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•,12,13,14•,15,16,17,18], and behavioral traits (i.e., regulation of activity, cognitive abilities, or aggression and nestmate recognition [19•,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•]. 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•,33]; for example, foraging behavior [34], thermoregulation, and nest cleaning [35•]. 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 reproductives until she is five [36]), consistent differences are apparently inherited in successive cohorts of workers

[37]. Since the regulation of foraging depends on inter-actions 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•], proba-bly 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, sen-sory 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 colo-nies [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 ex-ample, 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 envi-ronmental factors might predict CHC profile better than colony of origin [50–52]. For example, leaf-cutter ant colonies (*Atta sextens*) 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 distribu-tion 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 ag-gression or exploratory behavior. For example, aggression in the wasp, *Vespula vulgaris*, tends to increase with age [57]. In the ant *Leptothorax acervorum*, 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 smar-agdina*, [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, octopa-mine, 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 colo-nies in life history traits within a species across a geo-graphic cline. For example, a temperature gradient is associated with variation in colony growth and activity in subterranean termites [66,67]. Gradients in environ-mental conditions are associated with intraspecific varia-tion 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 har-vester ant colonies in the regulation of foraging by feed-back from ant–ant interactions [29,76], are associated with differences in reproductive success, in numbers of off-spring 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 colo-nies may have a competitive advantage in the invasive range [82,83], until population densities become very high [81]. When the invasive wasp *Vespa velutina* is sympatric with the native wasp *Vespa crabro*, its foun-dresses tend to be more active, bolder, and more explor-atory 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 bottle-neck effect on *V. velutina* when they were introduced