shift in periodicity. More than two hundred genes of *C. floridanus*, including the clock genes *period* and *shaggy*, oscillate every 8 hours in the nurses' brains; the same genes show a 24-hour rhythm of expression in foragers' brains [23]. In *P. occidentalis*, like *C. floridanus*, foragers' brains show a 24-hour rhythm in *period* expression but nurses do not [21]. The study with *P. occidentalis* tested only for the presence of near 24-hour rhythms of gene expression in both foragers and nurses; the possibility of shorter ultradian patterns in *period* expression in *P. occidentalis* nurses remains to be investigated. More work is necessary to delineate the underlying mechanism and the role of social cues.

The plasticity of an ant's circadian clock may influence its capacity to switch tasks. The temporal patterns in the expression of such differentially expressed genes (DEGs) over a 24-hour day have been characterized for only one species *C. floridanus*. The task-associated DEGs in *C. floridanus* show a highly synchronized daily fluctuation in their expression levels in foragers' brains but not in nurses [67]. This finding in *C. floridanus* is consistent with the results obtained in *P. barbatus*; the expression of *foraging*, a task-associated DEG, shows circadian oscillations in foragers' brains but not in nurses [24].

Conclusion

The cellular machinery that produces biological rhythms in ants is plastic. The temporal patterns of gene expression, which can shift in periodicity when ants change tasks, seem to depend on the rhythmic properties of the abiotic cues and the social cues associated with a particular task environment. The plasticity of the ant's clock raises interesting questions about the role of biological rhythms in task allocation. We highlight two sets of questions:

1. Circadian rhythms in neurotransmitters: Little is known about the mechanisms that lead social cues to influence the expression of clock-controlled genes in ant brains. Ants show task-associated differences in the expression of biogenic amine receptor genes [68] and in the levels of neurohormone (reviewed in [69]). Several neurotransmitters, especially biogenic amines, also play a role in synchronizing insect clocks [19,20]. This suggests that there may be daily rhythms in the neurotransmitter activity that influence behavior.
2. Colony variation in temporal patterns of activity: Colonies vary in how daily temporal patterns of

activity shift in response to changing conditions. For example, red harvester ant colonies differ consistently in how they regulate daily foraging in response to changing humidity; some *P. barbatus* colonies reduce foraging in dry and hot conditions, sacrificing food intake to conserve the water lost while outside the nest, while other colonies do not [70]. Colonies that forage less when it is hot and dry outside were more likely to have offspring colonies than colonies that did not [71], demonstrating that natural selection can act on how colonies regulate activity. Variation among colonies in activities with important ecological functions may be associated with colony-specific differences in the phase, amplitude, or periodicity with which genes are expressed inside foragers' brains.

The temporal patterns in task performance depend on the rhythmic physiological state of the individual ants performing a task, as well as the patterns of interaction among ants within and between task groups. The rhythmic state of an ant, arising from an ant's internal clock-controlled processes, is plastic and can be influenced by changing colony needs. The plasticity of the biological clock in individual ants influences their capacity to switch tasks, which in turn leads to plasticity in the task performance of the colony.

Data Availability

No data were used for the research described in the article

Declaration of Competing Interest

None.

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