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AN INTERACTION BETWEEN ENVIRONMENTAL TEMPERATURE AND GENETIC VARIATION FOR BODY SIZE FOR THE FITNESS OF ADULT FEMALE *DROSOPHILA MELANOGASTER*

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Abstract.—*Drosophila* and other ectotherms show geographic genetic variation in body size, with larger individuals at higher latitudes and altitudes. Temperature is implicated as an important selective agent because long-term laboratory culture of *Drosophila* leads to the evolution of larger body size at lower temperatures. In this paper, we tested the hypothesis that, in *Drosophila melanogaster*, larger size is favored at lower temperatures in part because of selection on adult females. We used replicated lines of *D. melanogaster* artificially selected for increased and decreased wing area with constant cell area. The resulting size differences between the selected lines were due solely to differences in cell number, and thereby were similar to the cellular basis of clinal variation in body size in nature. We examined life-history traits of adult females at 18 and 25°C. Rearing for two generations at the two temperatures did not affect the extent of the size differences between lines from the different selection regimes. There was a strong interaction between temperature and size selection for both survival and lifetime reproductive success, with larger females living significantly longer and producing more offspring over their lifetime only when reared and tested in the colder environment. There was also an increase in average daily progeny production in large-line females relative to the control and small lines again, only in the colder environment. Thus, the females from the large selection lines were relatively fitter at the colder temperature. At both experimental temperatures, especially the lower one, the small- line females rescheduled their progeny production to later ages. Larger body size may have evolved at higher latitudes and altitudes because of the advantages to the adult female of being larger at lower temperatures.

Key words.—Body size, *Drosophila melanogaster*, life history, longevity, fertility, temperature.

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Temperature is strongly implicated as a determinant of ectotherm body size. The thermal environment experienced by an individual during development has a direct effect on final size, with body size increasing as temperature decreases for most (Ray 1960; von Bertalanffy 1960; Precht et al. 1973; Atkinson 1994), although not all (Atkinson 1994) species for which the relationship has been investigated. In addition to this purely environmental effect, temperature can exert an evolutionary effect on body size. Body size clines, with genetically larger individuals at higher latitudes, have been reported for a diverse array of ectotherms including several *Drosophila* species (e.g., David and Bocquet 1975; David et al. 1983; Lemeunier et al. 1986; Coyne and Beecham 1987; James et al. 1995), the house fly *Musca domestica* (Bryant 1977), the honey bee *Apis melifera* (Alpatov 1929a), and a copepod *Scottolana canadensis* (Lonsdale and Levinton 1985). This repeatability suggests that size clines are a result of natural selection rather than drift.

Although many ecological variables change with latitude and could therefore be implicated as selective agents for size clines, several lines of evidence suggest temperature may be of particular importance. First, body size has been shown to increase not only with latitude, but also with altitude in *Drosophila* (Stalker and Carson 1948) and a frog *Rana sylvatica* (Berven 1982), and in the cooler periods of the breeding season in *Drosophila* (Stalker and Carson 1949; Tantawy 1964). Second, there is evidence from laboratory studies of thermal evolution in *Drosophila*. Replicated populations have been maintained at different temperatures in the laboratory for many generations, and the resulting cold-adapted lines are larger than the warm-adapted ones when reared at a common temperature, irrespective of whether the comparison is conducted in the warm or the cold environment (Anderson 1966, 1973; Cavicchi et al. 1985, 1989; Partridge et al. 1994). In the present study, we set out to test the hypothesis that larger size evolves at lower temperatures at least in part because of the way that natural selection acts on the adult female stage of the life history.

In contrast to the consistently larger size of cold-adapted thermal selection lines, adult females and males lived longer and adult females produced more offspring than flies from the other selection regime when they were reared and tested at their own evolutionary temperature (Partridge et al. 1995). Laboratory comparisons of female fecundity for natural populations of *Drosophila* showed similar results (*D. pseudoobscura*: Dobzhansky 1935; *D. melanogaster*: Tantawy and El Helw 1970). Females derived from cooler environments produced more eggs than females from warmer environments when they were tested at a lower temperature, whereas females from warmer environments produced more eggs at a higher testing temperature. These studies demonstrate adaptation of life-history traits of adult males and females to temperature, but cannot be used to deduce any role of body size in producing that adaptation. Because lines selected by evolutionary temperature undoubtedly differ in many aspects of adaptation to temperature, any effect of body size per se is potentially confounded by the correlated selective changes in these other traits. A similar difficulty would occur if the effects of body size on performance at different temperatures were deduced from differences in body size induced by tem-

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perature during rearing, because rearing temperature has been demonstrated to affect other traits in addition to body size (e.g., Huey et al. 1995; Zamudio et al. 1995; Crill et al. 1996). To test whether evolutionary changes in size per se affect fitness at different temperatures, it is necessary to manipulate body size alone and to examine the consequences for fitness at different experimental temperatures.

The association between body size and fitness traits at a single temperature has been frequently investigated in *Drosophila*. Mating success of males appears to be both phenotypically (Partridge and Farquhar 1981, 1983; Partridge et al. 1987a,b) and genetically (Ewing 1961; Wilkinson 1987) correlated with body size. Strong phenotypic correlations between the size of adult females and their fecundity have also been reported (e.g., Alpatov 1929b; Sang 1950; Tantawy and Vetukhiv 1960; Partridge et al. 1986; Partridge 1988), whereas genetic correlations have been reported, in general, as positive but weak (Robertson 1957; Tantawy 1961; Tantawy and Rakha 1964; Tantawy and El Helw 1966; Hillesheim and Stearns 1992). Strong positive phenotypic correlations between body size and longevity have been reported (e.g., Partridge and Farquhar 1981, 1983; Partridge et al. 1986), although under extremely benign conditions further increase in body size can be associated with a decline in longevity (Miller and Thomas 1958; Chapman and Partridge 1996) while genetic correlations have been reported as either positive (Tantawy and Rakha 1964; Tantawy and El Helw 1966; Partridge and Fowler 1992) or absent (Zwaan et al. 1995). The general picture, therefore, is one of a positive association between size and adult fitness. In contrast, in the pre-adult period selection for increased adult size has been reported to result in increased developmental period and lowered survival to adulthood (Robertson 1963; Partridge and Fowler 1992; Santos et al. 1992, 1994), suggesting that stabilizing selection may act on body size through conflicting fitness effects on adults and juveniles. Larger body size could evolve at lower temperatures because of an effect on the fitness of either life-history stage. We have tested the hypothesis that larger size evolves at lower temperatures because of an altered pattern of natural selection on adult females. We have looked for an interaction between the effects of genetically altered body size and environmental temperature upon longevity, lifetime progeny production, and daily fecundity.

A response to selection for altered body size can be achieved by a change in cell size, cell number, or both. Genetic differences in body size between populations of *D. melanogaster* from different latitudes, at least as assayed in the wing blade, have been reported to be attributable mainly to differences in cell number, with little variation in cell size (James et al. 1995). To achieve a similar pattern of size variation through artificial selection, it is necessary to control cell size because directional selection for increased and decreased body size can result in an asymmetrical response, with increased body size being due to more cells, and decreased body size being due to a decrease in cell size (L. Partridge, K. Fowler, R. Langelan, and V. French, unpubl. data; B. Zwaan and L. Partridge, unpubl. data).

In this paper, we investigate the adult longevity and progeny production of females from replicated lines that were artificially selected for increased and decreased wing area, while cell area was held constant. Thus, the differences in wing area between the selection lines were caused by differences in cell number, like the clinal variation in size. Associated with the change in wing area was a correlated change in thorax length (McCabe et al. 1997). High genetic correlations between the size of different anatomical regions of the fly have been reported (Cowley and Atchley 1990; Wilkinson et al. 1990), and it was obvious to the eye that our selection-line flies were different in overall size from the controls. If larger body size has evolved at higher latitudes and altitudes in part because of natural selection on the adult female, then there should be an interaction between body size and experimental temperature for some aspect of adult female fitness.

