Genet. Res., Camb. (1962), **3**, *pp.* 388–404
With 4 text-figures
Printed in Great Britain

The estimation of generation interval in experimental populations of *Drosophila*

By J. S. F. BARKER
Department of Animal Husbandry, University of Sydney, Sydney, Australia

(*Received* 9 *December* 1961)

I. INTRODUCTION

The problem of generation interval in experimental populations of *Drosophila* has been briefly considered by Moree (1955). Difficulty arises because in theoretical investigations the unit of time is one generation, whereas in experimental population data the unit is one day. Thus, theoretical models and predictive equations can only be applied to experimental data when these two units can be converted to a common scale, i.e. days per generation. Generation interval is defined as the average time from a specific point in the reproductive life of one generation to the same point in the next. Any experimentally convenient reference point may be used, provided the same one is used in both generations. The mean time of egg-laying is used in the experiments reported here.

Several workers have estimated the generation interval in experimental populations of *Drosophila* (Table 1). Some of these estimates have been based on observed changes in gene frequency, and relating these to changes expected due to postulated selection effects (Ludwin, 1951; Merrell, 1953). Others have been based on average

Table 1. *Estimates of generation interval in experimental populations of* Drosophila

Reference	Population technique	Species	Temperature (°C.)	Generation interval (days)
Buzzati-Traverso (1955)	Vial series	*D. melanogaster*	25	15
Susman & Carson (1958)	,,	,,	25	13
Carson (1958)	,,	,,	25	14
Reed & Reed (1950)	Bottles	,,	20	21
Ludwin (1951)	,,	,,	20	30
Merrell (1953)	,,	,,	20	24
This study	,,	,,	25	14
This study	,,	*D. simulans v*	25	16–18
Wright & Dobzhansky (1946)	Cages	*D. pseudoobscura*	25	24·5
Wallace (1950)	,,	*D. melanogaster*	25	14
Prout (1954)	,,	,,	25	14
Erk (1955)	,,	,,	25	12–15
Hochman (1958)	,,	,,	25	15
This study	,,	,,	25	23

time of eclosion after the insertion of a medium jar into a population cage (Wright & Dobzhansky, 1946; Erk, 1955), or the minimum time from egg to adult (Carson, 1958; Susman & Carson, 1958). Other workers have assumed a value for the generation interval in their populations, but give no information as to how this was arrived at (Reed & Reed, 1950; Wallace, 1950; Prout, 1954; Buzzati-Traverso, 1955; Hochman, 1958). The estimates in Table 1 are quite variable, and some are certainly not valid estimates of the generation interval.

An experimental method that may be used to estimate generation interval was discussed by Birch (1948). The data required are the female life table giving the probability at birth of being alive at age x (designated l_x), and the age-specific fecundity table giving the mean number of female offspring produced in a unit time by a female aged x (designated m_x). These may be experimentally determined for some convenient interval of age, but an accurate estimate of the generation interval cannot be obtained until the value of the intrinsic rate of increase (r) is known. An approximate estimate (T) may be calculated independently of r if l_x and m_x are experimentally determined:

$$T = \frac{\sum x l_x m_x}{\sum l_x m_x} \tag{1}$$

This method, however, is not of much value for studies of *Drosophila* populations because l_x and m_x would be estimated in culture bottles or vials, where external conditions such as crowding would be quite different from those in experimental populations. As these external conditions affect survival and longevity (l_x) (Sang, 1949*a*, *b*, *c*; Lewontin, 1955; Birch, 1955) and fecundity (m_x) (Robertson & Sang, 1944; Chiang & Hodson, 1950), the generation interval estimate so obtained would have little relevance to experimental populations.

In this paper, two sets of experiments are described in which the generation interval has been determined for populations maintained at $25 \pm 0{\cdot}5°$ C. in population cages and in population bottles. The cages and bottles used, and associated techniques, have been described by Barker (1960*a*, *b*). Briefly, the cage consists of a glass-topped wooden box, with space for 16 media jars, one of which is used for egg sampling and the remainder to maintain the population. Each week, five of the latter are replaced, one each day, Monday to Friday, so that a jar remains in the cage for 3 weeks. Each jar contains 15 to 20 ml. of medium. The population bottle is made up of two cylindrical bottles joined by plastic tubing. The older of the bottles is replaced by one containing 10 ml. fresh medium every 2 weeks, so that a medium bottle remains in position for 4 weeks.

2. POPULATION CAGE EXPERIMENTS

(i) *Method of estimation*

Given that a sample of eggs can be placed in the population cage, the aim is to determine the mean time of egg-laying of the adults emerging from them. The time interval between the laying of the initial egg sample and this mean time of egg-laying is then an estimate of the generation interval.

The methods used were: approximately 1000 flies were placed in each of five cages; one cage being set up with wild-type *D. melanogaster* (Oregon-R-C), the other four with the *vermilion* (*v*) mutant of *D. simulans*. These cages were maintained for 9 weeks to allow the population numbers to build up and stabilize to some extent. A sample of *D. melanogaster* eggs was then obtained by taking all the media jars from a *D. simulans v* cage and placing them in the *D. melanogaster* cage for 7·5 hours (9 a.m. to 4.30 p.m.), after which the jars were replaced in the *D. simulans* cage. All *D. simulans* flies that had emerged into the *D. melanogaster* cage during this period were removed and replaced in the *D. simulans* cage. An initial egg sample whose mean egg-laying time was known was thus obtained.

From the 7th day after this initial egg sample, daily egg samples were taken from the *D. simulans* (experimental) cage, by placing a medium jar in the cage for 24 hours. When removed, samples of eggs were taken from the surface of the medium and each placed in a culture bottle containing dead yeast fortified medium. Each egg sample was taken on a sector of the medium surface, the size of the sector being variable as an attempt was made to take approximately 200 to 300 eggs on each. On dead yeast fortified medium, competition between larvae is reduced and the count of adults emerging from an egg sample is essentially a measure of the numbers of viable eggs in the sample. The flies emerging from these egg samples were collected daily and counted by eye colour as wild-type (*D. melanogaster*) or vermilion (*D. simulans*) until there were no further emergences. Thus, from each daily egg sample, an estimate was obtained of the percentage of *D. melanogaster* eggs laid in the cage that day.

