Theor Appl Genet (1983) 66:225–232

Genetic population replacement for insect control: a new method for estimating fitness and generation time of continuously-breeding competing strains

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Received August 8, 1982; Accepted February 25, 1983
Communicated by A. Robertson

Summary. A model of complete underdominance that applies to population replacement for insect control by compound autosomes or compound; free arm strains, has been used to develop a new technique for estimating fitness and generation time in continuously-breeding competing populations, without resorting to measurement of birth rate, survivorship etc. The method is statistical and uses successive intervals of various sizes in an estimation equation. Estimates of fitness and generation time are revealed as a result of convergence of data from competitions in which a strain either becomes fixed or is eliminated in a mixed population. The technique has been applied to data from *Drosophila melanogaster* cage competitions with believable results. Difficulties resulting from the frequency dependence of the estimates over time and the inherent cyclicity of the population competition data are evaluated. Fitness estimates from this method of successive intervals are lower than those from another unstable equilibrium method. The former technique measures fitness in population at carrying capacity in which density-dependence is prominent, whereas the latter method is applicable only to populations in which density-dependence is negligible. The implications to insect control of an estimation procedure which yields fitness values for continuously-breeding populations under conditions of density dependence are discussed.

Key words: Population replacement – Genetic control – Estimating fitness – Continuously-breeding – Competition – Frequency dependence – Density dependence

Introduction

Genetic methods of pest control offer the virtues of being highly specific and relatively non-polluting. However, they have tactical problems, as illustrated by the many failures in attempting population control by means of the sterile insect release method (S.I.R.M.). This illustrates the need to understand more fully the population and genetic dynamics of pest insects. To this end a body of literature is gradually being assembled on the theoretical bases of S.I.R.M. (Barclay 1980; Barclay and Mackauer 1980), but there is a lack of comparable studies on other genetic insect control techniques.

One such technique, that has received much attention experimentally, has been the replacement of an entire population bearing standard chromosomes (hereinafter called 'standards') by the release of strains carrying rearranged chromosomes. Strains of insects carrying such rearrangements as translocations, compound autosomes (hereinafter called 'compounds') and compound; free arm combinations (hereinafter called 'free arms') have been tested extensively in the laboratory and the field for their ability to replace wild types (for a review of the literature on genetic population replacement see Fitz-Earle and Holm 1982).

Of especial relevance to a theoretical understanding of population replacement is negative heterosis (or complete underdominance), whereby chromosomal rearrangements and standards separately have higher fitness than the hybrids between them.

In an extensive examination of various cases of negative heterosis Prout (1977) considered frequency changes within populations over discrete generations for a number of initial fitness values. In addition he was concerned with the genetic load (Wallace 1970) imposed upon populations in which negative heterosis was operative (Prout 1980). Computer models for population replacement in the two-spotted spider mite *Tetranychus urticae* have been developed by Feldman and Sabelis (1981). Their simulations showed good correspondence with their experimental results. Curtis and Hill (1971) used computer simulations to explore population replacement

for translocation strains. Karlin and McGregor (1972) have examined the effects of immigration on genetic equilibria under negative heterosis.

The present paper uses the model of complete underdominance with differential fitness of the homozygotes as a basis for estimating both fitness and generation time from several population replacement experiments (in population cages) involving different strains of the fruitfly *Drosophila melanogaster* breeding over continuous generations (Fitz-Earle et al. 1973; Fitz-Earle 1975; Fitz-Earle and Holm 1976). In a theoretical paper in which fitness was estimated from counts at some stage of development in two successive generations, Prout (1965) cautioned that fitnesses cannot be estimated satisfactorily unless the selection process has been completed at the time the genotypes are observed. This would be most unlikely if selection were against adults. In a later paper (Prout 1969) the above procedure was extended but discrete generations were still used. Jungen and Hartl (1979) related the frequency of wild-type and compound adult *D. melanogaster* in one generation with those of the next generation to obtain an index of fitness. They used bottled cultures with discrete, non-overlapping generations. In a companion paper (Hartl and Jungen 1979), 'semicontinuous' conditions were devised but again in bottled cultures that were never at sufficient number to approximate realistic native populations at carrying capacity. Estimates of effective generation length (2½–3 weeks) in the latter case were within the realm of the length given in the literature. However, the fitness estimates from both short and long term experiments were most difficult to interpret, no doubt due to the methodology of the study. One explanation given for the unreliable results, namely the impact of compound detachment, seems most unlikely since compounds are known to have a spontaneous detachment rate of only 1 : 50,000 (Hilliker and Holm 1978) and in over 160 cage population experiments detachments were not observed (Holm et al. 1980).

