

The results reported here suggest subdivision of the field populations but not subdivision of the cellular populations, and that selection for or against the *Adh*<sup>S</sup> allele acting on the entire content of the inversion will influence the  $\alpha$ -Gpdh alleles. This phenomenon may be a factor helping to explain the maintenance of polymorphism in the *Adh* and  $\alpha$ Gpdh loci and also the maintenance of the *In*(2*L*)*t* inversion.

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## High level of genetic heterozygosity in the hyperparasitic wasp, *Mesochorus nigripes*<sup>1</sup>

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**Summary.** The hyperparasitic ichneumonid wasp, *Mesochorus nigripes*, from Southern Sweden was found to have an over-all heterozygosity ( $H_a$ ) of 0.187 based on allele frequencies of 12 loci in 10 enzyme systems. This high level of genetic heterozygosity has not been reported in any hymenopteran species.

**Key words.** *Mesochorus*; Hymenoptera; Ichneumonidae; electrophoresis; heterozygosity.

Over the last 20 years it has become clear that natural populations of animals possess a wealth of genetic polymorphism. However, very low levels of electrophoretic variation have been found in hymenopteran species. Some species even lack variation altogether<sup>3,4</sup>. Several hypotheses concerning these low levels of intraspecific genetic variability in Hymenoptera have been proposed<sup>5-10</sup>. We report here a case of genetic heterozygosity of a much higher level than previously reported for any hymenopteran species.

The ichneumonid wasp, *Mesochorus nigripes*, is a well-known hyperparasite of two other ichneumonid wasps, *Bathyplectes curculionis* and *B. stenostigma*. These two *Bathyplectes* wasps are themselves larval parasites of the alfalfa weevil *Hypera postica*. Three trips were made to Skurup in Southern Sweden to collect larvae of the alfalfa weevil from which the *Bathyplectes* parasites and *M. nigripes* hyperparasites would emerge. Rearing experiments indicated that this population was arrhenotokous<sup>11</sup>. A total of 92 females and 14 males of *M. nigripes* were obtained and stored at -65°C for use in isozyme analysis. Starch gel electrophoretic techniques and staining methods are described elsewhere<sup>11</sup>. The following enzyme systems were examined: aldehyde oxidase (AO), esterase (EST), alpha-glycerophosphate dehydrogenase (GPDH), hexokinase (HK), isocitrate dehydrogenase (IDH), leucine aminopeptidase (LAP), lactate dehydrogenase (LDH), malate dehydrogenase (MDH), malic enzyme (ME), phosphoglucose isomerase (PGI), phosphoglucomutase

(PGM), and superoxide dismutase (SOD). Two buffer systems of Siciliano and Shaw<sup>12</sup> were used: the tris-citrate buffer system for HK, LAP, LDH, MDH, ME and SOD; and the tris-versene-borate buffer system for AO, EST, GPDH, IDH, PGI and PGM.

Although we originally planned to survey 12 enzyme systems, no usable gels were obtained for EST and LAP. Variations were observed in AO-1, EST and GPDH-1 gels, but they could not be clearly scored, and were thus excluded from the analysis. With the exception of HK-2 locus, the genetic basis of observed isozyme variation was confirmed by examining the electromorphs of 11 haploid males (hemizygote pattern). The gels for HK-2 locus in males could not be scored.

Allele frequencies for the 12 loci that could be scored are listed in the table with the results partitioned into the P,  $H_p$ , and  $H_a$  components of Pamillo and Crozier<sup>8</sup>. As shown in the table, the level of electrophoretic variation in *M. nigripes* is much higher than any hymenopteran species reported in the literature<sup>5,6</sup>. The highest level of heterozygosity in Hymenoptera other than Ichneumonidae was found in the ant, *Conomyrma bicolor*, with  $H_a = 0.100$  based on 9 loci<sup>5</sup>. The greatest degree of genetic polymorphism reported among insects is that of the tobacco budworm, *Heliothis virescens*, having an average H value of 0.389<sup>13,14</sup>.

So far, only 7 species of ichneumonid wasps have been studied electrophoretically. The proportion of polymorphic loci (P) in

Allele frequencies for 12 enzyme loci in *Mesochorus nigripes* (based on female wasps)

AO-2	GPDH-2	HK-1	HK-2	IDH-1	IDH-2
N = 69 1.000 h = 0	N = 72 1.000 h = 0	N = 52 0.337 0.634 0.029 h = 0.483	N = 56 0.411 0.553 0.036 h = 0.524	N = 67 1.000 h = 0	N = 67 1.000 h = 0
LDH	MDH	ME	PGI	PGM	SOD
N = 83 0.813 0.187 h = 0.304	N = 91 0.368 0.632 h = 0.466	N = 84 1.000 h = 0	N = 57 0.079 0.921 h = 0.146	N = 87 0.017 0.948 0.035 h = 0.100	N = 77 0.130 0.870 h = 0.226

Proportion of polymorphic loci, P = 0.583. Gene diversity at polymorphic loci,  $H_p = 0.321 \pm 0.065$  SE. Gene diversity over all loci,  $H_a = 0.187 \pm 0.060$  SE.

