



# The Ecology of Nest Movement in Social Insects

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## Abstract

Social insect colonies are typically mobile entities, moving nests from one location to another throughout the life of a colony. The majority of social insect species—ants, bees, wasps, and termites—have likely adopted the habit of relocating nests periodically. The syndromes of nest relocation include legionary nomadism, unstable nesting, intrinsic nest relocation, and adventurous nest relocation. The emergence of nest movement is a functional response to a broad range of potential selective forces, including colony growth, competition, foraging efficiency, microclimate, nest deterioration, nest quality, parasitism, predation, and seasonality. Considering the great taxonomic and geographic distribution of nest movements, assumptions regarding the nesting biology of social insects should be reevaluated, including our understanding of population genetics, life-history evolution, and the role of competition in structuring communities.

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**Nest:** the physical structure inhabited by a colony

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## INTRODUCTION

It is a popular misconception that social insect colonies are sessile entities. The bulk of social insects do not spend their lives anchored to a single nest location. Social insects are itinerantly unsettled critters like much of their animal brethren, in which individuals may occupy a variety of domiciles throughout their lifetimes. In 1990, Hölldobler & Wilson (32) argued in their field-defining tome on ant biology that the prevalence of nest movements of ant colonies was underestimated. Since that time, investigators have accidentally and by design learned much about the systematic movements of colonies of ants and other social insects.

Making a nest is hard work. Both time and energy are invested into the construction or excavation of a nest. Why would an ant colony emigrate from a good hole or a honey bee colony abscond from a fine comb? Although the investment into nest structures is a disincentive for movement, even species that utilize expensive nests move on a regular basis. Investigators often have made the perfectly reasonable assumption that colonies depart from intact nests because there is a problem with the nest itself or the location of that particular nest, that moving from one nest site to another serves the function of fixing a particular deficiency. Sometimes colonies move because things have gone wrong at home. It is now clear, however, that most nest relocations do not occur because a nest is spoiled.

The preponderance of data and observations shows that periodic nest movements are built into the life histories of many social insect species, probably the vast majority of all described species. This conclusion is drawn from numerous discoveries over the past few decades in which researchers have observed the spontaneous disappearance of known colonies. Historically, nest movements have been considered to be anomalous or uncommon events (79). The phenomenon is gaining recognition and is best described in ants perhaps because of the frequency of observations of many of species and the relative ease of tracking movements.

Although the ecology of nest movements remains enigmatic, the behavioral patterns of colony organization in the process of nest movement have been well characterized in model systems such as acorn ants, *Temnothorax* spp., and honey bees, *Apis mellifera* (95). Because the behavioral processes associated with nest movements in model systems have been well summarized (25, 70), the present review addresses the distribution and ecology of nest movement among social insects.

## NEST MOVEMENT SYNDROMES

Many social insects colonies are not bound to their nests throughout their lifetime, and the spatial and temporal aspects of nest movement are highly variable. The patterns of nest movement may be categorized into four discrete syndromes that range along a continuum indicating the frequency and relative role in the biology of the colony. The four stages in this continuum, described below, are legionary nomads, unstable nesters, intrinsic relocators, and adventitious nest relocators.

### Legionary Nomadism

Army ants are a monophyletic group of legionary predators inhabiting temporary nests called bivouacs, characterized by a biphasic nest movement pattern (42). In the nomadic phase, colonies move from one temporary nest to another nest each night. The stately phase is of equal duration to the nomadic phase, and the same bivouac is occupied continuously while the colony conducts hunting raids from this central nesting site. As the ecology of nest movements in the doryline clade of army ants is particularly well described (9, 42), the review focuses on the remaining and more enigmatic nest movement patterns.

**Table 1** A partial list of species whose nest movement behavior has been studied in the field

Species	Taxon	Syndrome	Reference(s)
<i>Aphaenogaster araneoides</i>	Ant	Intrinsic nest relocation: serial monodomy	54, 56, 57, 59
<i>Aphaenogaster rudis</i>	Ant	Intrinsic nest relocation: itinerant relocation	82–84
<i>Aphaenogaster senilis</i>	Ant	Intrinsic nest relocation: serial monodomy	5
<i>Apis mellifera</i>	Bee	Intrinsic nest relocation: seasonal migration	48, 81
<i>Apis dorsata</i>	Bee	Intrinsic nest relocation: seasonal migration	21, 41, 66
<i>Cataglyphis iberica</i>	Ant	Intrinsic nest relocation	15
<i>Cubitermes fungifaber</i>	Termite	Intrinsic nest relocation: itinerant relocation	65
<i>Euprenolepis procera</i>	Ant	Legionary nomadism	98
<i>Linepithema humile</i>	Ant	Unstable nesting	28, 29
<i>Messor andrei</i>	Ant	Intrinsic nest relocation: itinerant relocation	11
<i>Myrmica punctiventris</i>	Ant	Intrinsic nest relocation: itinerant relocation	85
<i>Pachycondyla analis</i>	Ant	Legionary nomadism	50
<i>Pheidole desertorum</i>	Ant	Intrinsic nest relocation: serial monodomy	18–20
<i>Pogonomyrmex californicus</i>	Ant	Intrinsic nest relocation: itinerant relocation	16
<i>Pogonomyrmex badius</i>	Ant	Intrinsic nest relocation: itinerant relocation	14
<i>Pogonomyrmex mayri</i>	Ant	Intrinsic nest relocation: itinerant relocation	43
<i>Pogonomyrmex barbatus</i>	Ant	Adventitious nest relocation	27
<i>Polistes bistrata</i>	Wasp	Adventitious nest relocation	17
<i>Polistes instabilis</i>	Wasp	Intrinsic nest relocation: seasonal migration	36
<i>Polyrhachis ammon</i>	Ant	Intrinsic nest relocation: itinerant relocation	26
<i>Pristomyrmex pungens</i>	Ant	Intrinsic nest relocation: serial monodomy	92