Our procedure for estimating fitness and generation time (the method of successive intervals) not only provides a means of analysing continuously-breeding populations, such as those to be found in *D. melanogaster* and many other pests, but furthermore it allows the evaluation of the two parameters under conditions in which the population is at carrying capacity. This paper includes a discussion of the impact of density dependence upon fitness estimates and the implications of these findings to the application of genetic insect control by population replacement in the wild.

Estimation of fitness and generation time

We start with the assumptions that mating is random among adults and that underdominance is complete, so that no heterozygotes survive beyond the egg stage. In addition, the homozygotes (standards and compounds) are unequally fit when in competition with each other, thus we start with the equation:

$$p_{i+1} = \frac{p_i^2}{p_i^2 + w q_i^2} \tag{1}$$

where p_i, q_i are the frequencies of the standards and compounds respectively at time i, while w is the fitness of the compounds. The fitness of the standards is assumed to be one; both fitnesses are assumed to be constant during the process of population replacement.

In the population cage competition experiments of Fitz-Earle and his colleagues, between compound or free arm and wild-type *D. melanogaster,* there was no immigration and it was determined that the fitness of any heterozygotes was indeed zero (Fitz-Earle et al. 1973; Fitz-Earle 1975; Fitz-Earle and Holm 1976). Mating preferences were not measured but will be assumed here not to exist.

Using equation (1) we can rearrange and obtain an estimate for the fitness from the (i–1)th to the ith generation:

$$\hat{w} = \frac{p_{i-1}^2 (1 - p_i)}{p_i (1 - p_{i-1})^2}. \tag{2}$$

Comparable formulae could be developed for application to other chromosome rearrangements such as with translocations, in which there may be partial survivorship of heterozygotes (semi-sterility), but they were not examined here.

While equation (2) applies strictly speaking only to populations breeding synchronously, it would apply approximately to continuously-breeding populations provided the generation time could be determined. The usual method of determining generation time in continuous populations is by measuring age-specific fertility and mortality rates and then using Lotka's Characteristic equation. This was not done, because such data had not been collected, but we employed another means described below.

We used two different estimates of the fitness, $\hat{w}$, of the compound autosome and compound; free arm strains. The first did not depend on the generation time and was simply an estimation based on the location of the unstable equilibrium gene frequency predicted from equation (1) and observed in the data as a result of using several different initial gene frequencies (see, for example, Fig. 2(d) in Fitz-Earle 1975). The second method used the estimator in equation (2) in which several different possible generation times (from 9 days to 27 days) were assumed and then $\hat{w}$ was calculated from all the data available. Since samples of cage populations had been taken roughly every three days until fixation of one or another chromosome type had been confirmed, this yielded a substantial number of estimates of w for each possible generation time of each cage replicate. Of course, these estimates were not independent since most sample frequencies were used twice, both as p_{i-1} and as p_i in equation (2).

Discrete generations – simulation

Here the problem of estimating generation time does not exist and the method was developed simply to

demonstrate its utility in estimating fitness using equation (2). Data from successive generations can be used to generate estimates of w, the fitness of chromosomally-rearranged homozygotes. The example given below applies to the cases of compound free-arm strains in competition with standards. Within certain limits pairs of adjacent frequencies from a sequence of generations should yield several reliable estimates of w.

