

LIFE-HISTORY CHANGES THAT ACCOMPANY THE TRANSITION FROM SEXUAL TO PARTHENOGENETIC REPRODUCTION IN *DROSOPHILA MERCATORUM*

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Abstract.—In spite of the predicted genetic and ecological costs of sex, most natural populations maintain sexual reproduction, even those capable of facultative parthenogenesis. Unfertilized eggs from natural populations of *Drosophila mercatorum* occasionally develop into viable adults, but obligately parthenogenetic populations are unknown in this species. To evaluate the microevolutionary forces that both favor and constrain the evolution of parthenogenesis in *D. mercatorum*, we have measured parthenogenetic rates across a natural, sexually reproducing population and characterized the life-history changes that accompany the transition from sexual to parthenogenetic reproduction in laboratory strains. A highly significant difference in parthenogenetic rate was found between two populations in close geographic proximity, with increased rate found with lower population density. Laboratory strains of parthenogenetic females suffered increased mortality and reduced egg viability relative to their virgin counterparts from a sexual strain. Lifetime egg production was similar across all strains, but a shift in peak egg production to an earlier age also occurred. The combination of these life-history traits resulted in a higher net reproductive value for sexual females, but because they also had a longer generation time, intrinsic rate of increase was not as dramatically different from parthenogenetic females. In environments with high early mortality, there may be no fitness disadvantage to parthenogenesis, but the predicted ecological advantage of a twofold increase in intrinsic rate of increase was not realized. These results support the theory of Stalker (1956) that parthenogenesis is favored in environments in which sexual reproduction is difficult or impossible.

Key words.—Cost of sex, *Drosophila mercatorum*, intrinsic rate of increase, life-history evolution, net reproductive value, parthenogenesis.

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Sex is the predominant mode of reproduction in nearly all multicellular taxa. Although development of unfertilized eggs by parthenogenesis is widespread in nature, it characterizes very few taxonomic groups above the species level (Maynard Smith 1988). The ubiquitous maintenance of sexual reproduction in spite of its inherent genetic and ecological disadvantages has long been considered a paradox in evolutionary biology (Williams 1975; Maynard Smith 1978). The ecological disadvantage of sex (the cost of males; Williams 1980) arises in multicellular organisms with separate male and female sexes because if a mating pair produced the same number of offspring as a parthenogenetic female, they would have only half the number of offspring per individual as that single female would (Maynard Smith 1971). The resulting lower intrinsic rate of increase would cause sexual females to be replaced by parthenogenetic females under the assumption that the same number of equally viable eggs are indeed produced in both modes of reproduction.

At least part of this assumption is regularly violated. Parthenogenetic insects generally have lower hatch rates than their sexual counterparts, sometimes by as much as an order of magnitude (Stalker 1956; Carson et al. 1957; Carson 1967; Lamb and Willey 1979; Hong and Ando 1998). The tremendous reduction in viability of parthenogenetic progeny suggests the real question is why parthenogenesis would exist at all (Templeton 1983).

Theoretical evaluations of the relative costs of sexual versus asexual reproduction often compare obligately sexual versus obligately asexual populations (Hurst and Peck 1996; but see Uyenoyama 1984). However, the fitness of obligate parthenogens is not likely to represent that present at inception of parthenogenesis. Selection has been shown to improve

parthenogenetic ability (Stalker 1954; Carson 1967), and obligate parthenogens have presumably been subject to such selection repeatedly. To understand the origin and present distribution of parthenogenesis, we must know what barriers there may be to its evolution or to what extent selection may initially favor parthenogenesis in a sexual population. The most relevant comparison between sexual and parthenogenetic reproduction would be in a sexual species that has only occasional parthenogenesis—it is in such species that selection has the opportunity to increase the frequency of parthenogenesis and establish obligate parthenogenetic populations (Templeton 1982).

Populations of *Drosophila mercatorum*, like many *Drosophila* species, are tycho-parthenogenetic (able to occasionally produce parthenogenetic offspring; Stalker 1954; Templeton 1979). Occasional or facultative parthenogenesis is also found in at least nine other insect orders and occurs with obligate parthenogenesis in genera within at least six of those orders, suggesting its evolutionary potential (Bell 1982). Indeed, the only obligately parthenogenetic species known in the genus *Drosophila*, *D. mangabeiri*, is thought to have evolved from a tycho-parthenogenetic species much like *D. mercatorum* (Carson et al. 1957).

Between 79% and 99% of parthenogenesis in *D. mercatorum* occurs by gamete duplication, the mitotic duplication of one meiotic product and the subsequent fusion of the two mitotic products to restore diploidy (Carson 1973). This mechanism results in complete homozygosity at all loci within one generation and enables establishment of completely isogenic and homozygous clonal lineages (Carson et al. 1969). Life-history parameters that are properties of cohorts rather than individuals can thus be characterized for particular

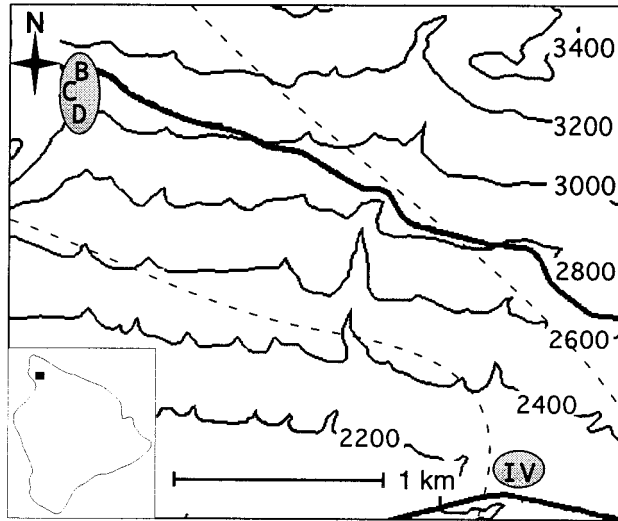


FIG. 1. The collecting sites near Kamuela, Hawaii. The contour lines show elevation above sea level in 200-foot increments. The thick solid line indicates road, and the dotted line shows the approximate distribution of the cactus *Opuntia megacantha*. A map of the Island of Hawaii is inset to show the approximate location of the sites.

parthenogenetic genotypes. Many studies have used *Drosophila* for investigations of life-history evolution (Birch et al. 1963; Malick and Kidwell 1966; Kidwell and Malick 1967; Clare and Luckinbill 1985; Partridge et al. 1987; Roper et al. 1996; Chippindale et al. 1997) because of the rapid generation time, the ease of laboratory rearing, and the availability of abundant ecological and genetic information about the genus. *Drosophila mercatorum* is thus an excellent system in which to compare the relative fitness advantages of parthenogenetic versus sexual reproduction that are likely to be present at the initial evolution of such ability.

This study measures rates of parthenogenesis in a natural population of *D. mercatorum* near Kamuela, Hawaii and characterizes the life-history changes (survival, egg production, and egg viability) and age-dependent selection values (net reproductive value, generation length, and intrinsic rate of increase) that accompany the transition from sexual to parthenogenetic reproduction in laboratory strains of *D. mercatorum* established from this natural population. These data are used to evaluate the true costs and benefits associated with parthenogenetic reproduction in *D. mercatorum*.

MATERIALS AND METHODS

Strains

In July and August 1990, collections of *D. mercatorum* were made in patches of the cactus *Opuntia megacantha* near Kamuela, Hawaii (Fig. 1). Most flies were aspirated directly off rotting cladodes; the remainder were captured in 1-gallon bags containing two to three rotten guavas placed well inside the cactus. All collections were made shortly after sunrise until about 1030 h. Almost all wild-caught females that were placed individually in shell vials had been inseminated and produced male and female offspring. In this manner, 55 site B-C-D lines and 33 site IV lines were established. The col-

lections at C and D were pooled with the B collections because they were so poor (they are within 100 m of one another and far from site IV; Fig. 1).

From each isofemale line, 10 virgin F_1 females (i.e., offspring of a mating that occurred in the wild) were isolated in a shell vial, placed on fresh food daily, and allowed to lay unfertilized eggs for 12 days after eclosion. The number of eggs produced by each virgin line was estimated from the equation:

$$y = n[8.1(t - 4)^{0.5} - 0.088(t - 4)^2]/3, \quad (1)$$

where y is the estimated number of eggs laid, n is the average number of females in the virgin line $(n_{initial} + n_{final})/2$, and t is the number of days of egg laying. This equation is empirically derived and validated in Templeton et al. (1976).

