CHROMOSOMAL INFLUENCES ON LIFE-HISTORY VARIATION ALONG AN ALTITUDINAL TRANSECT IN *DROSOPHILA ROBUSTA**

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Although many examples of heritabilities and genetic correlations among fitness characters in natural and experimental populations document the extent to which life-history variation is genetically based (see Law 1979; Etges 1982; Istock 1982; Rose 1983; Reznick 1985; Travis et al. 1987), only a few examples document direct associations between putative selective factors in nature and the resulting genetic differences among life-history characters (Istock et al. 1976; Reznick and Endler 1982; Templeton and Johnston 1982; Berven and Gill 1983). Understanding the direct causes that are responsible for the *maintenance* of genetic variation underlying variable life histories in populations may clarify the genetic constraints and processes leading toward life-history variation so often observed among species (Cole 1954; Williams 1966; Stearns 1976).

Istock (1978) forcefully argued that additive genetic variance in components of fitness may be an adaptive response to environmental variability (see also Istock et al. 1976; Istock 1982; Lynch 1984; Reznick 1985; Mitchell-Olds 1986), rather than the accumulation of polygenic variation by mutation or recombination, balanced by short-term natural selection (Fisher 1930; Lande 1976; Simmons and Crow 1977; Mackay 1985). The possibility that antagonistic pleiotropy will maintain polygenic variation among life-history characters reconciles the existence of additive genetic variance in components of fitness with Fisher's view (Caspari 1950; A. Robertson 1955; Williams 1957; Wright 1977; Rose and Charlesworth 1981; Rose 1982, 1983). However, positive genetic correlations among fitness components are not unknown in laboratory studies (Giesel et al. 1982; Murphy et al. 1983; Giesel 1986; Mitchell-Olds 1986). Without detailed knowledge of the causes in nature that have shaped the genetic structure of life histories, we cannot accurately predict their form or evolution.

The course of life-history evolution depends on the magnitudes of heritabilities and genetic correlations among characters as well as the genetic determination of the traits, that is, the frequencies of alleles at loci and amounts of genic dominance and interaction influencing the traits (Lewontin 1974). As for any polygenic trait,

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the maintenance of genetic variation depends on the levels of selection, on mutation, pleiotropy, and linkage, and on the numbers of loci and alleles (Lande 1976, 1980; Turelli 1984, 1985; Gimelfarb 1986). Genetic analysis of quantitative traits provides two major insights: inference into their architecture (Reeve and Robertson 1953; Breese and Mather 1960; Spickett and Thoday 1966; Kearsey and Kojima 1967; Sved 1975; Chapco 1977, 1979; Thoday 1977; Yamazaki and Hirose 1984), and an understanding of their dynamics and potential evolutionary constraints if few major genes are segregating (Kallman and Borkoski 1978; Lumme and Keranen 1978; Yoo 1980; Templeton and Johnston 1982; Lande 1983; Templeton et al. 1985; DeSalle et al. 1986). Once some modest description of the genotypic or chromosomal arrays determining life-history traits is made, study of short-term microevolutionary dynamics based on the environmentally sensitive genetic variances and covariances of life-history traits in populations can be extended to long-term evolutionary changes based on genotype frequencies.

Inversion polymorphisms in natural populations provide a means by which life-history variation can be associated with discrete genetic elements that are often selectively maintained (Dobzhansky 1970; Lewontin et al. 1981). Maintenance of life-history variation will involve the mechanisms controlling the inversion polymorphisms if segregating gene arrangements contain arrays of alternative (+ or −) alleles that constitute life-history polygenes. Inversions may not always be appropriate markers for investigating genic effects on life histories because many linked genes may be involved, but their ubiquity and association with selection in nature make them useful markers for studying how variable life histories are maintained in many species.

This study portrays life histories in association with inversion polymorphisms within and among populations along an elevational transect of *Drosophila robusta*, detailing the chromosomal architecture underlying correlated groups of life-history traits. These populations harbor 14 gene arrangements on five of the six major chromosome arms, including over 75% of the genomic chromatin in heterokaryotypic individuals (Carson 1958). The inversions in *D. robusta* are likely to contain a number of genes controlling fitness characters, and they can be used to localize the influence of single or interacting chromosomal arms on life-history characters on natural genetic backgrounds.

Gene arrangements in this species show latitudinal (Carson and Stalker 1947) and elevational clines (Stalker and Carson 1948; Levitan 1978; Etges 1984*a*), as well as short-term seasonal changes (Levitan 1973) and long-term frequency changes (Etges 1984*a*). Natural selection is implicated in maintaining several X-chromosome clines because similar clinal patterns are found repeatedly in eight separate elevational transects (Levitan 1978). Similarly, second-chromosome clines show equivalent patterns in all transects studied (Levitan 1982; Etges 1984*a*). Cage experiments with laboratory populations have suggested that balancing selection maintains several of the inversion polymorphisms (Levitan 1951*a*; Carson 1961). Thus, a priori we may find that the causes for the clines in gene arrangements are due to environmental changes with elevation expressed through variable life histories.

Environmental gradients associated with altitude encompass many selective factors that can influence life histories and point out likely environmental factors

influencing their evolution. Dearn (1977) showed that during the growing season, females of three species of univoltine grasshoppers lay fewer eggs in larger clutches with increasing elevation; he proposed that the decreasing length and the greater unpredictability of the reproductive season at higher elevations were responsible. Populations of frogs living at high elevations exhibit longer larval developmental times than those found at lower elevations: *Rana pretiosa* (Licht 1975), *R. clamitans* (Berven et al. 1979), and *R. sylvatica* (Berven 1982). Ballinger (1979) showed that montane populations of a lizard, *Sceloporus jarrovi*, are characterized by an increased age at first reproduction in field transplant experiments. Ground squirrels, *Spermophilus lateralis*, show smaller litter sizes, increased age at first reproduction, and increased female survival at high elevations (Bronson 1979). Columbian ground squirrels, *Spermophilus columbianus*, have higher adult survival rates and slower maturation rates at higher elevations (Zammuto and Millar 1985). Changes in life history with elevation appear to be widespread.

Thus, changes in temperature, vegetation, and precipitation along the Smokies transect, spanning 1000–4840 feet (′) (305–1475 m; elevations are reported in feet to correspond to notation of earlier studies) in elevation over 30 km, are probably related to the maintenance of the inversion clines in the Smokies and elsewhere (Stalker and Carson 1948; Levitan 1982). Migration and gene flow along these transects undoubtedly smooth the pattern of inversion-frequency change with elevation (Etges 1984*a*). If we assume that the principal resources for larval growth and development are sap fluxes (Carson and Stalker 1951), then lower-elevation populations may be better adapted to warmer and drier conditions (Shanks 1954, 1956), which should be conducive to greater unpredictability of breeding-site duration. Direct adaptation to warm temperatures may also produce smaller adult sizes and correlated life-history differences, as in *D. pseudoobscura* (Anderson 1966). Thus, larval developmental time should be shorter in lower-elevation populations. As average temperatures decrease with increasing elevation, breeding-site duration and larval developmental times may be longer. *Drosophila robusta* adults are genetically larger above 2000′ (610 m; Stalker and Carson 1948), implying higher ovariole numbers and longer larval developmental times (F. Robertson 1957).

In addition to testing for these life-history differences, the specific aims of this study are (1) to determine the extent of differences in age at first reproduction, in fecundity, and in longevity along the Smokies transect; (2) to determine the influences of temperature differences like those existing along the Smokies transect on these life-history characters; (3) to determine the extent to which variation in these life-history characters is influenced by gene arrangements and/or karyotypes in populations from the transect; and (4) to describe the karyotypic structure of life-history variation in an effort to understand the maintenance of the inversion clines.