If the generation time was not known and two successive observation periods happened to be at the same point in the life cycle, but it was not known how many generations this represented, then little confidence could be placed in the estimates of w. To illustrate this and to lay the groundwork for the section on continuous generations, estimates of w were made from Monte-Carlo simulations for intervals of one, two and three generations. The simulations allowed random union of 400 pairs of gametes chosen from an infinite gamete pool whose gene frequency (with respect to the chromosomal rearrangements) was exactly that of the parental generation. Each gamete was chosen from the gamete pool with the genotype determination being a Bernoulli event (Parzen 1960). The probability of the gamete being a wild type was exactly the proportion of wild gametes present and this was accomplished by generating random numbers using the fortran subroutine RANDU which was initially seeded for each run using the time of day. In this way a binomial distribution of offspring resulted from the parents. The initial gene frequency and initial fitness of rearrangements were prescribed and the frequencies in succeeding generations were tabulated. Estimates of w were made by means of equation (2) using p_i and p_{i-1}, p_i and p_{i-2}, and p_i and p_{i-3} to obtain estimates 1, 2, and 3 generations apart. Several runs were made for each of several combinations of initial gene frequency and fitness of rearrangements. The estimates from these replicated runs were averaged, since there was considerable variability over generations, and these averages are plotted in Fig. 1. The direction of bias in using step sizes of 2 or 3 generations to estimate w depends on which genotype is eventually lost to the population. From equation (2) it can be seen that if the population gene frequency is declining towards $p=0$ (i.e. fixation of rearrangements) and if the step size is two generations, then p_i and p_{i-2} differ from each other more than do p_i and p_{i-1}. Furthermore the estimate of w will be too large since in the numerator of equation (2)

$$p_{i-2}^2(1-p_i) > p_{i-1}^2(1-p_i)$$

while in the denominator of equation (2)

$$p_i(1-p_{i-2})^2 < p_i(1-p_{i-1})^2.$$

Thus a plot of $\hat{w}$ against step size (i.e. number of generations used in estimating w) should yield a graph

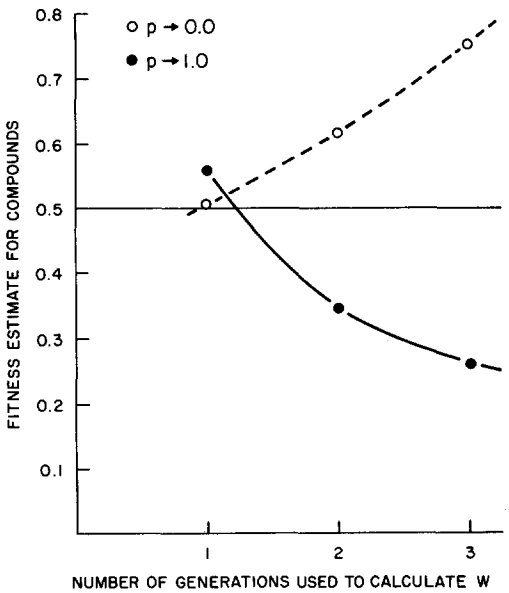


Fig. 1. Estimates of fitness, w, using equation (2) in a simulation with discrete generations. In each case w was estimated using step sizes of 1, 2 and 3 generations to illustrate the determination of the correct estimate of w and the generation time at the intersection of the graphs

which increases with step size. Symmetrically, a corresponding graph would decrease with step size if the gene frequency was increasing towards the fixation of wild types with $p=1.0$. The two graphs should coincide at the true value of w and at a step size of one generation; in fact this occurs in the simulated population (Fig. 1), in which the initial fitness used in the simulation was $w=0.5$.

