

whether the conversion of progesterone was catalyzed by hemoglobin or by a specific enzyme. It was reported that the 20 $\alpha$ -hydroxysteroid dehydrogenase activity disappeared from hemolysates during purification of 17 $\beta$ -hydroxysteroid dehydrogenase by (NH<sub>4</sub>)<sub>2</sub>SO<sub>4</sub> precipitation<sup>3</sup>. However, the presence of a specific enzyme for this converting activity is apparent, because no hemoglobin was detected in our enzyme preparation.

Concerning human blood, it has been thought that the steroid metabolic system could have a rather large capacity<sup>6</sup>. Although it is not possible to predict this enzyme activity in blood in vivo quantitatively from the present results, the total activity in this system is considered to be 10–25% of that of human testes<sup>11</sup>, and 1–4 times as much as in human placenta<sup>12</sup>.

The physiological significance of the presence of 20 $\alpha$ -

hydroxysteroid dehydrogenase activity in erythrocytes is still not known. In testes, a role for 20 $\alpha$ -hydroxysteroid dehydrogenase has been described in the regulation of steroid biosynthesis by the feed-back of products of this enzyme towards progesterone<sup>11</sup>. This steroid dehydrogenase in erythrocytes may have a role in supporting the metabolic regulation of the steroids.

Partial purification of 20 $\alpha$ -hydroxysteroid dehydrogenase activity from a human hemolysate fraction

Fraction	Total protein (g)	Total activity*	Specific activity**	Total hemoglobin (μmoles)
Total hemolysate	15.3	115.5	7.55	1.26
Centrifuged supernatant	11.7	137.9	11.8	1.00
membranes	3.74	13.2	3.53	0.29
DEAE-cellulose eluted	0.39	38.2	97.9	<0.000.2

\*pmoles 20 $\alpha$ -hydroxyprogesterone-4-en-3-ones/min; \*\*pmoles 20 $\alpha$ -hydroxyprogesterone-4-en-3-ones/min/g.

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## Mating patterns of virgin and inseminated *Drosophila melanogaster* of different alcohol dehydrogenase (*Adh*) genotypes

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**Summary.** Female choice mating experiments showed virgin female *D. melanogaster* of the 3 *Adh* genotypes chose heterozygous (*Adh<sup>F</sup>/Adh<sup>S</sup>*) males most commonly. Inseminated females chose mates randomly, but the likelihood of a female remating was genotypically dependent.

The description of mating patterns in natural populations of *Drosophila* is complicated by a common incidence of multiple inseminations<sup>2–8</sup>. Multiple insemination may be of considerable evolutionary significance as it has the potential to influence the level of genetic variability in a population<sup>3</sup> and may influence components of fitness such as fertility and fecundity<sup>5,9</sup> although this has not been demonstrated in all studies<sup>10,11</sup>. Furthermore, the choice of a 2nd mate may be influenced by previous mating experience<sup>12,13</sup>. These, and other, mating characteristics may contribute to the maintenance of enzyme polymorphisms in *Drosophila*<sup>8,14–16</sup>. This paper reports the results of female choice experiments designed to test the effect of the initial mating choice on subsequent mating behaviour and to compare the mating patterns of *Adh* phenotypes in the initial and subsequent matings.

**Materials and methods.** The *Adh* genotypes of females collected individually from the 'Chateau Tahbilk' vineyard population<sup>17</sup> were determined by cellophore electrophoresis<sup>18</sup>. Homozygous (*Adh<sup>F</sup>/Adh<sup>F</sup>* or *Adh<sup>S</sup>/Adh<sup>S</sup>*) females were progeny tested and iso-female strains started from females

inseminated by males of the same *Adh* genotype as their own. 10 iso-female strains of each homozygote were pooled to generate the 2 pure breeding strains used in this study. Heterozygotes were produced by crossing these strains. Individual 2–3-day-old virgin females of each genotype were placed with 3 2–3-day-old males, 1 of each genotype, in a 10×2.5 cm cylindrical glass vial. Prior to each trial males of each genotype were marked with 1 of 3 coloured UV-fluorescent dusts, thereby making them visibly distinguishable. The colour used for each genotype was randomized between experiments. A 30-min mating period was allowed. When mating occurred the genotype of the successful male was ascertained and at the cessation of copulation the female was placed in a vial containing standard medium. Inseminated females were held until 7–10 days old and then the mating choice procedure was repeated. 200 virgin females of each genotype were initially tested over a 9-generation period. At 3-generation-intervals 7–10-day-old virgin females were tested as in the original female choice experiment, a total of 45 being tested for each genotype.

