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Genetic structure and cohesion of insect societies

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One of the major transitions in evolutionary history occurred when individual organisms came together to form complex societies. The advanced social insects (ants, termites, social bees, and social wasps) possess some of the most remarkable examples of such cooperative societies. The development of these social systems represented a highly successful event. Social insects now dominate many terrestrial communities because they effectively manage ecological problems through their integrated social systems.

The evolution of the cooperative behaviors that define social insect societies depended on the genetic structure of populations. Moreover, genetic structure in contemporary populations influences the strength of kin selection and kin conflict. Population genetic structure arises in a variety of ways including intraspecific behaviors associated with mating strategies and dispersal, as well as interspecific interactions related to competition, predation, and parasitism.

My research program focuses on understanding how variation in genetic structure arises within insect societies and how changes in genetic structure affect group members. I use molecular genetic markers in combination with theoretical models to understand the genetic makeup of social insect populations. I then compare patterns of genetic structure to expectations derived from kin selection theory in order to understand the evolution of insect societies. Here, I review research concerned with genetic structure in three social insect taxa: the red imported fire ant, *Solenopsis invicta*, the yellowjacket wasp *Vespula germanica*, and the giant northern termite, *Mastotermes darwiniensis*.

The fire ant *S. invicta* is one of the most widespread and damaging social insect pests. We use genetic markers in combination with mathematical models to understand how *S. invicta* reproduces and comes to occupy new habitats. We assessed nestmate queen relatedness in polygyne (multiple-queen) *S. invicta* using both nuclear and mitochondrial markers. Surprisingly, estimates of queen relatedness calculated with both types of markers did not differ statistically from zero. Furthermore, there was no significant relationship between the genetic similarity and geographic proximity of nests within sites. In contrast, there was strong mitochondrial, but no nuclear, genetic differentiation among sites. These results indicate that nonnestmate queen recruitment occurs at a high frequency in this species. Therefore, kin selection models that rely on the recruitment of only nestmate queens to explain the persistence of polygyny do not apply to *S. invicta*. The genetic structure of polygyne *S. invicta* was further investigated to determine the influence of gene flow and selection in polygyne populations. A novel mathematical model was used to delimit the effects of male gene flow from monogyne (single-queen) populations and selection operating on polygyne ants. Our results indicate that selection on polygyne queens and workers alone, with no monogyne male

gene flow, provided the most parsimonious explanation for observed genotype frequencies in *S. invicta*.

We next turned our attention to genetic structure of the termite *M. darwiniensis*. *M. darwiniensis* is the sole extant member of its family and occupies the basal position in the phylogeny of termites. This study focused on genetic structure of *M. darwiniensis* in its native range in Australia. Workers were sampled from infested trees in distinct locales. Each locale was found within two broader geographic regions. The genotypes of all termites were assayed at six polymorphic microsatellite loci. Statistical analyses indicated that colonies typically fed on multiple trees within locales and extended over vast linear distances. Single colonies were frequently headed by multiple reproductives. Workers were highly related and substantially inbred. Thus, *M. darwiniensis* colonies are characterized by the input of alleles from multiple reproductives, which sometimes engage in consanguineous matings. In addition, our analyses of population structure indicated that locales and regions were significantly differentiated. We suggest that the genetic patterns displayed by *M. darwiniensis* result from selective pressures acting to maintain high relatedness among colony members while allowing colonies to grow rapidly and dominate local habitats.

Finally, we investigated the reproductive patterns of the invasive social wasp *V. germanica* in its introduced range in Australia. The genotypes of all wasps were assayed at three DNA microsatellite markers. Our analyses uncovered significant differentiation among four *V. germanica* populations. Pairwise estimates of divergence between populations indicated that an island population was particularly distinct from populations on the mainland. Within-population analyses revealed that genetic similarity declined with spatial distance, indicating that wasps from nests separated by more than ~25 km belonged to separate mating pools. These data suggest that the observed genetic patterns resulted from bottlenecks experienced by *V. germanica* as it colonized Australia. We also studied patterns of queen reproduction in *V. germanica*. We found that queens typically mated multiply. In addition, the distribution of the minimum number of male mates of queens followed a Poisson distribution, suggesting that the probability of a queen remating was not affected by previous copulations.

Overall, our research on the genetic structure of social insects has uncovered considerable variation in colony structure. Some species display simple genetic structure with colonies headed by one, singly-mated queen. Such colonies represent idealized social structure in insect societies. Other species may be headed by one, multiply-mated queen. In this case, group relatedness is somewhat depressed and can set the stage for conflict among group members. However, this slight drop in relatedness can be offset by benefits derived from mating multiply. Finally, some taxa display very low levels of nestmate relatedness, whereby cooperating individuals are virtually unrelated to one another. These situations run counter to expectations from kin selection theory and likely result from secondary loss of the conditions that originally promoted highly social systems.