Continuous generations – simulation

In keeping with the nature of the data available, a simulation was written to approximate roughly the biology of *D. melanogaster.* A larval period of two weeks and a maximum adult life span of 6 weeks in the population cages were assumed for the simulation. The survivorship curve for the adults was type II (i.e. exponential decline) but since larvae do not contribute to the egg production, all the larval mortality was imposed immediately after emergence from the eggs. In addition all selection was assumed to operate at the time of larval mortality; equation (1) was used to determine selection on larvae. The formation of zygotes was binomially distributed, as with the previous simulation. Several values of initial gene frequency and fitness were tried and the results were all qualitatively similar to those given in Appendix Table A 1 and graphed in Fig. 2. The initial value of fitness chosen for the graphs in this figure was $w=1.0$ (unrealistic for compounds but perhaps possible for translocations). The step size

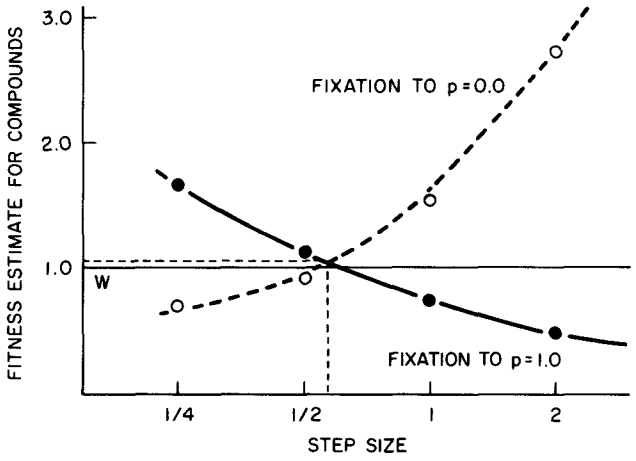


Fig. 2. Estimates of fitness, w, using equation (2) in a simulation with continuous population growth. In each case w was estimated using four different possible generation times. The true value of larval fitness of the rearrangements was set at 1.0, while the two graphs intersect at about w = 1.05

used for calculating $\hat{w}$ varied between twice the maximum life of a fly (i.e. 16 weeks) and ¼ of this maximum life (i.e. 2 weeks). We recognize that under ideal conditions *D. melanogaster* can live for up to 3 months, but in the crowded conditions of cage experiments, such as those considered here, 6 weeks may not be an invalid approximation. The gene frequencies of each 2-week age class were tallied separately while the gene frequency of the total parental group contributing eggs consisted of the weighted average of the three adult age groups present; it was from these parents that the gametic frequencies were obtained. Since the population was assumed to be in equilibrium with respect to size (i.e. at carrying capacity), the generation time was calculated using the approximation given by Pielou (1969) (based on Lotka's characteristic equation) namely

$$G \doteq \frac{\sum_{x=1}^{\infty} x \cdot l_x \cdot m_x}{\sum_{x=1}^{\infty} l_x \cdot m_x} \qquad (3)$$

where m_x is natality, l_x is survivorship and x is age of cohort.

The estimate of fitness, by our method of successive intervals outlined above, should be best at the true generation time. Assuming that this is indicated by the intersection of the various curves generated by graphing estimated fitness against possible generation time, the estimates of fitness and generation time from the simulation are about 1.05 and 0.57 (or $0.57 \times 8 = 4.56$ weeks) respectively. In the simulation, m_x (natality) was taken as 1.0 for all adult classes while l_x (survivorship) values were assumed to be 0.625, 0.25 and 0.125 for the proportions of age groups 2, 3, and 4 respectively. Thus $\sum_{2}^{4} l_x m_x = 1.0$ while $\sum_{2}^{4} x \cdot l_x m_x = 2.5$ giving $G = 2.5$ two week intervals, which represents $2.5/4 = 0.625$ of the maximum life span. The estimated fitness and generation time of 1.05 and 0.57 (or $0.57 \times 8 = 4.56$ weeks) are remarkably close to 1.0 and 0.625 (or $0.625 \times 8 = 5$ weeks) actually used in the simulation.

The survivorships used in the simulation are somewhat misleading since the first value (0.625) will obviously depend on both the normal mortality and the relative selection against the rearrangements occurring in the larval stage, and this has not been made explicit in the simulation; here selection was assumed to act on gene frequencies rather than on numbers. Any simulation which tried to reproduce the biology of a given species fairly precisely would have to make selective mortality explicit.