A selected number of other ant species have evolved legionary nomadism in a pattern reminiscent of army ants. These species are specialized predators and often move their nests to new locations, finding prey en route. However, unlike army ants, the nest movements of other legionary nomads do not follow the temporally consistent phases of army ants that track brood development. The nonarmy ant legionary nomads are typified by ants such as *Pachycondyla apicalis* and *P. marginata*, which periodically move nests presumably to track access to termite prey (46, 50). Similar legionary and predatory nest movements are found in other lineages (Table 1), such as *Leptogenys* spp. (97). While the prey acquisition strategy of the group-hunting ants *Pheidologeton diversus* and *P. silenus* is reminiscent of army ants, these ants lack the nomadic habit; colony movements occur in most if not all mature colonies and may be as infrequent as once a year (62). In a unique find, Witte & Maschwitz (98) have recently discovered that the ant *Euprenolepis procera* demonstrates characteristic traits of other legionary nomads, except for the fact that its prey are fungi.

### Unstable Nesting

Many species of ants are perennially located in ephemeral nesting environments and do not require long-term physical stability of nests for colonies to thrive. For example, the ant *Wasmannia auropunctata* opportunistically nests in open areas that experience high rates of local disturbance, such as the undersides and bases of leaves in plantations and orchards (87). Some litter-dwelling species of ants, such as *Nylanderia steinbeili*, nest opportunistically in dried leaves and in other relatively exposed surfaces that are ephemeral (55).

**Legionary nomadism:** a condition in predatory ants in which colonies do not inhabit established nest structures and move at a high frequency to gain access to prey

**Emigration:** a term used for the nest relocations in social insects

**Absconding:** describes nest relocations in which bees and wasps fly away from their nest to a new nest location

**Serial monodomy:** a nest movement pattern in which a single colony occupies one nest at a time but maintains multiple nests for its exclusive use

**Seasonal polydomy:** a pattern of nest movement in which colonies converge during the winter and spread among multiple nests in warmer periods, potentially as a thermoregulatory mechanism

**Polydomy:** a condition in which a single colony occupies multiple nests

**Seasonal migration:** a nest movement pattern in which colonies move nest locations, tracking changes in the seasons

Many invasive ant species exhibit unstable nesting patterns and are capable of rapidly occupying and departing temporary nests (93). This unstable nesting habit may predispose these animals to more frequent human-mediated jump-dispersal events, rapid colonization of new areas, and enhanced acclimation to microclimates that facilitate ecological success. Although some species of unstable nesters may occupy low-cost and low-quality nest sites because other nests are not available as a result of competition (55), unstable nesting may also be an adaptive approach to tracking and maintaining access to ephemeral resources.

### Intrinsic Nest Relocation

Intrinsic nest relocation occurs in species with colonies that occupy a discrete nesting environment and periodically depart for another similar nesting environment as a part of their life history. This pattern of nest movement is more widespread than commonly recognized among observers of social insects. Nest relocation events have often been described as “emigration” in ants or “absconding” in bees and wasps, but this review avoids these terms as their use implies that such relocation events are uncommon or elicited by circumstances external to the colony. Owing to page limitations, and to nest movement behaviors that remain undocumented, a complete list of intrinsic relocating species is not possible; several are listed in **Table 1**.

Intrinsic nest relocation may be subdivided into a four mutually exclusive categories. Serial monodomy is a pattern of nest movement in which a colony occupies a single nest at a time but maintains multiple nests for the colony’s exclusive use (56, 88). Serial monodomy is described in a number of ant species from a broad variety of biomes. This habit is likely to serve an adaptive function for the colony, although the benefits vary from species to species. A number of ants species practice serial monodomy, including *Aphaenogaster araneoides* (56), *Pheidole desertorum* (19), *Pristomyrmex pungens* (92), and *Stenamamma expositum* (51); this pattern is not known to occur outside of ants.