Methods

Selection Lines

The selection lines have been described elsewhere (McCabe et al. 1997). In brief, they were derived from a random-bred, wild-type base stock collected in Dahomey, West Africa, in 1970 and maintained since in population cage culture at 25°C. Three replicate large, control, and small lines were artificially selected for wing area with constant cell area. Selection was performed at 25°C. For each selection line, the wing area and cell area of 25 males and 25 females was measured in each generation. To measure wing area and cell area, the wings were fixed in propanol and mounted in Aquamount on a microscope slide. The areas of the mounted wings were measured at ×50 magnification using a *camera lucida* attached to a dissecting microscope and Quora graphics tablet connected to a computer. The outline of each wing was traced starting at the alar-coastal break. Using a compound microscope at ×400 magnification with a *camera lucida* attachment, the trichomes within a 0.01^2 mm area of the posterior medial cell of the wing (equidistant from the fourth longitudinal vein, the posterior cross vein and the fifth longitudinal vein) were marked on a piece of paper. An index of the average cell area of a wing was estimated by dividing 0.01^2 mm by the trichome count.

For each of the three replicate large and small selection lines, the flies with the 10 largest or smallest wing areas out of the 25 individuals measured of each sex were selected as the parents of the next generation (Fig. 1A). In order to maintain constant cell area, we applied the condition that the mean cell area of the 10 selected pairs should correspond to the overall mean cell area of the controls. For the three control lines, 10 males and 10 females were selected at random. Each replicate line was propagated by setting up 100 first instar larvae in a bottle of 70 ml medium seeded with live yeast.

Experimental Design for Measurement of Life-History Traits

After eight generations of selection, correlated changes in adult female life history characters were investigated at two temperatures, 18 and 25°C. The flies used in the experiment were the products of two generations of rearing at the experimental temperature, so that parental and early embryonic effects of temperature and temperature shift were avoided (Fig. 1B). Eggs were collected from each replicate line by

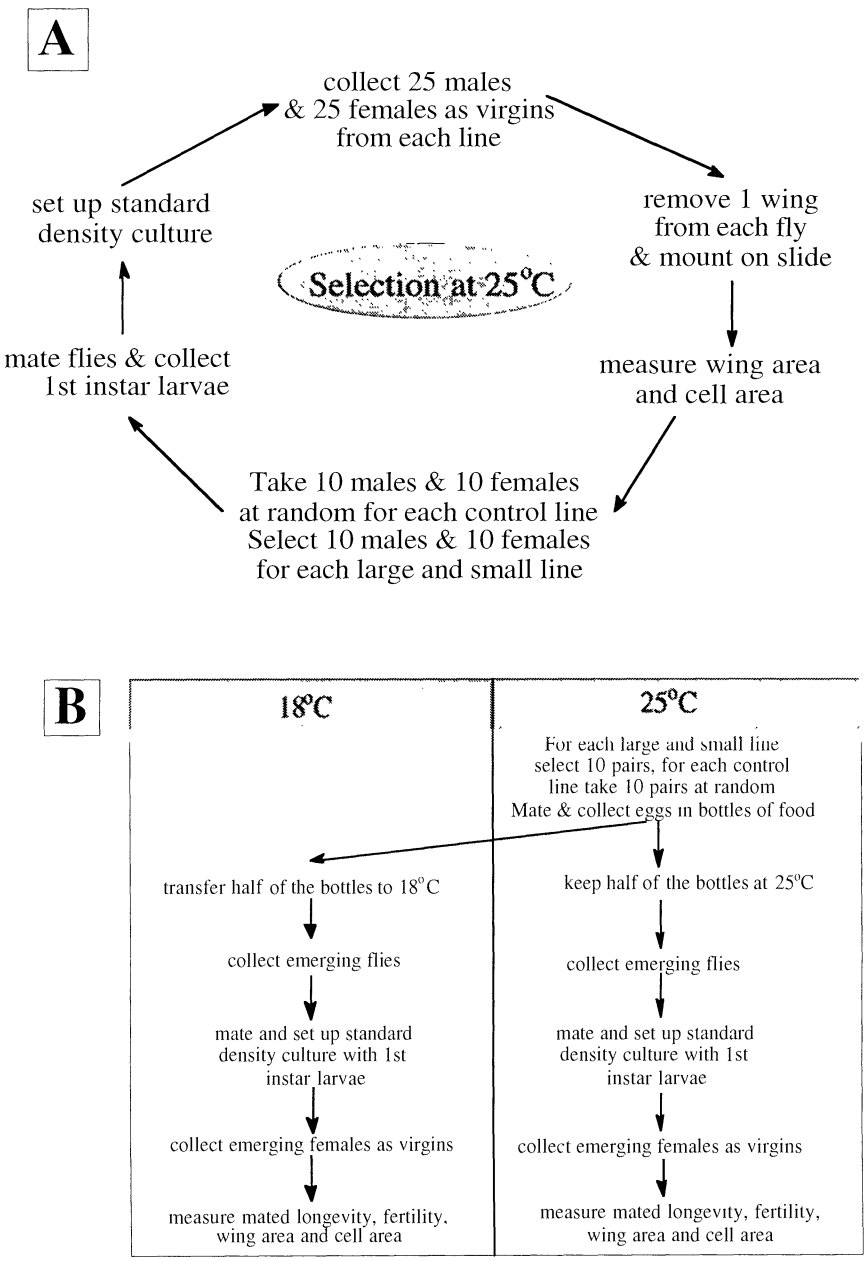

FIG. 1. Diagram of (A) the selection protocol and (B) the experimental design for the measurement of adult female life-history traits. Replicated lines were selected for increased and decreased wing area with constant cell area. After eight generations of selection adult female life-history traits were measured at 18 and 25°C. See text for further details.

allowing the 10 selected pairs to lay in fresh-yeasted bottles of medium for 10 sequential periods of 6 h. Half of these bottles were then cultured at each temperature. The flies eclosing from these bottles were the parents of the experimental individuals, and were transferred to laying pots containing yeasted grape juice medium. After an acclimatory period of 48 h at 18°C or 24 h at 25°C, the flies were transferred to fresh medium for a 2 h pre-lay period and then transferred again to fresh medium for egg collection, which lasted for 6 h at 18°C and 3 h at 25°C. First instar larvae were collected 46 h after the midpoint of the lay at 18°C, and 23 h after the midpoint of the lay at 25°C; and 30 larvae were placed in vials containing 7 ml medium seeded with live yeast, with 15 vials per replicate line. The eclosing females were collected as virgins and two females from each rearing vial were used for the measurements of female mated longevity, progeny production, and size characters at the two experimental temperatures.

The wing area and cell area of the experimental females were also assessed but, to avoid any harmful effects of wing removal on fertility and longevity, the wings were removed once the experimental female had died. The wing area and cell area data were both analyzed using two-way nested analyses of variance, with temperature and selection regime as

fixed main effects and with the replicate lines nested within selection regimes. Examination of the residuals confirmed that both data sets had normal error distributions (wing area: Shapiro Wilk $W = 0.98$, $P = 0.56$; cell area: Shapiro Wilk $W = 0.99$, $P = 0.94$).

Female Longevity

At both 18 and 25°C, 30 replicate vials for each of the six selection lines and three control lines were set up with one selected line female plus two, four-day-old virgin base stock males in each vial. The flies were transferred to fresh food every two days. Longevity was assessed by checking the vials daily for deaths and recording the date of death for each female. Dead males were replaced with virgin males of the same age, and all males were replaced every fortnight with four-day-old virgin base stock males.

The longevity data were analyzed parametrically using general linear modeling techniques available in the GLIM statistical package (McCullagh and Nelder 1983; Crawley 1993). This approach allowed us to investigate whether there was a significant interaction between temperature and selection regime while dealing the non-normal error distribution (Shapiro Wilk $W = 0.97$, $P=0.0015$).

Longevity (age at death) was analyzed as the response variable and a Weibull distribution was fitted to the data with constant rate and shape parameter. The Weibull distribution is a two parameter model that has the exponential distribution as a special case. This distribution allows the death rate to increase or decrease with age, and therefore it can be used to analyze Type I, Type II and Type III survivorship curves. A two-way nested analysis of deviance was then performed, with temperature and selection regime as fixed main effects and the replicate lines nested within selection regimes. Analysis of deviance is analogous to analysis of variance, but in GLIM maximum likelihood methods are used to fit linear models to the data, and deviance is the measure of discrepancy between the model and the data. The deviance of a model is twice the difference between the maximum log likelihood attainable and that achieved using the particular model under investigation (Crawley 1993).