Data from Drosophila melanogaster

The data on frequencies of compound autosome, compound; free-arm strains in competition with wild strains over time were taken from three sources (Fitz-Earle et al. 1973; Fitz-Earle 1975; Fitz-Earle and Holm 1976). These studies involved replacement experiments in population cages in which measurements were made of gene frequencies about every three days until the fixation of one type. Fifteen such experiments were reanalyzed using the method of successive intervals from equation (2) to estimate fitness and effective generation times as was done in the previous section. Estimations

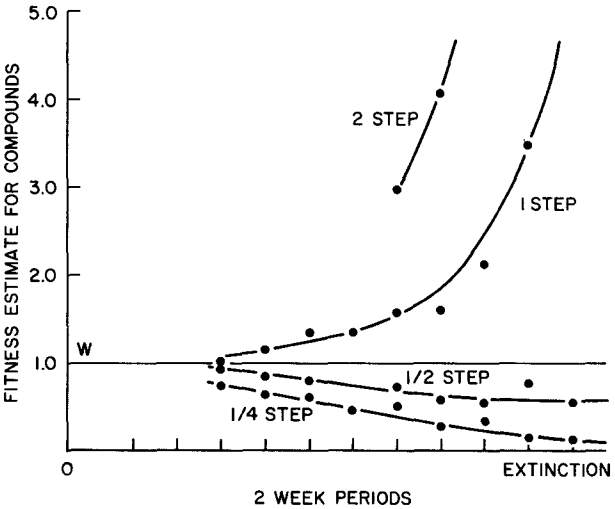
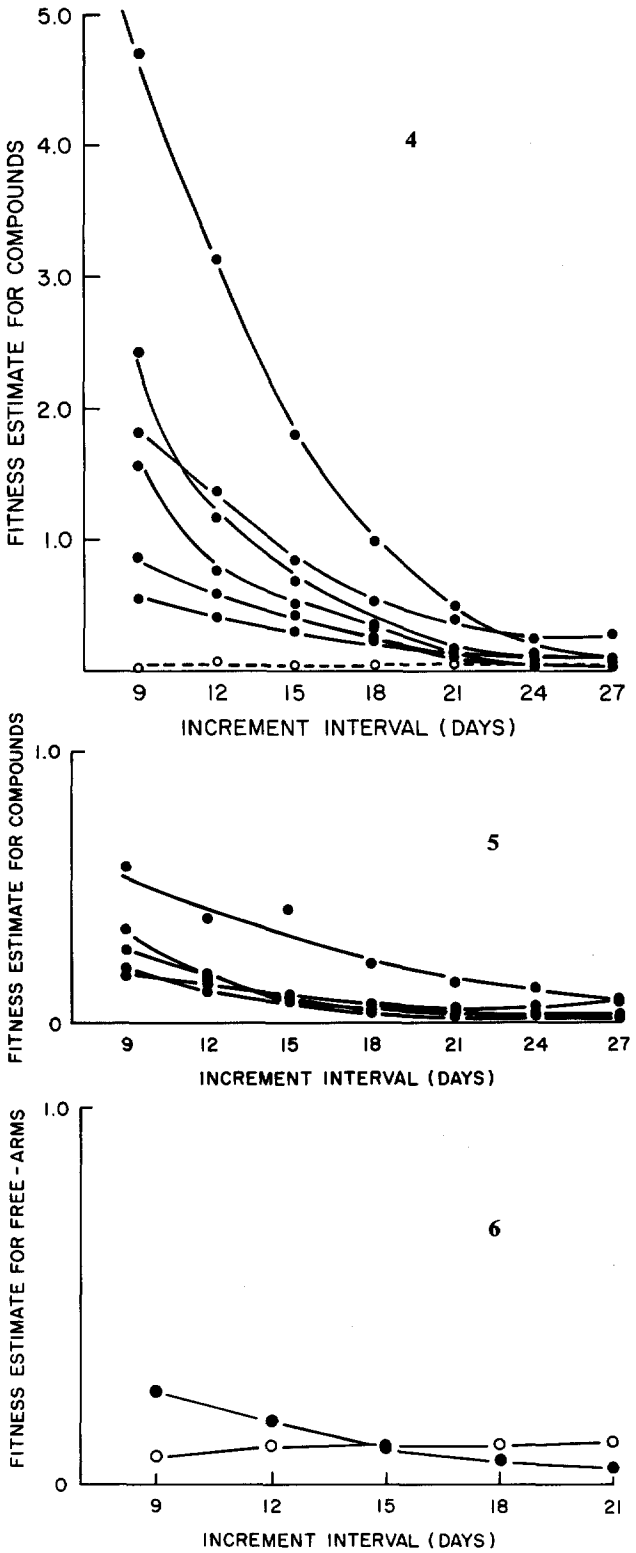


