RELATIVE FITNESS OF GEOGRAPHIC RACES OF *DROSOPHILA SERRATA*

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The purpose of this study is to measure differences in ecological characteristics of populations of a species of *Drosophila* from widely separated geographic regions. The species selected, *Drosophila serrata* Malloch, belongs to the *melanogaster* group of the subgenus *Sophophora*. Its known geographic distribution extends along the eastern coast of Australia from just north of Sydney to Queensland, and then to New Guinea and New Britain. The southernmost populations inhabit a temperate climate; the northern populations live in the tropics.

As a measure of relative fitness we use the statistic known variously as the "intrinsic rate of natural increase" (Lotka, 1925), the "Malthusian parameter" (Fisher, 1930), and the "innate capacity for increase" (Andrewartha and Birch, 1954). This statistic is designated r_m, to distinguish it from r, the actual rate of increase of a population at any specified time. The statistic r_m is the estimated geometric rate of increase in numbers at optimal density when all other components of environment are defined. That is to say, temperature and moisture are kept constant and the quality and quantity of food is controlled. It is calculated from two sets of experimental data, the age-specific birth rates, and the age schedule of deaths. It has been used in the past in comparing the capacities of different species to increase in numbers (Andrewartha and Birch, 1954). Bateman (1958, unpublished, see Andrewartha and Birch, 1960) used it to compare geographically separated populations of the tephretid fruit fly *Dacus tryoni*.

Capacity to increase in numbers at optimal density is only one aspect of the fitness or adaptedness of a species to its environment. However, it is our conviction that the difficult and complex concept of fitness must be studied analytically, and this is one component of the analysis. Even though it may prove difficult to relate the findings of such a study to what happens in nature, the measurement of r_m can serve as a means of measuring precisely the ecological differences between populations which may not be recognizable by other means. One objective of these experiments was to devise a way of measuring the innate capacity for increase of *Drosophila* with an accuracy such that small differences between populations could be reliably measured. There are numerous well-known means of identifying genetic differences between populations within species of *Drosophila*. Methods of measuring ecological differences with reliability are less well established.

We chose a species which has a wide geographic range, extending along some 3,000 miles of coastline from south to north and through a variety of climatic zones. Within such a distribution we would expect to find ecological differences between populations living far apart. Early in the study two morphologically distinguishable subspecies were recognized (Dobzhansky and Mather, 1961). These were designated *D. serrata serrata*, distributed from just north of Sydney in New South Wales to Proserpine in northern Queensland, and *D. serrata birchii*, distributed from Cairns in northern Queensland (300 miles north of Proserpine) to Rabaul in New Britain.

Procedure

Source of flies.—Adult flies were collected over banana bait from five local-

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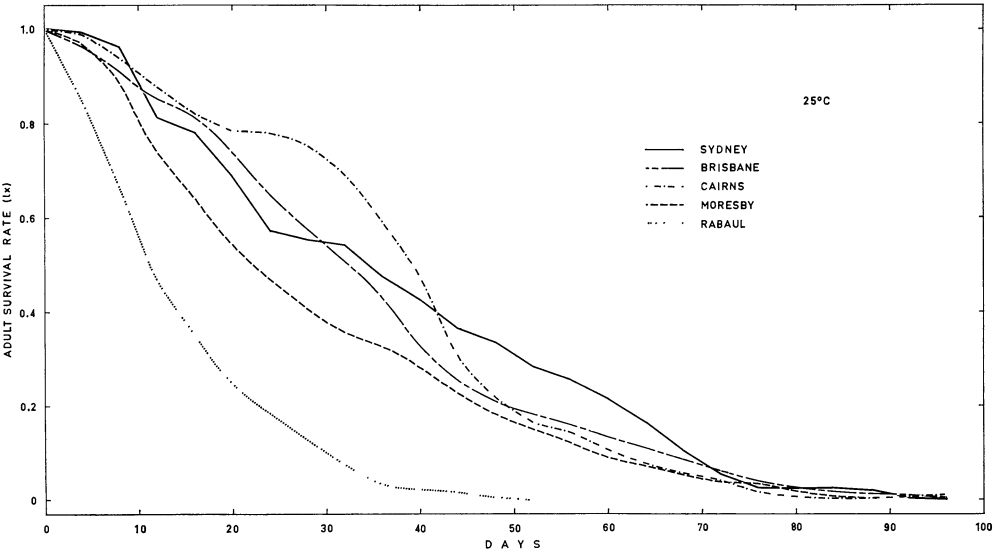

FIG. 1. The adult life tables (survival rate) of five geographic races of *D. serrata* at 25° C.

ities. The population collected from the southernmost known part of the distribution is called Sydney, though the collections were made some 130 miles north of Sydney at Bulahdelah. Proceeding some 500 miles north of Sydney, the next population was collected at Brisbane. One thousand miles north of Brisbane a population was collected at Cairns. The remaining two populations were collected across Torres Strait at Port Moresby in New Guinea and at Rabaul in New Britain. Collections from the three southernmost populations were made in March, 1960. Those from New Guinea and New Britain were made in May, 1960. Ten "strains" were established in the laboratory from each region from ten groups of flies which were kept separate from the time they were collected; they were kept as stock cultures at 25° C on standard *Drosophila* medium. By this means we hoped to maintain the natural variability and minimize the effects of selection in the laboratory. The flies used in all experiments were the first or second generation of crosses between these ten strains for a region. Experiments were done at 20° C and 25° C.

