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Temporal and spatial trends in allozyme frequencies in house fly populations, *Musca domestica* L.*

W. C. Black IV and E. S. Krafsur

Department of Entomology, Iowa State University, Ames, IA 50011, USA

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Summary. Allelic and genotypic frequencies were sampled from a single age class of the common house fly, *Musca domestica* L., at five farms on six dates from July 6 to October 12, 1982. Allozymes at six loci were resolved with vertical polyacrylamide gel electrophoresis. No consistent departures from random mating were detected. No consistent linkage disequilibrium was observed. Allele frequencies at the farms changed in independent and unpredictable ways. Gene frequencies at the five farms were initially divergent, converged in midsummer, and then progressively diverged. The divergence occured in mid-August when fly populations were large. Variation in gene frequencies at adjacent farms accounted for a large proportion of the variance in allele frequencies among all farms. These observations are consistent with the hypothesis that allele frequencies in young adult flies reflected the habitat in which they matured as larvae.

Key words: Breeding structure – Allozymes – Linkage disequilibrium – *Musca domestica*

Introduction

The house fly, *Musca domestica* L., enjoys a cosmopolitan distribution and is genetically one of the best known insects (Milani 1975). In temperate climates, populations seasonally become dense and the age structure and dynamics vary continuously (Krafsur et al. 1985; Krafsur 1985). Its broad distribution and capacity to colonise rapidly a wide variety of habitats suggest that house flies are greatly adaptive.

In a study of genetic variability and ecological genetics of house flies, we electrophoretically surveyed 51 loci distributed among 26 enzyme systems and found that 40% of loci were polymorphic (Black and Krafsur 1985a). Observed and expected heterozygosities were 0.0981 and 0.1148, respectively. These approximated the heterozygosity estimates made electrophoretically in other Diptera (excluding *Drosophila* spp) (Graur 1985).

We report here the results of work on the spatial and temporal variation in gene frequencies in flies sampled at farms in central Iowa. Gene frequencies were surveyed in flies of the youngest adult age group. These were assumed to represent flies which had matured at each farm. Flies were sampled from a variety of farms that differed qualitatively in the breeding resources they offered reproducing fly populations, thus presenting the possibility of local adaptation. We sought to determine if gene frequencies at six loci were homogeneous among flies emerging at different farms and if frequencies remained constant through time.

Materials and methods

Field procedures

Adult house flies were captured with sweep nets at five farms near Ames, Iowa (Fig. 1), that included a beef cattle farm, a swine farrowing facility, a dairy farm, a sheep farm, and a pork confinement unit. House fly larvae utilized for resources the dung and spilled feed.

Flies were collected for electrophoresis and age grading on six sampling occasions, from early July until mid-October, 1982. In each collection, adults were captured with sweep nets, placed in cages, returned alive to the laboratory, frozen, and stored at –70 °C. Later, female flies were brought individually to room temperature, dissected in 0.75% saline and age graded.

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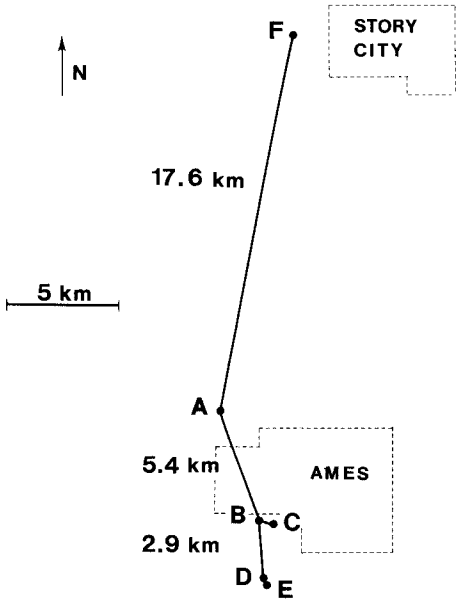

Fig. 1. Relative locations of the five farms surrounding Ames, Iowa. *A* = Beef nutrition farm, *B* = Swine farrowing sheds, *C* = Dairy farm, *D* = Sheep Farm, *E* = Pork production farm

The relative densities of male and female house flies at the different farms were monitored on white can sticky traps. Traps consisted of coffee cans painted white and secured on posts. Plastic bags coated with Tacky Trap diluted with petroleum ether were placed over the cans and allowed to capture flies for 1 to 2 h. Estimates of densities at the various farms were standardized by converting fly numbers to a trap-hour basis. Sampling was done two or three times weekly, for a sum of 30 samples extending from 1 June to 16 October.