Seasonal polydomy is likely to be practiced by many ant species in the temperate zone, in which colonies converge during the winter and spread among multiple nests in warmer periods, potentially as a thermoregulatory mechanism (6, 45, 85). Several widespread human commensal ant species with unicolonial habit and unstable nests, such as the Argentine ant, *Linepithema humile*, practice seasonal polydomy (12, 29), if not for thermoregulation then perhaps for foraging efficiency. Some seasonally polydomous ants, such as mound-building *Formica* spp. (22), however, maintain their nests in the same locations for many years.

Seasonal migration, often along elevational gradients, is practiced by many tropical bee species as well as a number of tropical wasp species. Seasonal migration may be more common in the tropics than across equivalent distances in temperate regions because seasonal shifts in elevation produce a greater relative change in temperature. In a seasonally migratory species, not all colonies migrate every year. Among the tropical honey bees, *Apis* spp., colony life history is coupled with seasonal migration, and the nutritional and brood status of the colony influences whether seasonal migration occurs (21, 80).

Itinerant relocation occurs when colonies periodically move their nests from one location to another and do not demonstrate fidelity to prior nesting sites. This mode of nest relocation prevails in ephemeral environments, such as continuously decomposing leaf litter and fine woody debris occupied by ants and termites on the floor of forests (13, 55). Itinerant relocation is distinguished from nomadism by the frequency of relocation, as truly nomadic species do not remain in a single nest for extended periods, and nomads are predators that move to track the access to prey. The termite *Cubitermes fungifaber* demonstrates itinerant relocation in Africa (65). Colonies of the harvester ant *Messor andrei* are itinerant relocators. In this species, single relocation events do not

result in a shift in foraging area, but the cumulative result of several relocation events results in a shift in the use of space. In the course of one year, one-third of colonies under observation had moved their nests outside of a fixed observation area (11).

### Adventitious Nest Relocation

It is likely that nearly all species have the capability of moving their nests in the event of some kind of traumatic event or destruction of the nest site. A few species are particularly known for their fidelity to nest sites, in which colonies can be observed and reobserved in the same nest for well over a decade. Such species, however, have the capacity to move nests on occasion, as observed in the leafcutting ants *Atta colombica* (72) and *Atta cephalotes* (T.P. McGlynn, personal observation). The wasp *Polistes occidentalis* apparently has a consistent behavioral repertoire for moving nests in response to damage (from weather or predation), but nest movements are not a regular part of its life history (86). In other species that tend to establish long-term nests, such as *Pogonomyrmex barbatus*, a fraction of colonies may be relatively mobile whereas most colonies stay put (27).

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**Swarming:** a collective behavior synonymous with budding in bees and wasps

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## THE TAXONOMIC AND GEOGRAPHIC DISTRIBUTION OF NEST MOVEMENTS

### Ants

In ants, nest relocation occurs throughout the phylogeny, and its occurrence appears to be independent of evolutionary history, aside from the evolution of legionary nomadic life history. Because many species are likely to demonstrate nest movement behaviors that remain undocumented, it is not yet possible to develop a robust phylogenetic test of the origins of nest movement behavior.

Nest relocations in ants occur in many kinds of environments: deserts, tropical rain forests, temperate deciduous forests, and the urban matrix. Researchers have surmised the function of nest relocation only in some circumstances, and there does not appear to be a tight association between biome and functionality. The author surmises, based on cumulative prior findings, that ants in temperate areas do not appear more or less likely to relocate for favorable microhabitats than ants in tropical environments are, and the effect of army ant predators on nest relocation may operate in the desert as well as in the rain forest.

Although the mode of nest relocation may be inferred for many terrestrial species, arboreal ants move their colonies quite readily, even though the underlying patterns remain unclear. Experimental work in forest and plantation canopies with supplemental nests indicates that mature colonies from many taxa of ants readily take up residence in artificial cavities (68). An increase in the diversity of cavity types increases the diversity of ants inhabiting these cavities, although the mechanism driving this pattern is not known (3). In arboreal *Cephalotes* of the Brazilian cerrado, species are differentiated by the characteristics of preferred nests (69).

Unlike ants, all adult residents of bee and wasp colonies have wings; therefore, tracking nest movements presents a greater challenge. Nevertheless, experimental and observational work has led to some understanding of nest movements in winged social insects.

### Bees

The biology of nest movements in honey bees has been comprehensively reviewed by Hepburn (30). Nest movements in bees are typically described as absconding. Swarming is different than

**Budding:** a form of colony reproduction in which a fraction of workers depart their natal nest to create a new colony at a new nest

absconding as swarms result in nest reproduction by the budding of a new colony, whereas an absconding colony merely flies away from its nest to a new nest location. Among bees, the long-term nesting patterns are best described in honey bees, *Apis* spp. Tropical honey bees apparently perform seasonal migration, this behavior does not occur with regularity in nontropical climates (30). Honey bee colonies demonstrate close fidelity to migratory nest sites, a remarkable feat considering that each migratory event is performed by separate generational cohorts of worker bees (64).