However, it must be remembered that the *D. melanogaster* would be laying eggs in another medium jars in the cage and that these would give rise to a second generation. This was prevented by imposing a secondary rotation of medium jars on the experimental cage. Once a jar has been in a cage for 6 days, it contains many larvae but these larvae have not begun to crawl out on to the floor of the cage to pupate. Therefore, if jars are removed after 6 days in the cage, no flies will enter the cage population from them. However, the population of *D. simulans v* in the cage must be maintained so that each jar was replaced by a 6-day-old jar from a cage containing this stock. Twelve-day-old jars were similarly replaced. This secondary rotation commenced 14 days after the initial egg sampling, when all jars 6-days-old or older were removed from the experimental cage and replaced by jars from a *D. simulans v* cage. Daily thereafter, 6-day-old and 12-day-old jars were removed and replaced.

The daily egg sampling from the experimental cage was continued until no *D. melanogaster* eggs were being laid. The data obtained were thus: (i) Time zero – mean time of egg laying of the initial egg sample, and (ii) an estimate of the percentage of *D. melanogaster* eggs among the total laid in the cage each 24 hours after Time zero. This latter may be taken as an estimate of the expectation of offspring for each day of age. That is, referring to the estimation procedure of Birch (1948), one obtains a direct estimate under population cage conditions of $l_x m_x$ for each day x, except that this does not refer to females only. Generation

interval can then be estimated from equation (1). If P_i is the estimate of the percentage of *D. melanogaster* eggs laid in each 24-hour period (x_i), then the variance of the mean is calculated as:

$$V(\bar{x}) = \sum P_i^2 \sigma^2 / (\sum P_i)^2 \quad (2)$$

where

$$\sigma^2 = \sum [P_i(x_i - \bar{x})^2] / \sum P_i \quad (3)$$

(ii) *Results*

Two estimates of the generation interval of *D. melanogaster* Oregon-R-C under population cage conditions were obtained. They were not strict replicates, as one estimation was carried out 9 months later than the other, and with one difference in the methods used. In Estimate 1, four samples of eggs were taken from each daily egg sample, while in Estimate 2, eight were taken. The means (and their standard errors) of the numbers of adults scored from each daily egg sample were, for Estimate 1, $1092{\cdot}9 \pm 55{\cdot}3$, and for Estimate 2, $2104{\cdot}6 \pm 145{\cdot}2$. The larger numbers scored in Estimate 2 might be expected to give a better estimate of the percentage of *D. melanogaster* eggs laid each day.

The results in Fig. 1 show both estimates to have a similar trend with two main peaks in the curve, although Estimate 2 lags about 2 days behind Estimate 1. The generation interval estimates, however, are not significantly different (Table 2).

Table 2. *Estimates of generation interval* ($\bar{x}$) *of* D. melanogaster *Oregon-R-C maintained in population cages*

	$\bar{x}$ (days)	Standard error
Estimate 1	22·7	1·70
Estimate 2	24·0	1·38

$t_{(83)} = 0{\cdot}62$; $0{\cdot}5 < P < 0{\cdot}6$.

3. POPULATION BOTTLE EXPERIMENTS

(i) *Method of estimation*

The method used was essentially similar to that for populations maintained in cages. Two experiments, with six replications in each, were carried out to estimate the generation interval of *D. melanogaster* Oregon-R-C. Concurrent with the second experiment, the generation interval of *D. simulans v* also was estimated, with four replications. Initially, six replications were started but two had to be discarded as very few flies emerged from the initial egg sample (4♂, 1♀ in one and 3♂, 2♀ in the other).

In each experiment, a number of population bottles, some *D. melanogaster* Oregon-R-C and some *D. simulans v* were initiated, each with 100 to 200 flies, and were maintained for 6 weeks. Then, when a fresh medium bottle was being attached to each population bottle, the adult flies from a *D. melanogaster* population were