Age grading

Gonotrophic age was determined by examining the degree of ovarian development according to criteria developed for house flies (Krafsur et al. 1985). Three age groups were recognized for the present study. Flies in the youngest age class were recognized by the lack of yolk deposition in their ovaries. These females were 0 to 3 days old at 21° (Trepte 1979) and are termed "previtellogenic nullipars". The next oldest age group consisted of females in which yolk occupied up to 66% of the developing eggs, but whose ovaries showed no signs of an earlier oviposition. These females were approximately 3 to 5 days old and are termed "vitellogenic nullipars". Samples of the youngest age class were desired for electrophoresis, but vitellogenic nullipars were included because of the small percentage (16%) of previtellogenics generally present in samples. Ovarioles in the third and oldest age group exhibited signs of previous ovipositions (Krafsur et el. 1985). These "parous" females were at least 6 days old and were included in age structure determinations, but not included in the electrophoresis samples.

For age structure indices, the proportions previtellogenic were calculated by dividing the number of previtellogenic flies by the combined numbers of previtellogenic, nulliparous and parous flies. The proportions parous were calculated by dividing the numbers parous by the numbers of nulliparous and parous.

Electrophoretic procedures

For each sampling date and location, 50 previtellogenic and vitellogenic nullipars (i.e., flies 0–5 days old) were examined electrophoretically. After age grading, nullipars were put directly into grinding buffer and frozen. Electrophoretic methods were described in Black and Krafsur (1984, 1985 a). Genotypes of flies were determined at six loci: Alcohol Dehydrogenase (*Adh*), Amylase + (fast) (*Amy*), Glutamate Oxaloacetate Transaminase (*Got*), Octanol Dehydrogenase (*Odh*), Phosphoglucomutase (*Pgm*), and Superoxide Dismutase (*Sod*). We found 26 alleles distributed among the 6 loci. *Sod* was the only diallelic locus. Electrophoretic assays were made on a total of 1,500 females representing 30 collections.

Analysis of data

"Linkdis" (Black and Krafsur 1985 b), was used to calculate linkage disequilibrium coefficients and check for significance. "Genestats" (Black and Krafsur 1985 c) was used to calculate allele frequencies and perform chi-square tests. Chi-square tests for significant departures from random mating and Wright's F-statistics were estimated in "Genestats" according to the methods of Weir and Cockerham (1985). Contingency Chi-square tests on allele frequencies were computed following Workman and Niswander (1970).

Wright's (1978) hierarchical analysis of breeding structure for a subdivided population was used to identify sources of spatial differentiation in gene frequencies. In the analysis, sampling units are grouped into subpopulations according to their relative distances from one another. Farms (*F*) were the sampling units. They were grouped into subpopulations (*S*), which formed the total population (*T*). Farms were grouped into subpopulations according to their relative proximities (Fig. 1). The swine farrowing facility and dairy farm constituted a subpopulation, the southern pork and sheep farms formed a second and the beef nutrition farm was treated as a third.

Three variance components were calculated. The variance in allele frequencies among farms (F_{FT}) is a function of the variance in allele frequencies among subpopulations (F_{ST}) and the variance in allele frequencies among farms in subpopulations (F_{FS}). The three statistics are related by the equation,

$$F_{FT} = F_{ST} + F_{FS} - (F_{ST} \times F_{FS}).$$

Where flies are completely panmictic, all F-statistics are zero. When flies produced at farms are differentiated by selection or genetic drift then allele frequencies within the same subpopulation will be heterogeneous and $F_{FS} \geqq F_{ST}$. If flies produced within subpopulations are panmictic and subpopulations are differentiated because of distance, local selection pressures, barriers to mating, etc., then $F_{ST} \geqq F_{FS}$.