Honey bees use dancing behaviors in different contexts to direct colonies to both food and new nesting sites. When nest relocations occur, the preceding dance bears some characteristics to the classic food “waggle dance” of foragers. However, the pattern of dancing prior to seasonal migration has a distinct manifestation, and directionality is communicated more clearly than distance (21, 41). In *Apis dorsata* colonies, nest relocation events are organized differently than reproductive swarming events are (81). However, in temperate *A. mellifera mellifera*, Lewis & Schneider (48) found the reproductive swarming dance and nest relocation dance to be equivalent and suggested to call this behavior the “relocation dance,” as it is performed prior to all relocation events, including seasonal migration and swarming.

Bees with annual life cycles, such as bumble bees, are not likely to demonstrate nest relocation behaviors. Little is known about the long-term establishment of nest sites in stingless bees; however, absconding events have been observed (39, 75). Because a number of colonies in a variety of species maintain nests in the same location for long durations, if nest relocations occur among stingless bees, then adventitious nest relocation may be the prevailing syndrome.

## Wasps

Nest relocations in social wasps are not well characterized, although the incidence is documented in a number of lineages. The Neotropical polistine wasp *Apoica pallens* apparently conducts seasonal nest movements tied to seasonal dry periods in the llanos of Venezuela (37); however, it is not clear if seasonal nest relocations occur throughout its broad range throughout the Neotropics. The Costa Rican wasp *Polistes instabilis* seasonally migrates from tropical dry forests to cooler, high-elevation dormancy sites (36). Nest relocation events have been observed in other tropical wasps, such as *Rhopalidia fasciata* (40), *Provespa anomala* (53), and several species of *Vespa* (63). Substantial circumstantial evidence suggests seasonal migration in a number of tropical wasp species (38). Seasonal migration may be the prevailing mode of nesting behavior of social wasps in tropical localities with suitable heterogeneity to afford the benefits of seasonal movement, such as an increase in prey availability or a reduction in metabolic rate. However, even in temperate regions, nest relocations occur in 25% to 88% of *Vespa simillima* and *V. crabro flavofasciata* wasp colonies to allow for nest expansion (74).

## Termites

Relative to our understanding of other social insects, the ecology of termites is enigmatic. Whereas other social insects forage for resources typically outside their nests, foraging behaviors of termites are constrained usually to locations that are not readily observed (76). Nevertheless, observations and experiments have been conducted on nest movements of a few termite species. Termite colonies are not sessile and shift locations even in the absence of significant changes in environmental conditions. Work on structure-infesting termites indicates that colonies may move their nests from one structure to another, effectively abandoning the old nest location for a new one. This pattern has also been documented in some species in the field outside of infested

structures (65). Areas once occupied by a colony may become vacant as that colony grows and expands. In carton-nesting termites, *Nasutitermes* spp., nest sites change with colony ontogeny (90). Colonies of termites move their nests to track seasonal changes (61).

## **HYPOTHESES FOR THE EVOLUTION AND MAINTENANCE OF NEST MOVEMENT**

Many functions are served by the movements of nests, which vary with the natural history of each species. Many selection forces may have worked to favor nest movement and have been evaluated with observational or manipulative approaches. Many of these hypotheses were posited and evaluated by Smallwood & Culver (84) and Smallwood (82). Not all these hypotheses apply to all systems, but it is likely that multiple factors, with varying temporal importance, may be assessed by nest-relocating species to influence nest relocation behavior (26).

### **Colony Growth**

Colonies, especially those that live in preformed cavities that do not have the potential for expansion, may outgrow their nesting space. This pattern of nest movements occurs in *Nasutitermes* termites, which initially grow in wood but then shift the bulk of the colony to carton structures as the colony grows (90). Colony growth may trigger adventitious nest movements in temperate honey bees and potentially in twig-dwelling ants. Colony growth is thought to influence the movement of vespid wasps from enclosed sites to more open areas to allow for expansion (63). Although this is a feasible hypothesis, there are no explicit tests to evaluate whether this is a cause for intrinsic nest relocation in any species. Colony growth does influence the pattern of nest movements in the serially monodomous Central American gypsy ant, *Aphaenogaster araneoides*, as colonies with higher growth rates maintain a greater number of unoccupied nests than slower growing colonies do; however, relocation rates in this species are governed by colony size (57).

### **Distance from Competition**

There is little evidence that nest movements occur in response to interactions with conspecific competitors. Even though distance from neighbors does not predict nest relocation events, once nest movements occur, there may be increases in conspecific nearest-neighbor distances (11, 16, 57). Encounter rates while foraging, nor distance to neighboring nests, have not been found to be predictive of movements (11, 57). However, in the polydomous nesting ant *Cataglyphis iberica*, relocation events from nests are triggered by heterospecific attacks by the behaviorally dominant ant *Camponotus foreli*, suggesting that the occurrence of polydomy may exist to reduce the costs of harassment by *C. foreli* (15).

