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Competition Between Strains With Autosomal and Standard Sex–determining Mechanisms in the Housefly *(Muscidae)*

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Abstract: Experimental cages started with a mixture of flies at three different ratios (1:9, 5:5, 9:1) from populations having heterosomal and autosomal sex–determining mechanisms were cytogenetically examined over six generations at two different temperatures (25 °C and 35 °C). In general, there was an increase in the frequency of XX males in all competitive population cages. Abnormal testes and intersex appearance, frequent X chromosome aneuploidies and deviation from a 1:1 sex ratio were observed.

Key Words: *Musca domestica* L. Competition, cytogenetics, autosomal sex–determining mechanism, evolution.

Karasinekte *(Muscidae)* Otozomal ve Standart Eşey Belirleme Mekanizmalı Irklar Arasında Yarış

Özet: Otozomal ve heterozomal eşey belirleme mekanizmalarına sahip populasyonlardan, üç farklı oranda (1:9, 5:5, 9:1) sineklerin karışımı ile başlatılan iki farklı ısıdaki (25 °C ve 35 °C) deneysel kafesler, altı generasyon boyunca sitogenetik olarak araştırıldı. Genel olarak bütün populasyon kafeslerinde XX erkek frekansında bir artış vardı. Anormal testisler, interseksüel görünüş, sık X kromosomu aneuploidisi ve 1:1 eşey oranından sapmalar gözlendi.

Anahtar Sözcükler: *Musca domestica* L., yarış, otozomal eşey belirleme mekanizması, evrim.

Introduction

It is known that in housefly populations, sex is generally determined by a heterosomal mechanism (XX females and XY males) (1, 2). However, researchers from different countries suggest that autosomal sex–determination has been rapidly spreading and replacing the standard heterosomal system (3, 4, 5, 6). This increase in the frequency of autosomal sex–determination in natural housefly populations has been found to be related to geographical altitude and latitude in European populations (3, 7, 8). Climatic factors and widespread usage of insecticides have been suggested as the reason for the rapid invasion of autosomal sex–determination factors in houselfy populations in different parts of the world (9, 10, 11). The most frequently mentioned chromosomes having both autosomal sex determining factors and resistance genes to insecticides are the second and the third chromosomes. The other explanation of why non–standard genotypes are being favoured by selection is that an invading male determinant creates new, competitively superior genotypes (10, 12). Transposition of male determining factors *(M)* mediated by one or more transposable elements has been suggested as a cause of autosomal *M* factor polymorphism (13).

The objective of this study was to compare the autosomal and standard sex–determining mechanisms in hybrid populations at different ratios and temperatures.

Materials and Methods

Strains of houseflies. Cytogenetic examination has shown the XX male frequency in the Trabzon and İzmit populations to be 100%. The Polatlı population only had 3% XX males (14) and thus was considered to be of the standard heterosomal type.

Laboratory conditions. Populations were reared at constant 24h illumination (60 watt fluorescent lamp), 25±3 °C temperature (except the competitive populations reared at 35±3 °C). Egg were collected from the population cages, and two rearing vials containing 350 eggs/100 g larval medium were prepared for each population over six generations. Adult flies were kept in

30x30x30 cm population cages and fed with powdered milk, cube sugar and water.

Experimental procedures. Experimental hybrid cages were started with a mixture of flies at three different ratios (1:9; 5:5; 9:1) from populations having heterosomal and autosomal sex–determining mechanisms. Two identical sets of population cages were prepared by a mixture of flies from Trabzon (T): Polatlı (P) and İzmit (I): Polatlı (P). One set of population cages was kept at 25±3°C and the other set was maintained at 35±3°C. All population cages uere initiated with 30 pairs of virgin adults. At every generation, emerged flies were counted and sex ratio was computed and the 25–30 males were taken from each population cage and examined cytogenetically to find out the ratio of XX males.