Female Progeny Production

To assess progeny production, the vials which had contained the experimental females for the longevity measurements were retained at the appropriate experimental temperature, and the adults that eclosed were counted. Since any differences in pre-adult survival between the selection lines or any interaction of survival with temperature could have biased this measure of progeny production, pre-adult survival at both 18 and 25°C were assayed in a separate experiment. First instar larvae from each of the size-selected lines were placed at a density of 150 in a vial of medium, with 10 replicates for each selection line at each temperature. This density was chosen to correspond to the maximum in any of the vials in the progeny-production experiment. The adults were counted on eclosion. There were no significant differences in pre-adult survival between the selection regimes ($F_{(2,6)} = 0.515$, $P > 0.25$). The interaction between temperature and selection was marginally nonsignificant ($F_{(2,6)} = 4.04$, $0.05 < P < 0.10$). To establish that this interaction could not explain subsequent results, we determined that it was caused by relatively greater pre-adult survival of the large selected lines at 25°C, with no pattern of differences between the selection lines at 18°C, the opposite pattern to that found in our progeny-production measurements (see Results).

As an overall measure of lifetime fertility, the number of progeny produced per sampling interval by each female was summed over her life, and these totals (henceforth referred to as lifetime progeny production) were analyzed in a two-way nested analysis of variance. Temperature and selection regime were analyzed as fixed main effects, and the replicate lines were nested within selection regimes. Examination of the residuals confirmed that the errors were normally distributed (Shapiro Wilk $W = 0.989$, $P = 0.91$).

The data for progeny production in each sampling interval provide further information on the timing of any differences in progeny production between the selection lines. However, these data present some problems for analysis because of the nonindependence of successive samples. To circumvent this problem, the data for lifetime progeny production were further subjected to an analysis of covariance, with longevity as an additional explanatory variable. This allowed any effect of longevity on total reproductive output to be controlled, and any difference of average daily fecundity between the selection and temperature treatments to be deduced.

RESULTS

Size Traits

As expected, there was a highly significant ($P < 0.005$) difference in wing area between flies from the different selection regimes (Fig. 2A). The two generations of rearing at 18°C significantly increased wing area, but this effect did not differ between the selection regimes, with no significant interaction between selection and experimental temperature. Cell area was also significantly greater at 18 than at 25°C (Fig. 2B) but not significantly different between flies from the different selection regimes, and there was no significant interaction between experimental temperature and selection regime for cell area.

Life-History Traits

Both experimental temperature and selection regime significantly affected survival, and there was a highly significant interaction between temperature and selection regime (Table 1; Figs. 3 and 4) with females from the three large-selection lines having higher survival rates when reared and tested in the colder, but not the warmer environment. The difference between the selection regimes was consistent across the replicate lines, with no significant difference in survival probability between the lines within the selection regimes nor any significant interaction between the lines within a selection regime and temperature (Table 1). The large females had higher survival rates than females from the small or control selection lines ($\chi^2_{(2)} = 32.1$, $P < 0.00001$) which were not significantly different from one another ($\chi^2_{(1)} = 0.0011$, ns). The interaction between the effects of temperature and se-

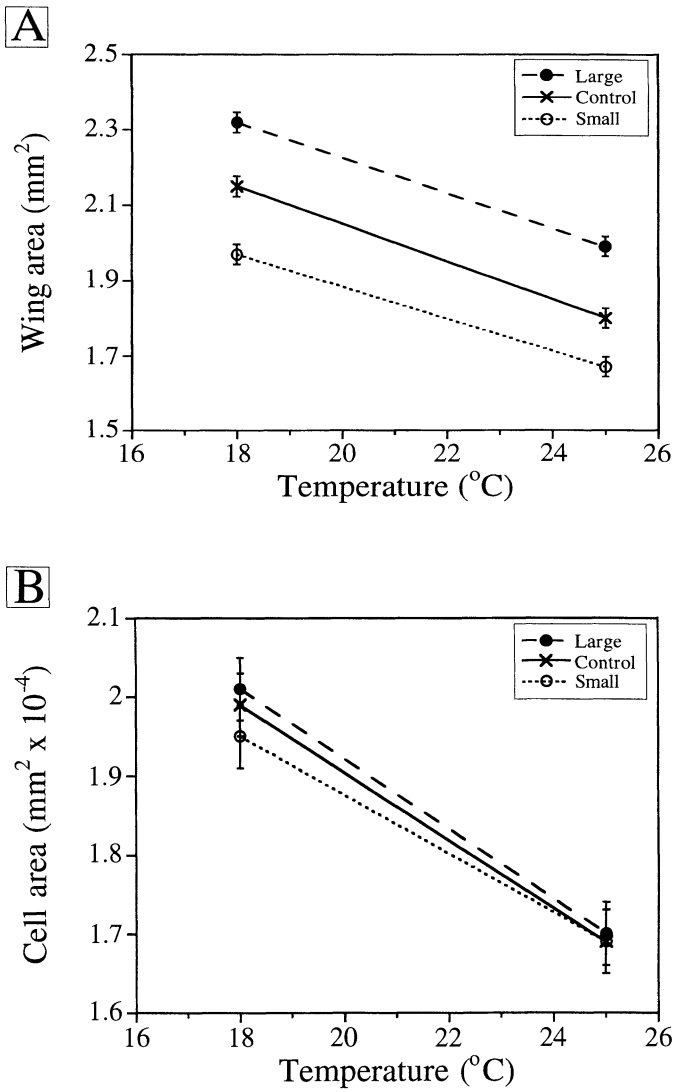

FIG. 2. Wing area (A) and cell area (B) of the females from the size selected lines which were used in the life-history traits experiment at 18 and 25°C. Each point gives the mean (± 95% CL) of the three replicate lines within each selection treatment. There was a highly significant difference in wing area between the selection regimes ($F_{(2,6)} = 16.21$, $P < 0.005$) and between rearing temperatures ($F_{(1,6)} = 3.7$;TS 10^5, $P<0.00001$), but there was no significant interaction between selection regime and temperature ($F_{(2,6)} = 0.016$, ns) for wing area. Cell area was significantly greater at 18 than at 25°C ($F_{(1,2)} = 3.4$;TS 10^5, $P < 0.00001$), but not significantly different between the selection regimes ($F_{(2,6)} = 2.02$, ns) and there was no significant interaction between temperature and selection regime ($F_{(2,6)} = 0.52$, ns).

lection regime is conspicuous when the mean longevity of the selection lines is plotted for the two temperatures (Fig. 4).

Females from the three large-selection lines produced more progeny over their lifetime than the control and small line females when reared and tested at 18°C (Table 2; Fig. 5). Analysis of variance revealed a significant interaction between temperature and selection regime ($F_{(2,6)} = 6.82$, $P < 0.05$) for lifetime progeny production. Since the data for preadult survival show that there was a tendency for relatively

TABLE 1. Two-way analysis of deviance on survival probability of females from the large-, control-, and small-size selected lines reared and tested at 18 and 25°C. Replicate lines were nested within selection regime, and selection regime and temperature were analyzed as fixed effects.