Survival and duration of development of immature stages.—The time for development from the egg to the adult must be known. The per cent survival of immature stages from egg to emergence of the adult must also be known. These two components of the innate capacity for increase turned out to be the most difficult of all components to measure accurately. Kalmus medium with live yeast on the surface gave very erratic results. Occasionally, survival rate was high on Kalmus medium but more often than not, survival was low. Varying the quantity of water in the medium did not help. Regular *Drosophila* medium with dead yeast instead of live yeast was worse still. After a great deal of trial and error, the procedure finally adopted was a modification of Stalker and Carson's (1959) method of measuring survival of larvae of *Drosophila robusta*. Stalker and Carson reared larvae on Kleenex tissue soaked in a suspension of live yeast. We found this quite unsatisfactory until we added sucrose to the yeast suspension. Without sucrose the yeast autolyzed, releasing ammonia which killed the flies in the pupal stage. With sucrose in the suspension this did not happen. The de-

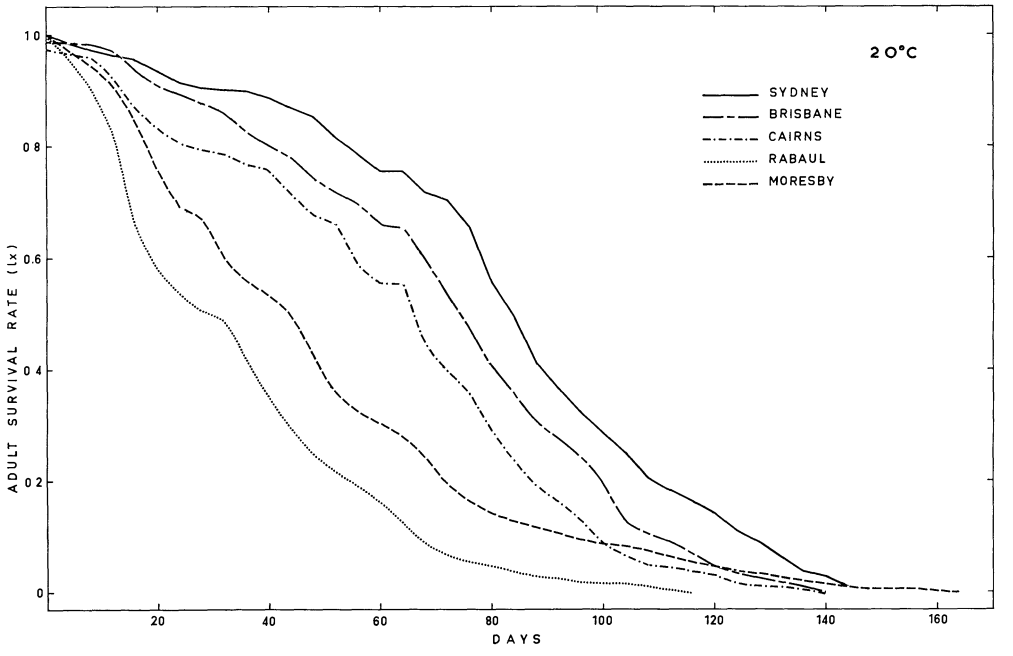

FIG. 2. The adult life tables (survival rate) of five geographic races of *D. serrata* at 20° C.

tails of the method were as follows: eggs were collected from adults of mixed ages by placing spoons with yeasted Kalmus medium in with them for 15 hours at 25° C. The eggs were then counted into groups of ten which were cut out as separate small blocks of medium. Each block with ten eggs was placed in a ¼-pint milk bottle on a piece of crumpled Kleenex tissue which had been saturated with 10 ml of yeast in sucrose solution. The solution was made with 50 g of yeast, 8 g of sucrose in 100 ml of water. Both bottles and Kleenex and cotton plugs were dry-sterilized beforehand. Only ten eggs were put into each bottle. It would have been impracticable to use fewer than ten eggs per bottle. We did not use more than ten, as preliminary experiments with Kalmus medium and regular *Drosophila* medium had indicated that mortality was higher when the number of eggs per bottle was 20. Experiments were replicated 20 times, half the replicates of all five races being done at one time and the other half at another time. The number of eggs hatched was recorded at 12-hour intervals.

Adult survival.—Newly emerged adults from 0–24 hours old at 25° C were put into ¼-pint milk bottles containing Kalmus medium (Kalmus, 1943) on the surface of which a few drops of dense suspension of yeast had been smeared. This provided ample food. A piece of Kleenex tissue was pressed into the medium. Twenty pairs of flies were put into each bottle. The number of dead males and females was recorded each day at 25° C and every alternate day at 20° C. At the same time the flies were transferred to new bottles with fresh Kalmus medium and yeast. Each experiment was replicated 20 times.

Birth rate or fecundity.—It is not practicable to measure fecundity and adult survival in the same flies. For adult survival ten times as many flies are needed as are required for measuring fecundity. The measurement of fecundity in so many flies would be impracticable and unnecessary.