Each parthenogenetically produced F_2 female was placed in a new shell vial every 3 days until death. The viable parthenogenetic rate is defined as the number of parthenogenetically produced F_2 offspring divided by the estimated number of eggs laid by the virgin F_1 females. The true parthenogenetic rate is defined as the number of parthenogenetically produced F_2 offspring that are themselves capable of parthenogenetic reproduction divided by the estimated number of eggs laid by the virgin F_1 females. Hypotheses of homogeneity of parthenogenetic rates across strains or with earlier studies are tested with the log-likelihood ratio test:

$$2[\sum x_i \ln(x_i/n_i) - \sum x_i \ln(\sum x_i / \sum n_i)], \quad (2)$$

where x_i is the number of parthenogenetically produced F_2 offspring (or number of parthenogenetically produced F_2 offspring that produced parthenogenetic progeny, depending upon the hypothesis of interest) in strain (or set of strains) i ; and n_i is the estimated number of eggs laid in strain (or set of strains) i . Statistic (2) converges to a chi-square under the null hypothesis of homogeneity, with the degrees of freedom being the number of strains (or sets of strains) being tested minus one.

Four different parthenogenetic strains of *D. mercatorum* were established from two gravid females collected at site IV. Three virgin offspring from female 23 and one virgin offspring from female 43 produced parthenogenetic progeny from which parthenogenetic lineages could be established. The strains were named Im23-6, Im23-8, Im23-C, and Im43-7 respectively ("Im" standing for impaternate). Each strain passed through several single female generations to ensure complete isogenicity. The natural population from which these strains were derived was also the source of a sexual laboratory strain of *D. mercatorum* named K + X established in 1987. The relatively small number of strains used in this experiment and the fact that the sexual strain was isolated 3 years before the parthenogenetic strains may limit the generality of our results, but there is no reason to expect that these strains are atypical.

Experimental Design

All flies used in each replicate of this experiment eclosed within the same 24-h period. Virgin females of the sexual strain (K + X) were used for comparisons of survival, egg production, and egg fate with parthenogenetic females be-

cause mating is known to affect life-history parameters in *Drosophila* (Malick and Kidwell 1966; Kidwell and Malick 1967; Crews et al. 1985; Partridge et al. 1987; Fowler and Partridge 1989). Flies of the sexual strain were anesthetized with carbon dioxide for sexing. Any impact from this brief exposure should have been minimal because regular exposure to carbon dioxide anesthesia was found to have no effect on female *Drosophila melanogaster* survival or egg production (Partridge et al. 1986).

The strains were housed separately, with 35 flies of each put together in 100-ml plastic beakers inverted onto 50-mm plastic petri dishes. The bottom of the beakers (the top of the fly houses) had been replaced by mesh covering. The petri dishes contained grape juice-agar medium for oviposition and facilitation of egg counting. A drop of wet yeast was placed on each dish for food. Petri dishes were changed daily at 0830 h and at 1730 h. Flies that had died or escaped during dish changing were recorded. All eggs were counted.

To determine the developmental fate of these eggs, a random sample of 300 were transferred to a new petri dish daily. A few drops of wet yeast on each dish attracted hatched larvae for later retrieval. After 24 h the eggs were classified into one of five categories: defective, not developed, aborted early, aborted late, and hatched. The defining characteristic of a defective or unhealthy egg was a lack of turgidity. These eggs were considered unable to develop, although in a few rare instances such eggs did initiate development and abort. Eggs aborted at early stages of development were recognized by their characteristic mottled brown appearance (Stalker 1954). Eggs aborted at late stages of development could be popped out of their vitelline envelope as larvae or had in fact started to emerge but failed to complete hatching. Such eggs were recognized by a loss of turgidity in an initially healthy egg.

Groups of up to 15 hatched larvae were transferred to plastic vials filled with standard cornmeal-agar media sprinkled with dry yeast. A small piece of Kim-wipe provided pupation sites. Fifteen larvae from the standard stock could successfully eclose from such vials with food remaining. Larvae were later classified based on the latest stage of development they reached: hatched, pupated, or eclosed. In total, there were seven mutually exclusive egg fates: defective, not developed, aborted early, aborted late, hatched, pupated, or eclosed.

This entire experiment was repeated four times. Replicates 1–4 were begun in August 1998, October 1998, January 1999, and March 1999, respectively. Throughout this experiment the flies were kept in a 25°C incubator on a 12:12 L:D photoperiod.

Additional experiments were done to measure overall fitness of mating females from the sexual strain. Twelve females and 24 males that had eclosed within a 6–8-h period were put together in a half-pint milk bottle filled with standard cornmeal-agar media sprinkled with dry yeast. A second and third group of flies was collected 3 days and 6 days later, respectively. Flies were transferred to new bottles daily, and any dead flies were recorded. Flies that were caught in the food were freed. If they could not be freed but were still alive, they were considered lost. Adult offspring that emerged from the bottles were counted and initially sexed, but no significant deviations from a 50:50 sex ratio were observed.

Although this method of housing flies enabled measurement of only survival and age-specific production of viable adults, it required much less effort and reduced the chance of escape. If a fly did escape during transfer, all others had to be anesthetized again to determine its sex.

Statistical Analyses

To test the null hypothesis that all strains had the same survival function, the Wilcoxon test was performed using JMP IN version 3.2.6 (SAS Institute, Cary, NC). This test allows for censored observations and gives more weight to early survival times, when survival's impact on fitness would be expected to be greater due to higher early fecundity. Details of this analysis can be found in Lee (1992).

Egg production characteristics were compared among strains with fixed-effects analyses of variance (ANOVAs) using strain as the only effect in the model (also with JMP IN). All ANOVAs were accompanied by pairwise comparisons between the strains using a Tukey-Kramer correction for multiple pairwise comparisons.

To test the null hypothesis of no association between strain and egg fate, the FREQ procedure in SAS was used (SAS Institute 1989). Only the parthenogenetic strains were compared because less than 0.2% of unfertilized eggs from the sexual strain initiated development. The data consisted of four sets of 4×7 tables corresponding to the four replicates, four parthenogenetic strains, and seven possible egg fates, respectively. Within each of the four sets there were between 46 and 61 4×7 tables, one for each maternal age at which females laid eggs. Because the response levels (the seven possible egg fates) were ordinally scaled, standardized mid-ranks were assigned as scores for each replicate-strain-age combination as a measure of how far those eggs developed on average. A Mantel-Haenszel procedure for analyzing sets of $s \times r$ tables was then used to test whether scores differed among strains or among maternal ages while accounting for the variation among replicates. The test statistic for this procedure, Q_s , is distributed approximately as a chi-square with $n - 1$ degrees of freedom. Because this test requires that each replicate-strain-age combination have a sample size of 20 distributed such that there are greater than five to both the left and the right of some point in the ordinal scale, replicate-strain-age combinations that did not meet this requirement were removed for this analysis.

Differences among strains and among maternal ages were found, therefore, we performed a logistic regression to further describe the relationship between strain and egg fate using the CATMOD procedure in SAS. Response functions were modeled as cumulative logits of the marginal probabilities for each of the possible egg fates so that separate slope parameters for each of the response functions could be fit. Separate slope parameters were necessary because the LOGISTIC procedure in SAS had shown that the common slope assumption of the cumulative logistic model with proportional odds was violated. With cumulative logits, model parameters are estimated using weighted least squares, so no zero-cell counts are allowed. Due to its large number of zero-cell counts, the sexual strain was excluded from this analysis as well. To remove many remaining zero-cell counts, the

response variables (egg fates) were pooled into five categories by putting hatched and pupated eggs into the ‘‘aborted late’’ category. A value of 0.00001 was added to all cells so no zero-cell counts would remain. The parameter estimates for several ages were recalculated adding 0.0001, and the significant parameter values were the same to the thousandth decimal place. Four cumulative response functions were thus calculated for each age and strain corresponding to the probability of an egg being healthy, initiating development, reaching the larval stage, and eclosing. Whereas the categories that the eggs were placed into were mutually exclusive, these cumulative response functions included all eggs that reached a particular stage of development whether or not they developed further.