Correlation coefficients between allele frequencies and house fly densities were calculated by using SAS (1982). These coefficients were converted to a normalized scale with Fisher's *z*-transformation. Chi-square tests for the homogeneity of *z*-values were computed following the procedure in Sokal and Rohlf (1969). A mean *z*-value of all possible correlations was calculated and back-transformed to estimate a common correlation.

Results

Temporal variation in fly density and age structure

Seasonal trends in fly densities were essentially similar at the five farms (Figs. 2 and 3). Correlation coefficients between fly densities at all pairs of farms were homogeneous ($\chi^2 = 4.88$, df = 5, $P = 0.43$) and statistically significant (common correlation = 0.53, $P < 0.001$). The proportions of previtellogenic and parous flies are given by sampling date in Table 1 and by location in Table 2. The proportions of parous flies (*PP*) were homogeneous among farms on each sampling date. The proportions of previtellogenic flies (*PPV*) were not homogeneous among farms on four of the six sampling

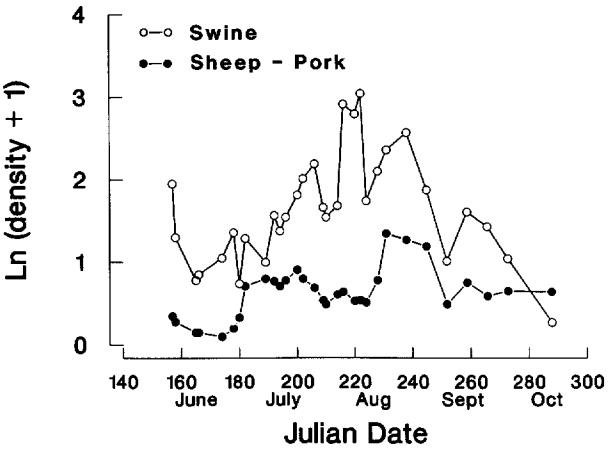

Fig. 2. Three day moving average log flies per trap-hour at swine farrowing sheds and the sheep and pork farms combined

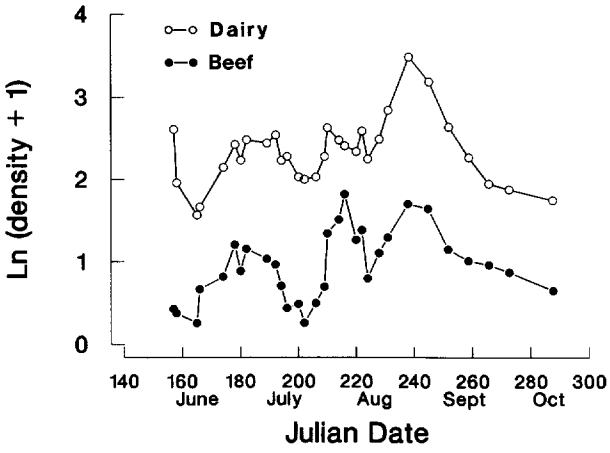

Fig. 3. Three day moving average log flies per trap-hour at dairy and beef nutrition farms

Table 1. Proportions of previtellogenic and parous flies according to sampling dates

Date	Previtellogenic	χ^2 (4 df)	Parous	χ^2 (4 df)
July 6	114/516 (22.1%)	49.0***	266/402 (66.2%)	2.5
July 19	119/436 (27.3%)	20.4**	186/317 (58.7%)	5.7
Aug. 2	123/511 (24.1%)	5.7	261/388 (67.3%)	6.1
Aug. 19	119/305 (39.0%)	9.5*	55/186 (29.6%)	6.5
Sept. 13	120/384 (31.2%)	26.5***	134/264 (50.8%)	4.4
Oct. 12	139/318 (43.7%)	64.6***	68/179 (38.0%)	6.2
Tests for seasonal homogeneity among:				
Previtellogenics χ^2 (5 d.f.) = 66.3***				
Parous χ^2 (5 d.f.) = 116.9***				

* $P \leqq 0.05$; ** $P \leqq 0.01$; $P \leqq 0.001$

Table 2. Proportions of previtellogenic and parous flies according to sampling location