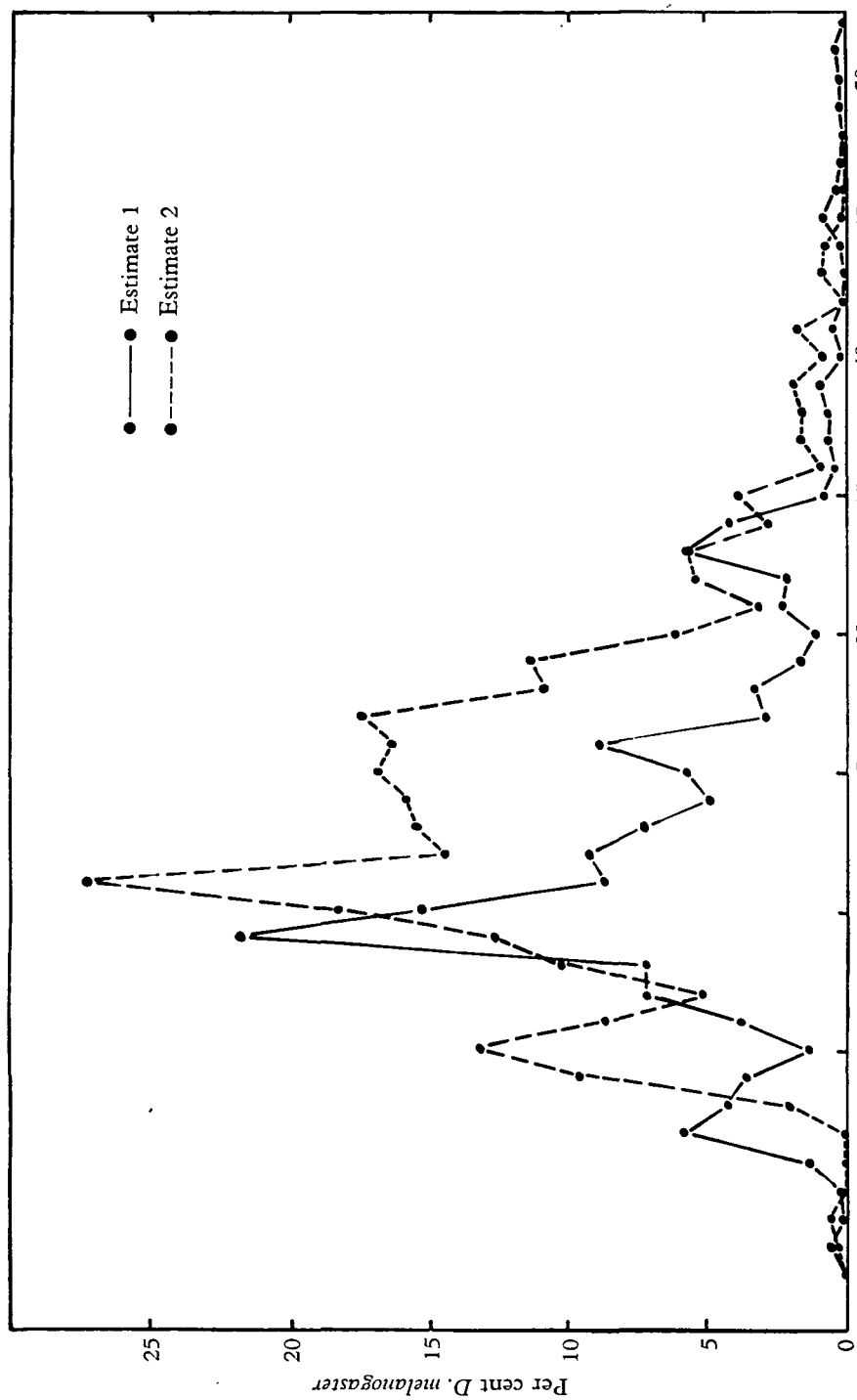

Fig. 1. Percentage D. *melanogaster* emerging from the daily egg samples for the two estimates of generation interval of this species maintained in population cages.

https://doi.org/10.1017/S0016672300003232 Published online by Cambridge University Press

placed into a *D. simulans* population bottle. In the first experiment, they remained there for periods varying from 24·5 to 29·5 hours, when they were removed and the *D. simulans* populations, which had been stored separately in culture bottles, replaced in the population bottle from which each had been taken. An initial egg sample whose mean egg-laying time was known was thus obtained for each replicate. In the second experiment, six populations of *D. melanogaster* and six of *D. simulans* were paired. When the fresh medium bottles were being attached, the adults from a *D. melanogaster* population were placed into the *D. simulans* population bottle with which it was paired and *vice versa*. For all populations, these adults were returned to their original population bottle exactly 24 hours later. In both experiments, from the 8th day after this initial egg sampling, the populations were lightly etherized at the same time each day and any adults of the appropriate species that had emerged from the egg sample removed. The first such adults collected were placed in a culture bottle. Those collected the next day were placed in another culture bottle and the previous day's collection transferred into this bottle without etherization. This procedure was repeated every 24 hours until no further adults emerged into the population bottle. Thereafter, the adults were transferred into fresh culture bottles at the same time each day until all had died, or in some cases, until a few males only remained in the bottles. The progeny emerging in these transfer bottles were counted daily until there were no further emergences. The data obtained for each population was thus: (1) Time zero – mean time of egg-laying of the initial egg sample, and (ii) the number of progeny (n_i) produced by the adults emerging from this initial egg sample, in each 24-hour period after Time zero (x_i). These numbers of progeny produced may be taken as an estimate of the number of eggs laid in each 24-hour egg collection period, or the expectation of offspring. Generation interval can then be calculated from equation (1) as:

$$\frac{\sum n_i x_i}{\sum n_i} \tag{4}$$

(ii) *Results*

D. melanogaster—*Experiment 1*

The generation interval estimates are given in Table 3, while Fig. 2 shows the distribution of the numbers of *D. melanogaster* adults that emerged from each 24-hour egg collection. These numbers are each presented relative to the day on which the eggs were laid.

Four of the replicates (Nos. 2, 3, 4, and 5) reached peak egg production on Day 13, one (No. 6) on Day 15, while the remaining one (No. 1) shows a number of peaks over the period Day 13 to Day 17. This latter distribution is spurious and due to an experimental error. The culture bottles used in the daily transfer for the 24-hour egg collections normally contained dead yeast fortified medium. The flies of Replicate No. 1 were accidentally placed in bottles containing unfortified medium on Days 14 and 16. The amount of food available per larva in these would be less than with fortified food and the mortality of immature stages would thus be increased.