The age schedule of egg laying was obtained as follows. Flies from 0 to 24 hours

TABLE 1. *Per cent survival of immature stages (egg to emergence of adult) at 25° C and 20° C*[1]

Race	25° C		20° C	
	Mean	C.V.	Mean	C.V.
Sydney (S)	62	15	66	13
Brisbane (S)	64	14	70	11
Cairns (B)	57	13	53	16
Port Moresby (B)	61	20	64	17
Rabaul (B)	64	13	61	7

[1] C.V. = per cent coefficient of variability; S = *Drosophila serrata serrata*; B = *D. serrata birchii.*

old were collected as they emerged from regular *Drosophila* media. Four pairs of adults were kept in a ¼-pint milk bottle which had in it a spoon filled with Kalmus medium (Kalmus, 1943) mixed with charcoal to make the eggs readily visible. Preliminary experiments had indicated that this was an optimum density for egg laying. The surface of the medium was smeared with a concentrated suspension of Fleischmann's yeast. Each day the spoon was removed, the eggs on it were counted, and a new spoon was put back in the bottle. The experiment was replicated 20 times for each of the five localities.

RESULTS

Survival of immature stages.—The per cent survival from egg to emergence of the adult at 25° C and 20° C is shown in table 1. Analysis of variance of the data transformed to arcsin $\sqrt{\text{per cent survival}}$ showed that neither temperature nor race was significant ($P = 0.01$). A Scheffe test of comparisons between pairs of means showed that the only significantly different pair were Cairns and Brisbane races at 20° C ($P = 0.05$).

Most of the mortality of the immature stages occurred in the larvae and pupae; less than 10% of the eggs died.

Duration of development of immature stages.—The duration of development from egg to emergence of the adult at 25° C and 20° C is shown in table 2. Analysis of variance showed that neither temperature nor race was significant.

Survival of adults.—Life tables of female adults at 25° C and 20° C are shown in figs. 1 and 2. The mean lengths of life of females and males are given in table 3. An analysis of variance on length of life showed that temperature and race and sex significantly influenced the length of life ($P = 0.01$). There was no interaction between race and temperature. A Scheffe test was made on these results to find out which comparisons were significantly different. The results of this test are summarized below, table 3.

Fecundity.—The total number of eggs laid per female per four-day period during the life-span at 25° C and 20° C is shown in figs. 3 and 4. The total eggs laid per female in the life-span is shown in table 4.

From the point of view of the influence of fecundity on the innate capacity for increase, eggs laid early in life make a very much greater contribution to r_m than eggs laid later. The rising parts of the curves in figs. 3 and 4, and the maxima reached are therefore the most relevant parts of the curves to consider in comparing the five races. The comparisons of races are shown in figs. 3 and 4. The comparison between temperatures (for two arbitrarily selected races only) is shown in figs. 5 and 6.

Total fecundity is shown in table 4. These are useful figures for comparing races, although they do not enter as such into the calculation of r_m. An analysis of variance of this data showed that both temperature and race had a significant effect ($P = 0.01$). There was no significant interaction between race and temperature.

TABLE 2. *Duration of development in days from egg to emergence of adult at 25° C and 20° C*[1]

Race	25° C		20° C	
	Mean	C.V.	Mean	C.V.
Sydney (S)	11.8	3.2	16.4	1.6
Brisbane (S)	11.6	1.7	16.0	1.4
Cairns (B)	11.7	0.9	16.1	0.9
Port Moresby (B)	11.5	2.8	16.4	2.4
Rabaul (B)	11.7	1.8	16.0	2.6

[1] C.V. = per cent coefficient of variability; S = *Drosophila serrata serrata*; B = *D. serrata birchii.*

TABLE 3. *Mean length of adult life in weeks at 25° C and 20° C*[1]

Race	25° C				20° C			
	Female		Male		Female		Male	
	Mean	C.V.	Mean	C.V.	Mean	C.V.	Mean	C.V.
Sydney (S)	27.1	17.7	14.8	22.9	50.1	8.7	41.3	16.4
Brisbane (S)	25.5	18.0	16.4	17.8	44.6	10.6	39.4	11.5
Cairns (B)	25.4	12.3	18.0	14.9	42.3	10.0	33.9	9.9
Port Moresby (B)	23.2	22.3	16.0	21.2	35.2	6.5	21.5	31.2
Rabaul (B)	12.5	23.8	9.9	27.3	27.9	30.4	17.9	61.1

Comparisons between races. Comparisons at 25° C are above the diagonal. Comparisons at 20° C are below the diagonal. n = not significant; 0.05, 0.01 = significant at P = *0.05, 0.01*

20° C	Sydney	Brisbane	Cairns	Port Moresby	Rabaul	25° C
Sydney		n	n	n	.01	Female
		n	n	n	n	Male
Brisbane	n		n	n	.01	Female
	.01		n	n	n	Male
Cairns	.05	n		n	.01	Female
	.01	.01		n	.01	Male
Port Moresby	.01	.01	n		.01	Female
	.01	.01	.01		n	Male
Rabaul	.01	.01	.01	.05		Female
	.01	.01	.01	.01		Male

[1] C.V. = per cent coefficient of variability; S = *Drosophila serrata serrata*; B = *D. serrata birchii.*

A Scheffe test was made on these results to find out which comparisons of means were significantly different. The results of this test are summarized in table 4. The sequence in total fecundity from lowest to highest (at both temperatures) was Rabaul, Port Moresby, Cairns, Sydney, Brisbane.

