N

Nest Relocation

Sarah Bengston[1] and Terry McGlynn[2,3]
[1]City University of New York: Baruch College, New York, NY, USA
[2]Department of Biology, California State University Dominguez Hills, Carson, CA, USA
[3]Entomology Department, Natural History Museum of Los Angeles County, Los Angeles, CA, USA

Synonyms

Nest moving; Nest transfer; Nomadism

The propensity and ability of a colony to relocate some or all components of their nest varies widely across social insects. Some species are relatively sessile, such as large, mature *Atta* leaf-cutting ant colonies, which may find it very difficult to move a very large colony (with or without its substantial fungus gardens) to a new site. Other species move readily, either as a result of their intrinsic life history or external stresses and environmental stimuli. Indeed, it is likely that nest relocation by social insects is a much more frequent occurrence than is generally perceived [3]. Some of this underestimation results from the assumption that colonies should be reticent to leave structures that require so much investment in labor and materials. Certainly, for some, especially mobile species, there is limited investment in nest structure. As examples, the aptly named house-hunting ants (genus *Temnothorax*) rely entirely on preformed cavities, and many species of army ants have forgone a nest altogether and instead build a shelter (bivouac) out of their own bodies. Yet, it is not only species with very low investment in nest structures that relocate readily. For example, the western honey bee, *Apis mellifera*, builds large combs that store significant food resources and yet these colonies move so frequently that they have become a model species for understanding nest relocation.

Types of Nest Relocation

As summarized by McGlynn [3], nest relocation can generally be classified along a continuum of four types: nomadism, unstable nesting, adventitious nest relocation, and intrinsic nest relocation. Nomadic species display a colony history dependent upon movement. They often show behavioral traits specifically tailored to constant movement, such as the bivouacs mentioned above. Colonies may stay in place temporarily, particularly to exploit an ephemeral resource, but move on after that resource has been depleted. Unstable nesting species may also be adapted to exploit ephemeral resources and as such use low-cost nest sites, such as under dried foliage in leaf litter. These disturbance specialists can often be found in areas with high levels of human disruption. Extrinsic disturbance, damage, or environmental change (such as the arrival of a predator) may also induce

C. Starr (ed.), *Encyclopedia of Social Insects*,
https://doi.org/10.1007/978-3-319-90306-4_84-1

relocation in species that would otherwise remain sessile. This strategy is known as adventitious nest relocation. It is likely that most social insect species are capable of adventitious nest relocation if the extrinsic threat is significant enough, though observing such a stochastic process poses many difficulties. Intrinsic nest relocation, as opposed to the other categories that rely on external stimulus, occurs as a result of a species' colony history. Season events such as migration or seasonal ► polydomy trigger relocation of some or all of the colony to a new or secondary nest site.

Causes of Relocation

There is not one overarching reason why a colony may abandon a nest and relocate to a new site. Certainly, one obvious explanation may be that the colony is facing extrinsic threat or stress in its current site. This may include problems with the nest itself or the immediate vicinity.

Compromised Nest

A nest structure may become compromised, forcing a colony to relocate. This may be the result of direct damage to the nest or a decrease in its quality through time. Physical damage to the nest may occur from any external trauma, though most common when structures supporting the nest fail. For example, the ► giant honey bee, *Apis dorsata*, builds large, exposed nests on the branches of trees or on rocky cliff overhangs. These are prone to damage when tree branches fall or the rock formation shifts. Nests in leaf litter or flood prone subterranean nests may also experience frequent disturbance, resulting in impressive adaptations such as the well-documented rafting behavior of red imported ► fire ants, *Solenopsis invicta*. Additionally, colonies may relocate if they perceive a new site as of higher quality than the current site [1]. The characteristics determining the quality of a nest site vary based on species-specific criteria; *Temnothorax* ants prefer a small nest opening, while *Aphaenogaster araneoides* prefers larger nest.

Resource Deficiency

Generally, nomadic species are the most likely to routinely relocate in response to insufficient resource availability. However, non-nomadic species may use proximity to resources as a trait affecting nest site selection, often preferring a site closer to better resources when other nest site traits are comparable. For example, in the ► slave-making ants *Formica subintegra* and *F. pergandei*, colonies are more likely to relocate their nest when raiding distances to host colonies increased. These nest relocations considerably shorten raiding distances by putting them into closer proximity to host colonies. Additionally, the new raiding distances are shorter than the distance traveled to relocate, meaning colonies are simply not evacuating their current nest for a nearby site but instead tracking resource availability and moving accordingly. Similar tactics may be used for seasonally polydomous species; satellite nests may be established closer to resources while the primary nest remains in place.