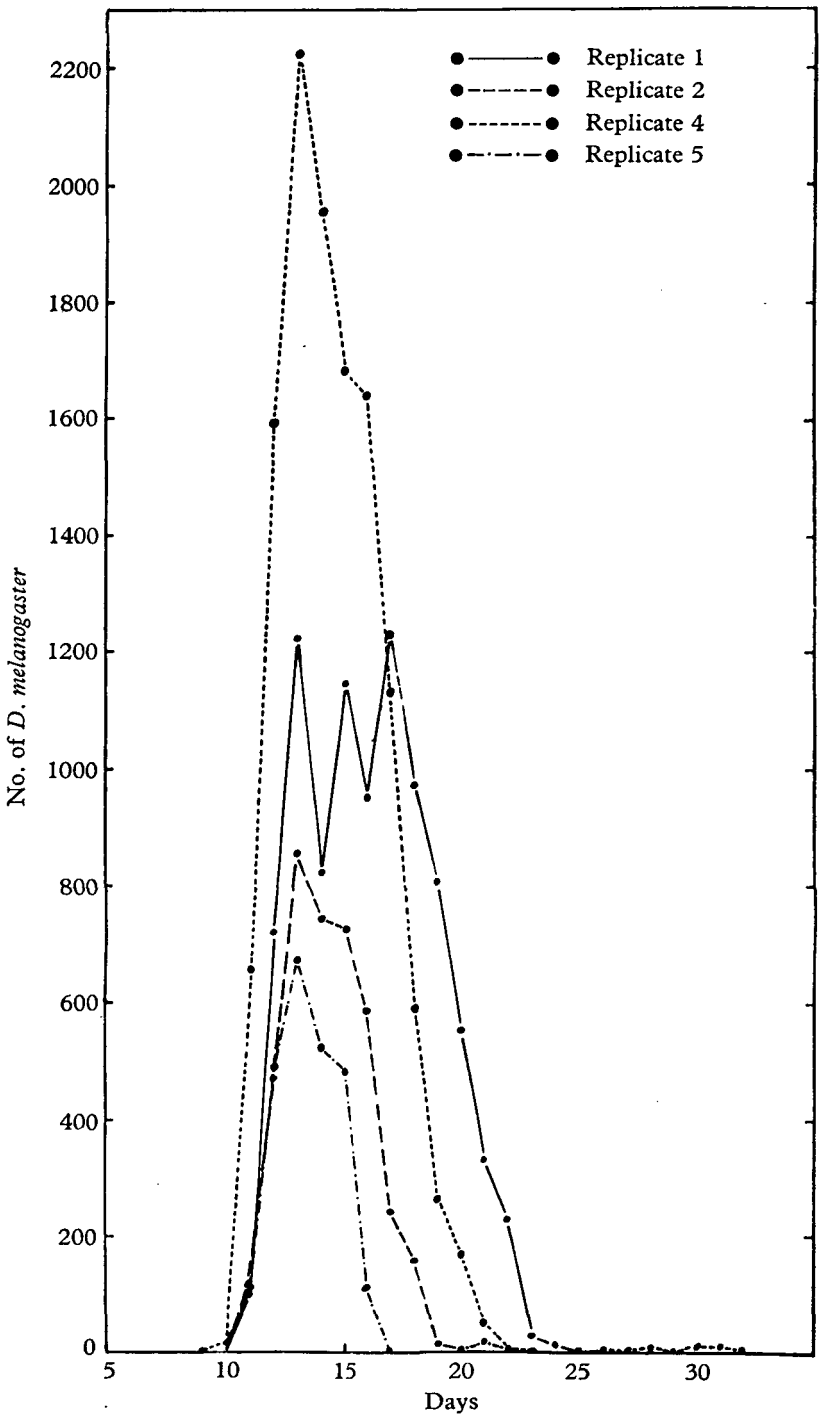

FIG. 2. Numbers of D. *melanogaster* emerging from the daily egg collections in Experiment 1, estimation of generation interval of D. *melanogaster* maintained in population bottles. Replicates 3 and 6 are omitted for clarity, as they largely overlap with replicates 4 and 2 respectively.

https://doi.org/10.1017/S0016672300003232 Published online by Cambridge University Press

Analysis of variance (Table 3) shows that the generation interval estimates are significantly different. The variance of each estimate is small because of the large numbers of individuals on which the estimate is based. The differences between

Table 3. *Estimates of generation interval* ($\bar{x}$) *in Experiment 1 for* D. melanogaster *Oregon-R-C maintained in population bottles, together with the total numbers of progeny scored in each estimate, and analysis of variance of the estimates*

Replicate No.	$\bar{x}$ (days)	$\sum n_i$
1	16·25	9156
2	14·39	3924
3	14·49	8102
4	14·73	12,031
5	13·73	2415
6	15·14	4130
Mean ± S.E.	14·79 ± 0·35	
Total		39,758

Analysis of variance

Source of variation	D.F.	Mean square
Between means	5	4521·98*
Within means	39,752	229·64

* $P < 0{\cdot}001$.

estimates could be due to a number of factors. Although the populations were started together and maintained in the same way, the micro-environment of each population bottle may be expected to be unique due to differences in population

Table 4. *Numbers of flies laying the initial egg samples and numbers of their progeny that emerged in the population bottles used in the estimation of generation interval of* D. melanogaster (*Experiment 2*), *and* D. simulans v

Replicate No.	No. of flies laying initial egg sample	No. of flies emerging from initial egg sample		
		Males	Females	Total
D. melanogaster				
1	158	29	26	55
2	198	47	37	84
3	401	42	73	115
4	218	11	19	30
5	339	51	63	114
6	240	18	21	39
D. simulans v				
1	237	42	38	80
2	181	25	15	40
3	217	13	13	26
4	255	24	18	42

size, in yeast growth, in degree of mould contamination, and other factors. Further, the number of flies laying the initial egg samples varied from population to population, as did the numbers that emerged from the initial egg sample (Table 4). The pattern of egg-laying over the 24 hours or so of the initial sample may vary from population to population. As it is most likely that the differences in the estimates from replicate populations were due entirely to such uncontrollable factors, the mean of the six estimates may be taken as a reasonable estimate of the generation interval. In experimental populations, one might expect the generation interval to vary from generation to generation for similar reasons. That is, each generation interval is unique. However, comparison of experimental results from such populations with theoretical expectations would have to be done by using the average generation interval over the period studied. This would be equivalent to the determination here of the mean of six generation intervals estimated at the same time in six different populations.

D. melanogaster—*Experiment 2*

Results are presented in the same way as for Experiment 1 in Table 5 and Fig. 3. In this experiment, conducted one year after Experiment 1, the populations reached peak egg production about the same time (five on Day 13 and one on Day 15), but maintained egg production at a higher level for slightly longer. Again, the estimates

Table 5. *Estimates of generation interval* ($\bar{x}$) *for* D. melanogaster *Oregon-R-C* (*Experiment 2*), *and* D. simulans v *maintained in population bottles, together with the total numbers of progeny scored in each estimate, and analysis of variance of the estimates*

Replicate No.	*D. melanogaster* Oregon-R-C		*D. simulans v*	
	$\bar{x}$ (days)	$\sum n_i$	$\bar{x}$ (days)	$\sum n_i$
1	13·85	3586	19·74	8508
2	14·64	3792	18·34	4186
3	14·74	9225	17·26	4145
4	15·25	2992	19·10	5655
5	15·02	5136		
6	14·22	2074		
Mean ± S.E.	14·62 ± 0·22		18·61 ± 0·53	
Total		26,805		22,494