### **Foraging Efficiency and Local Food Depletion**

Legionary nomads may continue to move nests to increase the probability of encountering specialized prey (46). It is unlikely that intrinsic nest relocation occurs to enhance access to resources, as in most cases the distances moved by species are not adequate to have such an effect, and a number of experiments with a variety of species have found that food availability has little effect on relocation behavior (57, 58). However, Aron et al. (4) found that in the laboratory the ant *Temnothorax unifasciatus* increases foraging effort after completing a nest relocation. Similarly, *A. araneoides* colonies closest to neighbors prior to relocation were more likely to forage over a

larger home range after relocation (59). Whereas the removal or supplementation of food did not result in nest movements in other ant species, the removal of resources from the serially monodomous ant *Pristomyrmex pungens* in the field resulted in nest movements (92).

Ant colonies, especially polydomous species, may move nests to localities that are closer to food resources with the result of increased foraging efficiency (33). There is less evidence to suggest that monodomous species relocate nests to improve foraging efficiency, because the other hypotheses listed more often apply to monodomous species.

### Microclimate

Nest relocation events have often been correlated with shifts toward more favorable microclimates. When *Aphaenogaster rudis* ant colonies move nests, the new nest locations are found in areas that afford greater insolation (83). The Neotropical ant *Ectatomma ruidum* frequently moves nests preferentially under experimental shade apparatuses from nests in adjacent sunny areas, with no effect of food supplementation on nest movement behaviors (58). Rates of nest relocation for the Florida harvester ant, *Pogonomyrmex badius*, increase greatly when shading treatments are applied (14). Unstable nesting species such as urban pest ants (e.g., *Linepithema humile*) move in response to changes in weather (28).

### Nest Deterioration

When nest structures are destroyed by an external trauma, colonies often move to a suitable environment or create a new nesting space. For example, the termite *Nasutitermes princeps* often creates nests in tree branches; if a nest-containing branch falls to the ground and the reproductives survive the trauma, a new nest will be created in the canopy (73).

Many species of ants typically nest in inexpensively constructed cavities, in ephemeral environments such as the fine woody debris, and in seed pods in the leaf litter of forests; other species construct inadequate nests that may be subject to decay from flooding and other environmental hazards. Nearly all litter-nesting ant species demonstrate intrinsic nest relocation (13, 31, 55). Laboratory experiments on the social organization of nest movements typically initiate relocation events by damaging the nest structure, such as removing the cover of a laboratory colony (24).

### Nest Quality

It is difficult to measure how social insects value the quality of one nesting space over another. During nest movements and swarming events, honey bees may communicate their own perception of nest quality as a component of the waggle dance as a part of the collective decision-making process (48). Once a nest is occupied, however, it is not clear whether nest movements occur for the selective advantage of higher-quality nesting sites as opposed to other incentives for relocation. Field colonies of the ant *Proformica longisetata* nest under rocks and will relocate to larger rocks if available (91). Likewise, in the ant *Polyrhachis ammon*, smaller nests are more subject to emigration than larger nests are (26). In *Temnothorax* ants, laboratory experiments indicate that colonies prefer certain nest characteristics, such as a small-sized opening to the nest and adequately large space for a mature colony (24). Preferential nest characteristics vary among taxa, as soil-nesting *A. araneoides* colonies will reoccupy nests with large-sized entrances more quickly compared with nests with small-sized entrances (54).

## Parasitic Load and Disease

Social insect nests house a wealth of concentrated resources and are prone to attract agents of top-down population regulation. Parasites and disease may not be subject to localized control. Although some ants support mutualists (e.g., actinomycetes) that work against the spread of parasites in nests, disease and parasites are often not readily controlled. Some colonies may adventitiously emigrate from nests that have been spoiled by disease or parasites to start anew at a new location, as is the case for the wasp *Mischocyttarus labiatus* (49). In other cases, a persistent load of parasites may keep colonies in a constant state of emigration. Many social parasites are adapted to the itinerant lifestyle of social insect colonies. This has been documented most extensively in the army ant *Eciton burchellii* (71).

An alternative explanation for the movement away from parasitized nests is host manipulation by parasites. Hughes et al. suggest that the aggregations of workers of the wasp *Polistes dominula* away from their natal nest may serve to complete the life cycle of strepsipterans that are infecting the workers (35). Whereas for *P. dominula* these aggregations do not result in the creation of a new colony, it is quite possible that for other species frequent nest relocations may occur due to a parasite manipulating a colony into moving its nest. This could explain the pattern of relocation in the red harvester ant, *Pogonomyrmex barbatus*, in which rates of relocation vary among colonies, with a small fraction of colonies relocating much more often than others. Because this pattern is not explained by competition and is not tied to any life-history variable that was measured, it is suggested that these colonies may have sought to escape an infestation or infection in their nests that was transferred during the move (27). As an alternative explanation, differences in the genetic diversity of the workforce may account for differential responses to nest movement decisions, as has been found for foraging decisions in another *Pogonomyrmex* species (96).