A separate model was fit for each age:

$$Y_{ij} = \mu + \alpha_i + \beta_{j(i)} + \epsilon, \quad (3)$$

where Y_{ij} equals the fate of eggs from strain i , replicate j ; μ equals the overall mean; α_i equals the differential effect of strain i ; $\beta_{j(i)}$ equals the differential effect of strain i nested within replicate j ; and ϵ equals the residual error. Nested-by-value effects ($\beta_{j(i)}$) were used in place of replicate and replicate-by-strain interaction terms because all ages had a significant replicate-by-strain interaction and such a substitution showed whether replicate had a significant effect for only some strains. When this was the case, a reduced model eliminating nonsignificant nested-by-value effects was fit because the additional model terms can reduce the quality of the individual parameter estimates (Stokes et al. 1995). The significant nested-by-value effects have no obvious biological explanation, but they were kept in the model because they were significant, although their values are not reported. Ages that had no significant intercept or no significant strain effect were dropped from further consideration. For one age (7 days) a model with a significant intercept could only be fit using strain and strain-by-replicate effects instead of nested-by-value effects, so such a model was fit for this age only. The parameter estimates from the model were used to calculate the probability of an egg reaching each of the four points of development described by the cumulative response functions, as well as odds ratios to measure differences between each pair of strains. For details see Stokes et al. (1995).

Logistic regression yielded very few significant values for the probability of eclosing because this event was so rare. To evaluate this probability, a Poisson regression was performed using the GENMOD procedure in SAS that fits generalized linear models. The probability distribution was assumed to be Poisson and the link function was the log. Deviance and Pearson chi-square statistics were used to assess model fit.

These analyses excluded the sexual strain because those unfertilized eggs so rarely reached any of the later developmental stages. To obtain the probability of an unfertilized egg from the sexual strain being healthy, all data were pooled into only two response categories: defective and healthy. Separate logistic regression models were fit for each age as before, using the CATMOD procedure. Parameter estimates for the parthenogenetic strains were generally consistent between the two logistic regressions, and all reported values for the

parthenogenetic strains are for the logistic regression including all five response categories.

To test the null hypothesis that there was no difference in overall fitness among the strains, age-dependent selection values were calculated for each replicate of each strain. A one-way fixed-effects ANOVA was then performed for each of these parameters using strain as the only effect in the model. Net reproductive value (R_0), the number of daughters expected per female per lifetime, was calculated as $\sum l_x m_x$, where l_x equals the probability of surviving from birth to the middle of age class x , and m_x equals the average number of female offspring produced per female of age class x . For the sexually reproducing strain, m_x was determined as one-half the average number of flies produced per fly per day. For the parthenogenetic strains, m_x was determined by the age-specific egg production rate multiplied by the age-specific eclosion rate. The generation length (T), the average age of a female when she produces female offspring, was calculated as $\sum (x l_x m_x) / R_0$. The intrinsic rate of increase, r , was determined by solving the Euler-Lotka equation in which newly enclosed flies are defined as age class 0:

$$1 = \sum e^{-r(x+1)} l_x m_x. \quad (4)$$

RESULTS

Parthenogenetic Capacity of the Isofemale Lines

Table 1 summarizes the results obtained for the 88 lines of virgin females scored for parthenogenetic capacity. The viable and true parthenogenetic rates of the B-C-D lines were both 4.2×10^{-5} . The site IV viable rate was 1.7×10^{-3} and the site IV true rate was 0.94×10^{-3} . The likelihood ratio test of homogeneity showed significant differences between site B-C-D and site IV for both the viable parthenogenetic rate ($\chi^2 = 38.69$, $df = 1$, $P = 5.0 \times 10^{-10}$) and the true parthenogenetic rate ($\chi^2 = 18.93$, $df = 1$, $P = 1.4 \times 10^{-5}$).

Survivorship

A separate survival curve was determined for each strain for each replicate of the experiment. The Wilcoxon test indicated that there were no significant differences among replicates for strains Im43-7 ($\chi^2 = 4.2665$, $df = 3$, $P = 0.2341$), Im23-C ($\chi^2 = 1.6143$, $df = 3$, $P = 0.6561$), virgin K + X ($\chi^2 = 2.3427$, $df = 3$, $P = 0.5044$), and mating K + X ($\chi^2 = 1.4225$, $df = 2$, $P = 0.4910$). There were significant differences among replicates for strains Im23-6 ($\chi^2 = 13.9237$, $df = 3$, $P = 0.0030$) and Im23-8 ($\chi^2 = 19.0443$, $df = 3$, $P = 0.0003$). In these two cases, removal of replicates one at a time showed that only one caused the differences: replicate 1 for strain Im23-8 and replicate 2 for strain Im23-6. Comparisons between strains were then done including and excluding the outlier replicates for the two strains in question. Results were qualitatively the same, and reported figures are for analyses including all data.

Analysis of survival curves calculated from all replicates grouped together (Fig. 2) showed that the strains were significantly different ($\chi^2 = 82.8768$, $df = 5$, $P < 0.0001$). There was no significant difference in survival between mating and virgin K + X females. Flies from the four parthenogenetic

TABLE 1. Results of the screen for parthenogenetic reproduction in the virgin female offspring of wild-caught inseminated females.

Line	Estimated number of eggs	Number of parthenogenetic offspring	Number of parthenogenetic offspring that reproduced parthenogenetically
B-30	379	1	1
33 other lines from site B	14,423	0	0
11 lines from site C	5113	0	0
10 lines from site D	3780	0	0
BCD Total	23,696	1	1
IV-1	461	1	1
IV-23	340	10	7
IV-24	379	1	0
IV-27	399	1	0
IV-30	379	1	1
IV-36	399	1	0
IV-43	399	5	3
IV-48	399	2	0
25 other lines from site IV	9668	0	0
IV Total	12,823	22	12

strains had higher mortality than virgin K + X females, and flies from three of the four parthenogenetic strains (Im23-6 being the exception) had higher mortality than mating K + X females. Among the four parthenogenetic strains, Im23-6 was significantly different from the rest, showing increased survivorship across the entire life span. Differences among

the remaining three parthenogenetic strains were not detectable with either the Wilcoxon or a Komolgorov-Smirnov test.

Egg Production

A comparison of spline curves fitted to the mean (averaged over all replicates) of the mean (averaged over all flies) number of eggs laid per day for each strain (Fig. 3) illustrates the general pattern of the egg-production data. Several attri-

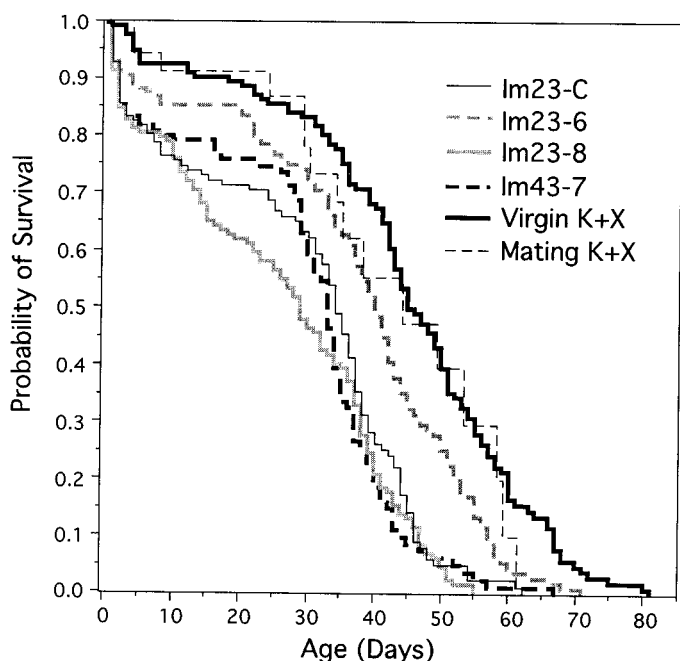


FIG. 2. Survival curves for four parthenogenetic strains and both virgin and mating females of a sexual strain of *Drosophila mercatorum*. Curves were calculated using data from all replicates of the experiment together. A Wilcoxon test showed significant differences among the strains. Pairwise comparisons indicated that there was no significant difference between virgin and mating females from the sexual strain (K + X); between mating females from K + X and virgin females from parthenogenetic strain Im23-6; and among parthenogenetic strains Im23-C, Im23-8, and Im43-7.