Analysis of variance

Source of variation	*D. melanogaster* Oregon-R-C		*D. simulans v*	
	D.F.	Mean square	D.F.	Mean square
Between means	5	908·34*	3	6163·00†
Within means	26,799	224·36	22,490	396·30

* $P < 0{\cdot}01$; † $P < 0{\cdot}001$.

https://doi.org/10.1017/S0016672300003232 Published online by Cambridge University Press

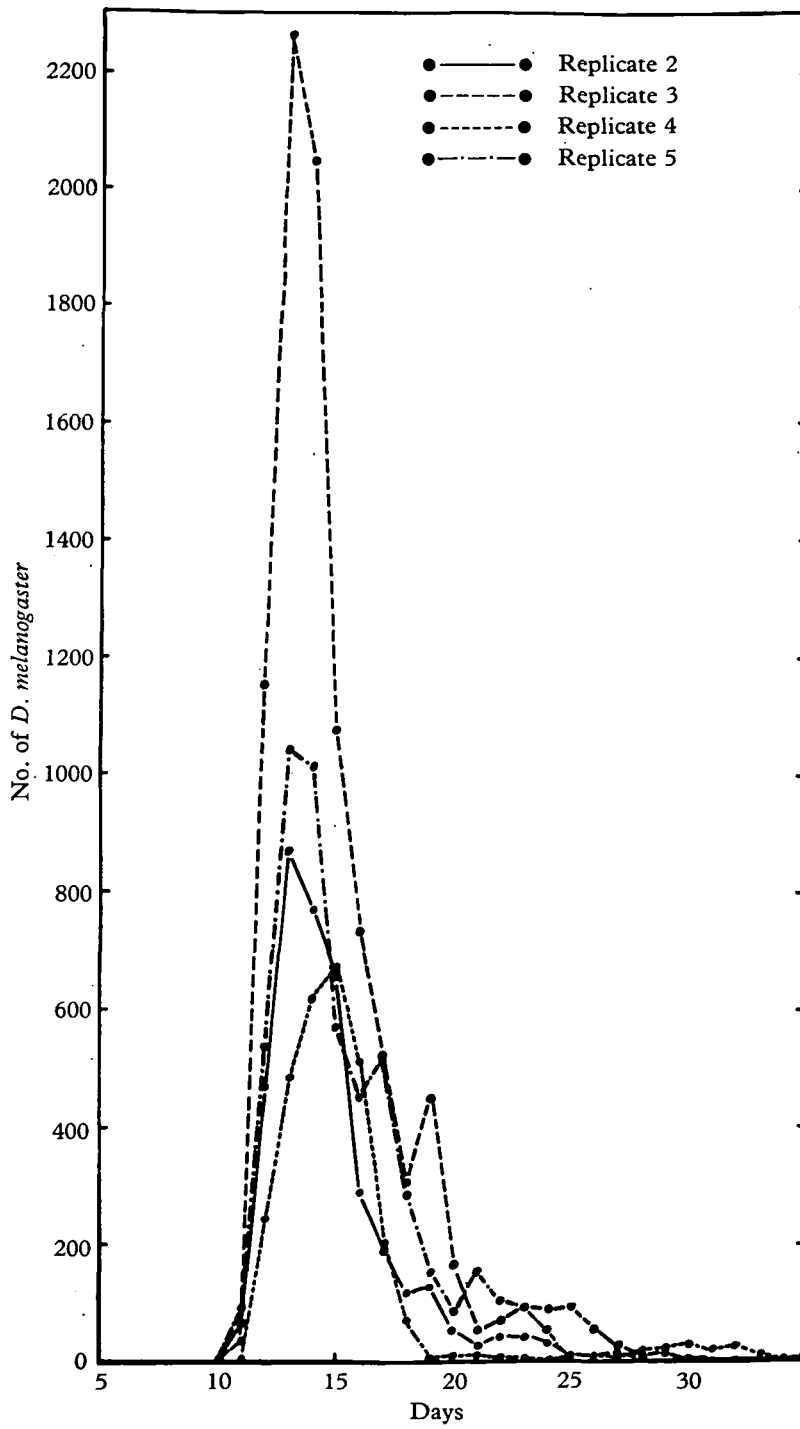

FIG. 3. Numbers of *D. melanogaster* emerging from the daily egg collections in Experiment 2, estimation of generation interval of *D. melanogaster* maintained in population bottles. Replicates 1 and 6 are omitted for clarity, as they largely overlap with replicates 2 and 4 respectively.

https://doi.org/10.1017/S0016672300003232 Published online by Cambridge University Press

are significantly different, although the between means variance is less than in Experiment 1. Although there were significant differences between the estimates in each experiment, their mean estimates do not differ significantly ($t_{10} = 0{\cdot}41$, $0{\cdot}7 > P > 0{\cdot}6$).

D. simulans v

The results are presented in Table 5 and Fig. 4. Peak egg production was reached in all replicates on Day 13 or 14. Beyond this point, there was considerable day to