The innate capacity for increase r_m.— The innate capacity for increase r_m is the rate of increase of a population which has a constant age schedule of births and deaths, and which is increasing in numbers in unlimited space. It is given by:

$$\frac{\delta N}{\delta T} = r_m N \qquad (1)$$

Lotka (1925) showed mathematically that the distribution of ages in a population in which death rates and birth rates remained constant for each age group, and which increased in unlimited space, would approach a certain age distribution known as the "stable age distribution." As the name implies, this age distribution does not change with time. So the innate capacity for increase r_m could be defined as the rate of increase of a population with a stable age distribution. The rate of increase of a population with any other sort of age distribution changes with time as will the age distribution itself. So in comparing capacities for increase there is great merit in comparing the rates of increase of populations of stable age distribution. Lotka showed, moreover, that for such a population the innate capacity for increase, r_m and the schedules of mortality and fecundity will be connected by the expression:

$$\int_0^\infty e^{-rx} m_x l_x \delta_x = 1 \qquad (2)$$

where 0 to ∞ is the life-span, l_x is the probability at birth of being alive at age x, and m_x is the number of female offspring produced in unit time by a female aged x (i.e., half the total eggs laid in unit time).

We may make use of expression (2) to estimate r_m by replacing the integration with a summation over discrete time inter-

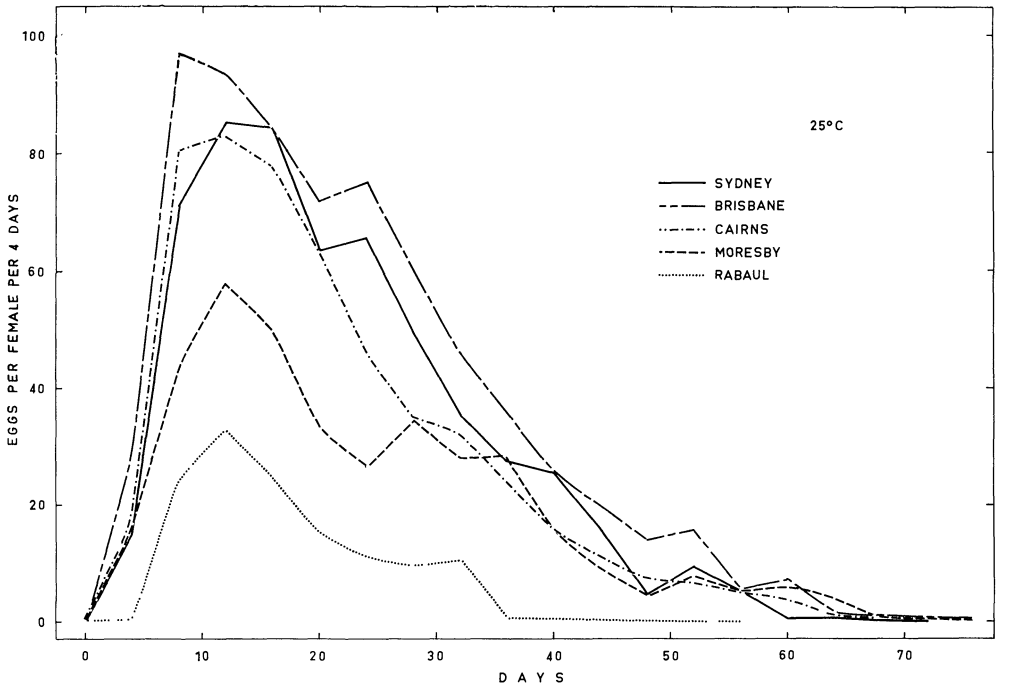

FIG. 3. Eggs laid per female per four-day period during her lifetime at 25° C for five geographic races of *D. serrata*.

vals. Thus we estimate r_m from the expression:

$$\sum_{0}^{t} e^{-r_m} x\, l_x\, m_x = 1 \qquad (3)$$

where 0 to t is the observed maximum lifespan of our experimental animals, and l_x and m_x are the observed probability of survival to age x and fecundity at ages x, respectively. Details of the procedure for estimating r_m from this expression are given by Birch (1948) and Andrewartha and Birch (1954).

The estimation of r_m.—Ideally, when r_m is estimated from formula (2), the schedules of age-specific mortality and fecundity (l_x and m_x schedules) should be measured on the same animals. This is because there is bound to be some real biological correlation between l_x and m_x. That is, a "vigorous" animal could be expected to have both great longevity and high fecundity, while a "weak" one might be poor in both respects. Unfortunately it is not practicable to determine both mortality and fecundity schedules from the same individuals because of the radically different sample sizes needed to make reasonable estimates of these two components. Ten times as many flies were used to determine the life tables as for the fecundity tables. It would have been impossible to determine fecundity schedules for all the females in these survival experiments, especially when it is borne in mind that mortality was determined from batches of ten females and ten males. Each of those females would have to be kept in a separate vial to determine its individual fecundity and mortality schedule. Since fecundity was measured on batches of four females, the amount of work involved in scoring individual fecundity and mortality schedules would have been 25 times as great as was actually done.