Predators and Parasites

External attacks from predators or parasites may elicit an adventitious nest relocation response if the damage or threat is severe. If predatory attacks are rare and episodic, the resulting relocation may be a one-time move to a new nest that must be established. However, species under continual threat of predation have adapted to this threat by maintaining multiple nests that they may move between at regular intervals or flee to when detected by a predator. For example, when army ants detect and attack the desert ant *Pheidole desertorum*, the colony immediately evacuates to a nearby unoccupied nest they had previously established. Similar to attacks from a predator, slave-making social parasites may provide selective pressure for colonies to move more frequently.

Both internal ► nest parasites and external parasitic threat may result in nest relocation. Nest movement may be the result of a colony moving away from burdensome parasites or may instead be the result of host manipulation by the parasites. Certain parasites and pathogens have been shown to manipulate host behavior and thus are able to oblige host movement away from the nest as a method of parasite dispersal. While this has not been demonstrated to result in whole colony relocation, substantial proportions of infected ► *Polistes dominula* colonies have been found aggregating away from their original nests.

Colony Growth

The growth of a colony, particularly in relation to worker and brood number, has not been clearly demonstrated to result in nest relocation in social insects. What is seen more commonly is that mature or rapidly growing colonies accommodate expanding numbers with seasonal polydomy. After alates have dispersed, the colonies contract for the winter (see below). However, for species that reside in preformed cavities or other unstable, space-constrained nest sites, it stands to reason that if worker number exceeds what can comfortably fit in the nest, the colony must move. Crowding within the nest may also inhibit signals that promote cohesion; in honey bee colonies, when the density of workers increases within the nest, queen pheromones are diluted, resulting in the rearing of virgin queens and subsequent swarming.

Seasonality

True seasonal nest relocation is mainly known from tropical bees and wasps. Often, relocation events occur within microclimates, such as moving the colony from a high-quality but exposed nest site to a lower-quality but more sheltered site during periods associated with heavy seasonal rainfall. Colonies of the western honey bee often relocate significant distances between the dry and wet seasons, effectively a seasonal migration.

Rather than a complete seasonal relocation, ants are biased towards seasonal polydomy. Many species show a significant expansion in colony size via nearby satellite colonies during spring and summer, followed by a contraction of colony size during a dry or winter season. For example, the dolichoderine ant *Dolichoderus mariae* expands from one or two overwintering nests up to 60 nests during the spring and summer. Colonies also maintain high fidelity to these satellite nests and often use the same sites repeatedly year after year. A similar pattern was found in the highly polydomous and invasive ► Argentine ant (*Linepithema humile*). Colonies show a repeated pattern of retraction to one or few nests in the winter and expansion in the spring. Inter-nest and foraging trails also shift seasonally to maintain connectivity between nests. They show little fidelity to satellite nests, as nearly half were occupied for less than a single month and 90% were occupied for less than 3 months. Laboratory experiments have demonstrated that much of their nest relocation was dependent upon humidity. Colonies are more likely to relocate to a site with higher humidity than to one with better food resources.

Collective Decision-Making

For a colony to relocate to a new nest site, it must find, assess, and select a new site. This requires substantial coordination and information flow among many individuals and a mechanism for reaching a decision. This process falls under the more general concept of collective decision-making, and researchers have borrowed many concepts and theories from sociology and psychology [5].

Before a decision can be made, information must be gathered, particularly about the quality of any potential nest site. This requires the assessment of numerous noisy variables, such as size of potential sites and of entrance passage ways, as well as proximity to neighbors and resources. Accurately sampling these variables takes time, resulting in an inherent trade-off between the accuracy and the speed of the assessment. Faster sampling will be less correct than taking a longer time to repeatedly sample the variables. Generally, the cost associated with the decision determines how much error is acceptable. If nest relocation is particularly risky, colonies are more likely to take the time to make a more accurate decision.

In social insects, it is not always necessary for individuals to visit multiple sites for a decision to be made. For example, in laboratory experiments with *Temnothorax* ants, this decision-making occurs through an entirely decentralized process. The ants have a strong preference for large cavities with small entrances and minimal light. When presented with two potential nests of varying quality, scouts may only visit one of the two sites to assess quality. They then choose to initiate recruitment to that site based on quality; the higher the quality, the more likely they are to recruit to it. Subsequently recruited individuals then also assess the site and in turn do or do not recruit based on quality. As a result, there is strong positive feedback into the colony when a high-quality site is discovered. Once recruitment to a site reaches a specific threshold, or quorum, the focus of recruitment switches from scouts to more passive members of the colony that are otherwise not involved in the decision-making process. While this process is decentralized, it does not mean that individual variation between workers is unimportant. In Argentine ant colonies, having more workers who are highly exploratory improves both the speed and accuracy of collective nest choice.

