GENE FLOW AND LIFE HISTORY PATTERNS

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ABSTRACT

Dispersal distances overestimate the gene-flow scale $l$ (the square-root of the mean squared distance travelled from birth to reproduction) when egg laying is concentrated early in dispersal and when there is mortality during dispersal. If egg laying follows a square-root normal distribution in time, as it does in several Drosophila species, then $l$ is reduced to about 0.6 of that estimated from dispersal alone, unless egg laying is concentrated in a very brief period. If mortality is such that the half-life is earlier than the mean fecundity day, then $l$ will be reduced still more relative to the dispersal estimate, and will be very sensitive to small changes in mortality. Overestimating $l$ yields overestimates of the amount of selection needed to maintain geographic differences in gene frequencies. If mortality increases in suboptimal habitats, then the neighborhood size will be smaller in those areas, because increased mortality decreases $l$. This means that $l$ is smallest, allowing the greatest differentiation and genetic innovation, precisely where it is most needed. This lends support to Wright's shifting balance hypothesis. If $l$ is adjusted to local conditions, then we do not necessarily expect a positive relationship between environmental and genetic heterogeneity. Data from Drosophila pseudoobscura are used to make the models realistic, and it is shown that $l$ depends on the distances among traps or breeding sites. It is therefore essential to know the geometry of breeding sites and the life history parameters to estimate $l$.

THE neighborhood is the area from which any two parents could have come with equal probability (after Wright 1943). It represents a geographical scale below which genetic differentiation is meaningless. If there are no geographic differences in fitness among genotypes, then the neighborhood represents the minimum area that can differentiate randomly from other such areas. If there are selective differences, then the neighborhood sets the lower limit on the area that can “track” microgeographic variation in fitness (Slatkin 1973; May, Endler and McMurtie 1975; Endler 1977), unless there is strong microhabitat choice (Taylor and Powell 1977). It is therefore essential to know something about the scale of gene flow in order to understand genetic variation and geographic differentiation (Wright 1969, 1978; Endler 1973, 1977).

In practice we have to estimate gene flow by using the distribution of movements from birth to reproduction; we use dispersal to estimate gene flow. For a
variety of reasons, dispersal is an overestimate of gene flow (see Endler 1977). The term migration is also often used, but migration can have even less to do with gene flow than dispersal (Endler 1977). The purpose of this paper is to show how life-history patterns affect gene flow, and to provide some approximations to the magnitude of these effects. Observations on the Drosophila pseudo-obscura group will be used to make the form of the models realistic.

GENE FLOW MEASURE

The neighborhood is determined by the dispersal of genes within a generation. If \( g(x,\theta) \) is a function that gives the probability that a gene originating at a given point \((s=0)\) will reach a radial (any direction \( \theta \)) distance \( x \) at a given time \( T \) (one generation), then the gene flow distance is \( l \), given by:

\[
l^2 = \int_0^{2\pi} \int_0^\infty x^2 g(x,\theta) \, dx \, d\theta,
\]

where \( \int_0^{2\pi} \int_0^\infty g(x,\theta) \, dx \, d\theta = 1 \).

In other words, the distance \( l \) is the square root of the mean squared distance from birth to reproduction (Fisher 1950; Slatkin 1973; May, Endler and McMurtrie 1975; Endler 1977).

The scale \( l \) is related to the radius of the neighborhood by \( r = l\sqrt{2} \), if dispersal follows a bivariate normal distribution. If the standard deviations along both axes of a bivariate normal distribution are equal to \( \sigma \), then \( l^2 = 2\sigma^2 \). The neighborhood radius is defined as \( r = 2\sigma \) (Wright 1946 [correcting the formula in Dobzhansky and Wright 1943], 1969, 1978); hence, \( r = l\sqrt{2} \). Strictly speaking, \( r \) refers to the radius of a circle including about 95% of the genes dispersing from the origin; these should be similar, provided that there are no drastic departures from random mating or strong microhabitat choice. The quantity \( l \) is also the scaling factor for gene flow when considering the balance between selection and gene flow in clines (Fisher 1950; Slatkin 1973; Endler 1977). Thus, the degree and scale of geographic differentiation is dependent upon \( l \).

DISPERSAL

The first step in estimating \( l \) is to measure the dispersal of individuals over a generation, or the time taken to go from ovum to ovum. It is usually not practical to measure dispersal over one generation unit \( T \) because recapture rates fall off so rapidly with time that there are not enough recaptures at time \( T \) to give a reliable estimate of the dispersal function. To get around this problem, we can measure dispersal at several times \( t \) over a period less than one generation \( T \), and extrapolate to time \( T \).