MATERIALS AND METHODS

Adult flies were sweep-netted over fermenting bananas at 1000′, 1360′, 2000′ in elevation (305 m, 415 m, 610 m, respectively) adjacent to the West Prong of the

TABLE 1

COLLECTION INFORMATION FOR *DROSOPHILA ROBUSTA* POPULATIONS IN THIS STUDY

Population	No. of Isofemale Lines*	No. of Wild Individuals	Late-Summer Air Temperature†	Precipitation‡
1000′	52	55 females 46 males	25°C	118 cm
1360′	69	257 females 480 males	22°C	140 cm
2000′	31	215 females 518 males	20°C	160 cm

* The number of offspring per wild-caught female varied. All offspring were combined with the wild-caught adults to start the lab populations.

† These approximate temperatures are from Shanks (1954, table 1; 1956, fig. 4) and from mean July-August temperatures during the 11-day collecting period in this study.

‡ Mean annual precipitation from 1935 to 1969 (unpubl. data provided by R. Matthews, Uplands Research Lab, Great Smoky Mountains National Park).

Little Pigeon River in the Great Smoky Mountains National Park. The two higher sites are described elsewhere (Etges 1984*a*), and the lowest site was located approximately 1 km west along Caney Creek from the site mentioned in Stalker and Carson (1948). Elevations are reported in feet to indicate that the populations were the same as those sampled in earlier studies.

Drosophila robusta adult males were mated immediately after capture with stock females of a known homokaryotype. All wild females were despermed by transferring them to vials of fresh food until no larvae were seen; the presence of only unhatched eggs indicated that all stored sperm were depleted. The females were then mated with stock males of a known homokaryotype. Determinations of adult karyotypes were made by examining the karyotypic configurations of 7–10 F_1 larvae from these crosses (Levitan 1978; Etges 1984*a*).

The inversion polymorphisms in Smokies populations of *D. robusta* involve five of the six chromosome arms: three common gene arrangements on the left arm of the X chromosome (XL, XL-1, and XL-2); two common arrangements on the right arm of the X (XR and XR-2); four common and one rare arrangement on the left arm of the second chromosome (2L, 2L-1, 2L-2, 2L-3, and 2L-5); two arrangements on the right arm of the second chromosome (2R and 2R-1); and two arrangements on the right arm of the third chromosome (3R and 3R-1) (Carson and Stalker 1947; Stalker and Carson 1948; Etges 1983, 1984*a*).

All F_1 progeny collected from each locality during desperming of wild females were introduced into one of three population cages (17 × 17 × 44 cm). All wild males and females not used for karyotyping were also introduced into these cages (table 1). The cages were maintained in an incubator at 20°C ± 1°, in a photoperiod of 16 h light and 18 h darkness. Two food cups per cage were changed on alternate days and retained. All eclosing offspring were returned to the cages to minimize inadvertent selection for short developmental time. The three population cages were treated uniformly: population densities and food availabilities were kept relatively constant to minimize systematic environmental differences between cages.

After 4 or 5 generations in the cages, 200 larvae per cage were karyotyped in order to determine the extent of inversion-frequency change caused by lab conditions. Larvae from each food cup were sampled for karyotyping.

Life-History Measurements

After accumulating on fresh food for 6 h, eggs were collected from each population cage each day; eggs were washed in insect saline, an antibiotic solution (1.6 g per liter of streptomycin sulphate + 0.8 g per liter of Penicillin-G™), 70% ethanol, and once again, insect saline. Lots of 100 eggs were then counted out onto 1-cm^2 squares of filter paper, placed into food cups with 0.5 g of baker's yeast and a folded Kimwipe™, and fitted with a plastic beaker fitted with a sponge cork. For each of the three experimental populations, at least 20 cups were cultured at each of three temperatures: 15°, 20°, and 25°C. Each food cup contained approximately 40 ml of cornmeal-molasses food, or 88 cm^2 of exposed food surface for the larvae; these were considered "optimal," noncompetitive growth conditions (Etges 1984*b*, unpubl. data).

Preadult life-history characters assayed were egg-to-adult viability and egg-to-adult developmental time (DEVT). Subsamples of adults from at least 10 replicates per treatment were used to measure the age at first reproduction (AFR) and adult longevity (LONG). Cumulative fecundity (FEC) of females from each population was measured for the first 3 wk after AFR for the 20°C treatment only. DEVT was determined by collecting eclosing adults daily. Egg-to-adult viability was measured by counting the number of eclosed adults per replicate, and by subtracting after correction for the number of dead or unhatched eggs. AFR was measured by placing virgin females with two aged, stock males (2-wk old at room temperature), changing vials daily, and observing when eggs hatched. For males, in the 20°C treatment only, AFR was determined similarly by placing virgin males in vials with two aged, stock virgin females. Adult female longevity was measured using the individuals from the AFR study; all females were kept with two stock males throughout their lifetimes. During the longevity study, 15°C vials were changed at 10–12-day intervals, 20°C vials were changed at 6–8-day intervals, and 25°C vials were changed at 4–5-day intervals in attempts to equalize growth conditions within vials cultured at different temperatures.

Karyotypic Determinations

A total of 1221 adult flies (801 females and 420 males) from the three experimental populations were karyotyped as before. Adults were chosen from each replicate culture across each day of emergence. Infrequently, complete adult karyotypes were not inferred because fewer than seven larvae per test cross were scored. These data were used for the single-arm inversion (haploid) analyses, whereas, for the karyotypic (diploid) analyses, all individuals not completely karyotyped were excluded (see below). Thus, sample sizes in the two analyses differed. I tried to sample several adults from each replicate-day class within each population-temperature combination representing the entire range of developmental time variation in each temperature treatment.

Data analysis proceeded in a hierarchical fashion by analysis of variance (ANOVA) for unbalanced designs using the SAS procedure GLM (Helwig and

Council 1979). The basic design in all analyses was a 3 × 3 × 2 ANOVA (Population × Temperature × Sex) with population, gene-arrangement, and karyotype considered random effects using Type IV sums of squares. Four variations of this design were evaluated. (1) Variation in life history for the entire experiment (N = 12,442 individuals), excluding karyotypes, was analyzed. (2) Differences among gene arrangements on each chromosome arm for each life-history character were assayed by ANOVA's, where single-arm effects were considered treatments in addition to population, temperature, and sex. This allowed determination of the average effect of gene arrangements on the variance for each life-history character across populations and temperatures as well as interactions between gene arrangements and each main effect. Each arm was tested separately, allowing any remaining population effects to be considered genetic background effects.

(3) Karyotypic influences were investigated by repeating the ANOVA's with observed single-arm karyotypes as treatment effects. This allowed significance testing of all possible within- and between-arm karyotype interactions for all life-history characters, as well as population-by-karyotype interactions. (4) Single-arm gene-arrangement and karyotype effects on life-history variation within each of the nine population-temperature treatments were determined in a posteriori ANOVA's to uncover the sources of significant main effects and interactions found using the complete model and to minimize Type I errors associated with simultaneous testing. Egg-to-adult viability data were arcsin-transformed and analyzed separately.

Tests for normality indicated that data for DEVT and AFR require log transformation before analysis but that LONG and FEC are normally distributed (Etges 1984*b*). Correlations between life-history characters were calculated with untransformed data.

RESULTS

Life-History Variation among Populations

The 2000-foot (′) population exhibited lower egg-to-adult viabilities than either the 1000′ or 1360′ populations (table 2). Temperature did not affect the expression of mean viability or the ranking among populations, suggesting that upper-elevation populations on this mountainside are less viable than lowland populations during egg-to-adult development. Embryonic lethality (brown eggs) was higher at 25°C than that at the other two temperatures combined (10.8% > 3.0%) and lower in the 1360′ population than in either the 1000′ or 2000′ population (4.7% < 6.6% or 5.8%, respectively; table 2). Decreased egg hatchability is not related to increased inversion heterozygosity in *Drosophila robusta* (Riles 1965); embryonic development may thus be sensitive to higher temperatures in these populations.