Table 1. Alcohol dehydrogenase (*Adh*) genotypes of mating pairs between virgin females of specified age and 2-3-day-old males

Female age <i>Adh</i> genotype	2-3-day-old				7-10-day-old			
	♀ <i>Adh<sup>F</sup>/Adh<sup>F</sup></i>	<i>Adh<sup>F</sup>/Adh<sup>S</sup></i>	<i>Adh<sup>S</sup>/Adh<sup>S</sup></i>	Totals	<i>Adh<sup>F</sup>/Adh<sup>F</sup></i>	<i>Adh<sup>F</sup>/Adh<sup>S</sup></i>	<i>Adh<sup>S</sup>/Adh<sup>S</sup></i>	Totals
♂								
<i>Adh<sup>F</sup>/Adh<sup>F</sup></i>	50	44	44	138	10	11	8	29
<i>Adh<sup>F</sup>/Adh<sup>S</sup></i>	84	85	81	250	19	19	18	56
<i>Adh<sup>S</sup>/Adh<sup>S</sup></i>	42	45	43	130	10	10	7	27
Totals	176	174	168	518	39	40	33	112
Male mating total $\chi^2_2$	52.14***				14.05***			
Female mating total $\chi^2_2$	0.20				0.77			
Contingency $\chi^2_4$	0.53				0.44			

\*\*\*  $p < 0.001$ .Table 2. *Adh* genotypes of 1st and 2nd males inseminating females of specified *Adh* genotypes

♂ <i>Adh</i> genotype	Female <i>Adh</i> genotype				<i>Adh<sup>F</sup>/Adh<sup>S</sup></i>				<i>Adh<sup>S</sup>/Adh<sup>S</sup></i>			
	<i>Adh<sup>F</sup>/Adh<sup>F</sup></i>	<i>Adh<sup>F</sup>/Adh<sup>S</sup></i>	<i>Adh<sup>S</sup>/Adh<sup>S</sup></i>	Totals	<i>Adh<sup>F</sup>/Adh<sup>F</sup></i>	<i>Adh<sup>F</sup>/Adh<sup>S</sup></i>	<i>Adh<sup>S</sup>/Adh<sup>S</sup></i>	Totals	<i>Adh<sup>F</sup>/Adh<sup>F</sup></i>	<i>Adh<sup>F</sup>/Adh<sup>S</sup></i>	<i>Adh<sup>S</sup>/Adh<sup>S</sup></i>	Totals
1st Male												
2nd Male												
<i>Adh<sup>F</sup>/Adh<sup>F</sup></i>	11	15	7	33	7	14	10	31	3	12	6	21
<i>Adh<sup>F</sup>/Adh<sup>S</sup></i>	10	20	10	40	11	13	8	32	8	12	4	24
<i>Adh<sup>S</sup>/Adh<sup>S</sup></i>	5	19	7	31	6	15	8	29	7	7	6	20
Totals	26	54	24	104	24	42	26	92	18	31	16	65
1st Male mating total $\chi^2_2$	16.23***				6.35*				6.12*			
2nd Male mating total $\chi^2_2$	1.29				0.15				0.40			
Contingency $\chi^2_4$	2.83				2.02				4.11			

\*  $p < 0.05$ ; \*\*\*  $p < 0.001$ .

**Results and discussion.** Table 1 provides the mating patterns of virgin females. The heterozygous male is much more successful than either homozygote, which mate with similar frequency, as assessed by comparison of the male mating totals of each genotype. Females of each genotype mate equally frequently and there is no evidence of assortative mating (contingency  $\chi^2$ ). The mating performance is independent of female age (table 1).

Of 518 initial matings, 261 females remated (table 2). Fast homozygotes remated more, and slow homozygotes less commonly than expected ( $\chi^2_2 = 7.41$ ;  $p < 0.005$ ) on the basis of the frequencies of the initial matings (table 1). The genotype of the 1st mating partner did not influence the probability of a female remating nor the subsequent choice of a 2nd mate (table 2), unlike the observations of other studies<sup>12,13</sup>. The 2nd male was equally likely to be of any of the 3 genotypes.

The relative mating advantage of heterozygous males and the similar mating propensities of females at the initial mating is supported by field data<sup>8</sup>. However, it is problematical if the male mating patterns can be explained specifically in terms of the *Adh* locus. For instance, wing area influences male mating success<sup>19</sup> and an association has been found between wing length and *Adh* genotypes<sup>20</sup>. This association may result from linkage disequilibria between the *Adh* locus and closely linked genes which influence wing dimensions<sup>21</sup>, the mating patterns observed being due to the effects of these. Whatever the cause, there is an obvious difference between the mating patterns of males with virgin and inseminated females. The reproductive condition of the female is, therefore, important in her response to male stimuli<sup>22,23</sup>.

The mating patterns observed in these experiments contribute towards the maintenance of the *Adh* polymorphism in natural populations<sup>8</sup>. More generally, a mating strategy

with the potential for both preferential and random insemination provides considerably more evolutionary flexibility than a system in which only single mating is possible, or one in which the outcome of matings subsequent to the 1st is determined by the initial choice of a mating partner.

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