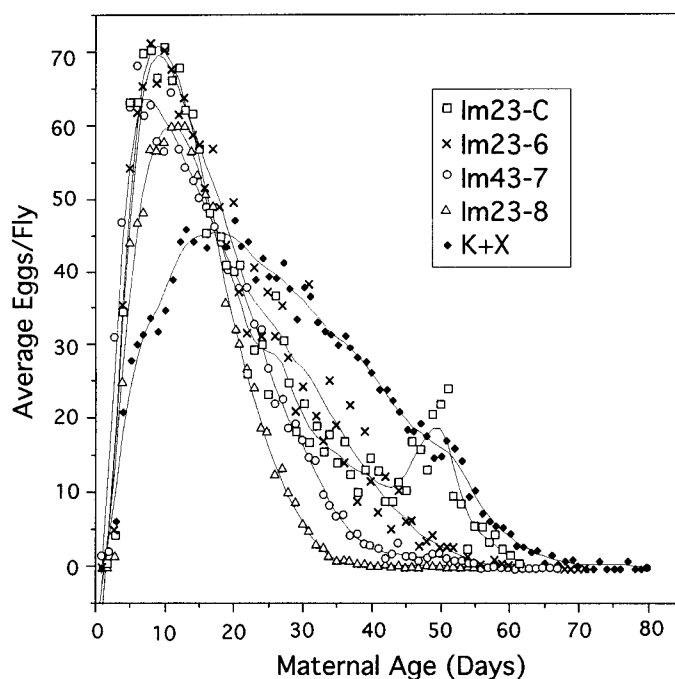


FIG. 3. Eggs laid per fly as a function of maternal age for virgin females of one sexual and four parthenogenetic strains of *Drosophila mercatorum*. Number of flies and number of eggs laid were summed over four replicates for each strain to calculate a single value at each maternal age. Splines were fit to the points from each strain.

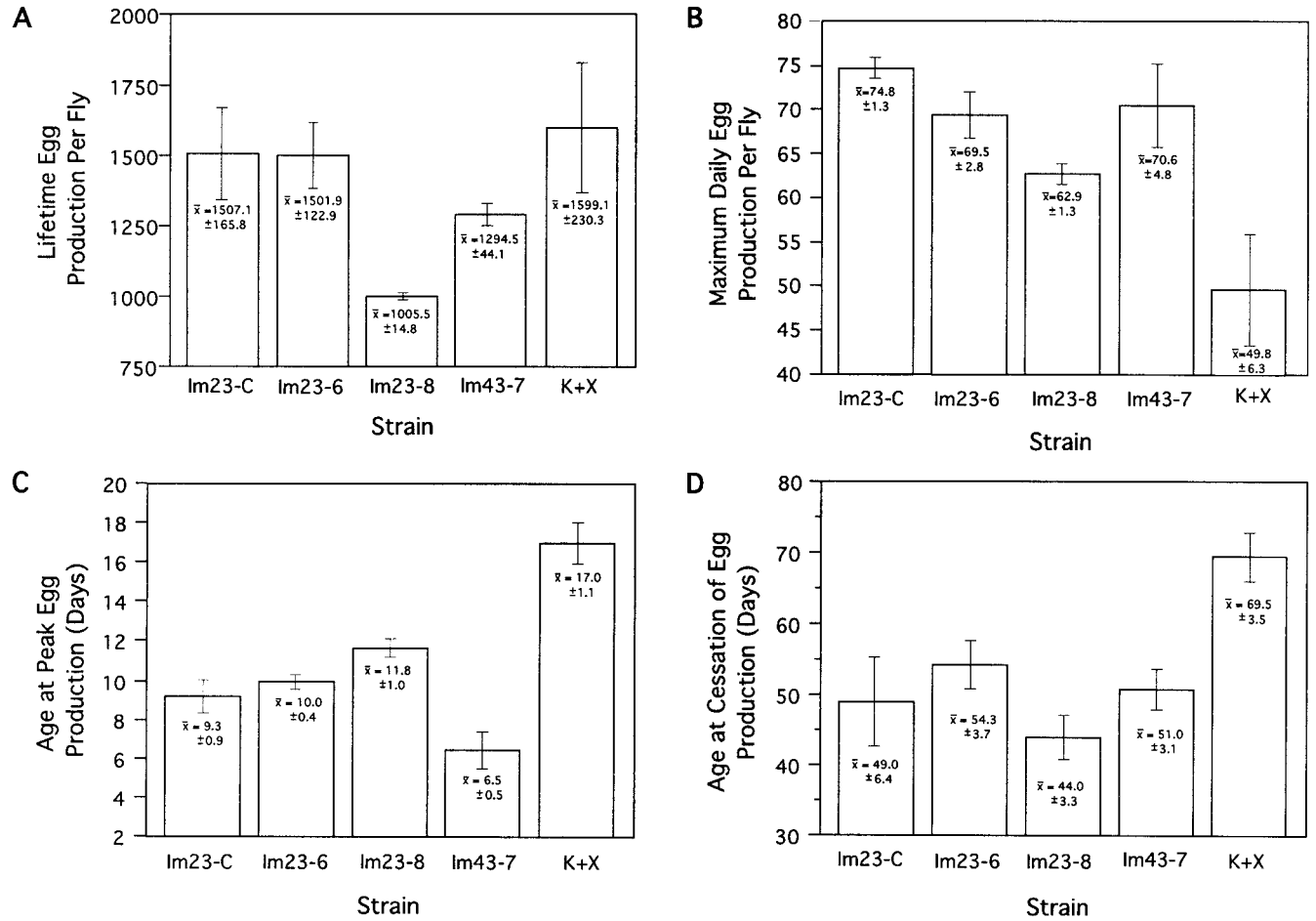


FIG. 4. Egg-production characteristics for virgin females of one sexual and four parthenogenetic strains of *Drosophila mercatorum*. (A) Total lifetime egg production per fly using the sum of daily average eggs/fly calculated for each replicate of each strain; (B) maximum daily egg production per fly using the highest daily average eggs/fly value observed for each replicate of each strain; (C) age at which the values for B were observed; (D) age at cessation of egg production. Two cases in which the last fly died on a day when it had laid eggs (replicate 2 for strain Im43-7 and replicate 4 for strain Im23-C) were excluded from the analysis in D.

butes of these data were used to analyze whether and how the strains differed.

The first attribute considered was total lifetime egg production (Fig. 4A). Significant differences among the strains were found using a Welch ANOVA to test whether the means were different because the standard deviations of the strains were not equal ($F_{4,6.348} = 12.6598$, $P = 0.0036$). Pairwise comparisons indicated that lifetime egg production of strain Im23-8 was significantly lower than the others. There were no significant differences among the other four strains.

The maximum daily egg production per fly (Fig. 4B) also varied among the strains according to an ANOVA performed on the highest value recorded for each replicate of each strain ($F_{4,15} = 6.4003$, $P = 0.0033$, $r^2 = 0.63$). Pairwise comparisons showed that virgin K + X females had a lower maximum egg production than parthenogenetic females, whereas there were no significant differences among the parthenogenetic strains.

An ANOVA indicated significant differences among the strains for age at peak egg production ($F_{4,15} = 22.5278$, $P < 0.0001$, $r^2 = 0.86$; Fig. 4C). Pairwise comparisons indicated that virgin K + X females reached peak egg production

significantly later than all parthenogenetic strains. Among parthenogenetic strains, Im23-8 and Im43-7 were significantly different from each other.

The age at cessation of egg production was compared among the strains with an ANOVA that indicated significant differences ($F_{4,13} = 6.3766$, $P < 0.0046$, $r^2 = 0.66$; Fig. 4D). Pairwise comparisons indicated that virgin K + X females were significantly different from all parthenogenetic strains except Im23-6. There was no significant difference among the strains in the mean length of the postreproductive period before death.

This set of results for egg production was verified by considering means and standard deviations at each age for all the strains together (data not shown). Three main results came from this analysis: (1) strain Im43-7 had significantly higher egg production at the earliest ages (2–3 days); (2) strain Im23-8 had a sharper decline in egg production with age so that, at 31 days, flies of this strain laid significantly fewer eggs than any of the other strains; and (3) virgin K + X females had lower egg production at early ages (5–12 days), and after peaking, had significantly higher egg production (32, 33, and 38 days) than the parthenogenetic strains.

Egg Fate

The Mantel-Haenszel test for strain differences in egg fate, controlling for both replicate and maternal age, was highly significant ($Q_s = 39326.190$, $df = 3$, $P < 0.001$), as was a test for differences among maternal ages, controlling for both replicate and strain ($Q_s = 15728.091$, $df = 43$, $P < 0.001$). Tests performed separately for each maternal age showed highly significant differences among the strains at all ages (data not shown). Pairwise comparisons indicated that strain Im43-7 is highly significantly different from the rest except at 3 days. Significant differences were seen between all other pairs of strains at most ages.