The measurement of age-specific mor-

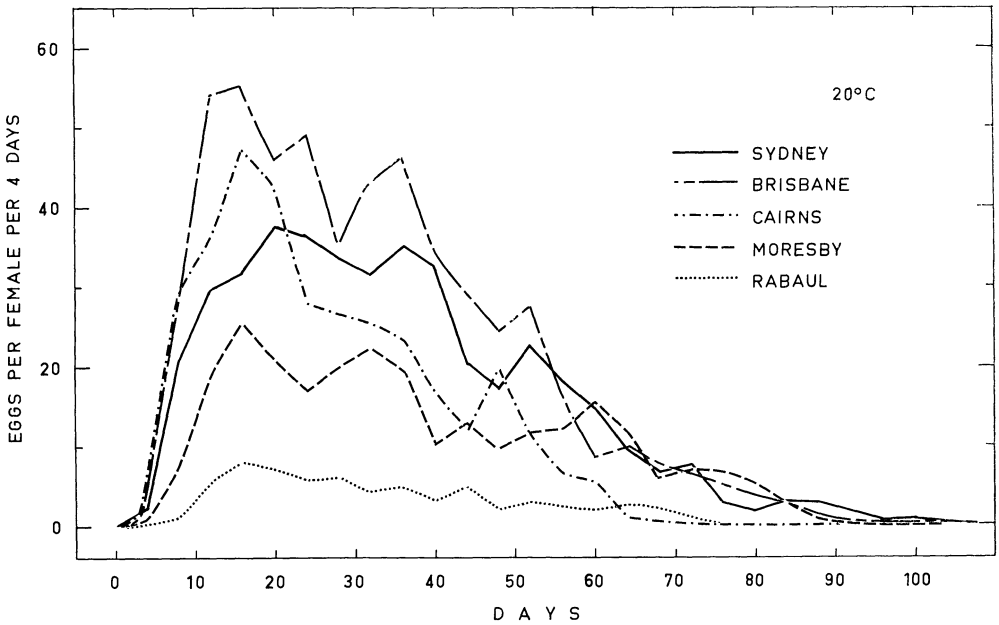

FIG. 4. Eggs laid per female per four-day period during her lifetime at 20° C for five geographic races of *D. serrata*.

tality and fecundity (and larval survival) on different batches of animals results in certain statistical difficulties. How are the replicated observations to be combined for estimation of r_m? It must be noted that *no method of combination will make up for the loss of information concerning correlation between* l_m *and* m_x. This loss of information is inherent in the way the observations were made.

There are two possibilities for estimating r_m. One is to take the mean larval mortality, the mean fecundity schedule, and the mean adult life table schedule over all replicates and get a single estimate of r_m, which we will designate as $\hat{r}_m$. These values are given in table 5 in parentheses. This method raises the problem of an estimate of the variance of such a statistic. It is possible to derive a large sample approximation to this variance in terms of the variances of the l_x and m_x schedules. This estimate of variance suffers from two disabilities. First, the covariances within fecundity and mortality tables also enter into the expression, and second, we really have no idea how such a large sample approximation will behave in the rather small samples (20 replicates) with which we are dealing. For these reasons we abandoned this approach.

A second method, one that has been used before in such situations (Bateman, unpublished), is to associate *at random* l_x and m_x tables. For example, if there are 10 replicated l_x tables and 10 replicated m_x tables, these can be paired arbitrarily to produce 10 replicated estimates of r_m. The advantage of such a procedure is that an empirical estimate of the variance of the estimate is provided. It suffers from the disability that no account is taken of the correlation between fecundity and mortality schedules. As we have already pointed out, however, since these correlations cannot be estimated in our experiment there is nothing that can be done about this problem.

We have used an extension of Bateman's approach. Rather than choosing ten pairs at random, we have made *all possible combinations* of the replicated life tables,

TABLE 4. *The total number of eggs laid per female at 25° C and 20° C*[1]

Race	25° C		20° C	
	Mean	C.V.	Mean	C.V.
Sydney (S)	559	37	428	72
Brisbane (S)	670	31	546	35
Cairns (B)	498	41	373	33
Port Moresby (B)	368	87	270	54
Rabaul (B)	151	73	69	158

Comparisons between races. Comparisons at 25° C are above the diagonal. Comparisons at 20° C are below the diagonal. n = not significant; 0.05, 0.01 = significant at P = *0.05, 0.01*

		Sydney	Brisb.	Cairns	Port M.	Rabaul	
	Sydney		n	n	n	.01	
	Brisb.	n		n	.05	.01	
20° C	Cairns	n	n		n	.01	25° C
	Port M.	n	n	n		n	
	Rabaul	.01	.01	.05	n		

[1] C.V. = per cent coefficient of variability; S = *Drosophila serrata serrata*; B = *D. serrata birchii*.

fecundity tables, and larval mortalities. To reduce the amount of computing somewhat, the 20 replicates of life tables and fecundity tables were reduced to ten each by random lumping. The result is 200 estimates of r_m for each geographical population at each temperature. The mean of these 200 estimates which we denote by $\hat{r}_m$ is given in table 5 for each population, along with the variance of the 200 estimates. A total of two thousand calculations of r_m was made using the electronic computor "Silliac."

The ten adult life table schedules are a random sample from the real distribution of such schedules, and the same is true for the ten fecundity schedules and the two values of larval mortalities. Then, if there were no correlation between these three components, the distribution produced by taking all possible combinations of the components would be a random sample from their true joint distribution. It would follow in turn that the values of $\hat{r}_m$ calculated from each combination would be a random sample from the true distribution of r_m. Since the mortality and fecundity schedules are almost certainly correlated in nature, however, the distribution of $\hat{r}_m$ we obtain differs from a random sample of the true distribution. In particular, the variance we get is certainly an *underestimate* of the true variance. This is because the positive correlation between l_x and m_x will result in more very small and very large values of $\hat{r}_m$ than we obtain by assuming l_x and m_x to be independent.