Farm	Previtellogenic	χ^2 (5 df)	Parous	χ^2 (5 df)
Beef	119/485 (24.5%)	39.2***	185/366 (50.5%)	18.3**
Swine	125/502 (24.9%)	41.9***	202/377 (53.6%)	27.9***
Dairy	139/546 (25.5%)	35.0***	246/407 (60.4%)	23.0***
Sheep	189/453 (41.7%)	38.6***	153/264 (58.0%)	21.8***
Pork	162/484 (33.5%)	42.4***	184/322 (57.1%)	46.8***
Totals	734/2470 (29.7%)		970/1736 (55.9%)	
Test for spatial homogeneity among:				
Previtellogenics χ^2 (4 d.f.) = 51.1***				
Parous χ^2 (4 d.f.) = 9.1				

** $P \leqq 0.01$; *** $P \leqq 0.001$

Table 3. Allele frequencies and standard errors (in parentheses) of the most common allele at six enzymatic loci in the house fly

Sampling dates	*Adh 2*						
	July 6	July 19	Aug. 2	Aug. 16	Sept. 13	Oct. 12	Mean
Farm							
Beef	0.786	0.840	0.840	0.830	0.710	0.740	0.791
	(0.041)	(0.037)	(0.037)	(0.038)	(0.045)	(0.044)	(0.017)
Swine	0.690	0.790	0.820	0.770	0.880	0.750	0.783
	(0.046)	(0.041)	(0.038)	(0.042)	(0.032)	(0.043)	(0.017)
Dairy	0.724	0.650	0.806	0.850	0.750	0.660	0.740
	(0.045)	(0.048)	(0.040)	(0.036)	(0.043)	(0.047)	(0.018)
Sheep	0.840	0.660	0.830	0.770	0.790	0.690	0.763
	(0.037)	(0.047)	(0.038)	(0.042)	(0.041)	(0.046)	(0.019)
Pork	–	0.760	0.850	0.770	0.740	0.714	0.767
	–	(0.043)	(0.036)	(0.042)	(0.044)	(0.046)	(0.017)
Population	0.760	0.740	0.829	0.798	0.774	0.711	0.768
	(0.021)	(0.020)	(0.017)	(0.018)	(0.019)	(0.020)	(0.008)
	Amy 4						
	July 6	July 19	Aug. 2	Aug. 16	Sept. 13	Oct. 12	Mean
Beef	0.680	0.656	0.678	0.690	0.670	0.740	0.686
	(0.047)	(0.048)	(0.049)	(0.046)	(0.047)	(0.044)	(0.019)
Swine	0.850	0.880	0.734	0.700	0.770	0.830	0.795
	(0.036)	(0.032)	(0.046)	(0.046)	(0.042)	(0.038)	(0.017)
Dairy	0.760	0.700	0.653	0.770	0.810	0.610	0.717
	(0.048)	(0.046)	(0.048)	(0.042)	(0.039)	(0.049)	(0.018)
Sheep	0.730	0.740	0.650	0.790	0.830	0.710	0.742
	(0.044)	(0.045)	(0.048)	(0.041)	(0.038)	(0.045)	(0.018)
Pork	0.770	0.750	0.760	0.750	0.730	0.844	0.767
	(0.042)	(0.043)	(0.044)	(0.043)	(0.044)	(0.037)	(0.017)
Population	0.758	0.746	0.695	0.740	0.762	0.746	0.739
	(0.019)	(0.020)	(0.021)	(0.020)	(0.019)	(0.020)	(0.008)
	Got 4						
	July 6	July 19	Aug. 2	Aug. 16	Sept. 13	Oct. 12	Mean
Beef	0.940	0.940	0.980	0.870	–	–	0.932
	(0.024)	(0.024)	(0.014)	(0.034)	–	–	(0.013)
Swine	0.767	0.920	–	0.833	0.960	0.920	0.884
	(0.042)	(0.027)	–	(0.039)	(0.020)	(0.027)	(0.015)
Dairy	0.867	0.922	0.940	0.900	0.930	0.940	0.917
	(0.034)	(0.028)	(0.024)	(0.030)	(0.026)	(0.024)	(0.011)
Sheep	0.970	0.862	–	0.830	0.908	0.930	0.900
	(0.017))	(0.036)	–	(0.038)	(0.029)	(0.026)	(0.014)
Pork	0.930	0.959	0.920	0.870	0.880	0.820	0.896
	(0.026)	(0.020)	(0.027)	(0.034)	(0.032)	(0.038)	(0.012)
Population	0.899	0.921	0.947	0.861	0.920	0.902	0.904
	(0.014)	(0.012)	0.013	(0.016)	(0.014)	(0.015)	(0.006)