*Diadromus pulchellus* is 0.273, and the mean heterozygosity ( $= H_a$  of Pamilo and Crozier<sup>8</sup>) can be calculated to range between 0.070 and 0.112 depending on whether Ldh-1 and Acp-2 are included in the analysis or not<sup>15,16</sup>. The other 6 species reported by Menken<sup>17</sup> have P ranges from 0 to 0.158 and  $H_a$  ranges from 0 to 0.056. The lack of variation in *Mesochorus vittator* is certainly due to the small sample size (2 males and 1 female)<sup>17</sup> and thus cannot be compared with the congeneric species *M. nigripes* in our study. Since genetic diversity is known to have a much greater value of standard error, Graur<sup>6</sup> used at least 15 loci to calculate expected heterozygosity ( $= H_a$ ) in 188 species of insects. If we include the other 4 loci (i.e. AO-1, EST, GPDH-1, and LAP) and assume that they were all monomorphic (although AO-1, EST and GPDH-1 showed variations, they could not be clearly scored), we still have  $P = 0.438$  and  $H_a = 0.141$ . This  $H_a$  value is still higher than reported for any hymenopteran species.

There are indications that some proteins are more likely to be polymorphic than others<sup>18-20</sup>. It is possible that many of the enzymes we surveyed in our *M. nigripes* samples are generally more polymorphic than those surveyed in other hymenopteran species, and thus produced a higher level of heterozygosity in our analyses. However, a comparison of the enzyme systems used in our study and those of Menken<sup>17</sup> and Shaumar et al.<sup>16</sup> revealed that HK-1, HK-2, and SOD are polymorphic in *M. nigripes* but are monomorphic in the other 7 species of ichneumonid wasps. MDH is polymorphic in both *M. nigripes* and *Triclistus yponomeutae*<sup>17</sup>.

Ignoring *M. vittator* for which only 2 males and 1 female were used<sup>17</sup>, our isozyme survey in *M. nigripes* is the first report of genetic variability in a hyperparasitic hymenopteran. Environmental stability conferred by the microhabitat usually results in an increase in the effective population size of a species, and this in turn will contribute to the high levels of intraspecific genetic

variability<sup>15,21</sup>. Our finding in this parasitic wasp seems to agree with this contention.

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## The role of assortative mating among age-classes in *Drosophila melanogaster*: preliminary results

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**Summary.** A series of experiments on age-related mating success and productivity provides evidence for assortative mating among three out of four age-classes in *D. melanogaster*. The preferred mating does not always result in the highest productivity. Three age classes of males contribute to reproduction while only females of the youngest age-class are involved. The progeny size is more affected by the age of the females than that of males. It is assumed that these findings must have important implications for generation overlap in natural populations.

**Key words.** Age-structured population; age-related mating success; assortative mating; generation overlap; *Drosophila melanogaster*.

In a population where individuals belong to different cohorts, the question can be raised as to whether there is effective reproductive isolation or completely random mating among cohorts. Populations of many species are age-structured and the results of natural selection in such populations are of particular importance for the evolution of life-history phenomena such as senescence and age-related patterns of reproduction<sup>1</sup>. In particular, the age-structure determines the frequencies of individuals subject to the age-specific fecundity and viability schedules<sup>3</sup>.

The effect of aging on the mating capacity of male *Drosophila* has been investigated<sup>4-6</sup>. The mating capacity of males declines with advancing age. The decline is not uniform, however, and the age at which flies become infertile or are no longer able to mate shows considerable variations<sup>6</sup>.

The present work attempts to answer two questions: 1) Is there assortative mating among age-classes of *Drosophila melanogaster* and 2) if so, what are the consequences in productivity of 'like' and 'unlike' aged flies. The objective is to analyze the possible relation of these to generation overlap.

The *Drosophila melanogaster* strains used in the experiments were established from wild-caught (1983) females originating from the Taï rainforest in southwestern Ivory Coast (Gif 255.1). Eight outbred strains were similarly synthesized. Each of them originated from 136 virgin individuals, i.e., 4 females and 4 males produced by each of 17 isofemale lines. Individuals were reared on a standard axenic medium<sup>7</sup> at 25°C. Under these conditions, we could observe up to five consecutive overlapping generations. Only the last four were used, however, owing to the small number of surviving individuals belonging to the oldest age-class when those from the youngest emerged.

Four identifiable age-classes were defined according to the generation span (about 13 days) and sexual maturation. These classes correspond to individuals aged 4, 17, 30 and 43 days.

A series of three independent experiments was carried out: 1) *multiple male experiment*: virgin males of the four age-classes were introduced into a 80 × 40 × 20 mm vial with virgin females of the youngest age-class (4 days old); 2) *multiple female experi-*