Significant differences were detected for developmental time (DEVT) among populations within each temperature treatment (tables 3, 5). Temperature and sex differences were significant, as were Population-by-Temperature and Sex-by-Temperature interactions, indicating individuality in the response of each popula-

TABLE 2

EGG-TO-ADULT VIABILITY (EAV) AND EGG HATCHABILITY FOR THREE POPULATIONS OF *DROSOPHILA ROBUSTA* AT THREE TEMPERATURES

TEMPERATURE	VIABILITY	POPULATION*		
		1000′	1360′	2000′
15°C	EAV	65.59 (4.56)	69.20 (2.44)	62.54 (4.56)
	d	4.6 (3.59)	3.2 (2.19)	2.5 (1.76)
	u	4.6 (2.92)	4.2 (3.82)	5.2 (1.85)
	N	22	23	20
20°C	EAV	68.86 (3.66)	70.15 (2.83)	56.08 (4.62)
	d	2.9 (2.49)	2.0 (2.05)	2.6 (1.14)
	u	6.3 (3.41)	4.1 (2.47)	5.0 (4.15)
	N	19	24	24
25°C	EAV	64.75 (2.22)	63.08 (2.80)	60.34 (2.22)
	d	11.4 (4.79)	8.8 (4.94)	12.2 (4.69)
	u	3.7 (3.14)	4.6 (3.65)	4.0 (3.33)
	N	23	33	23

NOTE.—Mean (standard deviation in parentheses) egg viability data: *d*, the number of dead embryos per replicate; *u*, the number of unhatched eggs per replicate; and *N*, the number of replicates per treatment.

* Egg-to-adult viability (EAV) of the 2000′ populations was significantly different from that of the other populations at each temperature by Duncan's multiple-range test ($P < 0.05$).

TABLE 3

EGG-TO-ADULT DEVELOPMENTAL TIMES IN THREE POPULATIONS OF *DROSOPHILA ROBUSTA* AT 15°, 20°, AND 25°C

Population	Temp., °C	Sex	*N*	DEVT (SE)	No. of Replicates
2000′	15	F	605	43.944^{a} (0.103)	20
1360′	15	F	786	43.832^{a} (0.087)	24
1000′	15	F	675	44.813^{b} (0.107)	22
2000′	15	M	552	45.647^{c} (0.100)	20
1360′	15	M	755	45.511^{c} (0.092)	24
1000′	15	M	624	46.904^{d} (0.116)	22
2000′	20	F	531	25.040^{e} (0.107)	23
1360′	20	F	801	24.377^{f} (0.085)	25
1000′	20	F	577	24.458^{f} (0.096)	19
2000′	20	M	659	26.426^{g} (0.086)	23
1360′	20	M	842	25.633^{h} (0.091)	25
1000′	20	M	592	25.816^{h} (0.093)	19
2000′	25	F	741	16.262^{i} (0.062)	30
1360′	25	F	858	16.490^{j} (0.065)	32
1000′	25	F	557	16.273^{i} (0.074)	21
2000′	25	M	799	17.304^{k} (0.066)	30
1360′	25	M	890	17.442^{l} (0.061)	32
1000′	25	M	598	17.114^{k} (0.075)	21
TOTAL			12,442		216

NOTE.—Temp., culture temperature; *N*, sample size; DEVT, developmental time, in days; SE, standard error.

* Population means having the same superscript are not significantly different by Duncan's multiple-range test ($P < 0.05$).

TABLE 4

AGE AT FIRST REPRODUCTION (AFR), LONGEVITY (LONG), AND FECUNDITY (FEC) FOR THREE POPULATIONS OF *DROSOPHILA ROBUSTA*

Population	Temp., °C	Sex	*N*	AFR (SE)	LONG (SE)	FEC (SE)
2000′	15	F	73	13.225[a] (0.314)	100.575[g] (6.210)	
1360′	15	F	73	14.274[b] (0.325)	109.542[g] (5.085)	
1000′	15	F	75	13.453[a] (0.349)	108.284[g] (5.549)	
2000′	20	F	66	6.849 (0.095)	79.682[h] (4.967)	751.712[j] (26.199)
1360′	20	F	69	5.812 (0.185)	84.000[h] (4.181)	812.333[j] (17.324)
1000′	20	F	58	7.345 (0.182)	81.224[h] (4.942)	766.310[j] (20.292)
2000′	25	F	64	4.703[c] (0.101)	57.403[i] (3.023)	
1360′	25	F	58	4.397[d] (0.120)	54.587[i] (3.367)	
1000′	25	F	61	5.016[c] (0.127)	62.919[i] (2.987)	
2000′	20	M	34	11.088[e] (0.186)		
1360′	20	M	37	11.595[f] (0.237)		
1000′	20	M	35	11.543[f] (0.210)		

NOTE.—Temp., culture temperature; *N*, sample size; SE, standard error. AFR and LONG in days; FEC in total number of eggs produced through 21 days of age.

tion and sex to different temperatures. The 1000′ population was almost a full day slower in DEVT at 15°C but was among the faster-developing populations at 20°C and 25°C, suggesting that lower-elevation populations are sensitive to colder temperatures for developmental rates (table 3). At 20°C the 2000′ population was slower in development than the 1360′ and 1000′ populations by about half a day. At 25°C, the 1360′ population was slower than either the 2000′ or 1000′ population. Results at the latter two temperatures were equivocal with respect to possible adaptation to temperature.

Temperature and sex accounted for much of the variance in age at first reproduction (AFR; tables 4, 5), with significant Population-by-Temperature and Sex-by-Temperature interactions. Over all temperature treatments, adults from the 1000′ population matured more slowly than adults from the 1360′ and 2000′ populations ($F = 10.95$, $P < 0.0001$). At 15°C, females from the 1360′ population exhibited slower rates of sexual maturation than females from the other two populations. At 20°C, all female AFR differed, with the 1000′ population the slowest and the 1360′ population the fastest. Males from the 2000′ population in this temperature matured faster than those from the other two populations (table 4). Despite population-specific responses to temperature, AFR was greater in the 1000′ population, suggesting that lowland populations not only have higher egg-to-adult viabilities and longer DEVT in colder temperatures, but also attain sexual maturity more slowly than the mountainside populations.

Female longevity (LONG) and early fecundity (FEC) did not differ between populations, but increasing temperatures vastly decreased longevity (tables 4, 5).

Inversion-Frequency Variation among Populations

Among the natural populations, a clinal pattern of genetic change consistent with previous work (Etges 1984*a*) was found; however, all three populations

TABLE 5

ANOVA RESULTS OF LIFE-HISTORY VARIATION AMONG POPULATIONS OF *DROSOPHILA ROBUSTA*

Source of Variation	df	Type IV Sum of Squares	*F*	*P*
EGG-TO-ADULT DEVELOPMENTAL TIME				
Population	2	0.0237	8.97	0.0001
Temperature	2	382.6347	1×10^5	0.0001
Population by Temperature	4	0.2367	44.68	0.0001
Sex	1	1.4281	1083.08	0.0001
Population by Sex	2	0.0013	0.49	NS
Temperature by Sex	2	0.0269	10.21	0.0001
Population by Temperature by Sex	4	0.0059	1.12	NS
Error	12,424	16.3814		
AGE AT FIRST REPRODUCTION				
Population	2	0.1258	10.38	0.0001
Temperature	2	22.6066	1864.56	0.0001
Population by Temperature	4	0.3891	16.04	0.0001
Sex	1	3.9370	49.43	0.0001
Population by Sex	2	38.1712	14.12	0.0001
Replicates	107	697.1800	2.26	0.0001
Error	689	4.1769		
EARLY FECUNDITY				
Population	2	1.35×10^5	2.24	0.1090
Replicates	36	1.73×10^6	1.85	0.0052
Error	190	5.71×10^6		
LONGEVITY				
Population	2	2428.02	0.85	NS
Temperature	2	1.28×10^5	44.84	0.0001
Population by Temperature	4	12786.77	2.24	0.0642
Replicates	103	2.07×10^5	1.40	0.0099
Error	498	7.12×10^5		
EGG VIABILITY				
Population	2	0.0219	4.15	0.0171
Temperature	2	0.2465	46.67	0.0001
Population by Temperature	4	0.0052	0.49	NS
Error	199	0.5256		
EGG-TO-ADULT VIABILITY				
Population	2	0.3743	4.84	0.0088
Temperature	2	0.1071	1.38	NS
Population by Temperature	4	0.1893	1.22	NS
Error	207	8.0086		