dates. The heterogeneity in *PPV* probably can be attributed to the relative proximity of collection sites to larval breeding sites. The greatest *PPV* were consistently found at the sheep and pork farms (Table 2). At the sheep farm, flies were collected indoors from walls above the moist straw, manure and spilled food in which larvae develop. At the pork farm, flies were collected outdoors in pig pens where faeces and spilled food accumulated.

House fly age structures fluctuated significantly by date of sampling, as in earlier studies (Krafsur 1985). The homogeneity in *PP* among farms, and the positive correlations in density among farms suggest that broadly similiar schedules of mortality and natality obtained among the house fly populations.

Table 3 (continued)

Sampling dates	*Odh 2*						
	July 6	July 19	Aug. 2	Aug. 16	Sept. 13	Oct. 12	Mean
Beef	–	–	0.980	0.890	–	–	0.935
	–	–	(0.014)	(0.031)	–	–	(0.017)
Swine	0.940	0.940	0.950	0.950	–	–	0.945
	(0.024)	(0.024)	(0.022)	(0.022)	–	–	(0.011)
Dairy	0.950	0.950	0.950	0.850	–	–	0.925
	(0.022)	(0.022)	(0.022)	(0.036)	–	–	(0.013)
Sheep	0.930	0.930	0.930	0.960	0.950	0.960	0.943
	(0.026)	(0.026)	(0.026)	(0.020)	(0.022)	(0.020)	(0.009)
Pork	0.960	0.960	–	0.880	–	–	0.933
	(0.020)	(0.020)	–	(0.032)	–	–	(0.014)
Population	0.945	0.945	0.952	0.906	0.950	0.960	0.938
	(0.011)	(0.011)	(0.011)	(0.013)	(0.022)	(0.020)	(0.006)
	Pgm 3						
	July 6	July 19	Aug. 2	Aug. 16	Sept. 13	Oct. 12	Mean
Beef	0.980	0.970	0.940	0.970	0.970	0.950	0.963
	(0.014)	(0.017)	(0.024)	(0.017)	(0.017)	(0.022)	(0.008)
Swine	0.980	0.990	0.990	0.990	1.000	0.980	0.988
	(0.014)	(0.010)	(0.010)	(0.010)	–	(0.014)	(0.004)
Dairy	0.980	0.980	0.990	0.970	0.990	0.990	0.983
	(0.014)	(0.014)	(0.010)	(0.017)	(0.010)	(0.010)	(0.005)
Sheep	0.980	0.980	0.980	0.980	1.000	1.000	0.987
	(0.014)	(0.014)	(0.014)	(0.014)	–	–	(0.005)
Pork	0.980	0.980	0.980	0.990	0.980	0.950	0.977
	(0.014)	(0.014)	(0.014)	(0.010)	(0.014)	(0.022)	(0.006)
Population	0.980	0.980	0.976	0.980	0.988	0.974	0.980
	(0.006)	(0.006)	(0.007)	(0.006)	(0.005)	(0.007)	(0.003)
	Sod 1						
	July 6	July 19	Aug. 2	Aug. 16	Sept. 13	Oct. 12	Mean
Beef	0.950	0.960	0.970	0.950	0.930	0.980	0.957
	(0.022)	(0.020)	(0.017)	(0.022)	(0.026)	(0.014)	(0.008)
Swine	1.000	0.980	1.000	0.920	0.960	0.950	0.968
	–	(0.014)	–	(0.027)	(0.020)	(0.022)	(0.007)
Dairy	1.000	0.940	0.990	0.950	0.990	0.950	0.970
	–	(0.024)	(0.010)	(0.022)	(0.010)	(0.022)	(0.007)
Sheep	1.000	1.000	1.000	0.970	0.970	0.960	0.983
	–	–	–	(0.017)	(0.017)	(0.020)	(0.005)
Pork	1.000	0.990	1.000	0.950	0.980	0.940	0.977
	–	(0.010)	–	(0.022)	(0.014)	(0.024)	(0.006)
Population	0.990	0.974	0.992	0.948	0.966	0.956	0.971
	(0.004)	(0.007)	(0.004)	(0.010)	(0.008)	(0.009)	(0.003)