Fig. 3. Estimates of fitness using equation (2) for continuous population growth as in Fig. 2, but graphed over time. The frequency dependence of w is apparent in this case as it was in all other cases tried. For the purpose of averaging, the estimates from different runs of the simulation were averaged starting at the last time period before fixation for each run and progressing backwards to the start



Figs. 4–6. Estimates of fitness for the three different *Drosophila* strains obtained using equation (2) and seven different possible generation times. The point of convergence of the fitness-step size curves is to the right of the graphs in Figs. 4 and 5, but longer step sizes would have been difficult given the length of time to fixation

were made for seven possible generation times from 9 to 27 days in three day intervals. Unfortunately in most experiments the times until fixation of one genotype were brief and this prohibited the use of longer time intervals than 27 days. For this reason only cages which took a relatively long time for fixation to occur were chosen for reanalysis in this way. The results of the reanalysis of the data for two compound strains C(3L)VH2, ri; C(3R)SH19, + (Fitz-Earle et al. 1973 Fig. 2) and C(2L)P, b; C(2R)P, px (Fitz-Earle 1975, Fig. 2) and a free arm strain C(2L)SH1, +; F(2R), bw (Fitz-Earle and Holm 1976, Table 4) in competition with wild types are given in Figs. 4–6 respectively. An example of one of the sets of reanalysed data is to be found in Appendix Table A2.

The estimates of w were strongly frequency dependent, especially for possible generation times other than the true one (i.e. where the curves intersect). The frequency dependence is apparent in both the *Drosophila* simulation (Fig. 3; Table A1 in the appendix) and also in the *Drosophila* data (Table A2 in the appendix). Here we assume that the observed frequency dependence represents a systematic bias in the estimates rather than an actual change of fitness during population replacement. To overcome the problem of frequency dependence, estimates of w for a given cage and a given interval size were obtained by averaging several estimates near the middle of the time sequence of estimates since these appeared to be relatively independent of frequency of compound (or free arm) strains. The averages thus obtained were then plotted against possible generation time as shown in Figs. 4, 5, and 6. Ideally all the lines should intersect in one point

Table 1. Estimates of fitness for two different compound strains and one free-arm strain using the methods of unstable equilibrium and successive intervals

Strain	Fitness estimates	
	Unstable equilibrium method	Successive intervals method[a]
C(3L)VH2, ri;[c] C(3R)SH19, +	–[b]	0.05
C(2L)P, b;[d] C(2R)P, px	0.075 – 0.11	0.05
C(2L)SH1, +;[e] F(2R), bw	0.25 – 0.33	0.10

[a] Recursion equation (2)
[b] Not available, see text
[c] Data from Fitz-Earle et al. (1973)
[d] Data from Fitz-Earle (1975)
[e] Data from Fitz-Earle and Holm (1976)

which would then give the best available estimates of fitness and generation time. Since it is unreasonable to except a unique intersection, due to sampling error for example, only visual estimates of fitness were made for the three strain pairs examined. These estimates are given in Table 1. As may be observed from any of Figs. 4 through 6 inaccuracies in the plotting of the graphs would not significantly affect these estimates of w. However, the estimates of generation time would seem to be quite sensitive to plotting errors.

