The behavioral ecology of variation in social insects
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Understanding the ecological relevance of variation within and between colonies has been an important and recurring theme in social insect research. Recent research addresses the genomic and physiological factors and fitness effects associated with behavioral variation, within and among colonies, in regulation of activity, cognitive abilities, and aggression. Behavioral variation among colonies has consequences for survival and reproductive success that are the basis for evolutionary change.

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Introduction
Investigating the sources of variation has been an important and recurring theme in social insect research [1]. Here we consider variation at two levels: among individuals within colonies, and among colonies within populations. Because of space limitations we do not provide a comprehensive review; each of our citations is only one example out of many studies.

Variation among individuals within colonies is ubiquitous. In addition, evidence is growing that colonies vary, which means that the range of individual phenotypes in one colony differs from the range in another. The behavior of colony A differs from the behavior of colony B because the combined outcome of the range of behavior among individuals of colony A differs from that combined outcome for colony B.

Many kinds of phenotypic differences lead to both individual and colony variation (reviewed in [2–4]); including: life-history traits (i.e., growth, reproduction, and queen mating frequency [5–10]), morphological traits related to social behavior and physiology [11\textsuperscript{*},12,13,14\textsuperscript{*},15,16, 17,18], and behavioral traits (i.e., regulation of activity, cognitive abilities, or aggression and nestmate recognition [19\textsuperscript{*},20,21]). The development and maintenance of individual and colony variation is influenced by resource availability, abiotic conditions along a geographic cline, social interactions within and between colonies, and population-level genetic factors such as dependent lineages (reviewed in [22]). In most cases, we do not know the source of variation among individuals or colonies. Mutation, small differences in microclimate and resource availability, the developmental noise that leads organisms with the same genotypes to differ, all probably contribute to the variation that we observe.

Behavioral variation
Regulation of activity
Individuals within a colony may exhibit consistent behavioral variation (see Table 2 in [3]) in their propensity to perform particular tasks [19\textsuperscript{*}]. Whether individuals work inside or outside the nest may be associated with a tendency to be in a certain location inside the nest, which affects the probability of interaction with nestmates [23,24]. In the ant Myrmica rubra, individuals that forage outside the nest are more active, exploratory, aggressive, and attracted to light than individuals that work inside nest [25]. Individuals often move from one task to another as they age, for example, from in-nest brood care to nest cleaning to out-of-nest foraging. The mechanisms for this have been best studied in honey bees (reviewed in [26]). In the ant Camponotus fellah, the age-mediated transition from in-nest to foraging tasks also corresponds to changes in social interaction networks [23]. Individuals within a colony may also vary in foraging strategies. In Ectatomma ruidum, some foragers are more likely to collect food by stealing from neighboring nests while others are more likely to collect food by searching the leaf-litter [27,28]. Colony variation in foraging behavior may then arise from variation in the foraging strategies of individuals.

Studies on behavioral variation among colonies have focused on the regulation of activity [29,30,31,32\textsuperscript{*},33]; for example, foraging behavior [34], thermoregulation, and nest cleaning [35\textsuperscript{*}]. Harvester ant colonies differ consistently, from year to year, in the extent to which they curtail foraging activity in dry conditions. Because individual ants live only a year (whereas the queen lives for 20–30 years, and does not begin producing new reproducitives until she is five [36]), consistent differences are apparently inherited in successive cohorts of workers.
[37]. Since the regulation of foraging depends on interactions between outgoing and returning foragers [38,39], it is likely that differences among colonies arise from the variation in individual sensitivity to interactions.

Colonies of bumble bees [40] and honey bees [41] vary in the extent of nectar and pollen foraging. In honey bees, genomic and physiological differences are associated with consistent within-colony variation in individual foraging behavior [26,42]. Social insect colonies also vary in their ability to thermoregulate and clean the nest [35], probably due to physiological variation among individuals within the colony in ability to perceive temperature fluctuations [43,44] or dead nestmates and parasites [35,45,46].

Cognitive abilities
Individuals and colonies vary in learning, memory, sensory bias, and decision-making [3]. In bumble bees, rapid learning is correlated with the ability to remember visual cues [47], and rate of decision-making is associated with nectar foraging [20]. Colonies that learn more slowly harvest less nectar compared to the fastest learning colonies [48]. Colonies also vary in sensory bias, such as color preferences, which may be associated with variation in foraging success and exploratory behavior [49]. For example, colonies of bumble bees that prefer violet collect more nectar than those that prefer blue [20].

Aggression and nestmate recognition
Individuals and colonies may both vary in aggression toward individuals of other colonies [3]. Differences among colonies in cuticular hydrocarbon (CHC) profile are the basis for nestmate recognition in most social insects. The results of nestmate recognition experiments in ants suggest that individuals modify over time their response to the odors of different ants that they meet, so that at any time individuals differ in their responses. Collectively, colonies respond because there are some ants that can identify the odor of any intruder as that of a non-nestmate [21]. Empirical studies suggest that environmental factors might predict CHC profile better than colony of origin [50–52]. For example, leaf-cutter ant colonies (Atta sexdens) that forage on the same plants have similar CHC profiles and are less aggressive toward one another than toward conspecifics with a different diet [53].

In some Polistes spp. (Vespidae, Polistinae), individuals assess variation among workers by their facial patterns. In P. dominula, specific facial patterns, such as the distribution of the black pigment on the clypeus, are associated with dominance rank and nesting success [54]. In P. fuscatus, workers can distinguish individual faces of both nestmates and non-nestmates [55]. In the hover wasp, Liostenogaster flavolineata (Vespidae, Stenogastrinae), individuals prioritize visual facial cues over CHC profiles to distinguish nestmates [56].