Let \( L(t) \) be the characteristic distance travelled at time \( t \), calculated according to equation (1):

\[
L(t) = \int_0^\infty x^2 f(x,t) \, dx,
\]

where \( f(x,t) \) is the probability of travelling to distance \( x \) by time \( t \). (For brevity we drop the direction summation, \( \theta \)).
If dispersal from the release point is uniform and random in all directions, then $L(t)$ will be proportional to the square root of time, or

$$L(t) = D\sqrt{t}, \quad (2)$$

where $D$ is the dispersal rate (Dobzhansky and Wright 1943; Bateman 1950; Richardson 1970; Endler 1977). Substituting in the generation time, $T$ we get our first estimate of $l$; call it $l_1$:

$$l_1 = L(T) = D\sqrt{T}. \quad (3)$$

If dispersal follows a random walk or Brownian motion model, then the dispersal function $f(x,t)$ follows a normal distribution, with variance $D^2t$, and has the form:

$$f(x,t) = \frac{K}{D\sqrt{t}} \exp(-x^2/2D^2t), \quad (4)$$

where $K$ is a constant such that $\int f(x,t)dx = 1$ (Dobzhansky and Wright 1943; Bateman 1950; Richardson 1970). Thus, if the distribution of dispersal distances at any given time is normal, then $L(t)$ is the radial standard deviation of the distances. Note that $f(x,t)$ does not have to follow (4), for equations (2) and (3) to be used. $L(t)$ is simply an empirical measure of the spread of the distribution that happens to be equal to the theoretical standard deviation from the release point if dispersal is normal in form (equation 4), and it is still a good approximation to $l$ when it has other forms (May, Endler and McMurtrie 1975). There is abundant evidence from a variety of organisms that the dispersal function $f(x,t)$ is usually leptokurtic relative to the normal distribution (Endler 1977; Richardson 1970), and this is true for Drosophila pseudoobscura, especially during the first two days following release (Dobzhansky and Wright 1943, 1947; Dobzhansky and Powell 1974; Powell et al. 1976). Because we are primarily interested in the relative effects of fecundity and mortality patterns on gene flow relative to dispersal, the leptokurtosis will have little effect on the conclusions.

Many data have been collected on dispersal rates in Drosophila pseudoobscura and its sibling species (Dobzhansky and Wright 1943, 1947; Dobzhansky and Powell 1974; Powell et al. 1976; Crumpacker and Williams 1973). At first sight, the data appear heterogeneous; the more recent experiments yield larger dispersal rates than did the earlier experiments. However, the experiments giving larger dispersal rates also had a greater spacing between traps: 40 m instead of 20 m. Johnston and Heed (1975) found that dispersal rates are related to trap spacing in a number of Drosophila species. The later experiments also covered a larger area than the earlier ones, so that larger estimates are also more likely.

We can eliminate some of the variation by measuring dispersal in terms of the average distance among traps. The rationale behind this is as follows: We assume that the flies move at random in two directions during the dispersal period, and when they come near an attractive area they move more slowly
and eventually stop on the bait or egg-laying site. As a consequence, traps with more distant neighbors will attract flies from further away on average than traps with close neighbors.

The published data for \textit{D. pseudoobscura} were reanalyzed as follows. For each experiment and each day, a quantity $L_m(t)$ similar to equation (1) was calculated according to:

$$L_m(t) = \sqrt{\frac{\sum x^2 f(x,t)}{\sum f(x,t)}} \, ,$$

where $f(x,t)$ is the number of marked flies recaptured at day $t$ at radial distance $x$ from the point of release, and the resulting $L_m(t)$ is in meters. To make $L_m(t)$ independent of trap spacing and study area size, we divide it by the average distance among traps, $B(t)$ to obtain $L(t)$:

$$L(t) = \frac{L_m(t)}{B(t)} \, .$$

The average distance among traps on day $t$ is the reciprocal of the square root of the trap density on day $t$, or

$$B(t) = \sqrt{\frac{A(t)}{N(t)}} \, ,$$

where $A(t)$ is the area occupied by traps and $N(t)$ is the number of traps set out on day $t$. The area occupied by the traps was determined by circumscribing a circle around the traps, using as its diameter the maximum distance among traps. $B(t)$ gives the average distance between traps if they were spaced at random. The average $B(t)$ for all experiments and days is 145 m.

$L(t)$ measures the average distance travelled on day $t$ in trap units. If $t = T$, the generation time, then $L(T) \approx l_i$; the object is to measure $L(t)$ at enough times to extrapolate to $t = T$.