Discussion

The method outlined here of using successive intervals in estimating fitness is new, as far as we know. It is likely to have considerable applicability to population replacement experiments such as those analyzed here and in the planning of replacement regimes for insect control in the wild. The estimates of fitness obtained by this new method, however, are somewhat less than those obtained by the other crude method of attempting to locate the unstable equilibrium frequency on the two sides of which fixation would be expected to proceed in opposite directions. In one of the sets of cage experiments (Fitz-Earle et al. 1973) a meaningful estimate of the unstable frequency of compounds could not be obtained since there was no clear boundary evident. In the other two sets of data those estimates for w both exceeded the corresponding estimates from equation (2) (Table 1).

A likely explanation for the discrepancies between the two methods is that they are measuring fitness under two different sets of conditions. The approximate unstable equilibrium method is based upon extrapolating back to the beginning of an experiment. At this time the population in the cage is still increasing in numbers and is well below carrying capacity. The higher estimates of fitness are thus a reflection of the meiotic behaviour of the competing strains and the differences in frequency to achieve equilibrium. By contrast, the method of successive intervals yields fitness estimates at a time when the cage population is at carrying capacity. The lower values of fitness of the rearrangements at this time are thus a consequence of both frequency and density. Thus the fitness, at least of compounds and free-arms, would appear to decline under density dependent conditions. Prout (1980) in an extensive paper largely devoted to a discussion of load theory has shown also that selection is influenced by density.

From the standpoint of genetic insect control these findings would suggest that competition should be effected at population densities well below the carrying capacity of the environment and in circumstances where the competing strain has a higher fitness. Where this is not possible, as in some tropical insects which may be continuously at carrying capacity, an alternative strategy would be to use, for competition, strains whose fitness improves, or is at least stable, with increased density.

It is encouraging to note that the fitness estimates by the method of successive intervals for the compound strains (approximately 0.05) are one half that of a free arm strain (approximately 0.10) which is entirely consistent with their known meiotic behaviour (Fitz-Earle et al. 1973; Fitz-Earle and Holm 1976).

One assumption of the method of successive intervals based on equation (2) for estimating fitness is that generation time is the same for both compounds (or free arms) and wild types. If the generation times of the two competing homozygotes differ, then estimates of w should change systematically over the time sequence of gene frequencies. For this reason it may be better to use the estimates near the start of the experiment on both sides of the unstable gene frequency equilibrium in order to minimize the differences in average generation time for the different graphs, otherwise different graphs would be based on quite different generation times and their intersections would be meaningless. It appears that this possibility may have to be tested independently.

Both the frequency of the wild type in the *Drosophila* data and the estimated fitnesses derived from them show considerable cyclicity. Appendix Table A2 shows these estimates for one cage experiment from the data given by Fitz-Earle et al. (1973). The example is given as being typical of the behaviour of the data throughout the caged experiments. This cyclic behaviour of the estimates is reflected also in Table A1 for the simulated population, which again is typical of the various runs made of the simulation. The cyclicity is likely a result of the time lag implicit in the dynamics of an iteroparous population in which the gene frequency of a given set of adults depends on the gene frequencies of several different age groups in the past (Maynard Smith 1968). This cyclicity makes the use of the method of successive intervals described above rather difficult in populations which go quickly to fixation since fitness values on the same horizontal lines in Appendix Tables A1 and A2 are from different parts of the cycle. This can be alleviated in two ways: (a) use the average of several successive values of $\hat{w}$ over time for each step size, and (b) displace the set of values of $\hat{w}$ by one for each successive time step, since the cycles appear to be so displaced in both the simulated and real data (Appendix Tables A1 and A2). This latter technique was adopted for comparing averages of fitness estimates in Figs. 4, 5, and 6 since fitness

estimates from the *D. melanogaster* data were highly variable.

A trend in the simulated data appears in Fig. 3; the estimates of fitness appear to be frequency dependent, especially for step sizes other than one generation. This may bias the estimates of w if values of $\hat{w}$ are used for genotype frequencies far from the unstable equilibrium; this is one more reason for using values of $\hat{w}$ near, and on both sides of, the equilibrium genotype frequency in constructing the graphs. This apparent frequency dependence of fitness estimates may be analogous to that described by Prout (1965, 1980) in populations which are tallied at stages before selection is complete, and may occur even if the actual fitnesses remain constant.