Cytogenetic examination. Cytological analysis consisted of microscopic examination of spermatogonial cells of the first meiotic divisions in the testes (15). Pive pairs of autosomes and one pair of heterosomes (sex chromosomes) were identified according to size and centromere position (16), and photographs were taken using Kodak ASA 400 film. The preparations were sealed with nail polish for re–examination. Images were magnified 500 times for chromosomal identification in order to determine the frequency of XX males from each population cage.

Results

The results of cytogenetic examinations of the populations in compettion reared at 25°C and 35°C are given in Table 1. The values in parentheses show an increased percentage of XX males in competing populations over six generations. The following karyotypes were identified in males: XY, XX, 0Y, XO, XXY, XXXY, XXX (Figure 1). The number of aneuploid males was slightly higher in the populations reared as 35°C (7.81%) than in the populations reared at 25°C (5.75%), but the difference was not significant. In general, there was an increase in the frequency of XX males in all population cages (except those started with a 5I:5P ratio at 25°C) over six generations.

Testes with abnormal formation were observed during dissection for cytogenetic examination (Figure 2). Some of these abnormal testes had ovarium–like tissues or reduced size. The presence of intersex individuals was also observed in these hybrid populations. The populations prepared with Trabzon and Polatlı strains produced more intersex individuals than the populations prepared with İzmit and Polatlı strains. There were more intersex individuals reared at 25°C than at 35°C, and the number of intersex individuals decreased over the generations at both 25°C and 35°C. Variations in the sex ratio were random.

Discussion and Conclusion

Latitudinal and altitudinal effects on the distribution of XX male frequency have been reported for housefly populations in Europe (3, 4, 8). Franco et al. (3) suggested that climate influences both the type and frequency of sexual determinants in housefly populations, and that it might affect the survival of the overwintering stage, the length of development or the adult life span. According to them, since higher temperature increases the number of generations, the localization of autosomal populations in Central and Southern Italy would represent the more advanced stage of a micro–evolutionary process by climate and involve autosomal sex–determinants. The mobile genetic elements have the potential to increase variability in a gene pool by acting as mutagenic agents. Green (13) has suggested that the *M* factors of different loci may be homologous in ancestry, and are capable of being transposed to different sites. According to Hickey's model (17), a transposon that causes sex–determination in the host would favour its own spread. Among eukaryotes, it is also known that mating type in yeast is controlled by a transposable genetic element (18). Some environment might produce a selective advantage for mutator activities associated with these elements (19, 20). The idea here is that the progeny of dysgenic crosses experienced very high mutation frequencies and some of the resulting mutants were selected, thus fixing the respective trasposable elements. In order to check these possibilities, the effects of environmental temperature, the competitive differences of Trabzon and İzmit populations and the ratio of non–standard: standard populations were tested. The direction of change in sex–determining mechanisms was found in favour of autosomal factors in these populations. There was an autosomal advantage in competition between flies with autosomal and heterosomal sex–determining factors (Table 1). The populations started with Trabzon and Polatlı flies showed more XX male advantage than the populations started with İzmit and Polatlı flies. Cytogenetically examined aneuploidy of X in males were XXX, XXY, XXXY, XO, YO (Figure 1) in these competitive populations, but flies without at least one X or Y were

