The identification of recombinant males in *Muscidifurax raptorellus* Kogan & Legner, secured from virgin hybrid ♀♀, formed by crossing cohorts from solitary and gregarious populations, supports chromosomal inheritance of gregarious oviposition behavior. Examination of parasitization behavior in female progeny that had recombinant male fathers, indicated the existence of recombinant ♀♂. Such ♀♂ also were able to elicit immediate phenotypic changes in their female mating partners, at intensities expected from their genetic character, as previously observed with original parental ♀♂ in this species. Progeny originating from F₁ mothers and recombinant fathers demonstrated the highest levels of heterosis, as measured by increased parasitization rates and numbers of eggs laid. Although extranuclear inheritance has not been eliminated, its influence on phenotypic changes in progeny seems minimal.

**KEY-WORDS :** Insecta, parasitic Hymenoptera, recombinant males.

Studies of quantitative inheritance of gregarious oviposition (> one individual developed per host) in the parasitoid genus *Muscidifurax*, have revealed that extranuclear factors influence phenotypic changes in females for certain traits (Legner, 1987, 1988a). In *Muscidifurax raptorellus* Kogan & Legner, a South American species parasitizing synanthropic Diptera, ♀♂ are capable of changing the female’s oviposition phenotype upon mating, by transferring an unknown substance. It appears as if a proportion of the genes change expression under the influence of substances in the male seminal fluid. The intensity of this response is different depending on the genetic composition of the male and female (Legner, 1988a, 1989a). Variable degrees of expression of this trait in offspring that result from backcrosses are consistent with a polygenic mode of inheritance.

The behavioral changes after mating are permanent as revealed by increases or decreases in the response maintained for 16 days following a particular mating (Legner, 1987, 1989a, c). Speculations on the nature of the substance in the male seminal fluid have included microorganisms, accessory gland fluids, and behavior modifying chemicals, such as prostaglandins (Legner, 1987, 1988a). Maternal inheritance of extranuclear substances as proposed by Corbet (1985) seemed plausible, although the linear additivity of the traits and variance changes in hybrid versus parental generations pointed to chromosomal inheritance (Legner, 1987, 1988a, 1989a).

Chromosomal inheritance of gregarious behavior could be substantiated further by the formation of recombinant males. Extranuclear influences on reproductive behavior at
mating can be minimized by observing virgin arrhenotokous parasitoids whose oviposition tendencies reflect their genome alone. This study examines the genetic character of \( \delta \delta \) produced by \( F_1 \) females and which possess varying ancestry from solitary and gregarious parents.

**MATERIALS AND METHODS**

**CHARACTER OF PARENTAL STOCK**

Parental parasitoid cultures were obtained from 25 mated \( \Phi \Phi \) each of the Peruvian (solitary) and Chilean (gregarious) races of *Muscidifurax raptorellus* in mass-cultured stock. They were perpetuated for 22 generations in 500 cc screened polystyrene containers with \( ca. 500 \) randomly mated female parasitoids ovipositing on 2000 *Musca domestica* L. puparia for 48-h.

Electrophoretic analyses had previously established extremely low levels of variability in the mass-cultured founder stock, especially when compared to recent field-collected wild cultures (Kawooya, 1983; Legner, 1989). Parasitoids used to start the original colonies were thought to possess only a fraction of the gene pool of the parental wild populations (Kawooya, 1983). In addition, Hymenoptera generally show lower genetic variability than other insect orders (Crozier, 1971, 1975; Metcalf et al., 1975; Kawooya, 1983).

**FORMATION OF RECOMBINANT HYMENOPTERAN MALES**

Some unique considerations are required in the formation of recombinant males in haplo-diploid breeding systems, which although discussed previously (Legner, 1990), will be summarized here because of their importance to the present case. Although normal oogenesis in arrhenotokous Hymenoptera does not deviate from that found in other diploid-diploid organisms, hymenopteran spermatogenesis is highly modified (Crozier, 1975; Legner, 1990). Because hymenopteran \( \delta \delta \) are haploid, marked modifications of spermatogenesis are necessary to ensure that a balanced set of chromosomes is transmitted via that sperm. The principal difference is that the first division is somewhat abortive, with no karyokinesis, so that there is only one true division, an equational one (Crozier, 1975). In most Hymenoptera, the sperm of any one haploid male are identical, at least in the genetic components they carry.

Considering a hypothetical hymenopteran example involving 2 loci in which parental cohorts are homozygous for different alleles at each locus, the \( F_1 \) generation of \( \Phi \Phi \) would be genetically identical and heterozygous. Assuming that the loci in question are unlinked, each \( F_1 \) female would be capable of producing 4 kinds of gametes: \( AB, A'B, AB' \) and \( A'B' \), in equal proportions. Similarly, such virgin \( F_1 \) hymenopteran \( \Phi \Phi \) produce 4 haploid and genetically distinct \( \delta \delta \) from unfertilized eggs: \( AB, A'B, AB' \) and \( A'B' \). However, only 50 % of these \( \delta \delta \) would be of the parental genotypes as opposed to none of the \( F_1 \) females. In this way the recombinant hymenopteran \( \delta \delta \) differ from diploid-diploid systems: there are different kinds of genotypes depending on the number of active loci.

In *M. raptorellus* there are probably more than 8 loci segregating for gregarious or solitary oviposition (Legner, 1990). Thus, the variety of recombinant \( \delta \delta \) in this system would be considerably greater than in the 2 locus example (e.g., \( 2^8 = 256 \) gametes). There would also be proportionally fewer parental genotypes produced among these \( \delta \delta \).

Recombinant \( \delta \delta \) were obtained by random manual selection from \( ca. 500 \) ovipositing \( F_1 \) females. This is believed to have simulated a true \( F_1 \) male population. These \( \delta \delta \) were then mated with another group of \( F_1 \) females that were timed to emerge in synchrony in order to create the \( F_2 \) female generation.