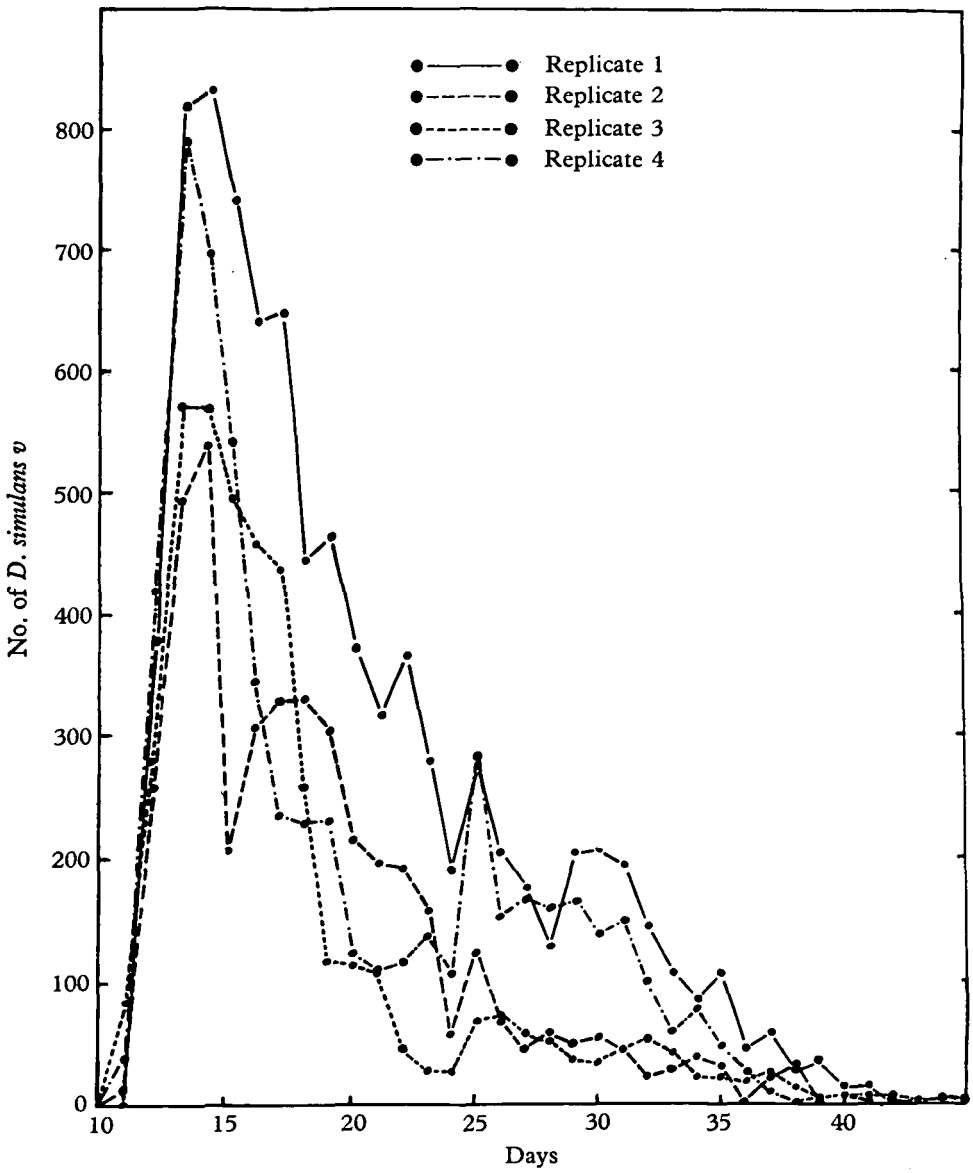

Fig. 4. Numbers of *D. simulans v* emerging from the daily egg collections in the estimation of generation interval of *D. simulans v* maintained in population bottles.

https://doi.org/10.1017/S0016672300003232 Published online by Cambridge University Press

day fluctuation, but egg production was maintained at a higher level for longer than in the *D. melanogaster* populations. Although the numbers of eggs produced by *D. melanogaster* in the first few days (up to and including peak production) were much higher than the numbers produced by *D. simulans*, the numbers of adults producing these eggs differed for the two species. The mean numbers of females collected into the transfer bottles by the day of peak egg production were 31 ± 7 for *D. melanogaster* and 21 ± 6 for *D. simulans*, considering only *D. melanogaster* Experiment 2, which populations were studied at the same time as the *D. simulans*. The mean numbers of eggs per female per day, up to and including peak egg production were $21{\cdot}9 \pm 3{\cdot}2$ for *D. melanogaster* and $23{\cdot}9 \pm 4{\cdot}1$ for *D. simulans*. On this rough estimation no differences in fecundity in the first few days of adult life are apparent.

Again, the replicate estimates are significantly different, but the mean is calculated as before. This mean generation interval of *D. simulans v* is about 4 days longer than that of *D. melanogaster* Oregon-R-C.

4. DISCUSSION

The estimation procedure presented here would seem to be a reasonable first approach, although there are some potential sources of error. The main assumption is that the competition provided by the other species is the same as intraspecific competition, as far as its effects on life cycle components are concerned. Considering the estimation for *D. melanogaster*, *D. simulans* certainly provides the high density conditions of the population cage or bottle, but it is not known to what extent these conditions are similar to those in a pure *D. melanogaster* population. Even within species, there is evidence that the viability and adaptive values of genotypes are dependent on what other genotypes are co-existing with them and on their frequencies (Levene, Pavlovsky & Dobzhansky, 1954, 1958; Lewontin, 1955; Spiess, 1957; Bonnier, Jonsson & Ramel, 1959; Parsons, 1959). As *D. simulans v* is rapidly eliminated from a population by *D. melanogaster* Oregon-R-C when the two are placed in competition (Claringbold & Barker, 1961), the competition provided by *D. simulans* is presumably of a lower order than that within a pure *D. melanogaster* population. Therefore, although the magnitude of the bias in the generation interval estimates is unknown, the effect probably would be an underestimate of the interval for *D. melanogaster* and an overestimate for *D. simulans*. In addition, underestimation will result if males tend to live longer than females and remain fertile.

In the population cage estimation, most of the *D. melanogaster* eggs in the initial sample would have been laid in the freshest medium jar, which was placed into the cage at the beginning of the egg sampling period and consequently had no *D. simulans* eggs on it. The rate of development of the zygotes hatching from these eggs may have been faster than that of equivalent first laid eggs in a population comprising *D. melanogaster* only. Basing the expectation of offspring on the percentage of *D. melanogaster* adults emerging from each 24-hour egg sample involves the assumptions that the propensity for egg-laying of the *D. simulans* population is constant,

and that the hatchability and survival of immature stages of *D. melanogaster* are not affected by the relative proportions of the two species. The total number of *D. simulans* flies in the cage will certainly not be constant. Variation in the size of this population may be the inverse of variation in that of *D. melanogaster*, because the *D. melanogaster* emerging from the initial egg sample are effectively replacing a portion of the *D. simulans* population. Although this would change the shape of the percentage *D. melanogaster* distribution, increasing the height of the peak, there appears to be no reason to expect that it will result in any change in the mean. It has been pointed out that the viability of a genotype depends on what other genotypes are co-existing with it and on their frequencies. If the survival of *D. melanogaster* is different when competing with *D. simulans* than when alone, this will affect the estimate of the percentage of *D. melanogaster* eggs in each 24-hour egg sample, but will introduce a bias only if there is a frequency-dependent effect. Unfortunately, there are no data on this, but any effect may be small as the flies of the 24-hour samples were reared under relatively uncrowded conditions on dead yeast fortified medium.