Effect	df	χ^2	P
Temperature	1	675.1	< 0.0001
Selection regime	2	29	< 0.0001
Lines within selection	6	4.6	ns
Temperature × selection	2	10.1	< 0.01
Temperature × lines within	6	2.2	ns

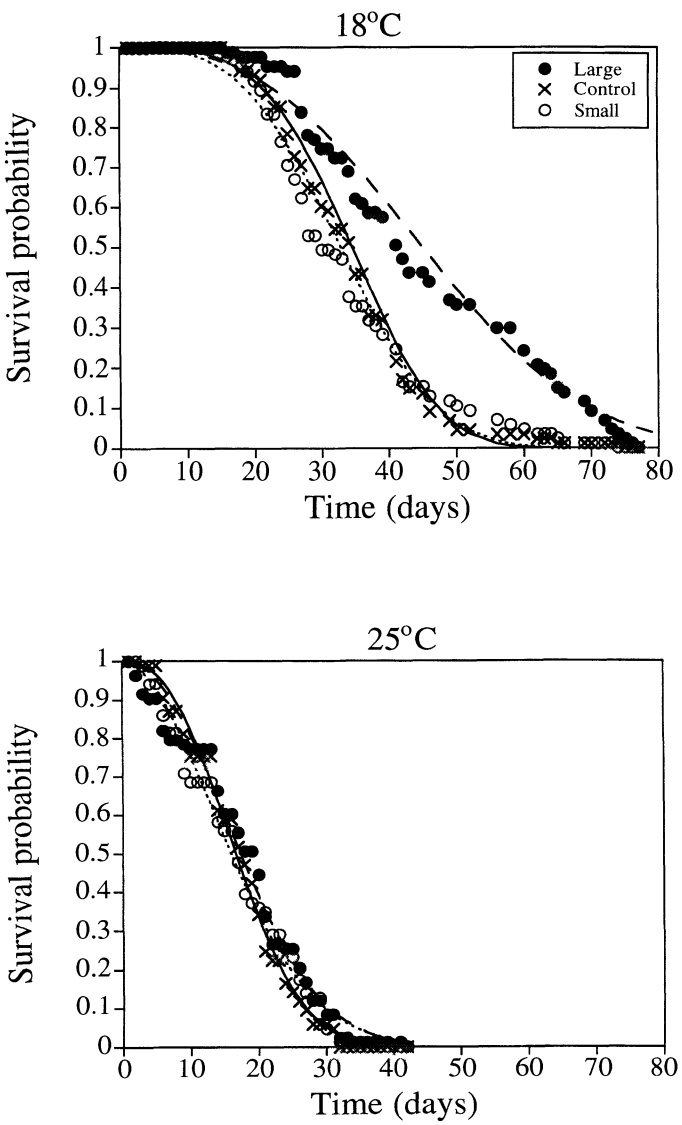

FIG. 3. Proportion of flies surviving each sampling interval (cumulative survival probability) plotted against time for mated females from the large-, control-, and small-selection lines at 18 and 25°C. The Weibull model provided a significantly better fit to the data than an exponential model ($\chi^2_{(1)} = 384.7$, $P < 0.00001$) with an estimated shape parameter of 2.5078, showing that mortality accelerated with age. The curves show the fitted Weibull survival function for each selection regime at each temperature.

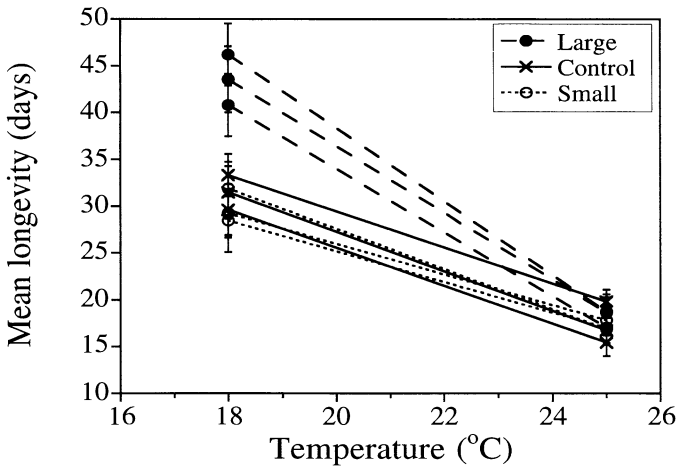

FIG. 4. Mean longevity (± 95% CL) of females from the large-, control-, and small- selection lines reared at 18 and 25°C. Longevity was significantly greater at 18 than at 25°C ($P < 0.0001$), differed between selection regimes ($P < 0.05$), and there was a significant interaction between temperature and selection regime ($P < 0.005$).

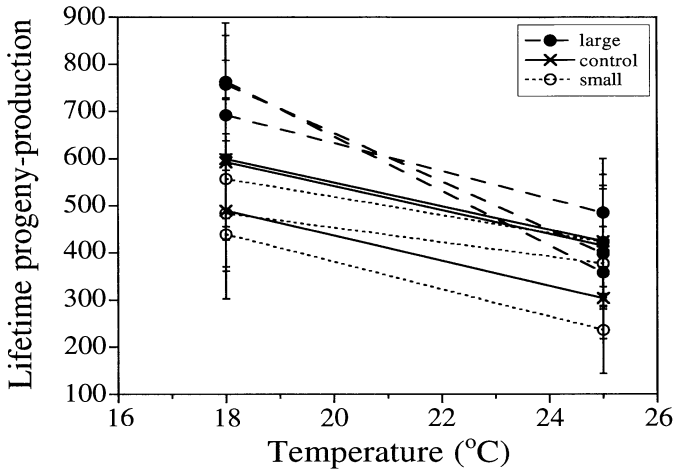

FIG. 5. Mean lifetime progeny production (± 95% CL) of females from the large-, control-, and small-selection lines reared at 18 and 25±C. Females produced significantly more progeny over their lifetime at 18 than at 25°C ($P < 0.0001$), differed in progeny production between selection regimes ($P < 0.05$), and there was a significant interaction between temperature and selection regime ($P < 0.005$).

greater pre-adult survival of the large lines at 25°C but not at 18°C, the interaction between temperature and selection regime for lifetime progeny production cannot be an artifact of differences in pre-adult survival.

The data for daily fecundity (Fig. 6) were analyzed indirectly because the data from successive time intervals were not independent due to the presence of many of the same females in each sample. Average daily fecundity was deduced from the relationships between lifetime progeny production and longevity at both temperatures (Fig. 7). At 25°C, there was no significant difference between the selection regimes in either the intercepts or the slopes of the regressions, nor was there any evidence for curvilinearity (Fig. 7). Thus, there was no evidence for any difference between the selection regimes in average daily progeny production at 25°C. The slope of the regression was significantly greater in the large-line females than in the small- and control-line females at 18°C ($F_{(1,253)} = 9.5$, $P < 0.05$). The relationship between longevity and lifetime progeny production was significantly curvilinear for the large-line females ($F_{(1,88)} = 7.8$, $P < 0.001$), but not for the small- or control-line females. For the 64% of large-line females at 18°C that lived for up to 50 days, lifetime progeny production increased more steeply with longevity than for the control- or small-line females, indicating that these large-line females produced more offspring per day than did the control- or small-line females. However, for the remaining 36% of large-line females which lived beyond 50 days, the relationship between longevity and lifetime progeny leveled, and then declined (Fig. 7). Part of the curvilinearity in the large females was accounted for by a greater postreproductive lifespan. In addition, some of the very long-lived, large-line females had increased longevity at the expense of reduced reproductive output. This type of analysis does not give an indication of any differences in the timing of progeny production by females from the different selection regimes. Inspection of confidence limits in Figure 6 shows that small-line females had significantly lower daily fecundity than controls, at least up to day 16 at 18°C and day 6 at 25°C, but not later in life. Thus the small lines rescheduled their progeny production towards later ages than the controls.

To quantify the performance of the selected lines relative to the controls, the mean lifetime progeny production and longevity of each of the replicate lines was calculated and was then divided by the overall control mean for each temperature. Thus defined, when relative longevity and lifetime progeny production are equal to unity, the selected lines performed no better and no worse than the control lines, whereas a value of greater than one indicates the extent to which the selected lines had increased relative to the controls. Selection for decreased wing area did not significantly increase or di-

TABLE 2. Two-way analysis of variance on lifetime progeny production of females from the large-, control-, and small-size selected lines reared and tested at 18 and 25°C. Replicate lines were nested within selection regime, and selection regime and temperature were analyzed as fixed effects.

Effect	df	SS	MS	*F*	*P*
Temperature	1	334 700 000	334 700 000	371	< 0.0001
Selection regime	2	3610499	1805249	7.5	< 0.05
Lines within selection	6	1444674	240779	2.5	ns
Temperature × selection	2	1275168	637584	6.8	< 0.05
Temperature × lines within	6	559786	93297.7	0.6	ns
Error	511	151482			

minish relative longevity or lifetime progeny production at either temperature (Table 3). Selection for increased wing area produced no significant improvement in relative longevity or lifetime progeny production at 25°C, but when females from the large- selection lines were reared and tested at 18°C, relative longevity was significantly increased by about 18% and relative lifetime progeny production by about 32% (Table 3). The increase in relative lifetime progeny production of the large lines at 18°C was significantly greater than the increase in relative longevity ($t = 3.121$, df = 4, $P < 0.05$), indicating that average daily progeny production was also increased.