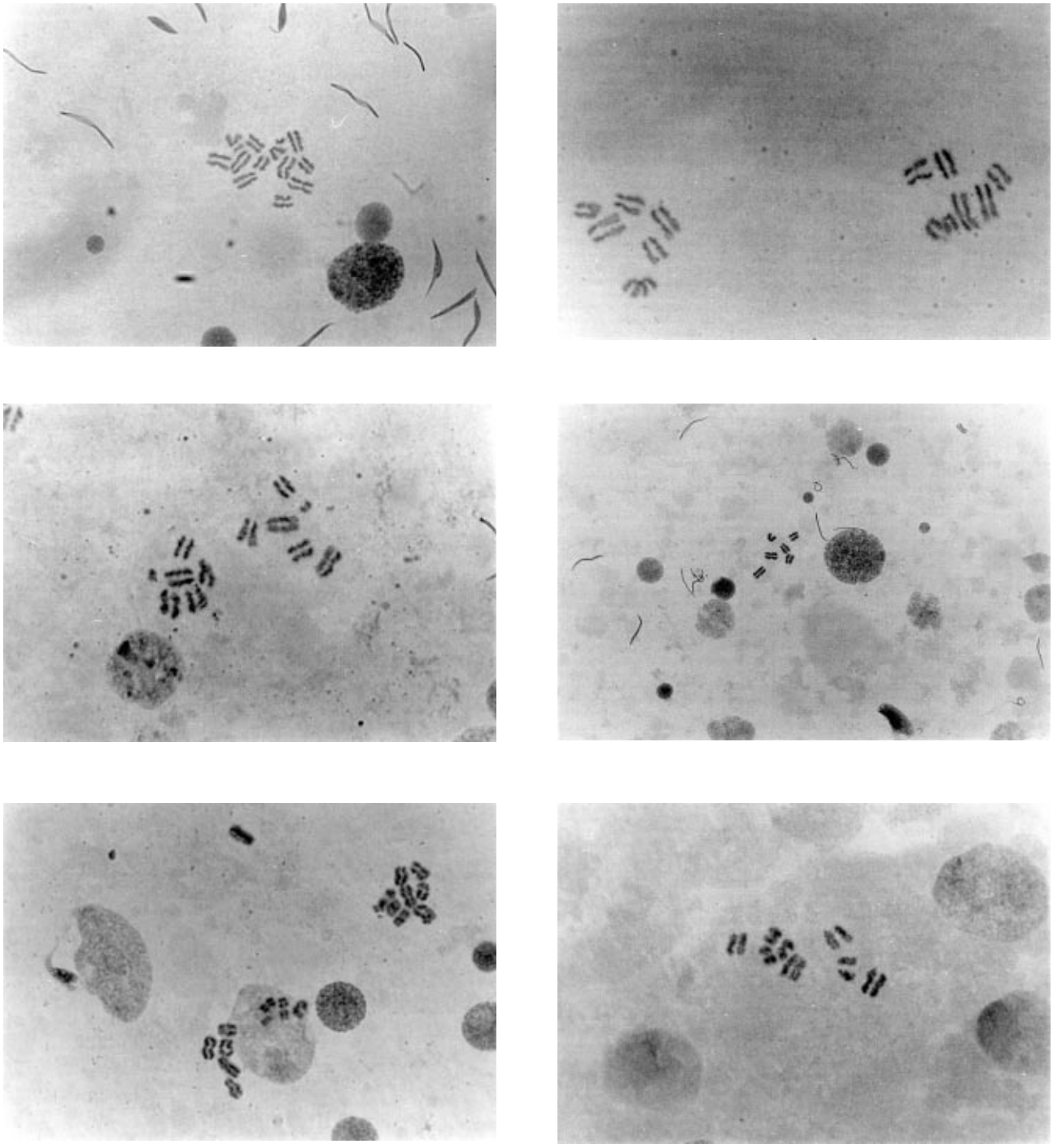

Figure 1. Testis squash meiotic preparations from houseflies having XY(a), XX(b), YO(c), XO(d), XXXY(e) and XXX(f) sex chromosomes. Magnification: 100X5.

never observed. As confirmed by many investigators (3, 10), chromosome X is neutral with regard to sex–determination, but the obligation of having at least one of X or Y for all flies examined indicated some vital function of sex chromosomes. Testes with abnormal formation (Figure 2) in hybrid populations (Trabzonx