NOTE.—NS, not significant.

responded to laboratory-cage conditions after 4 or 5 generations (table 6). Frequency changes were greatest for inversions of the left arm of the second chromosome with an increase in frequency for 2L-1 and a decrease in 2L-3. Frequency changes in the left arm of the X chromosome were not as marked as those on the second chromosome, and only the 2000′ population showed any significant changes with an increase in XL-1 and a decrease in XL. Third-chromosome inversion frequencies did not vary significantly from nature. Thus, laboratory-induced changes in inversion frequencies were restricted to gene arrangements showing clines in nature.

TABLE 6

INVERSION-FREQUENCY CHANGE (%) AFTER FOUR OR FIVE LABORATORY GENERATIONS IN THREE POPULATIONS OF *DROSOPHILA ROBUSTA*

	POPULATION					
	1000′		1360′		2000′	
CHROMOSOME	Field	Lab	Field	Lab	Field	Lab
X chromosome						
N^a	176	329	200	321	124	330
Left arm						
XL	44.9	42.9	33.5	35.2	22.6	12.4
XL-1	34.7	37.4	54.5	55.1	65.3	78.5
XL-2	20.4	19.7	12.0	9.7	12.1	9.1
χ^2	0.37 NS		0.77 NS		9.02[d]	
Right arm[b]						
XR	25.0	26.1	37.0	34.9	50.0	56.4
XR-2	75.0	73.9	63.0	65.1	50.0	43.6
Second chromosome						
N^a	237	400	247	400	180	400
2L	21.1	18.3	19.7	17.0	7.8	15.5
2L-1	28.7	42.3	17.7	37.0	16.7	31.8
2L-2	7.6	9.0	8.0	7.0	4.5	2.5
2L-3	42.6	30.4[c]	54.6	38.8[c]	71.0	50.2
χ^2	15.5[e]		29.5[e]		26.7[e]	
Third chromosome[b]						
3R-1	69.6	69.8	70.2	71.0	71.3	76.0

NOTE.—NS, not significant.
[a] N, the number of chromosomes sampled.
[b] Lab-induced changes in frequency were not significant.
[c] Including one 2L-5 not used in the calculations.
[d] $P < 0.025$.
[e] $P < 0.0001$.

No inversions were lost (table 6), and the clines from nature (W) persisted in the lab (L) for gene arrangements on the left arm of the second chromosome (W, $\chi^2 = 38.70$, $P < 0.001$; L, $\chi^2 = 41.47$, $P < 0.001$), left arm of the X chromosome (W, $\chi^2 = 30.80$, $P < 0.001$; L, $\chi^2 = 122.29$, $P < 0.001$), right arm of the X chromosome (W, $\chi^2 = 19.88$, $P < 0.001$; L, $\chi^2 = 66.83$, $P < 0.001$), but not the right arm of the third chromosome (W, $\chi^2 = 0.14$, NS; L, $\chi^2 = 4.36$, NS). Since karyotypic frequencies had changed, but the clines were retained, the slight shift in genetic backgrounds probably biased the expression of life histories.

Life-History Differences among Gene Arrangements

Chromosome arms in the ANOVA's were designated as follows: EXL, left arm of the X chromosome; EXR, right arm of the X chromosome; TWL, left arm of the second chromosome; and THR, right arm of the third chromosome. Of two gene arrangements on the right arm of the second chromosome, 2R and 2R-1, the latter is rarely encountered in the Smokies populations in frequencies greater than 5%–10% (table 2; Carson 1958; Etges 1984*a*). No life-history differences were associated with these gene arrangements.

X chromosome.—No main effect of gene arrangements on the left arm of the X chromosome on DEVT was apparent; yet variation among populations persisted, indicating a genetic background effect (Appendix A).

A four-way interaction (Population by Temperature by Sex by EXL) stemmed from differences among EXL gene arrangements in the 1000′ population at 25°C ($F = 3.31$, $P = 0.039$, $N = 190$). Here, gene arrangement XL was associated with a mean DEVT of 16.5 days, XL-2 with a mean of 17.4 days, and XL-1 with an intermediate mean of 17.0 days. This suggests a temperature-specific pattern where gene arrangement XL, which increases in frequency toward lower elevations in the Smokies (Etges 1984*a*), expressed some advantage in warmer temperatures.

Differences in AFR resulted in part from a significant interaction between temperature and EXL gene arrangements (Temperature by EXL; Appendix A). Greater AFR was associated with gene arrangement XL-1 at 15°C and 25°C, but at 20°C, this arrangement was associated with the lowest mean AFR. Differences among EXL gene arrangements in LONG were detected in the 1000′ population at 20°C ($F = 6.45$, $P = 0.003$, $N = 66$). Here, gene arrangement XL-1 was associated with a significantly lower mean LONG of 77.8 days when XL and XL-2 were associated with greater mean life spans of 109.6 and 103.2 days, respectively.

Variation between gene arrangements XR and XR-2 in DEVT was not significant overall, but a significant interaction with sex (SEX by EXR) was found (Appendix B). Collectively, these results suggest that expression of life-history differences among X-chromosome gene arrangements was sensitive to temperature and sex. Significance of the population effect, with all other sources of variance accounted for, indicated that non-sex-linked genes affected both DEVT and AFR.

Second chromosome.—Gene arrangements on the left arm of the second chromosome were associated with significant differences in DEVT (Appendix C). Because the main effects of temperature and sex were significant sources of variance in this model and the effect of population was not, the background effect revealed in the X-chromosome ANOVA's was therefore at least partially due to the influence of second-chromosome gene arrangements because these populations differ with respect to TWL inversion frequencies (table 6). An interaction between sex and TWL gene arrangements (Sex by TWL) resulted from a shorter mean DEVT of gene arrangement 2L in males (25.4 days) than in females (28.2 days), and a longer mean DEVT, relative to the rest of the gene arrangements in each sex, associated with 2L-1 in males (26.2 days) than in females (26.4 days). Thus, DEVT was influenced by TWL inversions, but potential selective differences were sex-specific, as Levitan (1951*b*) noted for karyotype frequencies in natural populations.

Within temperature treatments, DEVT differences between gene arrangements of TWL provide evidence for the possibility that selection maintains the clines in TWL gene arrangements along the Smokies transect. In the 1360′ experimental population at 25°C, 2L and 2L-3 were associated with longer DEVT than were 2L-1 and 2L-2 ($F = 8.19$, $P = 0.001$, $N = 197$); at 20°C, 2L, 2L-2, and 2L-3 had

longer DEVT than did 2L-1 ($F = 3.52$, $P = 0.016$, $N = 306$). Thus, 2L-1 was associated with shorter DEVT in warmer temperatures.

Differences between second-chromosome gene arrangements were significant for AFR but not for LONG (Appendix C). The Temperature-by-TWL interaction for AFR exactly paralleled that for EXL: rankings of gene arrangements at 15°C and 25°C were similar for 2L-1 and 2L-3, and reversed at 20°C. At 15°C, the rankings were 2L-3 > 2L-2 > 2L > 2L-1; at 25°C, the rankings were 2L-3 > 2L-1 > 2L > 2L-2; and at 20°C, the rankings were 2L-2 > 2L-1 > 2L > 2L-3 (Etges 1984*b*). Temperature-dependent expression of second-chromosome differences for maturation rates involved those gene arrangements showing clines in nature.