Figure 5 shows the probability of an egg reaching a particular developmental fate as a function of maternal age for each strain. Eggs from virgin K + X and Im23-8 females generally had the highest probability of being healthy (Fig. 5A). Strains Im23-6 and Im23-C had a slightly lower probability until age 24 days, when nearly all differences among these four strains disappeared. Strain Im43-7 was clearly very different from the others; it produced an extremely low proportion of healthy eggs, with values dropping as low as 0.05. Strain Im43-7 was also significantly less likely than the others to produce an egg that initiated development, with values just barely above zero beyond 15 days (Fig. 5B). Significant differences among the other three strains caused their relative ranking to change with maternal age. The probability of an egg developing to the larval stage could only be calculated for ages up to 12 days, after which the event was too rare to be detected as statistically significant (Fig. 5C). Eggs from strain Im43-7 had the smallest probability of developing to the larval stage. Im43-7 was also significantly less likely than the other strains to produce eggs that would go on to eclose (Fig. 5D). Differences between the other pairs of strains were not detectable at this stage.

Comparisons between each pair of strains for the above probabilities are shown by odds ratios, or the odds of an egg from one strain reaching a stage of development relative to the odds of an egg from the other strain reaching that same stage (Fig. 6). Although differences between strain Im43-7 and the others were most dramatic (Fig. 6A, C), there were significant differences among the other strains. Eggs of strains K + X and Im23-8 were five to seven times more likely than eggs of strains Im23-6 or Im23-C to be healthy around the ages of peak egg production (Fig. 6B). Eggs of strain Im23-C had the greatest probability of initiating development at early ages (two to four times greater than strains Im23-6 and Im23-8; Fig. 6D). Differences among these three strains decreased further when looking at the odds an egg will reach larval stage (Fig. 6E), and differences were not detectable at all when considering the odds of eclosing (Fig. 6F).

Phenotypic Correlations

Correlations between life-history parameters can be directly calculated only from individual data, but the decline and then rise of the probability of producing a healthy egg for strains Im23-6, Im43-7, and Im23-C (Fig. 5A) could be explained by a correlation between the ability to lay healthy eggs and longevity. Graphs of the proportion of eggs that

initiated development, reached larval stage, and eclosed versus maternal age (not shown) suggested that all of these parameters were correlated with longevity for strain Im23-C. A correlation between longevity and egg production also should have been evident in the shape of the age-specific egg production curve as a rise at later ages after less-fecund flies died off. There was a clear rise in two replicates for strain Im23-C and a less dramatic rise in one replicate each for strains Im23-6, Im43-7, and K + X (data not shown).

In spite of their genetic homogeneity, such correlations must be due to within-strain differences. Such differences would have also been apparent in variability between replicates because a different sample of flies was used in each. The absolute values of the residuals from the fitted age-specific egg production splines were compared with a one-way ANOVA (Fig. 7). There were significant differences among the strains for the average residual ($F_{4,1143} = 22.9180$, $P < 0.0001$). Pairwise comparisons showed that Im23-8 had significantly less variation among replicates than the other strains and Im23-C had significantly more.

Age-Dependent Selection Values

An ANOVA for net reproductive value (R_0) indicated there were significant differences among the strains ($F_{4,14} = 647.3073$, $P < 0.0001$, $r^2 = 0.99$). Pairwise comparisons showed that mating K + X females had a significantly greater value of R_0 than parthenogenetic females (Fig. 8A). An ANOVA for generation length (T) showed no significant differences among the strains ($F_{4,14} = 0.7232$, $P = 0.5904$, $r^2 = 0.17$). Generation length was also calculated substituting hatch rate for eclosion rate to reduce the effect of single values. An ANOVA for generation length calculated using hatch rate showed significant differences among the strains ($F_{4,14} = 5.2857$, $P = 0.0083$, $r^2 = 0.60$). Pairwise comparisons showed that strains Im43-7 and mating K + X were significantly different from each other (Fig. 8B). An ANOVA for intrinsic rate of increase (r) also showed significant differences among the strains ($F_{4,14} = 11.7848$, $P = 0.0002$, $r^2 = 0.77$), and pairwise comparisons indicated K + X had a significantly greater value than the parthenogenetic strains (Fig. 8C).

DISCUSSION

Parthenogenetic Capacity in Natural Populations

The Kamuela population of *D. mercatorum* had previously been screened for parthenogenetic capacity in 1974 (Templeton et al. 1976) and 1976 (Templeton 1979). The 1974 collections were made in a garbage dump located about 1 km east of site IV (Fig. 1). The viable and true parthenogenetic rates from this collection were 3.9×10^{-5} and 1.6×10^{-5} , respectively. The 1976 collections were made at site B and yielded a viable rate of 1.1×10^{-5} and a true rate of 1.6×10^{-6} . The 1990 viable rate of 4.2×10^{-5} for sites B-C-D is not significantly different from either the 1974 viable rate (ln-likelihood ratio $\chi^2 = 0.004$, $df = 1$, $P = 0.95$) or the 1976 viable rate (ln-likelihood ratio $\chi^2 = 1.08$, $df = 1$, $P = 0.30$). The 1990 true rate of 4.2×10^{-5} for sites B-C-D is not significantly different from the 1974 true rate (ln-

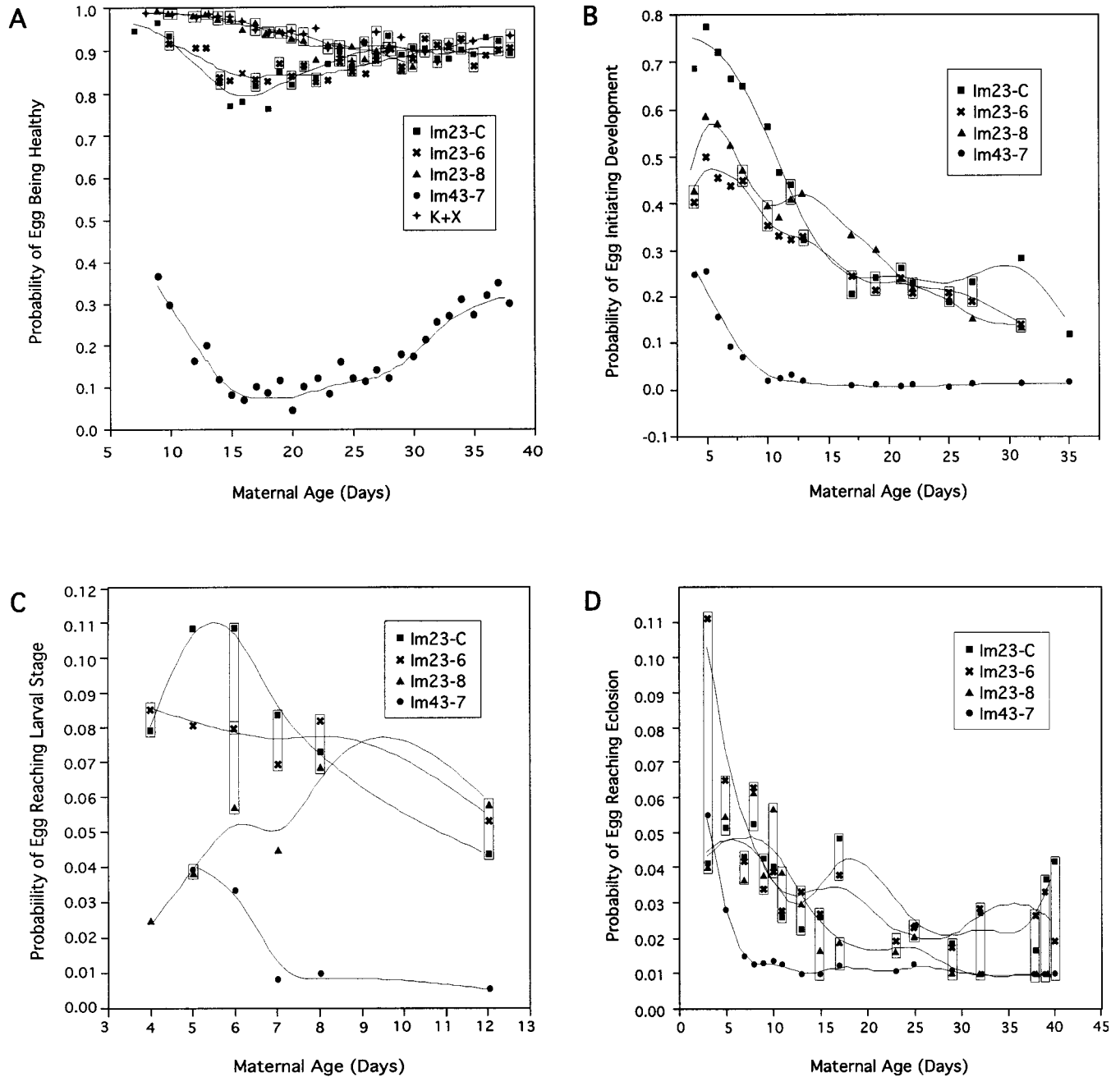


FIG. 5. Probability of an egg (A) being healthy, (B) initiating development, (C) reaching larval stage, and (D) reaching eclosion, as a function of maternal age for virgin females of one sexual and four parthenogenetic strains of *Drosophila mercatorum*. Datapoints are shown only if all parameters involved in their calculation were significant at the $\alpha = 0.05$ level. Points that were not significantly different from each other at each age have been boxed. Splines were fit to the points from each strain.

likelihood ratio $\chi^2 = 0.66$, $df = 1$, $P = 0.42$) and is barely significant at the 5% level from the 1976 true rate (ln-likelihood ratio $\chi^2 = 3.88$, $df = 1$, $P = 0.049$).