Discussion

Replicate lines of *D. melanogaster* selected for increased and decreased wing area with constant cell area showed clear temperature dependence of adult female life history traits. There was a highly significant interaction between temperature and selection regime for both age specific survival and total progeny production. Both the longevity and daily progeny production of the large females were significantly increased relative to the controls when they were reared and tested at the lower temperature, leading to increased lifetime progeny production. Therefore selection for larger size increased total adult female performance at low temperatures. Selection for decreased wing area did not significantly improve or diminish relative longevity or lifetime progeny production, although it resulted in a rescheduling of progeny production toward later ages, especially at the lower experimental temperature. The rescheduling of progeny production to later in life in the small lines at 25°C could lower fitness because in nature this species may do much of its reproduction in expanding populations, where an early age of first reproduction is favored. Indeed, one phenotypic response of females to increased nutrition is to bring forward the average age at which progeny are produced (Chapman and Partridge 1996). The data therefore support the idea that body size of adult females is selected differently at high and low temperatures through its effects on longevity and on the extent and timing of reproduction, with genetically larger body size being favored in cooler environments.

The improved performance of large females in the cold was not because of a change in the relative size of the selection lines at the lower rearing temperature. There was no interaction between temperature and size selection for either wing area or cell area. Yet, the small line females did not suffer significantly reduced lifetime progeny production relative to controls at either experimental temperature, and the controls did not suffer any significant reduction in progeny production relative to the large lines at the higher experimental temperature. One possible explanation is that the sample size of females may not have been sufficiently large to detect such differences. Another is that the lifetime progeny production of adult females may increase with their size more rapidly as size increases. The mean lifetime progeny production of females from the three selection regimes at the two experimental temperatures is plotted against their mean wing area in Figure 8. Inspection of confidence limits shows extensive overlap between the lifetime progeny production of large-line females at 25°C and small line females at 18°C, when they are similar in size. It is possible, therefore, that the relationship between progeny production of adult females and their overall size does not change with experimental temperature. Rather, the environmental increase in body size at lower experimental temperatures, combined with the increase from artificial selection, may have taken the females into a size range where fitness increases more rapidly with increasing size. The data in Figure 8 do suggest such an upwardly accelerating relationship.

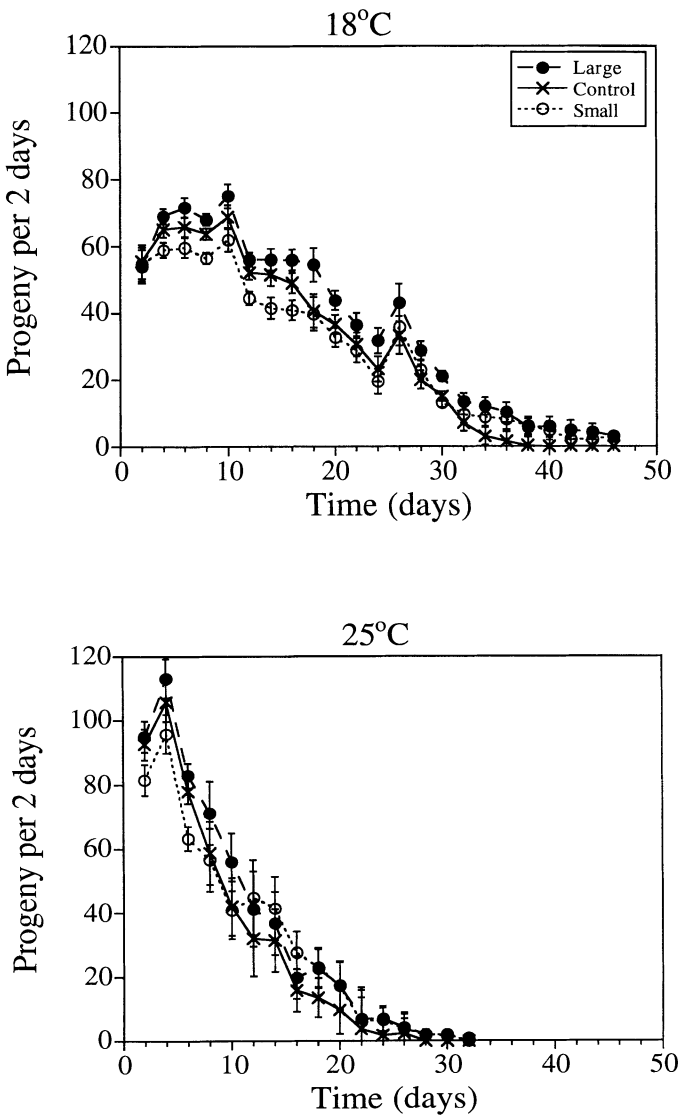

FIG. 6. The number of adult offspring produced per sampling interval by females from the size selected lines raised and tested at 18 and 25°C. Each point shows the mean (± 95% CL) for each selection regime calculated across replicate lines. Statistical analysis was not applied directly to these data because of the nonindependence of successive samples.

Distinguishing this interpretation from one where the relationship between size and adult female fitness is altered by experimental temperature will be difficult. As pointed out in the introduction, attempts to establish relationships between adult fitness and size per se, at any experimental temperature,

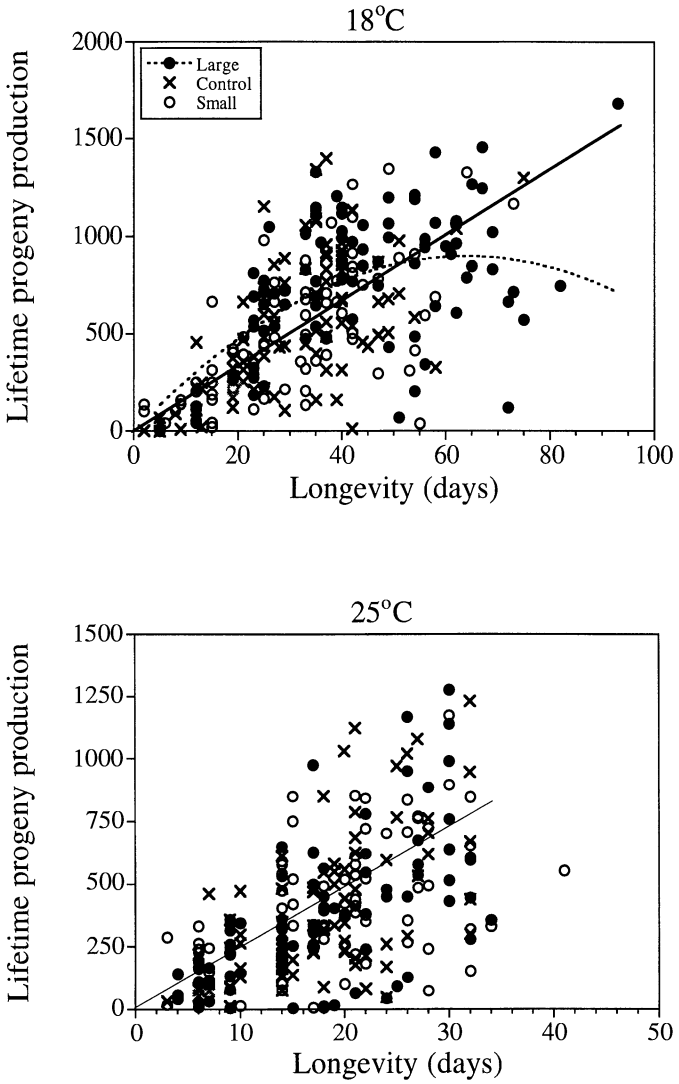

FIG. 7. The relationship between lifetime progeny production and longevity for females from the large-, control-, and small-selected lines reared and tested at 18 and 25°C. There was no significant difference between the selection regimes at 25°C in either the intercepts ($F_{(2, 6)} = 1.2269$, ns) or the slopes ($F_{(2,6)} = 0.5347$, ns) of the regressions. The line shows the overall regression for large, control and small lines. At 18°C the slope of the regression was significantly different between the large- line females and the small- and control-line females ($F_{(1, 253)} = 9.5$, $P < 0.05$), with significant curvilinearity for the large-line females ($F_{(1, 88)} = 7.8$ $P < 0.001$), but not for the small or control lines. The solid line shows the fitted regression line for the small- and control-line females, and the dashed line shows the fitted regression for the large-line females.

using flies whose size has been varied by rearing temperature, is doomed because of the confounding effects of rearing temperature on other aspects of physiology (e.g., Huey et al. 1995; Zamudio et al. 1995; Crill et al. 1996). Direct selection on the degree of phenotypic plasticity of body size in response to temperature could be used to settle the issue, and this trait has been demonstrated to be heritable and to respond to artificial selection (Scheiner and Lyman 1989, 1991).