Genotypic frequencies

Chi-square tests were performed for goodness of fit of observed genotypic frequencies to those expected under random mating. Eleven of 153 (7.2%) tests proved statistically significant. This frequency was not significantly greater than the 5% expected for a Type I Error. Nor were significant values clustered on specific dates, loci, or farms. These results suggest that mating was random at all farms and dates.

Table 4. Chi-square tests for temporal differentiation of allele frequencies among sampling sites

Locus		Farm					Population
		Beef	Swine	Dairy	Sheep	Pork	
Adh	χ^2	31.75**	29.88*	69.24***	37.17*	27.47*	116.05***
	df	15	15	20	20	16	20
Amy	χ^2	28.09	49.35**	40.71*	44.14**	36.62	45.81**
	df	25	25	25	25	25	25
Got	χ^2	12.17	64.65***	17.56	21.03	63.07***	69.67***
	df	9	16	20	12	15	25
Odh	χ^2	6.89*	0.23	22.98***	7.72	7.49	18.65*
	df	2	6	6	10	4	10
Pgm	χ^2	24.35	7.03	6.53	4.05	8.64	34.54**
	df	15	10	10	5	10	15
Sod	χ^2	3.70	15.93**	11.68*	10.58	14.63*	28.23***
	df	5	5	5	5	5	5
Total	χ^2	106.95**	167.07***	168.70***	124.69**	157.92***	
	df	71	77	86	77	75	

* $P \leqq 0.05$; ** $P \leqq 0.01$; *** $P \leqq 0.001$

Table 5. Correlation coefficients between allele frequencies at five farms

Farm	Allele				
	Adh 2	*Amy 4*	*Got 4*	*Pgm 3*	*Sod 1*
Beef × swine	−0.23	−0.05	0.08	0.06	0.13
Beef × dairy	0.29	−0.57	0.42	−0.60	−0.39
Beef × sheep	−0.02	−0.23	0.68	−0.17	0.04
Beef × pork	0.68	0.91*	0.69	0.45	−0.25
Swine × dairy	0.21	−0.23	0.95*	0.11	0.59
Swine × sheep	−0.02	−0.14	−0.25	0.17	0.84*
Swine × pork	0.20	0.31	−0.26	0.52	0.88*
Dairy × sheep	0.66	0.82*	−0.27	0.63	0.33
Dairy × pork	0.58	−0.77	−0.33	−0.60	0.62
Sheep × pork	0.65	−0.47	−0.05	−0.66	0.90*
Common correlation	0.53	0.01	0.14	0.13	0.49

* $P \leqq 0.05$

Linkage disequilibrium

To test for linkage disequilibrium in fly populations at farms, composite linkage disequilibrium coefficients were calculated for all locus pairs (Weir 1977). Weir's chi-square test was employed to detect significance. Chi-square values in Weir's test became inflated when expected frequencies were small (i.e., when rare alleles at both loci appeared in a single fly). Fifty-four of 321 disequilibrium coefficients were significantly greater than zero. But only 13 of these 54 involved common alleles, a proportion not significantly less than that expected for a Type I Error. The 54 significant values, moreover, were homogeneously distributed among dates, farms, and locus pairs. Thus, no consistent pattern of linkage disequilibrium was observed in house fly populations at farms.

Temporal shifts in allele frequencies

The frequencies and standard erors of the most common alleles are presented in Table 3. Chi-square tests for homogeneity of allele frequencies among dates are set forth in Table 4. Heterogeneity at two or more loci was detected at each farm. *Adh* alleles were temporally heterogeneous on all farms. *Pgm* alleles were temporally homogeneous on all farms.

To determine if gene frequencies followed similar seasonal patterns, correlations were calculated between allele frequencies for all possible pairs of farms (Table 5). Six of the 50 correlations proved statistically significant. Common correlations at the *Adh* and *Sod* loci were large, but not statistically significant, and the individual correlations were not consistently large or positive.