In contrast to this temporal consistency for parthenogenetic rate at site B-C-D, the 1990 collection revealed great geographic variation in parthenogenetic rate between this site and another nearby site. Both the viable and true parthenogenetic rates differed by two orders of magnitude between populations only 2 km apart (with flies continuously distributed between). Moreover, the previous parthenogenetic rate of the initial par-

thenogenetically produced F_2 offspring was usually about 10^{-2} . However, in the 1990 site IV collection, four of the 11 parthenogenetically produced F_2 lines shown in Table 1 had rates of 10^{-1} . Thus, not only did flies have an extremely high rate of facultative parthenogenesis at site IV, but their parthenogenetically produced offspring had a capacity for continued parthenogenetic reproduction that is unparalleled in studies of the genus *Drosophila* (Templeton 1983).

The highly significant difference between two such geographically close populations in their rates and success of

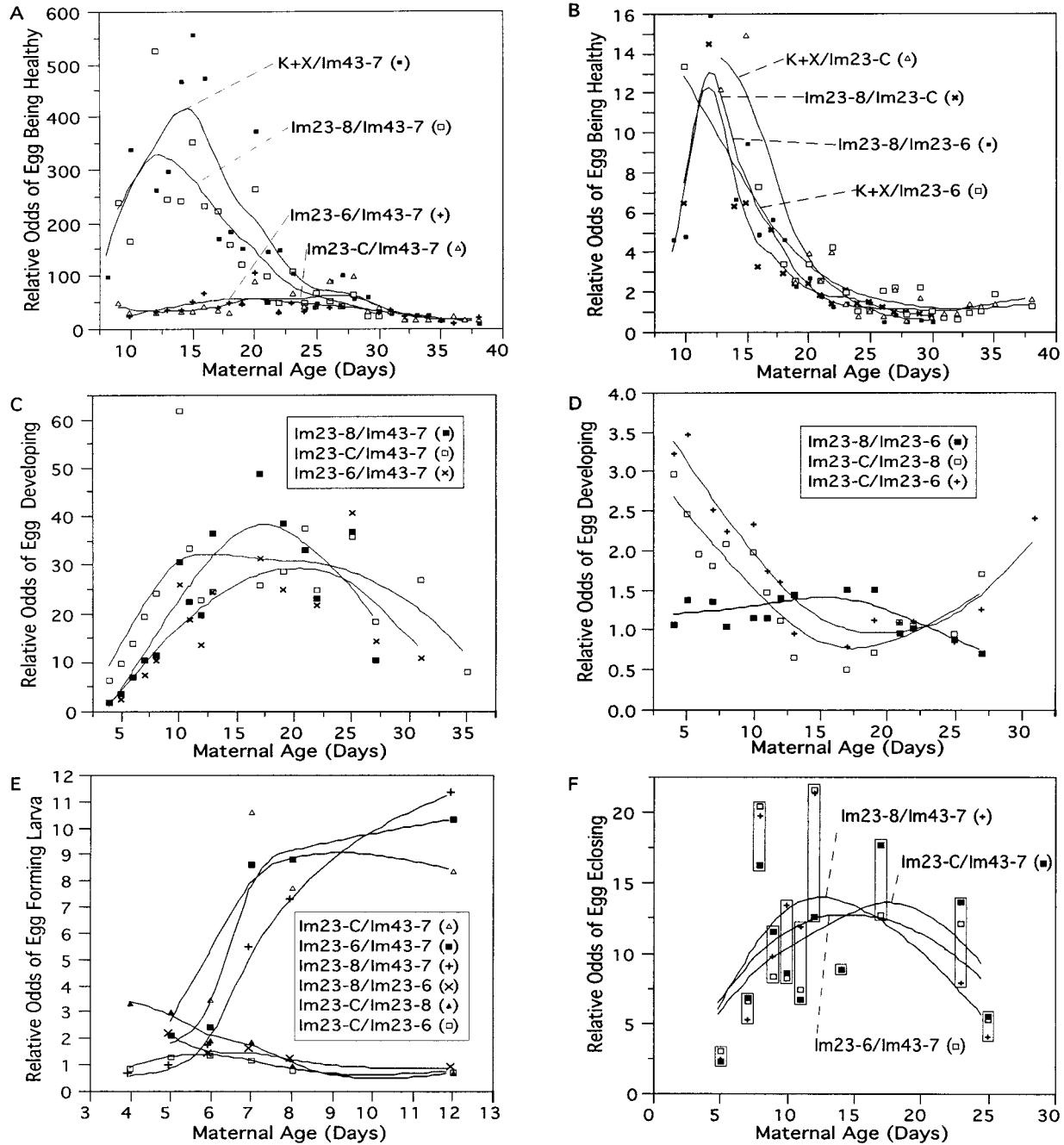


FIG. 6. Relative odds of an egg (A, B) being healthy, (C, D) initiating development, (E) reaching larval stage, and (F) eclosing, for each pair of strains. The scale of (A) and (C) obscured the details that are shown instead in (B) and (D), respectively. Pairs for which the probability of being healthy were not significantly different for more than half of the maternal ages are not shown (K + X/Im23-8 and Im23-6/Im23-C). Datapoints for odds ratios are only shown if the probability of the event (Fig. 5) was significant for each strain. Splines were fit to the points from each strain.

parthenogenesis is unprecedented in the literature and cannot be explained by genetic drift and population subdivision. Previous studies on these populations revealed that sites IV and B-C-D are virtually panmictic for nuclear genetic systems, with an estimated number of effective migrants per generation (Nm) between four and eight (DeSalle et al. 1987). Such high values of gene flow preclude any significant differentiation of adaptively neutral systems between sites IV

and B-C-D. However, these levels of gene flow are sufficiently restricted to allow significant differentiation to arise and be maintained for genetic systems under selective regimes that differ between these sites (Templeton et al. 1989, 1990). Given that parthenogenetic capacity has a strong genetic component in *D. mercatorum* (Templeton 1983), there must be some selective difference between these sites with respect to facultative parthenogenesis.

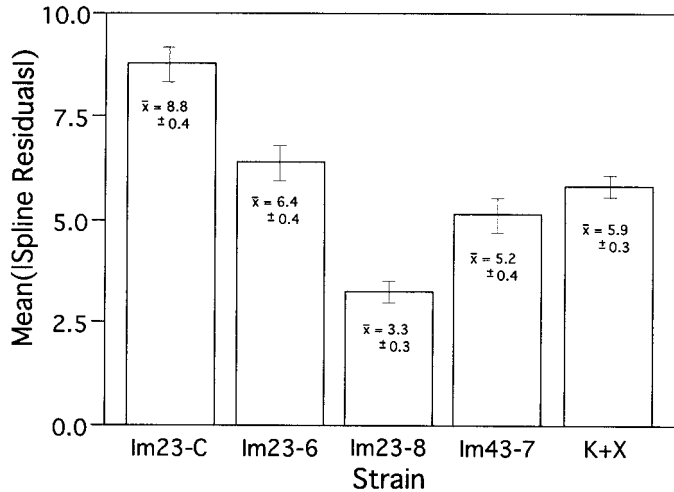


FIG. 7. Mean absolute value of residuals from spline curves ($\lambda = 1000$) fit to average daily egg production by maternal age for each replicate of each strain.