The mechanisms responsible for the superior performance of adult females from the large selected lines at the lower temperature are not clear. Large flies may be more resistant to desiccation, but the advantage of increased size would be greater at higher, not lower temperatures. Heat dissipation and retention are also unlikely to be of importance because adult *D. melanogaster* are in a size range where they immediately adopt the temperature of their surroundings (Stevenson 1985). Processes affecting the acquisition, conservation, and use of resources necessary for adult survival and offspring production are more likely candidates. At 18°C, the longest lived large-line females produced fewer offspring over their lifetime than their shorter lived counterparts, suggesting their increased longevity may occur as a consequence of decreased allocation of resources to reproduction. Zwaan et al. (1995) found that direct selection for increased longevity in *D. melanogaster* resulted in decreased reproductive output. But our data do not simply suggest a temperature dependent reallocation of resources in the large-selection lines, because the net effect of selection for increased size was to increase both reproductive output and longevity at 18°C. This suggests that when temperature is reduced, either the large lines are able to acquire greater stores of metabolites or are using equivalent stores more efficiently, or both.

Fat is important for both maintenance and reproduction (e.g., Geer et al. 1970) and fat content has been implicated in the increased longevity of flies selected for increased virgin longevity (Zwaan et al. 1995), late reproduction (Service 1987) and starvation resistance (Service et al. 1988). For several species of ectotherm, fat content is increased when culture temperature is reduced (e.g., Lang 1963; Gilbert and O'Connor 1970; Collatz 1973). However, such a temperature effect alone could not explain the superior performance of the large lines; an interaction between temperature and body size for the ability to build up energy stores would be necessary.

Energy expenditure could be reduced if the large-line females had relatively lower routine metabolic rates when reared and tested at the lower temperature. Metabolic rate increases with body size, but mass specific metabolic rate decreases with size (e.g., Prosser 1986). Thus, larger individuals expend less energy per unit mass on their routine metabolism. Temperature also directly affects metabolic rate, decreasing it at lowered temperature (e.g., Hunter 1964). There is some evidence that for several species of ectotherm, mass specific metabolic rate decreases with increasing size more rapidly at lowered temperature (Rao and Bullock 1954; Meuwis and Heuts 1957). If temperature affected the relationship between metabolic rate and size in this way, then the relative cost of being large would be lower at 18 than at 25°C, thereby making more energy available for use in maintenance and reproduction. This could be directly tested by measuring the metabolic rates of the selection lines at the two different temperatures.

Given the holometabolous development of *Drosophila,* the size of the adult is largely dependent on its pre-adult growth period. Increased size must be achieved by increased development time, increased growth rate, or both. Large selected lines have previously been shown to take longer to develop (Reeve 1954; Sang 1956; Robertson 1957; Partridge and Fowler 1993). Because slow larval development may incur greater mortality in the pre-adult period (Santos et al. 1992,

TABLE 3. The performance of the large- and small-selected lines relative to the control lines at each temperature. For each trait at both 18 nd 25°C, the mean of each of the replicate lines was calculated, and this divided by the control mean. The significance of any deviation from unity for the large- and small-selected lines at each temperature was assessed using a two-tailed t-test with $n - 1 = 2$ degrees of freedom.

	Large			Small		
	Grand mean	SE	t	Grand mean	SE	t
Relative longevity						
18°C	1.18	0.023	7.71*	0.97	0.0152	−1.537
25°C	1.02	0.018	1.29	0.99	0.0098	−0.654
Relative progeny-production						
18°C	1.32	0.04	8.01*	0.88	0.06	−1.90
25°C	1.08	0.10	0.89	0.91	0.15	−0.62

* $P < 0.05$.

1994; Partridge and Fowler 1993), the advantage of large size for adult fitness may be counterbalanced by increased costs of growth to large size during the pre-adult period. However, lines selected for increased and decreased thorax length showed no evidence of temperature dependence of larval competitive ability (Partridge and Fowler 1993), and present evidence suggests the large selection lines studied in this paper did not suffer increased pre-adult mortality at either temperature. The assay of larval survival showed no significant differences between the selection regimes, and the nonsignificant interaction between temperature and selection indicated a tendency for increased pre-adult survival of the large selection lines at the warmer temperature. Thus, the increased progeny production of the large lines at 18°C can be attributed to increased levels of offspring production by the females rather than superior survival by the developing larvae, and the superior performance of the large-line females at the lower temperature was not offset by reduced survival of their offspring at the densities used in these experiments. It would be interesting to examine the longevity and fertility of males from these selection lines and to examine the fitness of larvae in different density regimes.

This study has shown that adult fitness components may be very important to thermal adaptation. By manipulating body size, this study has allowed us to identify a direct effect of increased body size on the fitness of adult females at low temperature. The results suggest that body size could indeed be selected differently at high and low temperatures through its effect on this life history stage.

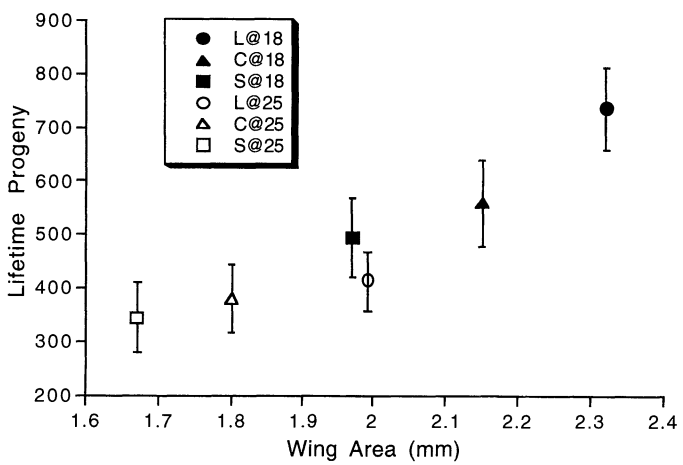

FIG. 8. Mean (± 95% CL) lifetime progeny production for females of the large (L), control (C) and small (S) selection regimes tested at 18 and 25°C, plotted against their wing areas at the same experimental temperatures.

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LITERATURE CITED

ALPATOV, W. W. 1929a. Biometrical studies on variation and races of the honey bee (*Apis melifera*). Q. Rev. Biol. 4:1–58.

———. 1929b. Growth and variation of the larvae of *Drosophila melanogaster*. J. Exp. Zool. 42:407–437.

ANDERSON, W. W. 1966. Genetic divergence in M. Vetukhiv's experimental populations of *Drosophila pseudoobscura*. Genet. Res. Camb. 7:255–266.

———. 1973. Genetic divergence in body size among experimental populations of *Drosophila pseudoobscura* kept at different temperatures. Evolution 27:278–284.

ATKINSON, D. 1994. Temperature and organism size—a biological law for ectotherms? Adv. Ecol. Res. 25:1–58.

BERVEN, K. A. 1982. The genetic basis of altitudinal variation in the wood *frog Rana sylvatica*. I. An experimental analysis of life history traits. Evolution 36:962–983.

BRYANT, E. H. 1977. Morphometric adaptation of the housefly, *Musca domestica* L., in the United States. Evolution 31:580–596.

CAVICCHI, S., D. GUERRA, G. GIORGI, AND C. PEZZOLI. 1985. Temperature-related divergence in experimental populations of *Drosophila melanogaster*. I. Genetic and developmental basis of wing size and shape variation. Genetics 109:665–689.

CAVICCHI, S., D. GUERRA, V. NATALI, C. PEZZOLI, AND G. GIORGI. 1989. Temperature-related divergence in experimental populations of *Drosophila melanogaster*. II. Correlation between fitness and body dimensions. J. Evol. Biol. 2: 235-251.

