SHORT COMMUNICATION

Genome Organization and Social Evolution in Hymenoptera

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Hunt and Page (1995) originally reported that *Apis mellifera* has an unusually large recombinational map and hypothesized that it is related to male haploidy in Hymenoptera. Our results clearly falsify this hypothesis because the Hymenoptera contain both very large (Hunt and Page 1995) and very small genome maps (Antolin et al. 1995; Gadau et al. 1999; Laurent et al. 1998; Fig. 1). An alternative, structural explanation is that *A. mellifera* has a large recombinational map because it has many chromosomes. In addition to needing to explain why it has more chromosomes, no correlation between chromosome number and recombination frequency was found in our study (Table 1). These results suggest functional rather than structural explanations for variation in recombinational size of genomes within the Hymenoptera.

One trend is apparent: parasitic Hymenoptera on average have fewer chromosomes (Sherman 1979) than do social species, but there are also significant differences between parasitic Hymenoptera in their recombination frequencies, suggesting adaptive differences in cross-over rates (e.g., compare *T. brassicae* and *Nasonia* both of which have five chromosomes; Fig. 1). Comparisons of differences in recombination rates of parasitic and social Hymenoptera are probably less illuminating than comparisons within the parasitic or social species because of the phylogenetic distances between them. *A. mellifera* and *B. terrestris* are members of the same family, Apidae, but differ in several aspects of their life histories as well as the genetic and social structure of their colonies (Table 1). *A. mellifera* demonstrates many genetic, anatomical, and behavioral characteristics that result in increased genotypic diversity among workers within colonies. Queens mate many times (polyandry) while in flight in drone congregating areas where large numbers of males from many colonies congregate, insuring outcrossing. *A. mellifera* queens have evolved a mechanism for filling the spermatheca that insures a mixture of sperm from their many mates. Along with high levels of genotypic diversity generated by polyandry, *A. mellifera* increases genotypic diversity among workers with increased rates of recombination (Hunt and Page 1995). These results suggest strong selection for genotypic diversity in honey bees compared with *B. terrestris*, a species that typically mates one time (Table 1).

How can these differences, notably between *A. mellifera* and *B. terrestris*, be explained? Increased recombination can increase the genotypic and, presumably, phenotypic diversity among workers within colonies for multigenic traits when variable genes are linked together on chromosomes. Polyandry can increase genotypic diversity for both multigenic and single gene traits. It has been proposed that polyandry in *A. mellifera* evolved to increase genotypic diversity at the sex locus (Page 1986). However, single locus sex determination should have no effect on recombination rates. It has also been proposed for both *A. mellifera* and *B. terrestris* that genotypic diversity should be selected to diminish pathogen and parasite loads associated with social living (Schmid-Hempel 1998). Some models predict the evolution of higher recombination frequencies

Table 1. List of genetic structure and life history traits of the species compared in Fig. 1

	Nasonia vitripennis × *N. giraulti*	*Trichogramma brassicae*	*Bracon hebetor*	*Bombus terrestris*	*Apis mellifera*
Relative map size	829 cM/80 markers	1330 cM/84 markers	1156 cM/79 markers	1091 cM/80 markers	2020 cM/80 markers
Chromosome number	5	5	10	18	16
Relative average marker distance (cM)	8.4	17.7	17.0	13.5	29.7
Life history traits	Parasitic	Parasitic	Parasitic	Primitively eusocial	Highly eusocial
Mating system	Regularly inbreed	–	Outbreed	Outbreed/monandrous	Outbreed/polyandrous
Sex determination	Not single locus	Not single locus	Single locus	Single locus	Single locus
Parasite load	–	–	–	High	High
Colony size ($n \approx$workers)	Solitary	Solitary	Solitary	Small colonies (200)	Large colonies (30,000–40,000)
Division of labor	–	–	–	Weakly developed	Strongly developed