It is interesting that the values of $\mathring{\hat{r}}_m$ given in table 5 are consistently higher than the corresponding values of $\hat{r}_m$. Again, ignoring the question of correlation between l_x and m_x, since both $\hat{r}_m$ and $\mathring{\hat{r}}_m$ fail to take account of it, our estimate $\hat{r}_m$ should be the unbiased one. That is, a mean of estimates will be unbiased as compared with a single estimate based on means. An analogous case is the well-known fact that the reciprocal of a mean has a different expectation from the mean of reciprocals. Probably both $\hat{r}_m$ and $\mathring{\hat{r}}_m$ are biased estimates of the true r_m, since the positive correlation between l_x and m_x will be reflected in the mean as well as variance of a nonlinear function.

What are the number of degrees of freedom to be associated with our variance estimate? Although 200 values are calculated, these are not independent, the same data being used over and over again. In fact, there are 19 degrees of freedom corresponding to nine for the fecundity schedules, nine for the adult mortality schedules, and one for the larval mortality values. Our procedure is analogous to a three factor analysis of variance in which the three factors, adult mortality, fecundity, and larval mortality have respectively 10, 10, and 2 random levels. The values of $\hat{r}_m$ for different populations have been compared by a series of t-tests using 19 degrees of freedom. The results of the t-tests are shown in the bottom half of table 5. Our aim of reasonably low variability in the estimate of the innate capacity for increase was realized with the one exception of the Rabaul race, which

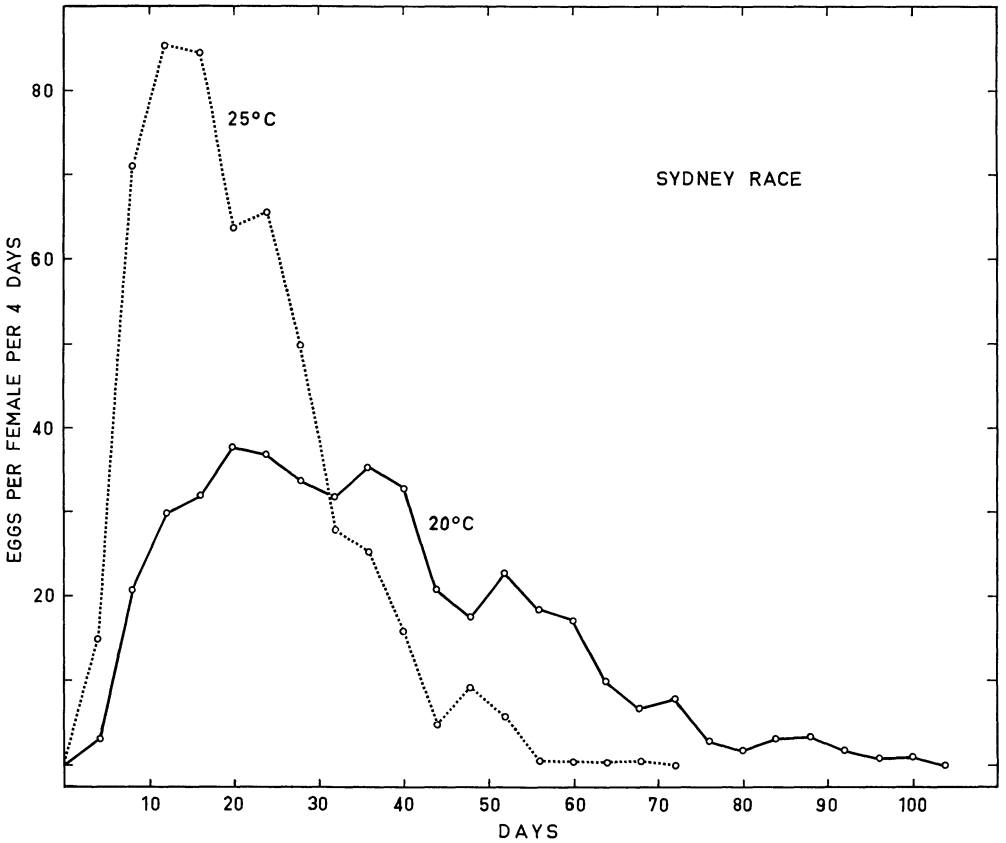

FIG. 5. Comparison of eggs laid per female per four-day period at 25° C and 20° C for the Sydney race of *D. serrata serrata*.

also had the lowest rate of increase. This race was very difficult to culture in the laboratory. Its high variability is a reflection of this.

Temperature had a significant effect on r_m for all races except Rabaul ($P = 0.01$). Rabaul was different from all other races at both temperatures. We made an analysis of variance on the data of table 5 (excluding the Rabaul race). They showed no significant effect on r_m (when Rabaul is excluded).

Since infinitesimal rates are not easy to visualize, the finite rates of increase are shown in table 6 and fig. 7. The finite rate of increase is obtained by a simple transformation of the figures in table 5. It is expressed as the multiplication of females per day (λ), and is given by $\lambda = \text{antilog}_e r_m$ (see Andrewartha and Birch, 1954). Small differences in λ can of course produce large differences in numbers in short periods of time. To get an idea of these differences, the estimated rate of multiplication per female in 20 weeks (λ^{20}) is also shown in table 6.