Parthenogens often have been found to live in marginal habitats relative to their sexual counterparts: at higher altitudes, on islands, in xeric environments, or in disturbed areas (Glesener and Tilman 1978; Bierzychudek 1985; Stenberg et al. 2000). Theoretical models have predicted that this distribution of sexual forms would arise to avoid migration load due to the arrival of less fit individuals from a more resource-rich central part of the distribution (Peck et al. 1998, 1999). Given the high amount of gene flow between our two sites, this model does not seem relevant here. Another possible explanation for our results is suggested by a model for the origin of facultative parthenogenesis given by Stalker (1954). Given its costs, parthenogenesis is expected to be favored only in environments where finding a mate is difficult or impossible, such as in marginal habitat with such low densities that stochastic fluctuations in the sex ratio may by chance eliminate males (Stalker 1956). Site IV is on the ecological margin for *D. mercatorum* and just such an environment. The only larval food resource on Hawaii is rotting cladodes of the cactus *O. megacantha*. The *O. megacantha* patches at site B are very large, supporting populations of up to 8000 individuals with single rots supporting hundreds of larvae. In contrast, the cacti grow poorly at site IV, where patches are small, widely scattered, and most usually do not have even one active rot. When they do, it is small and produces on average five to eight flies (Templeton et al. 1989). Finally, the wind in site IV is so strong it may prevent effective dispersal between patches for several weeks at a time (Johnston and Templeton 1982). Under such circumstances females may often be stranded on a cactus patch with no available males—a condition that is highly unlikely at the higher elevation sites of B, C, or D. The extremely low parthenogenetic rate and the ecological conditions found in the environment of *D. mercatorum* suggest that the costs or difficulty of finding a mate are the principle explanation for the distribution of parthenogenesis seen in nature.

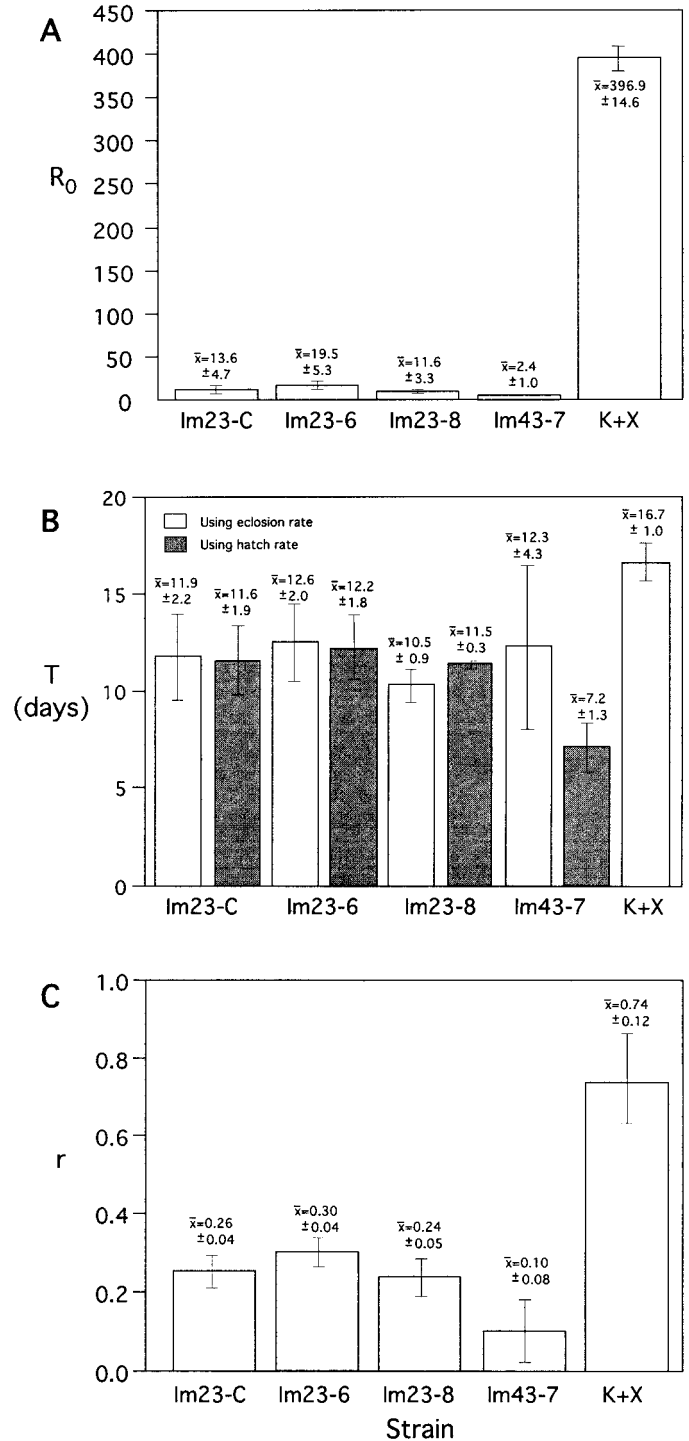


FIG. 8. Age-dependent selection values calculated for mating females of a sexual strain and virgin females of four parthenogenetic strains of *Drosophila mercatorum*: (A) net reproductive value, (B) generation length, and (C) intrinsic rate of increase.

Survival Analysis

Survival appears to be a cost of parthenogenetic reproduction, as females from three of the four parthenogenetic strains showed decreased survival relative to mating K + X females and females from all four parthenogenetic strains

showed decreased survival relative to virgin K + X females (Fig. 2). The lack of difference between mating and virgin females from the sexual strain is contrary to other experimental evidence that mortality of female *Drosophila* increases with mating (Malick and Kidwell 1966; Partridge et al. 1986; Fowler and Partridge 1989). This result may be due to differences in experimental conditions. Mating flies reared on cornmeal-agar medium sometimes became trapped in their food, unlike virgin flies kept on grape juice-agar medium. If all mating females that were considered lost after getting stuck in the medium were instead considered dead (based on the assumption that flies near death are more likely to become trapped in the food), then mating flies did experience increased mortality relative to virgins, although the relationship of the mating flies to flies of all four parthenogenetic strains was the same.

Although mortality of female *D. mercatorum* increases with multiple copulations (Ikeda 1974) and mortality of female *D. melanogaster* increases with mating and with egg production per se (Partridge et al. 1987), neither of these factors could account for the increased mortality of parthenogenetic over sexual *D. mercatorum* because parthenogenetic females (except strain Im23-6) in fact suffered greater mortality than mating females, and lifetime egg production was similar for all strains (except Im23-8). Homozygosity has also been found to decrease an individual's ability to buffer its development against environmental change (Lerner 1954; Biemont 1983; Leary et al. 1983) and may thereby affect mortality, but homozygosity per se probably could not account for the observed differences either. Although we did not empirically determine the degree of homozygosity, and the sexual strain has since been taken through several generations of single sib-pair matings, it had been maintained in the laboratory for more than 10 years (approximately 260 generations) as a single culture subject to recurrent bottlenecks as tend to occur in laboratory stocks. Unless selection for disassortative mating were strong over many loci, the degree of heterozygosity remaining in the strain is unlikely to have been great enough to account for the differences between the sexual and parthenogenetic strains.

A major difference, however, between the sexual and parthenogenetic strains is in the *manner* by which genetic homozygosity was attained. Homozygosity in the sexual strain would have been built up over many generations with selection increasing the likelihood that favorable genes or gene combinations would become fixed in the population. The parthenogenetic flies are the result of a genetic system that forces complete homozygosity in one generation, and selection would be so extreme it would favor any combination of genes that enabled parthenogenesis regardless of their antagonistic pleiotropy. The genetic effect of such an abrupt fixation of all genetic variation would be expected to involve the fixation of genes deleterious for overall survival. A cost of parthenogenesis, in the case of survival at least, is thus perhaps inherent to the genetic system of parthenogenesis in *D. mercatorum*.

Egg Production

The relative costs and benefits of parthenogenesis with respect to egg production appear to depend largely on en-

vironmental context. Three of four parthenogenetic strains had the same lifetime egg production as virgin K + X females (the exception being Im23-8, one of the three related strains; Fig. 4A). In spite of the similarity in total production, there was a dramatic and consistent change in the apportionment of eggs over the lifetime. All four parthenogenetic strains showed an increase in egg production early in life, followed by a relatively rapid decline (Fig. 3). Mating likewise increases early egg production (Bouletreau 1978) and decreases later egg production in *D. melanogaster* (Partridge et al. 1986). If the same result holds for *D. mercatorum*, total lifetime egg production of mating flies may also be similar to that observed here for virgins. Mating was found to increase egg production for *D. mercatorum* (Crews et al. 1985), but it was measured for only four consecutive days, and the maternal age was not reported.