The problem of defining fitness in continuous populations is difficult and we have made no attempt at an unequivocal definition in this paper. Even the problem of defining generation time for continuous populations is not trivial. Charlesworth (1970, 1972) and Charlesworth and Giesel (1972 a, b) have addressed this problem at some length, but completely adequate definitions remain elusive. In view of these potential ambiguities it may be premature to insist that what we are measuring by our method are in fact fitness and generation time but it seems clear that the quantities measured are at least closely related to fitness and generation time.

Acknowledgements. We thank Lefteri Zouros, Chung-I Wu, David Holm, Arthur Hilliker and an anonymous reviewer for discussion and comments on our ideas contained herein. A portion of this work was supported by Canada Council Killam Grant S71-1687 to M. F.-E.

Table A1. Estimates of fitness from one run of the *Drosophila* simulation illustrating both the cyclic behaviour of the gene frequencies and fitness estimates and the frequency dependence of the fitness estimates.

Freq. of standards 0.2200		Fitness of compound 0.2500			
Freq. of standards		Estimated fitness			
Adults	Eggs	2-step	1-step	1/2-step	1/4-step
0.220	0.241	0.000	0.000	0.000	0.282
0.220	0.241	0.000	0.000	0.282	0.282
0.220	0.241	0.000	0.000	0.282	0.282
0.241	0.286	0.000	0.250	0.250	0.250
0.269	0.263	0.000	0.216	0.216	0.275
0.266	0.495	0.000	0.219	0.279	0.374
0.411	0.300	0.000	0.114	0.194	0.189
0.344	0.794	0.152	0.193	0.250	0.926
0.633	0.449	0.046	0.078	0.281	0.159
0.517	0.952	0.074	0.123	0.257	2.787
0.807	0.844	0.019	0.116	0.713	0.274
0.821	0.988	0.022	0.060	0.249	3.794
0.984	0.992	0.007	0.165	0.963	1.171
0.973	1.000	0.004	0.032	0.593	9.182
0.997	1.000	0.002	0.060	1.078	4.322

Table A2. Estimates of fitness from one cage experiment. These illustrate both the frequency dependence of the estimates and the cyclic behaviour of the gene frequencies and fitness estimates

Frequency of standards[f]	9-step	8-step	7-step	6-step	5-step	4-step	3-step
0.222	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.140	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.239	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.294	0.000	0.000	0.000	0.000	0.000	0.000	0.196
0.397	0.000	0.000	0.000	0.000	0.000	0.124	0.040
0.388	0.000	0.000	0.000	0.000	0.128	0.042	0.156
0.796	0.000	0.000	0.000	0.021	0.007	0.025	0.044
0.707	0.000	0.000	0.034	0.011	0.041	0.072	0.180
0.783	0.000	0.023	0.007	0.027	0.048	0.120	0.111
0.690	0.037	0.012	0.044	0.078	0.195	0.181	6.840
0.891	0.003	0.012	0.021	0.053	0.049	1.858	0.712
0.851	0.017	0.030	0.076	0.070	2.658	1.018	2.280
0.930	0.013	0.033	0.030	1.143	0.438	0.978	0.373
0.957	0.019	0.018	0.682	0.261	0.584	0.222	3.002
0.960	0.017	0.633	0.242	0.541	0.206	2.760	1.359
0.977	0.358	0.137	0.306	0.117	1.560	0.764	4.154
0.987	0.077	0.171	0.065	0.873	0.428	2.278	6.520
0.980	0.266	0.101	1.352	0.663	3.529	9.580	11.748
0.993	0.035	0.467	0.229	1.219	3.311	3.820	12.696
0.962	1.225	0.595	3.170	8.605	9.926	27.735	105.027
0.990	0.329	1.747	4.744	5.473	15.304	36.443	24.191
0.993	1.244	3.311	3.820	10.686	25.462	13.521	139.000

[f] Data from Fitz-Earle et al. (1973)

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