Third chromosome.—THR gene arrangements influenced DEVT in a population-specific manner, as indicated by the significant interaction term, Population by THR (Appendix D). Gene arrangement 3R was associated with longer mean DEVT than 3R-1 in the 2000′ population (at 25°C, 17.1 vs. 16.4 days, $F = 6.75$, $P = 0.01$) and 1360′ population (at 20°C, 25.4 vs. 24.6 days, $F = 8.63$, $P = 0.004$; and at 25°C, 17.5 vs. 16.5 days, $F = 18.17$, $P = 0.001$) by an average of 0.5 and 0.8 days, respectively. Conversely, 3R-1 was associated with a greater mean DEVT than 3R over all temperatures in the 1000′ population, suggesting that the genic contents of third-chromosome gene arrangements vary along this elevational transect.

A Temperature-by-THR interaction was significant for AFR: at 15°C and 25°C, 3R was associated with greater mean AFR than 3R-1 (13.7 vs. 13.5 and 4.8 vs. 4.5 days, respectively); at 20°C, 3R-1 was associated with greater mean AFR than 3R (6.8 vs. 6.3 days). AFR was thus influenced by gene arrangements on three chromosome arms, EXL, TWL, and THR, and always through interaction of particular gene arrangements with temperature.

Adults from the 1360′ population at 20°C varied in FEC for 3R versus 3R-1, 779.6 versus 843.0 eggs, respectively ($F = 4.50$, $P = 0.037$, $N = 87$). Thus, THR differences were associated with DEVT, AFR, and FEC together, but in different ways: 3R was associated with longer DEVT, lower FEC, but lower AFR. Thus, third-chromosome gene arrangements influenced suites of life-history traits, indicating a genetic trade-off between DEVT and AFR, but not FEC.

Karyotypic differences in life history.—Karyotype treatments were denoted as diploid pairs of all observed gene arrangements (e.g., TWL/TWL). Karyotype-temperature interactions were not calculated because of the size of the model.

Both second- and third-chromosome karyotypes were associated with differences in DEVT with some evidence for a heterokaryotype advantage for short DEVT, but only for particular TWL/TWL heterokaryotypes (Appendix E). The most common karyotype, 2L-1/2L-3, was associated with shorter DEVT than either 2L-1/2L-1 or 2L-3/2L-3. This may explain the absence of a greater DEVT difference between 2L-1 and 2L-3 (Appendix C). Karyotypes containing 2L were consistently associated with slower development. Any temperature-specific ranking of karyotypes is glossed over in this analysis since karyotypic differences may emerge in a temperature-specific fashion (cf. Dobzhansky et al. 1964).

Third-chromosome heterokaryotypes were intermediate in DEVT as compared with both homokaryotypes (Appendix E). Only third-chromosome karyotypes

showed any indication of population-specific variation (Population-by-THR/THR interaction). In the 2000′ population, 3R-1/3R-1 karyotypes were associated with the shortest mean DEVT (26.7 days), whereas in the 1360′ population, they were associated with the longest DEVT (27.1 days), similar to the single-gene-arrangement results. Only in the 1360′ population at 25°C were there karyotypic differences ($F = 4.38$, $P = 0.003$, $N = 122$). Here, 3R-1/3R-1 karyotypes were associated with a mean DEVT of 18.3 days, 3R/3R-1 with a mean of 17.3 days, and 3R/3R with a mean of 16.6 days. No significant interactions were found for any pairwise combination of single-arm karyotypes.

Karyotypic variation associated with differences in AFR and LONG was absent (Appendix E) but that for FEC was detected (Appendix H). Both EXR/EXR and TWL/TWL karyotypes were associated with differences in FEC. Population-specific interaction between TWL/TWL and EXL/EXL karyotypes was also significant for this trait. A complex ordering of second-chromosome karyotypes revealed no clear pattern in FEC except that 2L-3/2L-3 females exhibited greater fecundities than average.

DISCUSSION

Parallel clines in X- and second-chromosome gene arrangements suggest the role of natural selection among populations of *Drosophila robusta* (Levitan 1978, 1982); yet no mechanism for the maintenance of these clines has heretofore been presented. Variation among gene arrangements and karyotypes in egg-to-adult developmental time (DEVT) in *D. robusta* is strong evidence for a selective mechanism involved in shaping the steep clines in TWL gene arrangements among the Smoky Mountains populations. Second-chromosome gene arrangements 2L-1 and 2L-2, common in low-elevation populations in this region, are associated with shorter DEVT under warm-temperature conditions. Conversely, in colder temperatures (15°C), high-elevation gene arrangement 2L-3 was associated with shorter DEVT. Overall, 2L-1/2L-3 heterokaryotypes tend to be faster than either homokaryotype, although not always significantly. Thus, there is a karyotypic basis to the population-level differences in DEVT (table 3) and an association with the underlying clines in gene arrangements (Levitan 1978, 1982; Etges 1984*a*, table 2).

Consistent second-chromosome differences in DEVT existed across populations, and to some extent temperatures, suggesting that the genic contents of TWL gene arrangements are more uniform than those of the third chromosome. Together with the higher frequency of 2L-1 and 2L-2 at lower elevations and the regularity with which 2L-1 increases in population cages at temperatures of 20°C and warmer (Levitan 1951*a*; table 6), the shorter DEVT of 2L-1 and 2L-2 are evidence that these gene arrangements are selectively favored at warm temperatures during preadult development. The association of 2L-3 with colder temperatures in nature (Carson and Stalker 1947; Carson 1958)—that is, regular increases in frequency along several elevational transects including the Smokies (Stalker and Carson 1948; Levitan 1978; Etges 1984*a*)—shorter DEVT at 15°C in the 1000′ population, and notable lack of population-specific interactions (Appendixes C,

D) support the hypothesis that the genic contents of second-chromosome gene arrangements are relatively invariant along the Smokies transect.

Populations from near 2000′ in elevation are characterized by karyotypic frequencies similar to all populations inhabiting this region up to 4840′, above which *D. robusta* has not been collected (Stalker and Carson 1948; Etges 1984*a*). The association of 2L-3 with longer DEVT in warmer temperatures (Appendix C) and shorter DEVT in colder temperatures, its clear increase in frequency with elevation, and the fact that the 2000′ population exhibited lower viability (table 2) and was among the faster-developing populations in two temperature treatments relative to the lower-elevation populations (two-way ANOVA, $F = 8.00$, $P < 0.0003$) all implicate 2L-3 with shorter DEVT in upper-elevation populations. Cooler temperature conditions have apparently produced shorter DEVT, as in *D. pseudoobscura* cage experiments (Anderson 1966), through counter-gradient selection (see Berven et al. 1979) by increasing the frequency of 2L-3.

However, DEVT was probably biased, since inversion frequencies changed because of population cage conditions (table 6). In just 4 or 5 generations, the frequencies of 2L-1 in each population doubled that found in nature, with a corresponding decrease in 2L-3. The ensuing increase in faster-developing 2L-1/2L-3 heterokaryotypes (Appendix E), from 23.7% (nature) to 31.9% (lab), in the 2000′ population produced a higher frequency of 2L-1/2L-3 than in either the 1000′ (25.7%) or the 1360′ (28.7%) populations. Frequencies of 2L-3 vary from 70% to 85% from 2000′ up to 4840′ in nature (Etges 1984*a*). Thus, phenotypic differences in DEVT among the experimental populations (table 3) were influenced by chromosomal gene arrangements, the frequencies of which had changed before the experiment.