CHAPMAN, T., AND L. PARTRIDGE. 1996. Female fitness in Drosophila melanogaster: an interaction between the effect of nutrition and of encounter rate with males. Proc. Roy. Soc. Lond. B. 263:755–759.

COLLATZ, K. G. 1973. Temperature-dependent storage processes in crayfish and spiders. Pp 195–197 *in* W. Wieser, ed. Effects of temperature on ectothermic organisms. Springer-Verlag, Heidelberg, Germany.

COWLEY, D. E., AND W. R. ATCHLEY. 1990. Development and quantitative genetics of correlation structure among body parts of *Drosophila melanogaster*. Am. Nat. 135:242–268.

COYNE, J. A., AND E. BEECHAM. 1987. Heritability of two morphological characters within and among natural populations of *Drosophila melanogaster*. Genetics 117:727–737.

CRAWLEY, M. J. 1993. GLIM for ecologists. Blackwell Scientific, Oxford, U.K.

CRILL, W. D., R. B. HUEY, AND G. W. GILCHRIST. 1996. Within-generation and between-generation effects of temperature on the morphology and physiology of *Drosophila melanogaster*. Evolution 50:1205–1218.

DAVID, J. R., AND C. BOCQUET. 1975. Similarities and differences in latitudinal adaptation of two *Drosophila* sibling species. Nature 257:588–590.

DAVID, J. R., R. ALLEMEND, J. VAN HERREWEGE, AND Y. COHET. 1983. Ecophysiology: abiotic factors. Pp 105–170 *in* M. Ashburner, H. L. Carson, and J. N. Thompson, eds. Genetics and biology of *Drosophila*. Academic Press, London.

DOBZHANSKY, T. 1935. Fecundity in *Drosophila pseudoobscura* at different temperatures. J. Exp. Zool. 71:449–464.

EWING, A. W. 1961. Body size and courtship behaviour in *Drosophila melanogaster*. Anim. Behav. 9:93–99.

GEER, B. W., R. M. OLANDER, AND P. L. SHARP. 1970. Quantification of dietary choline utilization in adult *Drosophila melanogaster* by radioisotope methods. J. Ins. Physiol. 16:33–43.

GILBERT, L. I., AND J. D. O'CONNOR. 1970. Lipid metabolism and transport in arthropods. Pp 229–253 *in* M. Florkin and B. T. Scheer, ed. Chemical zoology, Vol. V. Arthropoda: part A. Academic Press, New York.

HILLESHEIM, E., AND S. C. STEARNS. 1992. Correlated responses in life history traits to artificial selection for body weight in *Drosophila melanogaster*. Evolution 46:745–752.

HUEY, R. B., T. WAKEFIELD, W. D. CRILL, AND G. W. GILCHRIST. 1995. Within-generation and between-generation effects of temperature on early fecundity of *Drosophila melanogaster*. Heredity 74:216–223.

HUNTER, A. S. 1964. Effects of temperature on *Drosophila*. I. Respiration of *D. melanogaster* grown at different temperatures. Comp. Biochem. Physiol. 11:411–417.

JAMES, A. C., R. AZEVEDO, AND L. PARTRIDGE. 1995. Cellular basis and developmental timing in a size cline of *Drosophila melanogaster*. Genetics 140:659–666.

LANG, C. A. 1963. The effect of temperature on the growth and chemical composition of the mosquito. J. Ins. Physiol. 9:279–286.

LEMEUNIER, F., J. R. DAVID, L. TSACAS, AND M. ASHBURNER. 1986. The *melanogaster* species group. Pp. 147–256 *in* M. Ashburner, H. L. Carson and J. M. Thompson, ed. Genetics and biology of *Drosophila*. Academic Press, London.

LONSDALE, D. J., AND J. S. LEVINTON. 1985. Latitudinal differentiation in copepod growth: an adaptation to temperature. Ecology 66:1397–1407.

MCCABE, J., V. FRENCH, AND L. PARTRIDGE. 1997. Joint regulation of cell size and cell number in the wing blade of *Drosophila melanogaster*. Genet. Res. Camb. 69:61–68.

MCCULLAGH, P., AND J. A. NELDER. 1983. Generalised linear models. Chapman-Hall, London.

MEUWIS, A. L., AND M. J. HEUTS. 1957. Temperature dependence of breathing rate in carp. Biol. Bull. (Woods Hole) 112:97–107.

MILLER, R. S., AND J. L. THOMAS. 1958. The effects of larval crowding and body size on the longevity of adult *Drosophila melanogaster*. Ecology 39:118–125.

PARTRIDGE, L. 1988. Lifetime reproductive success in *Drosophila*. Pp. 11–23 *in* T. R. Clutton-Brock, ed. Reproductive success. Univ. of Chicago Press, Chicago.

PARTRIDGE , L., AND M. FARQUHAR. 1981. Sexual activity reduces lifespan of male fruitflies. Nature 294:580–582.

———. 1983. Lifetime mating success of male fruitflies (*Drosophila melanogaster*) is related to their size. Anim. Behav. 31: 871–877.

PARTRIDGE, L., AND K. FOWLER. 1992. Direct and correlated responses to selection on age at reproduction in *Drosophila melanogaster*. Evolution 46:76–91.

———. 1993. Responses and correlated responses to artificial selection on thorax length in *Drosophila melanogaster*. Evolution 47:213–226.

PARTRIDGE, L., K. FOWLER, S. TREVITT, AND W. SHARP. 1986. An examination of the effects of males on the survival and egg-production rates of female *Drosophila melanogaster*. J. Insect Physiol. 32:925–929.

PARTRIDGE, L., A. HOFFMANN, AND J. S. JONES. 1987a. Male size and mating success in *Drosophila melanogaster* and *D. pseudoobscura* under field conditions. Anim. Behav. 35:468–476.

PARTRIDGE, L., A. EWING, AND A. CHANDLER. 1987b. Male size and mating success in *Drosophila melanogaster*: the roles of male and female behaviour. Anim. Behav. 35:555–562.

PARTRIDGE, L., B. BARRIE, K. FOWLER, AND V. FRENCH. 1994. Evolution and development of body-size and cell-size in *Drosophila melanogaster* in response to temperature. Evolution 48:1269–1276.

PARTRIDGE, L., B. BARRIE, N. H. BARTON, K. FOWLER, AND V. FRENCH. 1995. Rapid laboratory evolution of adult life-history traits in *Drosophila melanogaster* in response to temperature. Evolution 49:538–544.

PRECHT, H., J. CHRISTOPHERSEN, H. HENSEL, AND W. LARCHER. 1973. Temperature and Life. Springer-Verlag, Berlin.

PROSSER, C. L. 1986. Adaptational Biology: molecules to organisms. J. Wiley, New York.

RAO, K. P., AND T. H. BULLOCK. 1954. Q_{10} as a function of size and habitat temperature in poikilotherms. Am. Nat. 88:33–44.

RAY, C. 1960. The application of Bergmann's and Allen's rules to the poikilotherms. J. Morphol. 106:289–306.

REEVE, E. C. R. 1954. Natural selection for body size in *Drosophila*. (Abstract) Caryologica Supplementary Vol., Proc. Int. Congr. Genet. 9:854–855.

ROBERTSON, F. W. 1957. Studies in quantitative inheritance. XI. Genetic and environmental correlation between body size and egg production *in Drosophila melanogaster*. J. Genet. 55:428–443.

———. 1963. The ecological genetics of growth in *Drosophila*. VI. The genetic correlation between the duration of the larval period and body size in relation to larval diet. Genet. Res. Camb. 4:74–92.

SANG, J. H. 1950. Population growth in *Drosophila* cultures. Biol. Rev. 25:188–219.

———. 1956. The quantitative nutritional requirements of *Drosophila melanogaster*. J. Exp. Biol. 33:45–72.

SANTOS, M., K. FOWLER, AND L. PARTRIDGE. 1992. On the use of tester stocks to predict the competitive ability of genotypes. Heredity 69:489–495.

———. 1994. Gene-environment interaction for body size and larval density in *Drosophila melanogaster*: an investigation of effects on development time, thorax length and adult sex ratio. Heredity 72:515–521.

SCHEINER, S. M., AND R. F. LYMAN. 1989. The genetics of phenotypic plasticity. I. Heritability. J. Evol. Biol. 2:95–107.