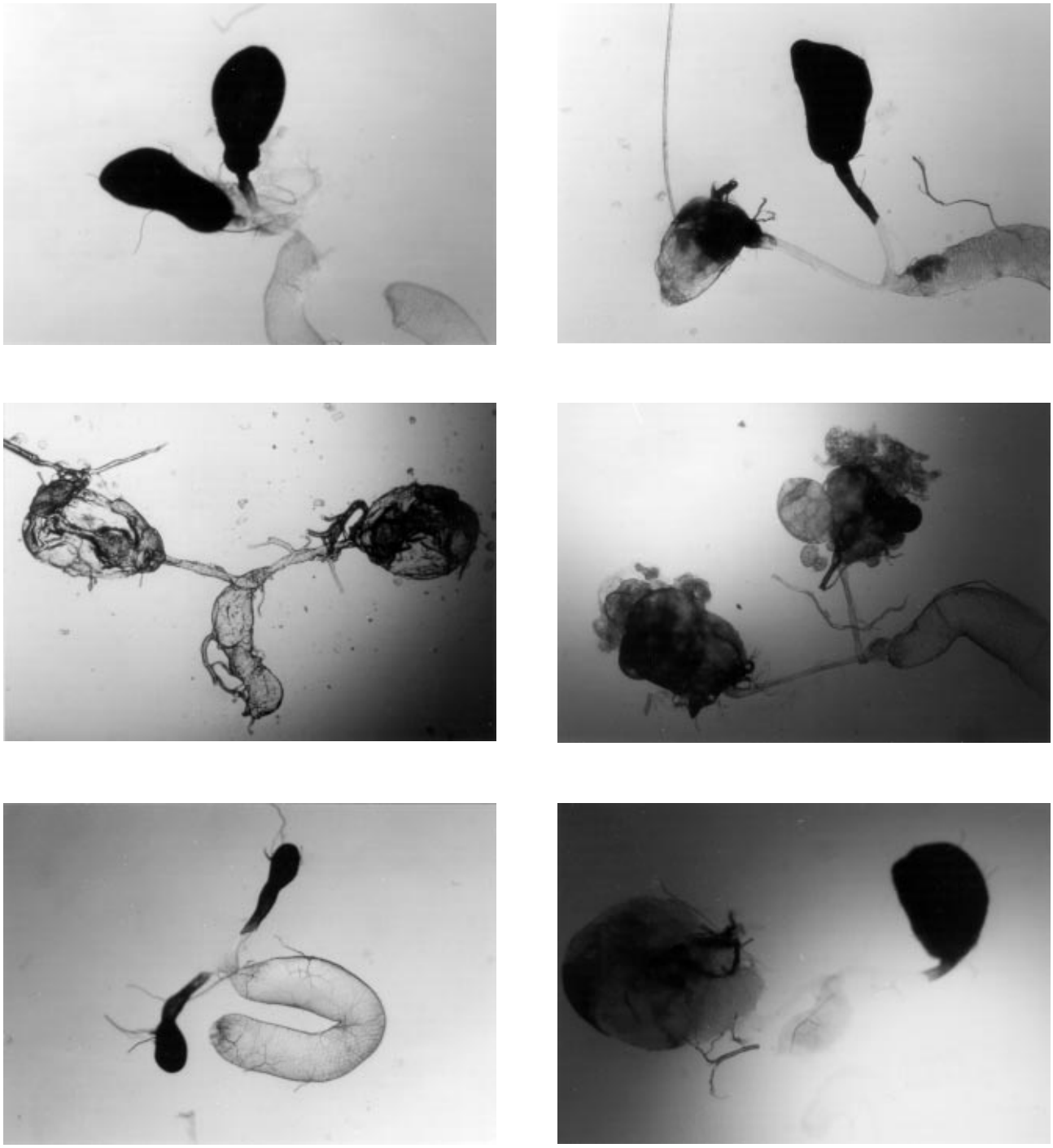

Figure 2. A pair of normal testes (a) and the abnormal testes (b–f) of houseflies. Magnification: 10X5.

Polatlı), especially those reared at 35 °C, are similar to the abnormal gonads of dysgenic *Drosophila* (25). Observation of abnormal gonads, intersex appearance, many cases of aneuploidy of X chromosome and strong deviations from the 1 male: 1 female sex ratio (22) suggest the possible existence of transposons in the housefly populations of Turkey.