Fig. 7 shows the trend in value of λ (the female rate of increase) at two temperatures. Considered as a sequence from south to north it rose from Sydney to Brisbane and fell progressively, north of Brisbane. The similarity of the trend at both temperatures suggests that the trend is real, though we were unable to demonstrate significance in the differences except for those indicated in table 5.

There is another way of looking at the data in fig. 7. For *D. serrata birchii*

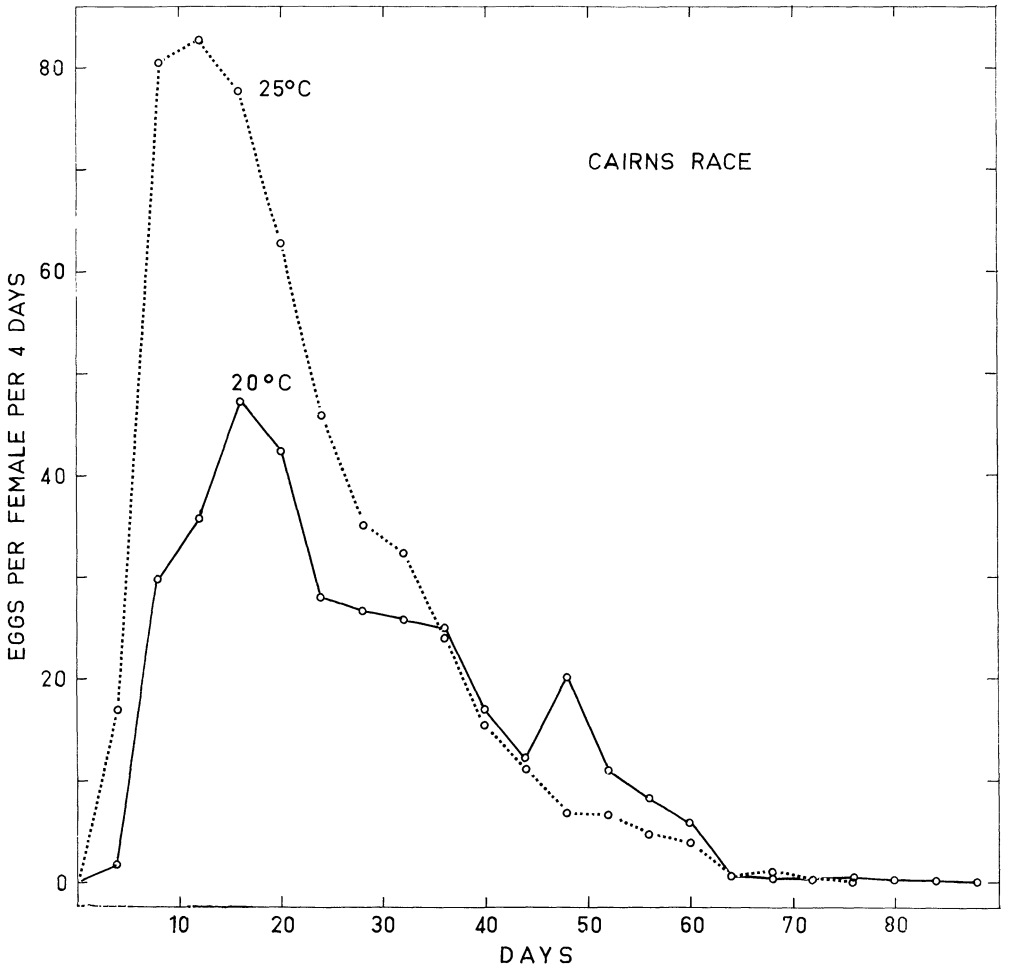

FIG. 6. Comparison of eggs laid per female per four-day period at 25° C and 20° C for the Cairns race of *D. serrata birchii*.

(Rabaul, Port Moresby, Cairns) there is a progressive increase of r_m from north to south. For *D. serrata serrata* (Brisbane and Sydney) the trend is the reverse, the value of r_m tending to decrease from north to south.

In table 7 the races are listed in order of total fecundity (F), mean longevity (L), and r_m. The order of races from higher to lower r_m is the same as the order of races from higher to lower fecundity, that is, Brisbane, Sydney, Cairns, Port Moresby, Rabaul, with the exception that at 20° C the value of r_m for the Sydney race is a little less than that for the Cairns race. This is probably due to the fact that the Cairns race laid more eggs earlier in its life than the Sydney race (an egg laid early in life contributes more to the value of r_m than an egg laid later). It is reasonable to conclude that the differences in fecundity have the over-riding influence in determining such differences in r_m as do exist between races.

SUMMARY

With appropriate techniques the innate capacity for increase (r_m) of two subspecies of *Drosophila serrata* has been reliably measured with low variance in the

TABLE 5. *The means and variances of the innate capacity for increase of five races of* D. serrata *at 25° C and 20° C. The means ($\grave{r}_m$) were based on 200 estimates. Figures in parentheses show $\hat{r}_m$ which is calculated from the mean values of the components of* r_m *over all replicates. The unit of time is a day*[1]

Race	25° C			20° C		
	Mean	Variance	C.V.	Mean	Variance	C.V.
Sydney (S)	0.233 (0.236)	.000755	11	0.124 (0.138)	.001235	24
Brisbane (S)	0.249 (0.253)	.000544	8	0.156 (0.158)	.000210	9
Cairns (B)	0.227 (0.236)	.001473	16	0.137 (0.138)	.000717	19
Port Moresby (B)	0.210 (0.219)	.001674	19	0.109 (0.112)	.000398	15
Rabaul (B)	0.135 (0.160)	.002798	40	0.051 (0.065)	.001132	60