Variation in the genic contents of third-chromosome gene arrangements between populations was probably responsible for the observed population-specific differences in DEVT (Appendixes D, E), but population-specific epistatic interactions between the third-chromosome gene arrangements and other parts of the genetic background cannot be ruled out. Differences among the genetic backgrounds of each population could simply be due to inversion-frequency differences among populations. Thus, contrasting sets of alleles influencing DEVT must be located in or near the segregating inversions of the left arm of the second and right arm of the third chromosomes.

Some chromosomal differences were consistent with the observed population-level differences in DEVT among populations at 15°C, where the 1000′ population exhibited slower DEVT than the other two populations (table 4). Here, second-chromosome differences associated with DEVT were significant ($F = 5.35$, $P = 0.002$, $N = 176$). Gene arrangements 2L, 2L-1, 2L-3, and 2L-2 were associated with mean DEVT of 46.6, 45.9, 45.0, and 44.8 days, respectively; the first two and the last three form overlapping groups ($P < 0.05$). Gene arrangements 2L and 2L-1 are in higher relative frequency in the 1000′ population than anywhere else along the Smokies transect (table 2; Stalker and Carson 1948; Levitan 1982; Etges 1984*a*, unpubl. data). Thus, 2L-1 was associated at 15°C with longer DEVT and at warmer temperatures with shorter DEVT.

Adaptation to the warmer conditions in lower-elevation populations was ob-

served where the 1000′ population exhibited significantly longer DEVT at 15°C than the two upper-elevation populations and was among the faster-developing populations at 20°C and 25°C (tables 1, 4). At 15°C, DEVT was negatively correlated with age at first reproduction (AFR) in females ($r = -0.528$, $P < 0.001$); that is, female larvae that develop slowly reach sexual maturity faster, once eclosed, than larvae that develop faster. Whether this is because slower-developing larvae are storing more energy and materials to be shunted into adult somatic or reproductive tissues, as in *D. melanogaster* (Sang 1950, 1956), is not known. Similarly, in the 20°C treatment, slower-developing male larvae mature faster as adults, and females reaching sexual maturity faster produce more eggs early in life ($r = -0.384$, $P < 0.05$).

Gene-arrangement interactions with temperature underlying variation in AFR signify possible adaptation to particular environments (Appendixes A, C, D). Gene arrangements associated with higher elevations—that is, XL-1 and 2L-3—were associated with lower AFR at 20°C but not at 15°C and 25°C, suggesting that 15°C and 25°C are not optimal temperatures for these high-elevation gene arrangements. The Temperature-by-THR interaction was caused by relatively shorter AFR associated with 3R at 20°C and longer AFR at 25°C, indicating that the selective values of gene arrangements on three of the polymorphic chromosome arms probably change throughout the season in nature.

How do these inversion–life-history associations help in understanding the maintenance of life-history variation? Since there was not always a strong pattern of inversion-frequency variation and life-history pattern along this elevational transect, functional interpretations for all life-history variation is unwarranted. Expression of fitness variation under laboratory conditions may also mask potential differences among gene arrangements. No interchromosomal interactions for any fitness character were detected, suggesting rather simple underlying patterns of inheritance, for example, differences in DEVT associated with 2L-1 and 2L-3 that correspond to their clinal patterns in nature.

If balancing selection (Dobzhansky 1970; Anderson et al. 1986) along the Smokies transect is responsible for maintaining the inversion polymorphisms, then the influence of selection in these populations is variable and depends on temperature and genetic background effects at different stages of the life cycle. Clinal or directional selection in addition to some heterokaryotype advantage may be operating, but only in certain temperatures and populations. Certainly, variation in components of fitness is associated with different gene arrangements; along with the clinal nature of certain of these arrangements, this life-history variation is probably not neutral with respect to fitness or likely to be eliminated by short-term selection. Frequency changes of these gene arrangements from 1947 to 1983 suggest that these populations are not at genetic equilibrium (Etges 1984*a*, unpubl. data), and thus the life histories may be changing.

Determination of both the magnitude and kind of selection operating at different stages of the life cycle are necessary for understanding how genetic variation in life histories is maintained (Prout 1965, 1971*a*,*b*, 1980; DuMouchel and Anderson 1968; Anderson and Watanabe 1974; Clegg et al. 1978; Anderson et al. 1979). Genetic covariation in components of fitness has been of central interest in the

study of inversion polymorphisms. Spiess et al. (1952) found that longevity and fecundity were positively correlated with karyotypes in *D. persimilis*. Dobzhansky et al. (1964) demonstrated karyotypic variation for fecundity, longevity, viability, and intrinsic rates of increase among experimental populations of *D. pseudoobscura*. Covariation in male mating speed and virility was found between karyotypes in *D. robusta* (Prakash 1967).

Gene arrangement 3R was associated with longer DEVT, lower FEC, and lower AFR in the 1360′ population at 20°C (see the Results). Here, the frequency of 3R may be held in equilibrium because it is favored at one life-cycle stage, AFR, but not during DEVT or through FEC (see Ruiz et al. 1986). Similarly, male DEVT and AFR in this population-temperature combination were inversely related ($r = -0.685$, $P < 0.001$); yet this correlation for females was not significant (Etges 1984*b*). In the 2000′ population at 25°C, 3R was associated with significantly greater DEVT and decreased LONG. Such manifold effects of inversions on fitness characters have also been noted in *D. persimilis* for DEVT and mating propensity, prompting Spiess and Spiess (1967) to describe a "developmental syndrome" associated with this polymorphism. Yet, since expression of these inversion-based correlations is population- and temperature-specific, plasticity of life-history patterns (table 4) may have a genetic basis.

A major problem that has hindered empirical verification of optimal models of life-history evolution is a lack of understanding of the evolutionary forces responsible—particularly which selective factors are important and when they act—for producing or maintaining alternative patterns in life history (Stearns 1976, 1983; Reznick 1985). Should genetic and phenotypic correlations correspond for life-history traits, then demographic and optimality arguments will suffice in explaining life-history variation (Schaffer 1974; Schaffer and Rosenzweig 1977). However, this is often not the case (Berven et al. 1979; Hegmann and Dingle 1982) either because populations are not at genetic equilibrium, the forces that produced variant life histories are not understood, or the environment in which quantitative genetic estimates are made is inappropriate (Service and Rose 1985; Clark 1987). The generality of optimal-life-history theory will become more tenable when many more examples of selectively maintained genetic correlations among life-history traits in natural populations are uncovered together with identifiable patterns of age-specific mortality that are consistent with the trade-off models.

However, because clinal variations in inversion polymorphisms in *D. robusta* are associated with life-history differences, and the presence of parallel altitudinal and latitudinal clines around the species range implicates selection, however weak, in maintaining some of these clines, the variation in life histories must in some part result from adaptation to different environments.

SUMMARY

Life-history variation was associated with the inversion polymorphisms on three of five of the chromosomal arms in experimental populations of *Drosophila robusta*. Karyotypic differences were associated with variation in egg-to-adult developmental time (DEVT), age at first reproduction, and early fecundity, but

not adult longevity. Variations in DEVT among gene arrangements on the left arm of the second chromosome were changed by temperature, but consistently across populations. Some low-elevation karyotypes were associated with shorter DEVT in warmer-temperature conditions. Third-chromosome karyotypes were also associated with differences in DEVT, but in a population-specific way, indicating variation in genic contents of third-chromosome gene arrangements among populations along this elevational transect. Third-chromosome gene arrangements were also associated with correlated sets of fitness characters. Not all life-history differences suggested adaptation to changes in elevation, but differences in DEVT were correlated with clinal variation in second-chromosome gene arrangements.

Since life-history differences were associated with karyotypic variation, changes in inversion frequencies through time may influence the course of life-history evolution for inversions with genic contents that are relatively uniform from population to population. Genetic variation in life histories can be preserved by inversion polymorphisms if alternative gene arrangements contain contrasting sets of alleles. Conversely, these data also suggest through which components of fitness long-term changes in gene-arrangement frequencies, previously documented in *D. robusta*, may be mediated.