## Predation

Predatory attacks may be the cause for adventitious nest relocation, as occurred in the wasp *Polistes bellicosus*, in which nest relocation events were precipitated by predatory attacks (89). Predation pressure produces an adaptive benefit to maintaining empty nests should they be needed in the event of an attack. For example, the serially monodomous desert ant *Pheidole desertorum* evacuates from the nest at the moment the colony is attacked underground by army ants (*Neivamyrmex* spp.), and the colony flees to unoccupied nests maintained by the colony (19). Army ants are also implicated in nest relocations by the serially monodomous rainforest ant *A. araneoides*, although upon attack by army ants, colonies evacuate to low-lying vegetation rather than occupy one of the empty nests maintained by the colony. Experiments on nest-bound odors suggest that army ants are attracted to colony odor buildup resulting from continuous nest occupation (54, 56).

In more temperate environments lacking army ants, it is possible that slave-making ants have an effect functionally similar to that of army ants. Slave-making ants attack relocating colonies (82). Intrinsic nest-relocating species are typically subject to attacks by slave-making ants; I suggest that these species relocate nests possibly to avoid the attraction of slave-makers, as continuous occupation of a nest is more likely to provide location cues to slave-making ants.

## Seasonality

Tropical honey bees and wasps perform seasonal nest movements (21). In the giant honey bee, *Apis dorsata*, high rates of swarming and absconding tied to seasonal events result effectively in seasonal migration (21). A similar pattern is found in *A. mellifera* in more tropical climates (80). The

tropical wasp *Polistes bistrriata* experiences high mortality associated with heavy seasonal rainfall events, and surviving colonies move their nests to microsites that receive less trauma from rainfall (17). Less work has been conducted on termites, but multiple species in northern Australia migrate seasonally to track weather conditions (61).

## MEASUREMENT OF NEST MOVEMENT

Nest relocation rates can be measured by marking nests and tracking the persistence of nest occupation over time. A comprehensive approach to fieldwork is required to track colonies as they move from one site to the other. To follow an individual colony, occupants of a nest should be marked; when the colony has departed the nest, the presence of marked individuals will distinguish the focal colony in its new abode.

In a system with short relocation distances and the possibility of locating all colonies in a prescribed area, an alternative tactic for monitoring nest movements is possible. Nests may be marked and monitored at high frequency. As one nest becomes empty and a newly occupied nest is found in the vicinity, the identity of the relocated colony may be inferred (11, 57). This method is reliable insofar as adjacent colonies do not move in the same time interval between observations.

Nest relocation rates have been evaluated by three measures. In all these approaches, marked and occupied nests are checked regularly for occupancy until the colony has departed the focal nest. The most common measure of nest relocation rate is the mean nest occupancy time, also called occupation duration or nest longevity (57). Nest occupancy time is simply calculated by the mean duration that colonies continuously occupy a single nest (11, 29, 57). This is most appropriately calculated by observing a nest regularly from the time it is initially occupied by a colony to the time the colony departs.

The second measure of nest relocation rate is relocation frequency, which ranges from 0 to 1 (57). Relocation frequency is calculated as follows:

$$\text{relocation frequency} = \frac{\text{the number of relocation events per observed unit time}}{\text{the number of occupied nests observed per unit time}}$$

The time unit for relocation frequency is the time interval between consecutive observation events. For example, if a researcher checks for nest occupancy every day, then relocation frequency would be measured as relocations per day. Unlike mean nest occupancy time, relocation frequency may be used to evaluate the rate of relocation without having to observe the initial occupation of a nest. To avoid bias, however, once a colony departs a nest, it should continue to be tracked in its new nest. The reciprocal of relocation frequency, without tracking individual colonies from initial occupation to emigration, has been called residence time (82).

A third measure of nest relocation rate is nest half-life (82). This measure uses the same information required for mean nest occupancy. Half-life is calculated as follows:

$$\text{half-life} = (\text{mean occupancy time}) \ln 2.$$

Caution is recommended in the calculation and evaluation of relocation frequency or residence time estimates. Noncomprehensive sampling (in space or time) may result in bias (82). This is most obvious in seasonally migratory species. However, even the rates of nest movements in adventitious and intrinsic nest-relocating species vary with environmental conditions. For example, colonies of *A. araneoides* are more likely to move nests during peaks in temperature and associated declines in humidity (57). Colonies in seasonally flooded forests move from the litter into low-lying vegetation during periods of high rainfall (60).