The similarity among strains in lifetime egg production in spite of differences in apportionment of eggs across the life span suggests lifetime egg production may be physiologically constrained. Rosenheim (1996) has shown that egg limitation is a plausible evolutionary outcome under the following conditions: there is some energetic cost to produce eggs, oviposition sites are limited with their discovery controlled by stochastic factors, and resources that are invested in egg production could be otherwise invested to increase fitness. These conditions are clearly met for *Drosophila* and may explain the lack of variation seen in lifetime egg production in spite of tremendous variation in other fitness components. Such a physiological constraint on egg production would strongly select for optimal oviposition strategy, because any eggs that were laid but could not develop would be truly wasted.

The oviposition strategy of parthenogenetic females parallels the strategy of inseminated females of sexual strains: an increase in early egg production is followed by a later decrease (Partridge et al. 1986), so that within a shorter life (as occurs for parthenogenetic and mated *Drosophila*), the same total reproductive output is possible. For sexual strains, oviposition strategy must involve a physiological response to mating because inseminated and virgin flies would have same the genetic makeup. In the case of parthenogenetic females, oviposition strategy probably has a genetic basis due to genes that cause a shift in egg production persisting in the population alongside genes conferring parthenogenetic ability. "Oviposition strategy" can thus have very different meanings, and selection may favor a particular strategy in very different ways.

These data on survival and egg production are similar to results of Templeton et al. (1976) for other parthenogenetic *D. mercatorum*. The apparent trade-off between early fecundity and later viability suggested by these studies is complemented by ecological data. Site IV not only has a relatively high parthenogenetic rate but also very high early mortality compared to the upper-elevation sites (Johnston and Templeton 1982). In such situations, there would be a tremendous advantage to reaching peak egg production at early ages, because flies do not live long enough to reap any advantage from later production. Selection for parthenogenesis may in fact be tightly connected to selection for early fecundity in areas with high early mortality.

Egg Fate

An additional cost of parthenogenetic reproduction appears to be an increase in the proportion of defective eggs, shown by the relative odds of an egg being healthy for each pair of strains (Fig. 6A, B). Three of four parthenogenetic strains showed such an increase (the exception being Im23-8, one of the related strains).

In spite of significant differences among parthenogenetic strains in what happens to the eggs that did *not* reach eclosion, the proportion of eggs that *did* reach eclosion is the same for the three related strains. Probability of eclosion is obviously the most important parameter to consider because only a fly that ecloses may reproduce, but consideration of this factor alone would obscure the fact that failure to eclose had very different developmental causes in each of the strains.

The differences among the parthenogenetic strains indicate that there were multiple genetic responses to the transition from sexual to parthenogenetic reproduction. In spite of the identical, extreme selection pressure involved in founding these strains, different genes were presumably fixed at the loci that affect survival, egg production, and egg fate, notably among the related strains. Because they were reared in identical environments, existing genetic variation in the sexual ancestor of the three related parthenogenetic strains must account for the differences. These life-history data support the existence of variation for fitness in *D. mercatorum* as has been documented to exist in *D. melanogaster* (Fowler et al. 1997).

The tremendous reduction in viability of eggs seen in parthenogenetic *D. mercatorum* suggests there may be a developmental constraint on the evolution of obligate parthenogenesis, as has been found for the facultatively parthenogenetic cockroach *Nauphoeta cinerea* (Corley and Moore 1998). In *D. mercatorum* artificial selection can cause an approximate 10-fold increase in the rate of parthenogenesis, and this increase can reach nearly 60-fold under a system of outcrossing that allows the introduction of new genetic variation (Carson 1967), but this still leaves hatch rates an order of magnitude lower than that for sexual reproduction. Future developmental analyses of parthenogenetic reproduction in *D. mercatorum* should provide insight into the causes and nature of the developmental constraints operating in this species.

Phenotypic Correlations

A correlation between longevity and both lifetime egg production and average daily egg production has been documented for *D. melanogaster* and *D. simulans* (Kidwell and Mallick 1967; Murphy et al. 1983), although Partridge et al. (1986) showed that longevity of *D. melanogaster* cannot be explained by either current egg laying rate or the cumulative number of eggs laid.

In this experiment a correlation between longevity and egg production appeared in five of 20 replicates. This result and the existence of variability among replicates within strains (especially for strain Im23-C; Fig. 7) indicate the existence of within-strain differences in spite of genetic homogeneity. Variation in mean fitness among populations can have dramatic consequences for how natural selection will act. Re-

duced variance in the probability of an egg surviving to adulthood allows for a decreased mean probability of survival (Gillespie 1977), and over time the most successful clonal population will be the one with the least temporal variation in fitness (Lynch 1984). Lifetime egg production was lower for strain Im23-8 than strain Im23-C, but Im23-8 had a lower variance for the number of eggs laid per fly per day. As seen below, this translated into equal intrinsic rates of increase.

Age-Dependent Selection Values

The ultimate consideration is how the life-history parameters interact to affect overall fitness. There was a dramatic difference between the sexual and parthenogenetic strains for net reproductive value (R_0). The average sexually reproducing female produced more than 20 times as many female offspring over her lifetime as the average parthenogenetic female from the most successful parthenogenetic strain (Im23-6) and more than 150 times as many offspring as the average female from the least successful parthenogenetic strain (Im43-7). In spite of such a large difference in total offspring production, the intrinsic rate of increase (r), was not as dramatically different. The average value of r for a sexually reproducing female was only 2.5–5.5 times greater than that of the average female from a parthenogenetic strain. Because the intrinsic rate of increase applies most appropriately to populations that are not regulated by density-dependent factors (Stearns 1992), density dependence in natural conditions may limit population growth (with greater impact on the fastest growing populations) and further decrease the differences observed here under density-independent conditions.

The discrepancy between net reproductive value and intrinsic rate of increase is due to generation length, or the average age of a female when she produces offspring. The theoretical importance of early growth and reproduction has long been recognized (Cole 1954; MacArthur and Wilson 1967; Meats 1971; Green and Painter 1975; Snell 1978; Caswell and Hastings 1980). Lewontin (1965) first showed that changes in developmental time of around 10% equal changes in fecundity of about 10 times that amount. The empirical results here further emphasize the importance of early reproduction for overall fitness. The fact that parthenogenetic flies are able to greatly compensate for a roughly one order of magnitude decrease in egg viability by shortening generation time is remarkable, but still the parthenogenetic *D. mercatorum* failed to break even with, much less exceed by twofold, the intrinsic rate of increase of their sexual counterparts.

Intrinsic rate of increase refers to how fast an allele with marginal effects on life history will spread in a population (Stearns 1992), thus, parthenogenetic alleles should spread more slowly than sexual alleles and their fixation would be unlikely. Nevertheless, such alleles have persisted in natural populations of *D. mercatorum*, due likely to the ecological situation in their natural habitat near Kamuela, Hawaii, which occasionally selects for parthenogenetic capacity when finding a mate is extremely difficult. Such periodic selection during which parthenogenetic ability (coupled with high early fecundity) may not only be the best, but also the only, re-

productive option appears to maintain parthenogenesis in natural populations.

Pairwise comparisons indicated that there were no significant differences among the parthenogenetic strains for either R_0 or r . Thus, in spite of the sometimes dramatic differences among the parthenogenetic strains for life-history parameters, they apparently all lead to the same result. The constraints of maintaining laboratory populations of these strains has undoubtedly selected for a certain minimum rate of population increase, but the fact that each parthenogenetic strain has achieved that in such a different way is nonetheless surprising. The existence of multiple combinations of life-history characteristics that achieve the same fitness outcome supports the idea of a ‘holey landscape’ that has many pathways from one adaptive peak to another (Gavrilets 1997).

CONCLUSION

A natural population of *D. mercatorum* was found to vary in rate and success of facultative parthenogenesis over very short distances in a way that is consistent with the predictions of Stalker (1956) that parthenogenesis should be favored only in marginal habitats where population densities are low. The low rate of parthenogenesis in nature cannot be explained by the supposed ecological benefit of parthenogenesis (a doubling of the intrinsic rate of increase), because parthenogenetic forms have a lower intrinsic rate of increase than their sexual counterparts. This is largely due to decreased survival and a tremendous reduction in egg viability that may, however, be largely compensated for under the appropriate ecological conditions (expected in marginal habitats) by a relatively small shift in egg production to earlier ages. These results show that only by examining the entire life history of parthenogenetic genotypes in an ecological context can the extent of variation upon which natural selection could act be understood.

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