Table 6. Chi-square tests of homogeneity among allele frequencies at farms and subpopulations in young female house flies. F-statistics indicate the relative contributions of variation among subpopulations (F_{ST}) and variation among farms in subpopulations (F_{FS}) to the total variation among farms in the population, (F_{FT})

Date	Farms		Subpopulations		F-Statistics		
	χ^2	d.f.	χ^2	d.f.	F_{FT}	F_{ST}	F_{FS}
July 6							
Locus							
Adh	10.3	9	7.7	6	0.011	0.016	−0.005
Amy	29.3	20	14.6	10	0.008	0.010	−0.002
Got	40.4***	12	23.2***	6	0.041	0.039	0.002
Odh	7.1	6	3.7	2	−0.005	−0.001	−0.004
Pgm	0.0	4	0.0	2	−0.010	−0.006	−0.004
Sod	20.2***	4	20.2***	2	0.041	0.056	−0.016
Total	107.3***	55	69.3***	28	0.013	0.016	−0.003
July 19							
Locus							
Adh	27.6*	12	7.6	6	0.018	0.008	0.010
Amy	22.1	20	10.3	10	0.014	0.006	0.008
Got	14.4	12	5.2	6	0.006	−0.002	0.008
Odh	2.0	6	0.4	2	−0.006	−0.005	−0.001
Pgm	8.8	12	8.4	6	−0.007	−0.003	−0.004
Sod	9.2	4	5.8	2	0.013	0.012	0.001
Total	84.1	66	37.8	32	0.012	0.004	0.008
August 2							
Locus							
Adh	9.5	12	2.9	6	−0.008	−0.005	−0.003
Amy	14.2	20	4.2	10	−0.002	−0.005	0.003
Got	11.7	6	11.7	6	0.014	0.014	0.000
Odh	4.2	6	3.1	4	−0.001	0.002	−0.003
Pgm	11.2	8	11.2*	4	0.003	0.010	−0.007
Sod	8.6	4	7.9*	2	0.012	0.019	−0.007
Total	59.4	56	41.0	32	−0.001	−0.001	0.000
August 16							
Locus							
Adh	25.7*	12	13.5*	6	0.003	0.000	0.003
Amy	46.6***	20	22.0*	10	0.011	0.008	0.003
Got	22.5	16	6.7	6	−0.002	−0.002	0.000
Odh	14.3	8	2.7	4	0.010	−0.003	0.013
Pgm	6.2	8	4.7	4	−0.005	−0.003	−0.002
Sod	2.6	4	1.3	2	−0.004	−0.002	−0.002
Total	117.9***	68	50.9*	32	0.005	0.001	0.004
September 13							
Locus							
Adh	23.5*	12	9.1	6	0.015	0.003	0.012
Amy	34.5*	20	23.6**	10	0.006	0.006	0.000
Got	17.5	15	5.7	4	0.003	0.008	0.005
Pgm	14.1	12	9.9	6	0.003	0.004	−0.001
Sod	6.5	4	4.9	2	0.007	0.009	−0.002
Total	96.1*	63	53.2**	28	0.009	0.005	0.004
October 12							
Locus							
Adh	14.7	16	6.8	8	−0.003	−0.005	0.002
Amy	43.1***	20	14.0	10	0.022	0.000	0.022
Got	30.5***	9	12.2*	3	0.032	0.017	0.015
Pgm	19.7	12	10.3	6	0.010	0.006	0.004
Sod	2.2	4	1.7	2	−0.005	−0.001	−0.004
Total	110.2***	61	45.1*	29	0.012	0.001	0.011

* $P \leqq 0.05$; ** $P \leqq 0.01$; *** $P \leqq 0.001$

Gene frequencies were not consistently correlated for any pair of farms, and in general, allele frequencies fluctuated independently of sampling location.

Spatial trends in allele frequencies

Contingency chi-square tests and hierarchical F-statistics are presented in Table 6. Heterogeneity was detected in allele frequencies among populations in early July and homogeneity in mid-July and early August. Significant spatial variation reappeared in mid-August and was maintained thereafter.