## CONSEQUENCES AND SIGNIFICANCE OF NEST MOVEMENTS

Ecologists have a predilection to draw parallels between social insects and plants mostly because both are rooted to a fixed location and demonstrate modular growth (1, 52). Because nest movements may be the norm rather than the exception, conclusions that assume the sessile nature of social insect colonies should be reconsidered. In particular, because social insect colonies move, caution must be used when applying spatially explicit models of foraging behavior and competition to the interpretation of hypotheses regarding the evolution and community ecology of social insects.

### Population Genetics

Gene flow is increased in seasonally migrating social insects. In *Apis dorsata*, colonies both migrate and aggregate together in large groups, and as may be expected, there is appreciable relatedness among colonies within aggregation sites. Nevertheless, migrations provide gene flow that minimizes genetic differentiation among sites (66).

The genetic origins of unicoloniality (in which colony boundaries dissolve at the local or regional scale) in nonclonal species remain unclear. In some species, such as the unstable nesting Argentine ant, *Linepithema humile*, it has been argued that unicoloniality emerged from the loss of diversity in nestmate recognition cues caused by a genetic bottleneck and exacerbated by increased aggression against colonies with higher genetic diversity (94). In the seasonally polydomous species *Formica truncorum*, it has been suggested that nest movements have facilitated the evolution of unicoloniality through the mixing of genotypes (22). Because *F. truncorum* also went through a genetic bottleneck, the hypothesis regarding *L. humile* may also apply. Nest movements might homogenize the existing genetic variance that might further reduce colony-level differences in recognition cues. However, not all species are unicolonial as a result of nest movements and genetic bottlenecks; in the case of the unstable nesting *Wasmannia auropunctata*, for example, genetic similarity may emerge as a result of clonality in reproductives, even though workers are produced sexually (23).

### Life Histories

Colonies that move nests on a regular basis may be predisposed to colony reproduction by budding (8). Legionary predators reproduce mostly by budding (42), and a number of intrinsic nest-relocating species also are facultative or obligate budders (67). Boulay et al. (8) suggested a mechanistic association between intrinsic nest relocation and reproduction by budding. The queen pheromone of the ant *Aphaenogaster senilis* suppresses the production of sexuals, so there is a selective advantage to and a functionally possible option for workers to leave their mother during nest relocation to raise sexuals in the absence of a queen.

### Competition

Even before Hölldobler & Wilson (32) pronounced competition as the “hallmark of ant ecology”, ant biologists have followed a tradition of invoking competition as a driving force behind behavioral phenomena in social insects. Nevertheless, there is little indication that competition is the cause of nest relocation in social insects. Experiments in a variety of systems have consistently convinced investigators that competition is not the cause of nest relocation, as demonstrated above. The spatial distribution of nests is one of the major lines of evidence supporting the primacy of competition in the organization of ant communities. Even if fine-scale nest distributions are

caused by competition, then this does not necessarily indicate that colony establishment, survival, or growth is contingent on competition.

A classic marker of competition in ants, both intraspecifically and interspecifically, is overdispersion, in which nests are spaced more evenly from one another than expected by chance alone (44). The scientific dialogue among myrmecologists regarding the spatial distribution of ant colonies, however, often overlooks the fact that colonies might move their nests throughout their life history.

A well-cited example of intraspecific overdispersion is the work of Ryti & Case (77, 78) on the harvester ants *Pogonomyrmex californicus* and *Messor pergandei*. Their analyses explicitly “ignore nest relocation, since nest relocation may or may not be related to the local competitive environment” (78). Nest movements in harvester ants may be directed away from the closest conspecific neighbor (16), and this may or may not affect nearest-neighbor distance (16, 27). The causes of relocation in harvester ants are unknown, although Gordon (27) suggested that the function of relocation may not be connected to the factors considered in the selection of a new nest site and that parasitism may likely be a cause for nest movements in *P. barbatus*.

After evaluating competing mechanisms to account for overdispersion, Ryti & Case (78) argued that resource competition and queen predation are responsible for spatial structuring of the community as a consequence of differential survival of young colonies. However, it has since become clear that nest relocation occurs in this system and may explain the pattern of overdispersion. Although competition among neighbors may cause this spatial pattern, it is probably not the result of differential survival among colonies and is not informative about the relationship between competition and community structure.

Interspecific and intraspecific overdispersion in Panama was documented in a classic study by Levings & Franks (47). Many of the colonies in this system nest in leaf litter and hence perform intrinsic nest relocation, and at least some of the common soil-nesting species also perform nest relocation (58). Because ants nesting in this environment may move their nests on a weekly to monthly basis (13, 55), the overdispersed pattern must be generated by the decisions to place nests away from competitors. A parsimonious explanation for overdispersion is that interspecific interactions are a factor in nest choice but not necessarily predictive of levels of competition, density, or species richness.