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APPENDIX A

ANOVA RESULTS FOR EXL GENE-ARRANGEMENT VARIATION IN LIFE HISTORY

	LIFE-HISTORY CHARACTER								
	DEVELOPMENTAL TIME (N = 1938)			AGE AT FIRST REPRODUCTION (N = 666)			ADULT LONGEVITY (N = 631)		
SOURCE OF VARIATION	df	Type IV Sum of Squares	F	df	Type IV Sum of Squares	F	df	Type IV Sum of Squares	F
Model	53	57.65	784.98****	34	25.89	107.23****	26	341696.7	9.19****
Temperature	2	11.51	4153.58****	2	14.66	1034.85****	2	178390.6	62.38****
Population	2	0.01	3.64**	2	0.06	4.44*	2	3503.7	1.23
Sex	1	0.04	30.12***	1	0.84	118.74****	—	—	—
Population by Temperature	4	0.01	2.45*	4	0.43	15.17****	4	7970.4	1.39
Temperature by Sex	2	0.01	4.33**	—	—	—	—	—	—
Population by Sex	2	0.00	0.04	2	0.07	4.70**	—	—	—
Population by Temperature by Sex	4	0.01	1.36	—	—	—	—	—	—
EXL	2	0.00	1.64	2	0.00	0.20	2	5679.3	1.99
Temperature by EXL	4	0.00	0.48	4	0.08	2.73*	4	4598.3	0.80
Population by EXL	4	0.00	0.73	4	0.01	0.19	4	2714.9	0.47
Population by Temperature by EXL	8	0.01	1.23	8	0.06	0.98	8	13787.9	1.21
Sex by EXL	2	0.00	0.96	2	0.01	0.49	—	—	—
Temperature by Sex by EXL	4	0.00	0.42	—	—	—	—	—	—
Population by Sex by EXL	4	0.00	0.83	3	0.00	0.21	—	—	—
Population by Temperature by Sex by EXL	8	0.04	3.34***	—	—	—	—	—	—
Error	1884	2.61		631	4.48		604	863702.5	

NOTE.—EXL, the left arm of the X chromosome. N, the number of X chromosomes sampled.
* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.
**** $P < 0.0001$.

APPENDIX B

ANOVA RESULTS FOR EXR GENE-ARRANGEMENT VARIATION IN LIFE HISTORY

	LIFE-HISTORY CHARACTER								
	DEVELOPMENTAL TIME (N = 1938)			AGE AT FIRST REPRODUCTION (N = 666)			ADULT LONGEVITY (N = 631)		
SOURCE OF VARIATION	df	Type IV Sum of Squares	F	df	Type IV Sum of Squares	F	df	Type IV Sum of Squares	F
Model	35	57.59	1174.67****	23	25.75	155.70****	17	317748.9	12.91****
Temperature	2	20.66	7373.28****	2	19.66	1366.85****	2	263566.2	91.01****
Population	2	0.01	3.10*	2	0.08	5.46**	2	5035.5	1.74
Sex	1	0.13	92.36****	1	0.95	131.47****	—	—	—
Population by Temperature	4	0.03	5.86****	4	0.51	17.67****	4	13520.2	2.33*
Temperature by Sex	2	0.03	11.37****	—	—	—	—	—	—
Population by Sex	2	0.00	0.49	2	0.12	8.05***	—	—	—
Population by Temperature by Sex	4	0.01	1.00	—	—	—	—	—	—
EXR	1	0.01	2.47	1	0.00	0.15	1	153.6	0.11
Temperature by EXR	2	0.01	1.97	2	0.00	0.19	2	1864.1	0.64
Population by EXR	2	0.00	0.37	2	0.00	0.29	2	1328.3	0.46
Population by Temperature by EXR	4	0.00	0.41	4	0.03	1.10	4	1525.9	0.26
Sex by EXR	1	0.01	7.43**	1	0.00	0.00	—	—	—
Temperature by Sex by EXR	2	0.00	1.14	—	—	—	—	—	—
Population by Sex by EXR	2	0.00	0.07	2	0.00	0.06	—	—	—
Population by Temperature by Sex by EXR	4	0.01	1.65	—	—	—	—	—	—
Error	1902	2.66		642	4.62		613	887650.4	

NOTE.—EXR, the right arm of the X chromosome. N, the number of X chromosomes sampled.
* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.
**** $P < 0.0001$.

APPENDIX C

ANOVA RESULTS FOR TWL GENE-ARRANGEMENT VARIATION IN LIFE HISTORY

	LIFE-HISTORY CHARACTER								
	DEVELOPMENTAL TIME (N = 2332)			AGE AT FIRST REPRODUCTION (N = 699)			ADULT LONGEVITY (N = 634)		
SOURCE OF VARIATION	df	Type IV Sum of Squares	F	df	Type IV Sum of Squares	F	df	Type IV Sum of Squares	F
Model	70	64.19	625.28****	46	26.61	85.66****	35	339115.4	6.63****
Temperature	2	23.88	8141.17****	2	10.10	747.46****	2	99824.6	34.15****
Population	2	0.00	1.40	2	0.07	5.21**	2	5791.7	1.98
Sex	1	0.15	101.54****	1	1.32	195.60****	—	—	—
Population by Temperature	4	0.03	5.31***	4	0.23	8.67****	4	5489.8	0.94
Temperature by Sex	2	0.03	8.69***	—	—	—	—	—	—
Population by Sex	2	0.01	3.57*	2	0.11	7.85***	—	—	—
Population by Temperature by Sex	4	0.00	0.80	—	—	—	—	—	—
TWL	3	0.01	3.18*	3	0.01	0.45	3	5455.0	1.24
Temperature by TWL	6	0.01	1.27	6	0.09	2.13*	6	8930.6	1.02
Population by TWL	6	0.01	0.94	6	0.01	0.27	6	13570.5	1.55
Population by Temperature by TWL	12	0.02	0.90	12	0.13	1.58	12	9030.4	0.51
Sex by TWL	3	0.02	3.47**	3	0.02	0.85	—	—	—
Temperature by Sex by TWL	6	0.00	0.43	—	—	—	—	—	—
Population by Sex by TWL	6	0.01	0.84	5	0.00	0.14	—	—	—
Population by Temperature by Sex by TWL	11	0.01	0.62	—	—	—	—	—	—
Error	2261	3.32		652	4.40		598	873895.5	

NOTE.—TWL, the left arm of the second chromosome. N, the number of autosomes sampled. Multiple comparisons for the TWL arrangement are in Appendix F.

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

**** $P < 0.0001$.

APPENDIX D

ANOVA RESULTS FOR THR GENE-ARRANGEMENT VARIATION IN LIFE HISTORY

SOURCE OF VARIATION	LIFE-HISTORY CHARACTER: DEVELOPMENTAL TIME (N = 2343) df	Type IV Sum of Squares	F	AGE AT FIRST REPRODUCTION (N = 700) df	Type IV Sum of Squares	F	ADULT LONGEVITY (N = 634) df	Type IV Sum of Squares	F
Model	35	64.44	1251.58****	23	26.51	171.19****	17	309250.0	12.40****
Temperature	2	33.29	11316.74****	2	20.01	1485.69****	2	258506.1	88.08****
Population	2	0.00	0.78	2	0.13	9.91****	2	2938.6	1.00
Sex	1	0.17	115.55****	1	2.06	305.64****	—	—	—
Population by Temperature	4	0.05	8.55**	4	0.56	20.68****	4	8885.0	1.51
Temperature by Sex	2	0.03	11.52**	—	—	—	—	—	—
Population by Sex	2	0.01	2.22	2	0.16	11.65****	—	—	—
Population by Temperature by Sex	4	0.01	1.54	—	—	—	—	—	—
THR	1	0.00	0.33	1	0.00	0.16	1	2.2	0.00
Temperature by THR	2	0.00	1.25	2	0.08	5.58**	2	1480.2	0.50
Population by THR	2	0.17	5.84**	2	0.01	0.55	2	630.6	0.21
Population by Temperature by THR	4	0.01	2.08	4	0.05	1.76	4	1755.2	0.30
Sex by THR	1	0.00	0.30	1	0.00	0.71	—	—	—
Temperature by Sex by THR	2	0.01	4.10*	—	—	—	—	—	—
Population by Sex by THR	2	0.01	1.87	2	0.01	0.50	—	—	—
Population by Temperature by Sex by THR	4	0.02	3.26*	—	—	—	—	—	—
Error	2307	3.39		676	4.55		616	903987.4	

NOTE.—THR, the right arm of the third chromosome. N, the number of autosomes sampled.
* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.
**** $P < 0.0001$.