F_{FT} and F_{FS} are plotted in Fig. 4. The variance in gene frequencies among farms (F_{FT}) was large in July, became small in early August, and then gradually increased. With the exception of the first sample, variation in allele frequencies between adjacent farms (F_{FS}) accounted for a large fraction of the total variance (F_{FT}).

Populations at farms were large in mid-August (Figs. 2 and 3) and even small migration rates would have maintained panmixia (Crow and Kimura 1970). Larval adaptation to the different breeding resources at each farm is a possible explanation of the observed differentiation. According to such an hypothesis, gene frequencies in young adults reflected the habitats in which they matured.

Discussion

Gene frequencies among flies at farms converged in midsummer and progressively diverged thereafter (Fig. 4). The initial divergence and midsummer convergence in allele frequencies are consistent with the hypothesis that house fly populations in early spring consisted of actively breeding but reproductively isolated subpopulations (Krafsur 1985). As the outdoor breeding season progressed, densities increased as new habitats were colonized. Age structures and densities showed similar seasonal trends among the farms. This suggests that the onset of reproduction in spring and succeeding schedules of natality and mortality were broadly similiar. Migration served to homogenize farm populations so that by midsummer they were panmictic.

But this theory fails to account for the fact that homogeneity in gene frequencies was not maintained when densities were great during August and September. Furthermore, a large proportion of the total variation in gene frequencies among farms was accounted for by differentiation between adjacent farms. This suggests that factors other than inadequate migration caused the gene frequency divergence late in summer.

The midsummer convergence and subsequent divergence of gene frequencies might be explained in principle by spatially different selection regimes. Farms differed qualitatively in the breeding resources they offered reproducing flies. Flies may therefore have experienced "fine-grained" environments and fitness was optimised by different genotypes. The divergence in allele frequencies between adjacent farms is consistent with the foregoing hypothesis. Larval crowding and reduced developmental time due to seasonally high temperatures cause smaller and less fecund flies (Black and Krafsur 1986a). These factors also probably increase larval mortality, perhaps making genotypic requirements for survival more exacting.

The hypothesis that differences in allele frequencies among farms reflected local adaptation also predicts that allele frequencies be uncorrelated. Such a result was obtained; only six of 50 correlations proved statistically significant (Table 5). Parallel shifts in frequency were not seen among farms.

Subsequent study of allele frequencies was made in all age groups and both sexes of the house fly in 1983 (Black and Krafsur 1986a). We observed the same pattern of seasonal convergence and divergence among teneral and nulliparous flies. But allele frequencies among the older, parous flies were spatially homogeneous from late June until November, supporting the hypothesis of local adaptation of larvae. Kinetic differences have been reported among allozymes at the *Adh* (van Delden 1982) and *Amy* (Doane 1980) loci in *Drosophila* species. Among house fly larvae, *Adh* may be an important detoxifying enzyme because they breed in fermenting substrates. House flies may prove valuable for research on the adaptive significance of amylase polymorphisms. Only a single amylase locus is known in *Drosophila,* but we have identified six amylase loci in the house fly (Black and Krafsur 1985a) one of which is very active and tran-

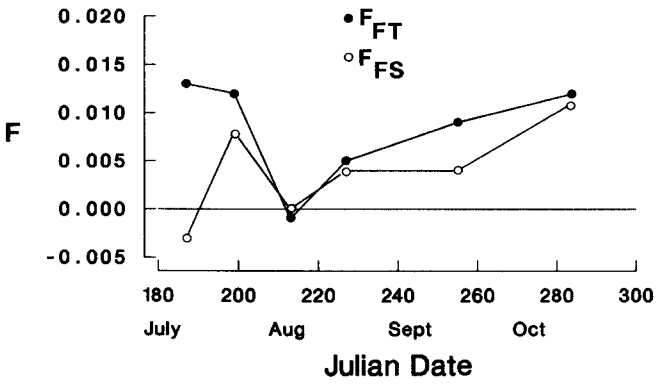

Fig. 4. Seasonal fluctuations in Wright's F_{FT} and F_{FS} among nulliparous flies

scribed only in larvae. The house fly is easily studied in the field or laboratory and thus presents opportunities for population geneticists interested in the evolutionary consequences of breeding structure and the functional significance of enzyme polymorphisms.

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