Similarly for the population bottle estimation, there are a number of potential sources of error. The major criticism is that the fecundity table of the adults emerging from the initial egg sample is not obtained under population bottle conditions, but under the more optimal conditions of daily transfer to fresh medium. This could affect two components of the generation interval, fecundity and longevity, possibly increasing both and consequently increasing the estimated generation interval. Robertson & Sang (1944) found, when comparing fecundity under more optimal conditions with population conditions, that (i) females reach peak fecundity at about the same time (the 3rd and 4th days after emergence), (ii) they maintain egg production for a longer time, and (iii) the mean number of eggs laid per day is increased. The second would result in an overestimate of the generation interval, while the last may increase the number of eggs laid each day without affecting the mean of the distribution. Any increase in longevity caused by the daily transfer to fresh medium is unlikely to affect greatly the *D. melanogaster* estimates. Figures 2 and 3 show that the numbers of eggs produced beyond Day 25 are very low, so that these eggs will be contributing relatively little information to the estimate. If they were, in fact, eggs that would not be laid under population bottle conditions, the generation interval would be overestimated, but the bias would be small.

In the *D. simulans* estimation, the daily transfer to fresh medium is likely to cause greater bias as *D. simulans* maintained egg production at a higher level for longer than did *D. melanogaster*. Under population bottle conditions, a fresh medium bottle is attached on Day 14, and probably only those eggs laid in the few days following this have any change of giving rise to adults of the next generation. Thus the generation interval of *D. simulans v* is certainly overestimated. However, when the next medium bottle is attached (Day 28), it would be expected from Fig. 4 that some of these *D. simulans v* will still be present in the population (along with their progeny), and that they will produce eggs. In other words, there will be generation overlap and the generation interval will be less than 18 days but probably

greater than 15 days. A more accurate estimate of the generation interval of *D. simulans v* might be obtained by daily transfer to a *D. melanogaster* population. The technique would be exactly the same, except that the fecundity table would be obtained under population conditions. However, this would involve daily anaesthetization of the flies and, as pointed out below, this might have a deleterious effect on their longevity. Thus, one source of error would be removed, but another introduced. As it would involve a large number of populations for daily transfer, it was not felt to be justified at this stage.

Some information on the degree of generation overlap in the population bottles was obtained during the collection of the flies emerging from the initial egg samples. Each day when the population was etherized and the flies from the initial egg sample collected, the numbers of flies of the other species present were counted (Table 6). For *D. melanogaster*, the numbers reach a minimum on Day 11 or 12, and then increase as the next generation starts to emerge. There is not likely to be any generation overlap as those few individuals present on Day 11 or 12 will almost certainly die before the next medium bottle is added on Day 14. The *D. simulans* populations (except for No. 6) also reach a minimum on Day 11 or 12, but these minimum numbers generally are much higher than those for *D. melanogaster*. Some of them could conceivably survive to enter the breeding population of the next generation, thus giving rise to some degree of generation overlap. Although the numbers of *D. simulans v* increase after Day 11 or 12, they do not increase as do the *D. melanogaster* and tend to fluctuate somewhat from day to day. This could be an artifact resulting from some adverse effect of the daily etherization. *D. simulans v* succumb to etherization far more rapidly than do *D. melanogaster*, so that to etherize the *D. melanogaster* emerging in these populations, the *D. simulans v* would receive more than is necessary merely to anaesthetize them. Repeated etherization then may reduce their longevity.

A further source of error in the population bottle estimates results from the counting of the numbers of adults emerging from each 24-hour sample as estimates of the numbers of eggs laid. Survival of immature stages is known to be dependent on their density (e.g. Lewontin, 1955), and as the numbers of adults emerging from these samples varied between 1 and over 2000, some error will be introduced. This could be overcome by counting the numbers of eggs laid each day.

There are, therefore, a number of potential sources of error in the estimated generation intervals. Nevertheless, this is a useful first approach to an experimental estimation under population conditions and the generation intervals estimated at 25° C. may be taken operationally as:

D. melanogaster (Oregon-R-C), population cages: 23 days
D. melanogaster (Oregon-R-C), population bottles: 14 days
D. simulans v: population bottles: 16 to 18 days

5. SUMMARY

A method for the experimental estimation of generation interval is presented together with results obtained at 25° C. for *D. melanogaster* Oregon-R-C maintained

Table 6. *Numbers of flies counted each day in the population bottles used in estimating the generation interval of* D. melanogaster (*Experiment 2*) *and* D. simulans v

Species	Population bottle no.	Days from Time zero (initial egg sampling) 8	9	10	11	12	13	14	15	16	17	18
D. melanogaster	1	—	440	263	152	6	51	187	296	314	327	334
	2	493	424	311	6	4	49	192	241	240	318	329
	3	—	20	9	3	39	169	276	302	311	302	—
	4	605	186	5	2	19	123	213	221	222	212	—
	5	—	492	7	7	5	66	255	374	—	—	—
	6	—	23	3	1	13	111	315	468	—	—	—
D. simulans v	1	128	101	74	47	43	65	67	48	41	45	44
	2	135	118	71	21	36	81	73	32	23	25	22
	3	152	138	115	78	136	173	155	53	40	38	40
	4	144	139	127	115	68	90	101	98	94	96	94
	5*	83	69	41	8	14	26	44	39	32	39	32
	6*	211	197	171	171	131	79	66	53	39	40	40

* These populations were discarded from the experiment as noted under Population Bottle Experiments—Method of estimation.

in population cages and in population bottles, and for *D. simulans v* in population bottles. Although there is significant variation between the replicate estimates obtained in population bottles, and although a number of potential sources of error have been discussed, it is suggested that this method provides useful operational estimates of the parameter, which may be taken as 23 days for *D. melanogaster* Oregon-R-C in population cages, 14 days for the same stock in population bottles, and 16 to 18 days for *D. simulans v* in population bottles.