Comparisons between races. Comparisons at 25° C are above the diagonal. Comparisons at 20° C are below the diagonal. n = not significant; 0.05, 0.01 = significant at P = 0.05, 0.01

		Sydney	Brisbane	Cairns	Port Moresby	Rabaul	
	Sydney		n	n	n	<.01	
	Brisbane	.05		n	.05–.01	<.01	
20° C	Cairns	n	n		n	<.01	25° C
	Port Moresby	n	<.01	.05		<.02	
	Rabaul	<.01	<.01	<.01	<.01		

[1] C.V. = per cent coefficient of variability; S = *Drosophila serrata serrata*; B = *D. serrata birchii.*

laboratory. This measure is a satisfactory ecological statistic for distinguishing between geographic races of the subspecies. It is also a satisfactory way of measuring the effect of temperature on increase in numbers. The main technical difficulty was to devise a method of measuring the survival of immature stages with low variance.

It is reasonable to consider that under some circumstances the innate capacity for increase (r_m) is a component of fitness. It certainly measures the capacity of the population to increase in numbers when density of flies is an optimum and food is in superabundance. In the subspecies *D. serrata birchii* the value of the innate capacity for increase at both 25° C and 20° C tended to increase north to south from Rabaul in New Britain, through Port Moresby in New Guinea to Cairns in northern Australia. In the subspecies *D. serrata serrata* the value of the innate capacity for increase tended to decrease from north (Brisbane) to south (Sydney) at both temperatures. Not enough is known about the ecology of the two races to speculate as to the possible adaptive significance of this pattern.

At both 25° C and 20° C the northernmost population (Rabaul) had a significantly lower value of r_m than all others. The Rabaul population was the only one which was completely sexually isolated from all others (Dobzhansky and Mather, 1961). Differences between the other races showed up more at 20° C than at 25° C. The components of the innate capacity for increase which primarily determine the order of the values of r_m for the races are concerned with fecundity. Adult longevity was also significantly different in the races, but contributed relatively little to the differences in r_m.

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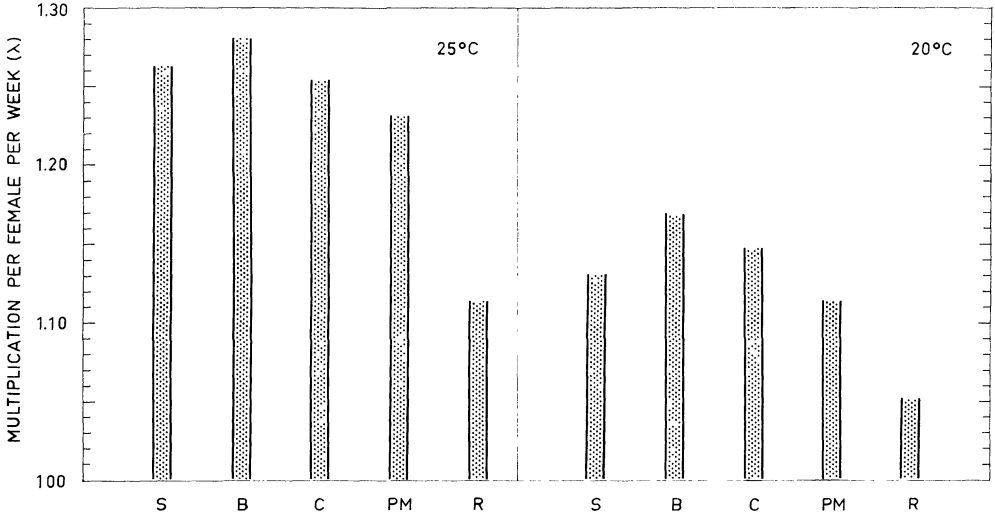

FIG. 7. The finite rate of increase (multiplication per female per week) of five races of *D. serrata* at 25° C and 20° C. S = Sydney; B = Brisbane; C = Cairns; PM = Port Moresby; R = Rabaul.

TABLE 6. *The rate of multiplication of* D. serrata *at 25° C and 20° C expressed as the finite rate of increase* λ *(multiplication per female per day) and as the multiplication in 20 days* (λ^{20})[1]

Race	Multiplication per female			
	25° C		20° C	
	Per day (λ)	In 20 days	Per day (λ)	In 20 days
Sydney (S)	1.263	107	1.132	12
Brisbane (S)	1.282	144	1.170	23
Cairns (B)	1.255	93	1.148	16
Port Moresby (B)	1.233	66	1.116	9
Rabaul (B)	1.145	15	1.053	3

[1] $\lambda = \text{antilog}_e\ r_m$; S = *Drosophila serrata serrata*; B = *D. serrata birchii.*

TABLE 7. *The five races placed in order 1–5, from higher to lower values of total fecundity* (F), *adult longevity* (L), *and innate capacity for increase* (r_m)[1]

Race	25° C			20° C		
	F	*L*	r_m	*F*	*L*	r_m
Sydney (S)	2	1	2	2	1	3
Brisbane (S)	1	2	1	1	2	1
Cairns (B)	3	2	3	3	3	2
Port Moresby (B)	4	4	4	4	4	4
Rabaul (B)	5	5	5	5	5	5

[1] S = *Drosophila serrata serrata*; B = *D. serrata birchii.*

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