An individual’s age or size may be associated with aggression or exploratory behavior. For example, aggression in the wasp, Vespuca vulgaris, tends to increase with age [57]. In the ant Leptothorax aceratorum, older workers with well-developed ovaries tend to be more aggressive and active than younger ones [58]. In some ant species, larger or major workers tend to be more aggressive than smaller workers (e.g., Acromyrmex echinatior, [59]; Oecophylla smaragdina, [60]).

Aggressive behavior appears to be heritable (reviewed for honey bees in [26]), but changes in gene expression are also associated with variation in aggressive behavior. In weaver ants, high expression of octopamine is linked to aggressive behavior [60], whereas in honey bees, octopamine, as well as glutamate and GABA signaling, is linked to exploratory behavior [61,62]. Aggression in honey bees, as in Polistes metricus paper wasps, is linked to a decrease in oxidative phosphorylation [63–65].

Ecological sources and outcomes of variation
Environmental conditions lead to variation among colonies in life history traits within a species across a geographic cline. For example, a temperature gradient is associated with variation in colony growth and activity in subterranean termites [66,67]. Gradients in environmental conditions are associated with intraspecific variation among colonies in life-history and breeding structure [68–70], in resource use [30], and in interactions with other colonies [71] or other species such as pathogens [72–74] and parasitoids [75].

Variation among colonies in behavior can have important ecological effects. For example, differences among harvester ant colonies in the regulation of foraging by feedback from ant–ant interactions [29,76], are associated with differences in reproductive success, in numbers of offspring colonies [37,77]. This suggests that selection is acting on variation among colonies in how individuals respond to interactions. Colony variation in interaction networks can lead to differences in parasite load and susceptibility to infection [78,79].

Variation among colonies may facilitate rapid evolution of invasive species [80,81]. Aggressive and active colonies may have a competitive advantage in the invasive range [82,83], until population densities become very high [81]. When the invasive wasp Vespuca velutina is sympatric with the native wasp Vespa crabro, its foundresses tend to be more active, bolder, and more exploratory than the native species [84]. On the other hand, there is more variation in these traits among the native V. crabro foundresses, perhaps because of a genetic bottleneck effect on V. velutina when they were introduced.
In the fire ant (Solenopsis invicta), colonies vary in queen number, due to epigenetic processes involving large numbers of genes [85]. A polygynous form spread within the invasive range [86] that may be associated with a decrease in aggression and high population densities [87].

Conclusions
Investigating the sources of variation is a central question in evolutionary biology. Variation is a fundamental element of the phenotypes that matter ecologically, and it is the starting point for evolutionary change. Variation among individuals, and among colonies, arises from differences in their behavioral, physiological and epigenetic response to their environments. Environments change, sometimes because organisms modify them, and this amplifies variation. It seems likely that when we compare individuals and colonies in any aspect of their biology, we will find that they vary.

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References and recommended reading
Papers of particular interest, published within the period of review, have been highlighted as:

• of special interest
•• of outstanding interest


The production of continuous size variation of Camponotus ant workers is regulated via DNA methylation, specifically through the conserved cell-signalling gene Epidermal growth factor receptor.


The production of large workers in a stingless bee depends on the spatial arrangement of brood inside the nest. Larvae reared in the center of the nest grow to larger cells and are provisioned with more food than those raised elsewhere. Larger bees are more likely to guard the nest than smaller ones.


Variation among workers within colonies arises from the interplay of worker interactions with each other and their environments. This leads to ecologically important variation among colonies.


31. Wray MK, Mattila HR, Seeley TD: Collective personalities in honeybee colonies are linked to colony fitness. Anim Behav 2011, 81:559-568.


33. Fire ant colonies vary in foraging activity, exploration, and discovery of and recruitment to resources. Variation in activity was correlated with colony growth, and there was evidence to suggest that activity and exploration are partially heritable.


36. Randt JM, Dornhaus A: Bumblebee response thresholds and body size: does worker diversity increase colony performance? Anim Behav 2014, 87:97-106. Continuous variation in worker size and in fanning in response to temperature increase was measured in bumble bee colonies. Colonies varied in their overall performance of removing dead nestmates and cooling the nest. Colony corpse removal was correlated with the average body size of workers in the nest, whereas colony cooling was correlated with the amount of behavioral variation in the nest.


59. Worker behavior, including brood care, aggression, and exploration, was consistent within and across settings. Some workers had a more aggressive and exploratory personality type than others. Ovarian development and age were also associated with worker behavior.


63. Liang ZS, Mattila HR, Rodriguez-Zas SL, Southey BR, Seeley TD, Robinson GE: Comparative brain transcriptomic analyses of scouting across distinct behavioural and ecological contexts in honeybees. Proc R Soc B – Biol Sci 2014, 281:20141868. Previous work [Liang et al. [61]] showed that honey bees that scouted for food also tended to scout for new nest sites, and that scouting behavior was associated with brain gene expression. Here, Liang et al. further investigate gene expression associated with scouting. Both food and nest scouts exhibit similar patterns of glutamate- and GABA-related genes,
but differ in their expression of other genes, such as odour-binding protein 4.


Vespa crabro (native) foundresses vary greatly within their native range. Vespa velutina (invasive) foundresses vary less within the sympatric range of V. crabro, but overall their foundresses tend me more active, bolder, and more exploratory than the native species. These traits may influence their ecological success as invaders.