Acknowledgement is due to Dr J. M. Rendel, Division of Animal Genetics, C.S.I.R.O., for his provision of laboratory facilities for carrying out some of the experiments, and for his many helpful discussions. The statistical advice of Dr P. J. Claringbold is greatly appreciated. I am indebted to Robin Johnston, Dorothy Allingham, and Gillian Davey for technical assistance at various stages in these experiments. The following undergraduate students assisted in the maintenance and scoring of the population bottle experiments: Judith Massasso, R. A. McIntosh, J. H. Medcalf, A. R. Rumsey, W. R. Scowcroft and T. T. The. The study was supported by a University of Sydney Research Grant.

REFERENCES

Barker, J. S. F. (1960*a*). Yet another population cage. *Drosophila Inform. Serv.* **34**, 113.

Barker, J. S. F. (1960*b*). An adaptation of the population bottle of Reed and Reed (1948). *Drosophila Inform. Serv.* **34**, 113–114.

Birch, L. C. (1948). The intrinsic rate of natural increase of an insect population. *J. Anim. Ecol.* **17**, 15–26.

Birch, L. C. (1955). Selection in *Drosophila pseudoobscura* in relation to crowding. *Evolution*, **9**, 389–399.

Bonnier, G., Jonsson, U. B. & Ramel, C. (1959). Experiments on the effects of homozygosity and heterozygosity on the rate of development in *Drosophila melanogaster*. *Genetics*, **44**, 679–704.

Buzzati-Traverso, A. A. (1955). Evolutionary changes in components of fitness and other polygenic traits in *Drosophila melanogaster* populations. *Heredity*, **9**, 153–186.

Carson, H. L. (1958). Increase in fitness in experimental populations resulting from heterosis. *Proc. nat. Acad. Sci., Wash.*, **44**, 1136–1141.

Chiang, H. C. & Hodson, A. C. (1950). An analytical study of population growth in *Drosophila melanogaster*. *Ecol. Monogr.* **20**, 179–206.

Claringbold, P. J. & Barker, J. S. F. (1961). The estimation of relative fitness of *Drosophila* populations. *J. Theoret. Biol.* **1**, 190–203.

Erk, F. C. (1955). Competition between chromosomal aberrations associated with Curly and their wild type homologues in laboratory populations of *Drosophila melangoaster*. *Genetics*, **40**, 331–342.

Hochman, B. (1958). Competition between wild type isoalleles in experimental populations of *Drosophila melanogaster*. *Genetics*, **43**, 101–121.

Levene, H., Pavlovsky, O. & Dobzhansky, Th. (1954). Interaction of the adaptive values in polymorphic experimental populations of *Drosophila pseudoobscura*. *Evolution*, **8**, 335–349.

Levene, H., Pavlovsky, O. & Dobzhansky, Th. (1958). Dependence of the adaptive values of certain genotypes in *Drosophila pseudoobscura* on the composition of the gene pool. *Evolution*, **12**, 18–23.

Lewontin, R. C. (1955). The effects of population density and composition on viability in *Drosophila melanogaster*. *Evolution*, **9**, 27–41.

Ludwin, I. (1951). Nautral selection in *Drosophila melanogaster* under laboratory conditions. *Evolution*, **5**, 231–242.

Merrell, D. J. (1953). Selective mating as a cause of gene frequency changes in laboratory populations of *Drosophila melanogaster*. *Evolution*, **7**, 287–296.

MOREE, R. (1955). The question of generation length in population models of *Drosophila melanogaster*. *Drosophila Inform. Serv.* **29,** 142–143.

PARSONS, P. A. (1959). Dependence of genotypic viabilities on co-existing genotypes in *Drosophila*. *Heredity*, **13,** 393–402.

PROUT, T. (1954). Genetic drift in irradiated experimental populations of *Drosophila melanogaster*. *Genetics*, **39,** 529–545.

REED, S. C. & REED, E. W. (1950). Natural selection in laboratory populations of *Drosophila*. II. Competition between a white-eye gene and its wild type allele. *Evolution*, **4,** 34–42.

ROBERTSON, F. W. & SANG, J. H. (1944). The ecological determinants of population growth in a *Drosophila* culture. I. Fecundity of adult flies. *Proc. roy. Soc.* B, **132,** 258–277.

SANG, J. H. (1949*a*). The ecological determinants of population growth in a *Drosophila* culture. III. Larval and pupal survival. *Physiol. Zoöl.* **22,** 183–202.

SANG, J. H. (1949*b*). The ecological determinants of population growth in a *Drosophila* culture. IV. The significance of successive batches of larvae. *Physiol. Zoöl.* **22,** 202–210.

SANG, J. H. (1949*c*). The ecological determinants of population growth in a *Drosophila* culture. V. The adult population count. *Physiol. Zoöl.* **22,** 210–223.

SPIESS, E. B. (1957). Relation between frequencies and adaptive values of chromosomal arrangements in *Drosophila persimilis*. *Evolution*, **11,** 84–93.

SUSMAN, M. & CARSON, H. L. (1958). Development of balanced polymorphism in laboratory populations of *Drosophila melanogaster*. *Amer. Nat.* **92,** 359–364.

WALLACE, B. (1950). Autosomal lethals in experimental populations of *Drosophila melanogaster*. *Evolution*, **4,** 172–174.

WRIGHT, S. & DOBZHANSKY, TH. (1946). Genetics of natural populations. XII. Experimental reproduction of some of the changes caused by natural selection in certain populations of *Drosophila pseudoobscura*. *Genetics*, **31,** 125–156.