Table 1. The results of cytogenetic examinations of the populations in competition reared at 25 °C and 35 °C. The values in parentheses show the percentage of XX males. T: Trabzon, İ: İzmit, P: Polatlı.

	1T: 9P		5T:5P		9T:1P		1İ:9P		5İ:9P		9İ:1P	
	25 °C	35 °C	25 °C	35 °C	25 °C	35 °C	25 °C	35 °C	25 °C	35 °C	25 °C	35 °C
1th Generation	12XX (50%) 12XX 3Y0	1XX (9.1%) 10XY	18XX (72%) 7XY	14XX (66.6%) 7XY	24XX (85.7%) 4XY	16XX (84.2%) 3XY 1XXX	2XX (12.5%) 14XY 1Y0	6XX (30%) 14XY 1Y0 1XXX	7XX (87%) 1XY	16XX (57.1%) 12XY	16XX (%) 9XY	15XX (88.2%) 7XY
	27	11	25		28	20	17	22	8	28	25	17
2th Generation	11XX (57.8%) 8XY 1Y0	1XX (4%) 24XY 1Y0	18XX (69.2) 8XY	8XX (57.1%) 6XY	15XX (83.3%) 3XY	14XX (85.7%) 2XY 4Y0	9XX (50%) 9XY	9XX (34.6%) 17XY 1Y0	18XX (69.2%) 8XY	2XX (10%) 18XY 3X0	14XX (60.8%) 9XY	14XX (60.8%) 9XY 3XXY 2XXXY 1XXX
	20	26	26	14	18	20	18	27	26	23	23	29
3th Generation	12XX (63.8%) 7XY 8X0 4Y0	6XX (33.3%) 12XY 1X0 3Y0	14XX (66.6%) 7XY 2X0	17XX (85%) 3XY 1XXX	22XX (81.5%) 5XY 2X0	17XX (85%) 3XY 3X0 1X0 1XXX	11XX (45.8%) 13XY 6X0	8XX (33.3%) 16XY 1X0 1Y0	13XX (46.4%) 15XY 4X0 2XXY	4XX (12.2%) 29XY	25XX (86.2%) 4XY	15XX (68.2%) 7XY 1XXY 1XXX
	31	22	23	21	29	25	30	26	34	34	29	24
4th Generation	20XY (74%) 7XY 1X0	17XX (51.5%) 16XY 2Y0	14XX (50%) 14XY	21XX (85%) 4XY	25XX (89.3%) 3XY 1Y0 1X0	14XX (87.5%) 2XY	8XX (33.3%) 16XY 2Y0 5X0	8XX (27.6%) 16XY 2Y0	10XX (32.3%) 21XY 1X0	10XX (30.8%) 23XY 2Y0 1XXY	35XX (100%) 0XY	16XX (55.2%) 13XY 3X0 1XXX
	28	35	28	25	30	16	31	30	32	36	35	33
5th Generation	22XX (78.5%) 6XY 1Y0 1X0	21XX (70%) 9XY 3Y0	17XX (62.9%) 10XX	22XX (78.5%) 6XY	19XX (86.3%) 3XY 1Y0	25XX (100%) 0XY	13XX (54.1%) 11XY 1Y0	7XX (23.3%) 23XY 6Y0	4XX (28.5%) 10XY 1Y0	12XX (34.2) 23XY	30XX (100%) 0XY	22XX (88%) 3XX 4XXX 1XXY
	30	33	27	28	23	25	25	36	15	35	30	30
6th Generation	22XX (84.5%) 4XY	15XX (60%) 10XY 2Y0 2X0	15XX (60%) 10XY	19XX (65.5%) 10XY 2X0 1XXY	22XX (88%) 3XY	13XX (100%) 0XY 5X0	8XX (40%) 12XY 1Y0 1XXY 1X0	6XX (33.%) 12XY 1Y0	10XX (33.3%) 20XY 2XY	10XX (47.6%) 11XY 1XXY	30XX (100%) 0XY	29XX (100%) 0XY 1XXY
	26	29	25	32	25	18	23		32	22	30	30

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