APPENDIX E

ANOVA RESULTS FOR SINGLE-ARM KARYOTYPE DIFFERENCES, INTER-ARM KARYOTYPE INTERACTIONS, AND POPULATION-BY-KARYOTYPE INTERACTIONS ON VARIATION IN LIFE HISTORY

	LIFE-HISTORY CHARACTER[a]								
	DEVELOPMENTAL TIME (N = 1126)			AGE AT FIRST REPRODUCTION (N = 347)			ADULT LONGEVITY (N = 315)		
SOURCE OF VARIATION	df	Type IV Sum of Squares	F	df	Type IV Sum of Squares	F	df	Type IV Sum of Squares	F
Model	152	31.02	134.41****	119	13.37	13.54****	94	275602.2	1.99****
Temperature	2	27.29	8986.48****	2	8.85	533.16****	2	111126.7	37.68****
Population	2	0.01	2.46	2	0.07	3.93**	2	520.8	0.18
Sex	1	0.00	3.06	1	1.39	168.04****	—[b]	—	—
EXL/EXL	7	0.01	0.77	7	0.02	0.29	5	3176.4	0.43
EXR/EXR	3	0.00	1.04	3	0.02	0.42	2	3431.3	1.16
TWL/TWL	9	0.03	2.24**	9	0.10	1.33	9	18600.6	1.40
THR/THR	2	0.01	3.07*	2	0.02	1.48	2	3111.2	1.05
EXL/EXL by EXR/EXR	7	0.02	1.42	6	0.02	0.34	6	5113.7	0.58
EXL/EXL by TWL/TWL	49	0.06	0.80	30	0.14	0.57	27	44723.5	1.12
EXL/EXL by THR/THR	13	0.02	1.02	8	0.06	0.88	8	10100.7	0.86
EXR/EXR by TWL/TWL	23	0.02	0.61	13	0.13	1.16	12	8655.8	0.49
EXR/EXR by THR/THR	6	0.01	0.82	5	0.07	1.64	4	4714.4	0.80
TWL/TWL by THR/THR	16	0.02	0.65	13	0.08	0.77	13	18438.7	0.96
Error[c]	973	1.48		227	1.88		220	324432.0	
Population by EXL/EXL[d]	14	0.02	0.91	11	0.06	0.63	9	2631.5	0.18
Population by EXR/EXR	6	0.01	0.59	5	0.04	0.89	4	5293.8	0.81
Population by TWL/TWL	17	0.03	1.23	13	0.15	1.42	13	13404.1	0.63
Population by THR/THR	4	0.01	2.43*	4	0.03	0.86	4	7836.9	1.20
Error[e]	1056	1.56		162	1.32		124	201858.1	

NOTE.—Multiple comparisons for the TWL/TWL karyotypes are in Appendix G.

[a] N, the number of adults karyotyped.

[b] Longevity was not measured for adult males.

[c] Error term for single-arm and inter-arm karyotype ANOVA.

[d] Population-by-karyotype interactions were calculated in a separate ANOVA with all main effects included. All three-way interactions were insignificant and are not reported.

[e] Error term for population-by-karyotype ANOVA.

* $P < 0.05$.

** $P < 0.01$.

**** $P < 0.0001$.

APPENDIX F

MULTIPLE-COMPARISONS TEST FOR TWL DEVELOPMENTAL TIME

Gene Arrangement	*N**	Developmental Time (days)†
2L-2	163	26.1^{a}
2L-1	785	$26.3^{a,b}$
2L-3	1014	26.6^{b}
2L	370	27.2^{c}

* *N*, the number of autosomes sampled.

† Values are the results of Duncan's multiple-range test; mean developmental times having the same superscript are not significantly different ($P < 0.05$).

APPENDIX G

MULTIPLE COMPARISONS OF TWL/TWL KARYOTYPES

TWL/TWL			THR/THR		
Karyotype*	*N*†	Developmental Time (days)	Karyotype	*N*†	Developmental Time (days)
1/2	66	25.1^{a}	3R/3R	84	26.1^{a}
1/3	351	$25.9^{a,b}$	3R/3R-1	499	$26.4^{a,b}$
2/3	64	$26.1^{a,b}$	3R-1/3R-1	543	26.9^{b}
3/3	201	26.9^{b}			
S/S	20	26.9^{b}			
1/1	109	27.1^{b}			
S/2	28	27.3^{b}			
S/3	166	27.4^{b}			
S/1	119	27.4^{b}			
2/2	2	35.2^{c}			

NOTE.—Mean developmental times having the same superscript are not significantly different ($P < 0.05$).

* Second-chromosome karyotypes are written in shorthand notation; for example, 2/3 refers to the observed karyotype 2L-2/2L-3, and S denotes the standard gene arrangement 2L.

† *N*, the number of adults karyotyped.

APPENDIX H

ANOVA RESULTS FOR OBSERVED KARYOTYPE DIFFERENCES OF A SINGLE CHROMOSOME ARM AND POPULATION-BY-KARYOTYPE INTERACTIONS ON VARIATION IN EARLY FECUNDITY

Source of Variation	df	Type IV Sum of Squares	*F*
Model	93	2870667.80	1.92*
Population	2	79698.40	2.48
EXL/EXL	4	68072.77	1.06
EXR/EXR	2	112798.60	3.51*
TWL/TWL	7	334914.88	2.98*
THR/THR	2	8594.15	0.27
Population by EXL/EXL[a]	7	112787.22	1.00
Population by EXR/EXR	3	1057.22	0.02
Population by TWL/TWL	9	201837.77	1.40
Population by THR/THR	4	141113.07	2.20
Population by EXL/EXL by EXR/EXR	2	49428.23	1.54
Population by EXL/EXL by TWL/TWL	5	215058.03	2.68*
Population by EXL/EXL by THR/THR	4	33821.85	0.53
Population by EXR/EXR by TWL/TWL	5	42241.87	0.53
Population by EXR/EXR by THR/THR	1	1484.92	0.09
Population by TWL/TWL by THR/THR	2	31718.29	0.99
Error	21	337000.99	

NOTE.—N = 115, the number of adults karyotyped.
[a] F ratios associated with inter-arm-karyotype interactions were not significant.
* $P < 0.05$.

DUNCAN'S MULTIPLE-RANGE TESTS FOR KARYOTYPIC DIFFERENCES IN FECUNDITY

X CHROMOSOME			SECOND CHROMOSOME		
Karyotype	*N**	No. of Eggs	Karyotype†	*N**	No. of Eggs
EXR-2/EXR-2	37	778.40[a]	1/2	2	556.5[b]
EXR/EXR-2	67	810.42[a]	S/2	3	634.3[b,d]
EXR/EXR	11	819.09[a]	S/3	23	741.3[b,c,d]
			1/1	7	812.6[c,d]
			1/3	41	816.4[c,d]
			2/3	7	828.9[c,d]
			S/1	8	830.5[c,d]
			3/3	24	851.5[c]

NOTE.—Number of eggs having the same superscript are not significantly different ($P < 0.05$).
* N, the number of adults karyotyped.
† Second-chromosome karyotypes are written in shorthand notation, as in Appendix E.

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