I offer an analogy to explain how overdispersion is not evidence that competition structures communities. A family is seeking to buy or build a new house in the woods. A real estate agent is hired, and the family evaluates several sites to build a new house. All these plots of land are near one another, though they differ in a variety of ways. After evaluating all the potential sites, the family chooses a plot of land that is far away from loud neighbors, on a large lot, close to the spouses' work, near the children's school, and has a great view. Clearly, living some distance from loud neighbors factored into this decision. However, why did this family need to buy or build a new house in the first place? They could have had many reasons. Their old house might have burnt down, or the family was growing and needed more space, or perhaps they were purchasing a vacation house. However, it is unlikely that the family moved away from their old home because of loud neighbors. Is it fair to compare neighborhood competition in ants with loud neighbors in this analogy? The comparison may be apt, but to know for sure one would require experiments demonstrating that the introduction of new neighbors triggers nest relocation events. As described above, in most systems there is no evidence to suggest that neighborhood competition triggers nest relocation.

Consider that ant colonies moving their nests are house-hunting on a regular basis. Colonies integrate many kinds of information to choose the best possible site (25). Colonies may reap many benefits from moving. However, a colony would preferentially choose a site distant from competitors. This fact does not necessarily indicate that competition is one of the more important variables

in the decision-making process, as competitive exclusion may not prevail even in environments with behaviorally dominant species (2).

Overdispersion among trees might indicate competition for light, because trees cannot walk (7). However, because ant colonies can walk, overdispersion may merely reflect a preference for colonies to separate themselves from one another, and this preference may have no bearing on the composition or assembly of communities.

In other social insects, there is even less evidence to suggest that competition might result in changes in spatial distributions that are caused by nest movements. Stingless bee colonies in Costa Rica maintain territories, though the mechanism by which colonies avoid inhabiting the territories of competitors is not known (10, 34). It is reasonable to suggest that colonies are spaced evenly as a cumulative effect of founding decisions, differential survival, and nest relocation, although more work is needed to determine the frequency and breadth of nest movements in stingless bees. On the other hand, as beekeepers can attest, honey bee colonies may happily coexist next door to one another and it is unlikely that relocation events in any *Apis* species reflect competition. Our limited knowledge of nest relocation events in wasps suggests that seasonal migration and predation are the principal causes of nest relocation.

## DIRECTIONS FOR FUTURE WORK

Our current understanding of the ecology of nest movements lacks depth. The bulk of research that has documented nest movements in social insects has been the product of serendipity: Field biologists investigating marked colonies are surprised to discover that the colonies they have marked refused to stay still. Most systems are not given further consideration after being subjected to a few tests of hypotheses to attempt to explain the function of nest movements. The majority of experiments have found correlates of movement events, but for the most part the natural triggers for relocation behavior remain mysterious.

To understand how environmental conditions mechanistically cause nest movements, detailed field experimentation on model systems is prescribed. A few potential systems that are understood better than most others include honey bees (*Apis* spp.), acorn ants (*Temnothorax* spp.), and gypsy ants (*Aphaenogaster* spp.). Functional tests of hypotheses may be conducted by developing field manipulations to observe the initiation and outcomes of nest relocation events. Iterative experiments to build on prior results are required to create a comprehensive understanding. Whereas scientific research (stereo)typically follows the course of building on prior results to construct a larger understanding of a phenomenon, this pattern has not emerged among field ecologists studying nest movements in social insects. Fieldwork on a particular species often ends when nest relocation has been discovered in the field. In most species, nest relocation in the field has been addressed only by a single publication before an investigator apparently moves on to a new research topic.

In addition to the prescription for experimental work on model systems, little work has been done to evaluate large-scale taxonomic or geographic patterns in nest movements. Working interspecifically within genera that demonstrate variation in nest movements, some lineages are likely to present patterns that may be predicted by phylogeography or large-scale climatic factors.

Continued experimentation in the field will inevitably reveal new examples of nest movements in social insects. This review has shown that there is no shortage of examples of species that exhibit this behavior, but what remains to be discovered are the overarching patterns that provide a more uniform theory for the evolution and maintenance of the phenomenon. Because social insect nest movements serve many functions and are presumably organized through a multitude of behavioral processes, the most fruitful avenues of research will synthesize colony organizational processes with ecological predictors and outcomes.

### SUMMARY POINTS

1. Nest movements commonly occur among social insects.
2. Many social insects relocate their nests on a regular basis as a part of their life history.
3. The behavioral processes of finding new nest sites are better described than the ecological causes and effects of nest movements are.
4. Nest relocations occur broadly across taxa and are more reflective of the ecology of a particular species than of a phylogenetic constraint.
5. Ants perform nest relocations in many biomes, whereas regular nest movements in bees and wasps predominate in the tropics.
6. Many selective forces may drive nest relocation, and the selective forces at work are different for each species, reflecting differences in life history and natural history. In most cases nest relocations are triggered by abiotic conditions and there is little evidence that nest relocations occur in response to biotic factors.
7. Although competition does not cause nest relocations, the positions of nests in ant communities reflect that colonies choose locations distant from competitors.

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