Like *Temnothorax* ants, honey bees also use a quorum-based collective decision-making process. When a colony buds, the dispersing colony establishes a bivouac structure, or a swarm, often on a tree branch. Scouts then fly out to inspect potential nest sites. These scouts report potential sites to the colony using the ▶ waggle dance, with high-quality sites yielding more vigorous dancing (100+ repetitions) while moderate- and low-quality sites yield less enthusiasm (10–20 repetitions). Multiple sites of similar quality or two sites of high quality both result in colonies taking longer times to reach a quorum, though a consensus between two competing sites does not need to be reached before the colony makes a decision [6]. Interestingly, behavioral variations between colonies may also affect how a decision is reached but not necessarily how long it takes to reach a decision. When 17 swarms were each presented with three new hives, there were consistent behavioral differences between colonies in the number of dances performed and scouting activity, yet this did not affect how long it took colonies to select a new nest site [7].

A challenge experienced by both social insect colonies and noninsect social groups making collective decisions is the management of irrational behavior of some group members. Best demonstrated in honey bees and *Temnothorax* while nesthunting experience with irrelevant alternatives can influence preference of individuals within the group but not the group as a whole. For example, when presented with two nests that trade-off between low light and nest entrance size, experience with irrelevant nests of low quality in one of these two variables (e.g., bright inside the nest or large nest entrance) biases lone *Temnothorax* workers towards the relevant nest of high quality on that axis. Accordingly, workers who have experienced a nest with a very large entrance will prefer nests with a smaller entrance despite that nest being more brightly lit. This preference, however, does not carryover to the colony as a whole. This group rationality, in spite of individual irrationality, may best be explained by scouts only assessing a single site when in a collective setting. Scouts are not then biased by unnecessary comparisons [4].

Previous experience with nest sites may also lead to in learning, with consequences for nest site selection. *Temnothorax* ants show short-term learning during emigrations, with increases in their migration speed if migrating multiple times over several days. They also become more accurate in their decision-making process, and experienced colonies are less likely than naive colonies to split between multiple nest sites. Colonies also learn to avoid low-quality nests and will avoid poor nests that they have already experienced, even if the other option is of identical quality [5].

Implications of Nest Relocation

As a result of the likely underestimation of the incidence of colony relocation, not much is known about its specific implications for social insects. However, some predictions can be drawn from the better known effects of animal movement generally. For example, relocation may have effects on competition between colonies or between species. Surprisingly, competition has not been shown to induce colony relocation or otherwise affect colony movement [3], though spatial distribution of colonies and competition for finite resources may affect other aspects of a species' natural history. Patterns of over-dispersion of nest sites seen in some social insect systems may not be directly explained by a colony moving to directly avoid competition. Rather, this pattern may arise through avoiding competition when selecting a new nest site, after already being induced to move by another intrinsic or extrinsic factor [2, 3], such as predation risk or seasonal migration.

Regardless of why colonies relocate, a necessary result of relocation is gene flow and increased genetic diversity within populations. This is perhaps best measured as a consequence of seasonal migration in *Apis dorsata*, where relatedness increases between colonies in close proximity to one another, while differentiation among populations is mediated by seasonal nest relocation. Similar patterns have been seen in highly ► invasive species, particularly when colonies relocate quickly and frequently, resulting in significant gene flow between geographically distant colonies. This has been thought to result in the evolution of unicoloniality (► supercolonies) by homogenizing populations, particularly after a population bottleneck, thus furthering the invasive potential of species such as the Argentine ant.

Because nest relocation may be more common than expected and holds significant implications for much of a species' biology and evolution, researchers must approach the question with caution. Assuming spatial permanence, for example, in spatially explicit models, may miss significant and important within-species variation. It may also not accurately reflect the genetic structure of the population or the connectedness of different populations. Instead, researchers must more carefully consider nest relocation as a critical component to social insect biology, as well as work to better understand the factors inducing and shaping nest relocation.

Cross-References

► Supercolonies
► *Temnothorax*

References

1. Dornhaus, A., Franks, N. R., Hawkins, R. M., & Shere, H. N. S. (2004). Ants move to improve: Colonies of *Leptothorax albipennis* emigrate whenever they find a superior nest site. *Animal Behaviour, 67*, 959–963.
2. Gordon, D. M. (1992). Nest relocation in harvester ants. *Annals of the Entomological Society of America, 85*, 44–47.
3. McGlynn, T. P. (2012). The ecology of nest movement in social insects. *Annual Review of Entomology, 57*, 291–308.
4. Sasaki, T., & Pratt, S. C. (2011). Emergence of group rationality from irrational individuals. *Behavioral Ecology, 22*, 276–281.
5. Sasaki, T., & Pratt, S. C. (2018). The psychology of superorganisms: Collective decision making by insect societies. *Annual Review of Entomology, 63*, 259–275.
6. Seeley, T. D., Visscher, P. K., & Passino, K. M. (2006). Group decision making in honey bee swarms: When 10,000 bees go house hunting, how do they cooperatively choose their new nesting site? *American Scientist, 94*, 220–229.
7. Wray, M. K., & Seeley, T. D. (2011). Consistent personality differences in house-hunting behavior but not decision speed in swarms of honey bees (*Apis mellifera*). *Behavioral Ecology and Sociobiology, 65*, 2061–2070.