Curtsinger, J.W. Stanford University, Stanford, California. [Present address: North Carolina State University, Raleigh, North Carolina] Embryonic lethality associated with multiple inversion heterozygosity in D. pseudoobscura.

In several species of Drosophila females heterozygous for two or more unlinked inversions produce high frequencies of inviable embryos (Riles 1965 and references therein). Intense selection against multiply heterozygous females can result: Terzaghi and Knapp (1960) reported 95%, 93%, 79% and 59% egg hatchability among progeny of D. pseudoobscura females heterozygous for zero, one, two, and three unlinked inversions respectively. The resulting selection might account for the restriction of inversion polymorphism mostly to one chromosome: once an inversion system is established, the increase of new inversions (initially present only in heterozygous condition) on nonhomologous chromosomes would be inhibited by reduced fitness of some carriers.

Maternal genotype[1]		Total eggs	Percent hatch	t-test	Probability[2]
X/X	ST/ST	225	.964	t=0.11	p=0.912
X/SR	ST/ST	186	.962		
X/X	AR/ST	231	.978	t=2.99	p=0.003
X/SR	AR/ST	206	.917		
X/X	TL/ST	196	.990	t=3.10	p=0.002
X/SR	TL/ST	202	.936		
X/X	PP/ST	186	.946	t=2.17	p=0.030
X/SR	PP/ST	150	.880		
X/X	CH/ST	227	.991	t=4.52	p<0.001
X/SR	CH/ST	215	.907		
All single hets.		1026	.974	t=5.85	p<0.001
All double hets.		773	.912		

[1] X = Standard (X)
SR = "Sex-Ratio" (X)
ST = Standard (III)
AR = Arrowhead (III)
TL = Tree Line (III)
PP = Pikes Peak (III)
CH = Chiricahua (III)

[2] Two-tailed test.

In D. pseudoobscura the X-linked "Sex-Ratio" inversions are the only widespread structural polymorphisms other than the extensive system of inversions on III. Anderson et al. have investigated possible selective interactions between the X chromosome and third chromosome inversions by measuring egg-to-adult viability among progeny of females jointly heterozygous for "Sex-Ratio" and third chromosome inversions. They found no reduced fitness compared to progeny of singly heterozygous or doubly homozygous females. However, the method of fitness estimatation employed confounds embryonic mortality with larval and pupal viability. Direct measures of embryonic mortality among progeny of females heterozygous for inversions on III and either homozygous on the X chromosome are presented here.

"Sex-Ratio" stocks were collected at Jasper Ridge Biological Preserve in San Mateo County, California. Third chromosome stocks were obtained from Dr. W. Anderson. Stocks were maintained on Carolina Instant Medium at approximately 21°C. Groups of ten 3-day-old females of each of the 10 genotypes shown in the table were mated with X/Y ST/ST males. Eggs were collected for 24 hours on day 5 and scored for hatching for 3 days. Dead embryos turn brown, while unfertilized eggs (two observed) remain white.

Results of the zygotic mortality observations are shown in the table. Standard X homozygotes and Sex-Ratio heterozygotes produce indistinguishable proportions of inviable embryos, provided individuals are also homozygous for inversions on III. However, among third chromosome heterozygotes, X chromosome heterozygotes consistently produce more inviable embryos than X chromosome homozygotes. Thus the deleterious effect of multiple inversion heterozygosity in D. pseudoobscura is confirmed for the two sets of inversions which are widespread in natural populations.

While the pertinent pair-wise comparisons of embryonic mortality shown in the table are statistically significant, the resulting selection differentials are small compared to those reported by Terzaghi and Knapp (1960) for other inversions. Excessive embryonic mortality among progeny of multiply heterozygous females might result from meiotic mis-pairing and subsequent production of aneuploid gametes. Sex-Ratio heterozygotes could be less sensitive to mis-pairing as a result of the unique inversion arrangement, consisting of three non-overlapping inversions which preserves chromosome "flexibility". On the other hand, the proportions of inviable embryos observed in this study show no obvious relation to the length of third chromosome inversions carried by double heterozygotes.

The selection differentials reported here are small compared with other modes of selection associated with Sex-Ratio, which can include strong viability, fertility, and sexual selection (Wallace 1948, Policansky 1979, Curtsinger and Feldman 1979). Thus these data confirm the assertion of Anderson et al. that third chromosome heterozygosity is unlikely to significantly influence the geographical distribution of Sex-Ratio inversions through increased embryonic mortality among progeny of multiple inversion heterozygotes.

References: Anderson, W.W., Th. Dobzhansky and C.D. Kastritsis 1967, Amer. Nat. 101: 89-93; Curtsinger, J.W. and W.M. Feldman 1979, Genetics, in press; Policansky, D. 1979, Amer. Nat. 114:672-680; Terzaghi, E. and D. Knapp 1960, Evol. 14:347-351; Riles, L. 1965, Genetics 52:1335-1343; Wallace, B. 1948, Evol. 2:189-217.

Eckstrand, I.A. and R.H. Richardson.
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Comparison of water balance kinetics between laboratory-reared and field-caught D. mimica.

Drosophila mimica are found on the island of Hawaii in a variety of habitats, ranging from rain forests to arid regions. The species is usually associated with the soapberry tree, Sapindus saponaria, and the flies are usually found courting, feeding, or fighting on the leaf litter. Although D. mimica are easily captured, the require special conditions to rear in the laboratory. However, the Drosophila Species Resource Center at the University of Texas maintains several stocks, including K85P1, which is the "standard" line.

The ability to remain in water balance is probably a highly selected character (Eckstrand 1979), and physiological, morphological, and behavioral adaptations are all important to survival in field animals. It is likely, however, that the fitness components of water balance control differ between field and laboratory flies. To test differences between field and laboratory flies, transpiration and sorption rates for each group were determined by using tritiated water to measure net water uptake and loss. The techniques for this procedure are found in Eckstrand (1979).

Table 1. Comparison of transpiration rate constants and sorption rates in laboratory and field-caught D. mimica.

		K85P1		Field	
a_V	Sex	k_T (%/hr)	m_S (mg/hr)	k_T (%/hr)	m_S (mg/hr)
0.99	F	-0.068	0.179	-0.328	0.838
	M	-0.094	0.168	-0.249	0.419
0.70	F	-0.165	0.273	-0.177	0.301
	M	-0.150	0.201	-0.229	0.279

Table 1 gives the net transpiration rates k_T or % body water lost each hour) and the net sorption rates (m_S or the mg of water taken up each hour) for laboratory-reared and field-caught flies tested at either 0.99 a_V or at 0.70 a_V (a_V = relative humidity/100). Laboratory animals have lower transpiration and sorption rates than do field-caught flies, especially at the high a_V. Culture conditions select for inactivity, and because laboratory flies expend little energy searching for food and mates, they probably have lower metabolic rates than do their wild counterparts. Field flies are noticeably more active than those reared in the laboratory. Their high activity level is probably supported by high metabolic rate which requires that the flies open their spiracles to obtain oxygen. This would result in increased transpiration. Sorption across the tracheal surfaces or the rectal pads might be enhanced to compensate for the increased water loss. At the low humidity, both field and laboratory D. mimica are less active, and their transpiration and sorption rates are similar. Field flies may additionally rely on behavioral adaptations and habitat selection to reduce water loss. Therefore, they may not require strict physiological regulation of water loss at low a_V's. However, laboratory animals, which cannot reduce water loss by habitat selection, may depend relatively more on physiological control of water balance.

References: Eckstrand, I.A. 1979, Ph.D. dissertation, The University of Texas at Austin, 190 pp.