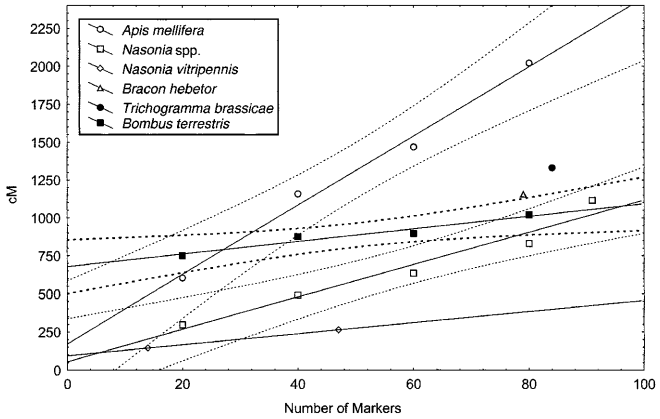

Fig. 1. Comparison of relative map sizes. To calculate relative map sizes for *A. mellifera*, *B. terrestris,* and *Nasonia* spp., the linked randomly amlified polymorphic DNA markers of *A. mellifera* ($n=365$), *Nasonia* sp. ($n=91$ markers, Gadau et al. 1999), and *B. terrestris* ($n=80$ markers, unpublished data) were randomized and map sizes were calculated for 20, 40, 60, 80, and 91 markers, respectively. For every set of markers, map sizes in centimorgans (a measure of recombination frequency) were calculated by adding the distances of linked markers and then adding an additional 40 cM for every unlinked marker. The additional 40 cM were added because we set 40 cM as the maximum recombinational distance allowable for linking two markers. Because all markers were known to be good markers and linked, any not joined into the map must therefore lie more than 40 cM from the end of any linkage group. Relative map sizes should be good predictors of absolute map sizes because for a given number of markers, larger genomes will contain fewer linked markers, and therefore more markers will lie at least 40 cM away from an established linkage group. Values for genome sizes for, *B. hebetor* (Antolin et al. 1995) *T. brassicae* (Laurent et al. 1998), and *N. vitripennis* (Saul 1993) were taken from the literature. For all species with more than two data points the regression line and the 95% confidence limits are shown

through parasite-mediated fluctuating selection under very restricted conditions (e.g., Otto and Michalakis 1998). However, it has also been suggested that an increase in recombination reduces interindividual genotypic variability within a colony, a condition which would potentially benefit the spread of parasites (Schmid-Hempel 1998). However, *A. mellifera* and *B. terrestris* both have significant loads of pathogens and parasites (Schmid-Hempel 1998) and differ dramatically in mating behavior and recombination frequency, suggesting that pathogens and parasites cannot explain their differences in mating behavior and recombination frequency (Table 1). *A. mellifera* and *B. terrestris* also differ in their social structure, especially with respect to division of labor (Table 1). One hypothesis is that more genotypic diversity results in more complex and stable division of labor. In this case, both polyandry and genetic recombination affect diversity, providing the behavioral traits involved in division of labor are multigenic and some of the genes are linked. Multiple, variable QTL have been demonstrated for foraging and defensive behavior in *A. mellifera* (Hunt et al. 1995. 1998), but it is still unknown whether the mapped QTL regions contain more than one linked gene.

We are aware that the information on the distribution of recombination frequency in the insect order Hymenoptera is currently very restricted and scattered. Nevertheless, we would predict, based on a first analysis, that highly eusocial hymenopteran species with large colonies and a highly developed system of division of labor, such as certain species of leaf cutter ants (*Atta* spp. or *Acromyrmex* spp.), yellow jackets (*Vespula* spp.) and stingless bees (*Trigona* spp.), should have higher recombination frequencies than their closely related but socially less developed relatives. Future studies of comparative genomics in Hymenoptera may therefore provide insights into causes, including the role of parasites and pathogens, that select for an increase in recombination.

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