———. 1991. The genetics of phenotypic plasticity. II. Response to selection. J. Evol. Biol. 4:23–50.

SERVICE, P. M. 1987. Physiological mechanisms of increased stress resistance in *Drosophila melanogaster* selected for postponed senescence. Physiol. Zool. 60:321–326.

SERVICE, P. M., E. W. HUTCHINSON, AND M. R. ROSE. 1988. Multiple genetic mechanisms for the evolution of senescence in *Drosophila melanogaster*. Evolution 47:387–399.

STALKER , H. D., AND H. L. CARSON. 1948. An altitudinal transect of *Drosophila robusta* Sturtevant. Evolution 2:295–305.

———. 1949. Seasonal variation in the morphology *of Drosophila robusta* Sturtevant. Evolution 3:330–343.

STEVENSON, R. D. 1985. Body size and limits to daily range of body temperature in terrestrial ectotherms. Am. Nat. 125:102–117.

TANTAWY, A. O. 1961. Effects of temperature on productivity and genetic variance of body size in *Drosophila pseudoobscura*. Genetics 46:227–238.

———. 1964. Studies on natural populations of *Drosophila*. III. Morphological and genetic differences of wing length *in Drosophila melanogaster* and *D. simulans* in relation to season. Evolution 18:560–570.

TANTAWY, A. O., AND M. R. EL HELW. 1966. Studies on natural populations of *Drosophila*. V. Correlated response to selection in *Drosophila melanogaster*. Genetics 53:97–110.

———. 1970. Studies on natural populations of *Drosophila*. IX. Some fitness components and their heritabilities in natural and mutant populations of *Drosophila melanogaster*. Genetics 64: 79–91.

TANTAWY, A. O., AND F. A. RAKHA. 1964. Studies on natural populations of *Drosophila*. IV. Genetic variances of and correlations between four characters *in D. melanogaster*. Genetics 50:1349–1355.

TANTAWY, A. O., AND M. O. VETUKHIV. 1960. Effects of size on fecundity, longevity and viability in populations of *Drosophila pseudoobscura*. Am. Nat. 94:395–403.

VON BERTALANFFY, L. 1960. Principles and theories of growth. Pp. 137–259 *in* W. N. Nowinski, ed., Fundamental aspects of normal and malignant growth. Elsevier, Amsterdam.

WILKINSON, G. S. 1987. Equilibrium analysis of sexual selection in *Drosophila melanogaster*. Evolution 41:11–21.

WILKINSON, G. S., K. FOWLER, AND L. PARTRIDGE. 1990. Resistance of genetic correlation structure to directional selection in *Drosophila melanogaster*. Evolution 44:1990–2003.

ZAMUDIO, K. R., R. B. HUEY, AND W. D. CRILL. 1995. Bigger isn't always better - body size, developmental and parental temperature and male territorial success in *Drosophila melanogaster*. Anim. Behav. 49:671–677.

ZWAAN, B., R. BIJLSMA, AND R. F. HOEKSTRA. 1995. Direct selection on lifespan in *Drosophila melanogaster*. Evolution 49:649–659.

Corresponding Editor: L. Meffert

Literature Cited

Biometrical Studies on Variation and Races of the Honey Bee (Apis mellifera L.)

W. W. Alpatov

The Quarterly Review of Biology, Vol. 4, No. 1. (Mar., 1929), pp. 1-58.

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Evolution, Vol. 27, No. 2. (Jun., 1973), pp. 278-284.

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Evolution, Vol. 36, No. 5. (Sep., 1982), pp. 962-983.

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LINKED CITATIONS

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Stable URL:

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Linda Partridge; Kevin Fowler

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Evolution, Vol. 47, No. 1. (Feb., 1993), pp. 213-226.

Stable URL:

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Linda Partridge; Brian Barrie; Kevin Fowler; Vernon French

Evolution, Vol. 48, No. 4. (Aug., 1994), pp. 1269-1276.

Stable URL:

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Rapid Laboratory Evolution of Adult Life-History Traits in Drosophila melanogaster in Response to Temperature

Linda Partridge; Brian Barrie; Nicholas H. Barton; Kevin Fowler; Vernon French

Evolution, Vol. 49, No. 3. (Jun., 1995), pp. 538-544.

Stable URL:

http://links.jstor.org/sici?sici=0014-3820%28199506%2949%3A3%3C538%3ARLEOAL%3E2.0.CO%3B2-Z

LINKED CITATIONS

Q 10 as a Function of Size and Habitat Temperature in Poikilotherms
K. Pampapathi Rao; Theodore H. Bullock
The American Naturalist, Vol. 88, No. 838. (Jan. - Feb., 1954), pp. 33-44.
Stable URL:
http://links.jstor.org/sici?sici=0003-0147%28195401%2F02%2988%3A838%3C33%3AQAAFOS%3E2.0.CO%3B2-5

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Philip M. Service
Evolution, Vol. 47, No. 2. (Apr., 1993), pp. 387-399.
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http://links.jstor.org/sici?sici=0014-3820%28199304%2947%3A2%3C387%3ALEOLAR%3E2.0.CO%3B2-9

An Altitudinal Transect of Drosophila robusta Sturtevant
Harrison D. Stalker; Hampton L. Carson
Evolution, Vol. 2, No. 4. (Dec., 1948), pp. 295-305.
Stable URL:
http://links.jstor.org/sici?sici=0014-3820%28194812%292%3A4%3C295%3AAATODR%3E2.0.CO%3B2-G

Seasonal Variation in the Morphology of Drosophila robusta Sturtevant
Harrison D. Stalker; Hampton L. Carson
Evolution, Vol. 3, No. 4. (Dec., 1949), pp. 330-343.
Stable URL:
http://links.jstor.org/sici?sici=0014-3820%28194912%293%3A4%3C330%3ASVITMO%3E2.0.CO%3B2-P

Body Size and Limits to the Daily Range of Body Temperature in Terrestrial Ectotherms
R. D. Stevenson
The American Naturalist, Vol. 125, No. 1. (Jan., 1985), pp. 102-117.
Stable URL:
http://links.jstor.org/sici?sici=0003-0147%28198501%29125%3A1%3C102%3ABSALTT%3E2.0.CO%3B2-S

Studies on Natural Populations of Drosophila. III. Morphological and Genetic Differences of Wing Length in Drosophila melanogaster and D. simulans in Relation to Season
A. O. Tantawy
Evolution, Vol. 18, No. 4. (Dec., 1964), pp. 560-570.
Stable URL:
http://links.jstor.org/sici?sici=0014-3820%28196412%2918%3A4%3C560%3ASONPOD%3E2.0.CO%3B2-B

LINKED CITATIONS

Effects of Size on Fecundity, Longevity and Viability in Populations of Drosophila pseudoobscura

A. O. Tantawy; M. O. Vetukhiv

The American Naturalist, Vol. 94, No. 879. (Nov. - Dec., 1960), pp. 395-403.

Stable URL:

http://links.jstor.org/sici?sici=0003-0147%28196011%2F12%2994%3A879%3C395%3AEOSOFL%3E2.0.CO%3B2-%23

Equilibrium Analysis of Sexual Selection in Drosophila melanogaster

Gerald S. Wilkinson

Evolution, Vol. 41, No. 1. (Jan., 1987), pp. 11-21.

Stable URL:

http://links.jstor.org/sici?sici=0014-3820%28198701%2941%3A1%3C11%3AEAOSSI%3E2.0.CO%3B2-W

Resistance of Genetic Correlation Structure to Directional Selection in Drosophila melanogaster

Gerald S. Wilkinson; Kevin Fowler; Linda Partridge

Evolution, Vol. 44, No. 8. (Dec., 1990), pp. 1990-2003.

Stable URL:

http://links.jstor.org/sici?sici=0014-3820%28199012%2944%3A8%3C1990%3AROGCST%3E2.0.CO%3B2-9

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Bas Zwaan; R. Bijlsma; R. F. Hoekstra

Evolution, Vol. 49, No. 4. (Aug., 1995), pp. 649-659.

Stable URL:

http://links.jstor.org/sici?sici=0014-3820%28199508%2949%3A4%3C649%3ADSOLSI%3E2.0.CO%3B2-6