$L(t)$ calculated by equation (6) is plotted versus $\sqrt{t}$ in Figure 1, using the data in \textit{Dobzhansky and Wright} (1943, 1947), \textit{Dobzhansky and Powell} (1974); \textit{Powell et al.} (1976). It is apparent that all experiments fall on about the same line as expected from equation (3). There is no evidence that the flies dispersed at different rates at different places or years when $L(t)$ is corrected for trap spacing. The data of \textit{Powell et al.} (1976) suggest that the same is true for \textit{D. persimilis, D. azteca} and \textit{D. miranda}, as their dispersal rates did not differ significantly from that of \textit{D. pseudoobscura}. The observed relationship for all experiments is $L(t) = 0.316 + 0.566 \sqrt{t}$. The regression of $L(t)$ on $\sqrt{t}$ is highly significant ($P < 0.001$), indicating that $L(t)$ is indeed linearly related to the square root of time.

The data of \textit{Crumpacker and Williams} (1973) are based upon a different experimental design in which the trap density during marking is different from that during recapture, and flies were not released from a single trap, making their experiments difficult to compare to those of \textit{Dobzhansky} and his col-
leagues. In addition, flies were removed from the outer traps and abducted from the study area, leaving a zone relatively empty of flies, surrounding the nine central traps where flies were released. The relatively high fly density in the center surrounded by a large area with relatively low fly density favors dispersal away from the central region more rapidly than would be expected if trapping intensity remained constant throughout the experiment. Since flies were continually being removed from the outer traps, we would expect the increased dispersal to become worse, and indeed the later experiments showed proportionally more long-distance movement than did the earlier experiments. This could be aggravated by crowding or dispersal effects. To make matters worse, Crumpacker and Williams recaptured only seven to 24 flies per day, making dispersal estimates extremely subject to sampling error and to the presence of even a single fly that happened to travel a long distance. For further discussion, see Chapter 2 of Endler (1977). Nevertheless, the calculated $L(t)$ for Crumpacker and Williams' (1973) experiments range from 0.95 to 1.5, placing them on or near the line calculated from the Dobzhansky experiments. The earlier experiments are closer to the line than the later experiments, again probably due to the above-mentioned density effects.
Multiple regression of L on time and temperature

Least squares surface: $L(t,C) = -0.376 + 0.640\sqrt{t} + 0.0255\, C$

Standard errors of the slopes: 0.0562 (time)
0.0082 (temperature °C)

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>F</th>
<th>d.f.</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Overall regression:</td>
<td>68.22</td>
<td>2,54</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Square-root time:</td>
<td>129.50</td>
<td>2,54</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Temperature °C</td>
<td>9.30</td>
<td>2,54</td>
<td>&lt;0.005</td>
</tr>
</tbody>
</table>

The effects of both time and temperature are significant.
95% confidence limits for predicted $L(T,C)$ are determined by:

$$L(T,C) = 2s \sqrt{1 + 1/N + c_{11}x_1 + c_{22}x_2 + 2c_{12}x_1x_2},$$

where $N = 57$, $s = 0.215$, $c_{11} = 0.0684$, $c_{12} = 0.00478$, $c_{22} = 0.00151$, $x_1 = \sqrt{T} - 1.639$, and $x_2 = C - 22.62$.

For a description of the method, see Chapter 13 of SNEDECOR and COCHRAN (1967).

Temperature is known to affect the rate of dispersal in insects (TAYLOR 1963; JOHNSON 1969). Experiment I of DOBZHANSKY and WRIGHT (1943) is often given as an example of a lower dispersal rate associated with lower temperature at the time of the experiment. Although it is also associated with the highest trap density, hence the smallest distance among traps, it yields $L(t)$ values that are still consistently below the overall regression line (Figure 1). The effects of temperature can be included by doing a multiple regression of $L(t)$ on temperature, as well as square-root time (Table 1). The relationship then becomes:

$$L(t,C) = -0.376 + 0.640\sqrt{t} + 0.0255\, C,$$

where C is the temperature in degrees centigrade. The effect of temperature is significant (Table 1). Thus $D$ is about 0.6 and is positively related to temperature.

To get our first estimate of $l$ or $l_1$, we need to know the generation time $T$, for substitution into equation (8). Because most organisms, including Drosophila, do not breed at discrete intervals, the value for $T$ relevant for dispersal will not be the same as the generation time for demographic considerations. To avoid confusion, we will define $T$ as the dispersal time.

**DISPERAL TIME**

DOBZHANSKY and WRIGHT (1943) estimated that about 50% of the marked flies died by about day seven of their experiments and, making a simple extrapolation, suggested that all flies will have died by 14 to 23 days. It is reasonable to define the dispersal time $T$ as the time it takes for all flies of a cohort to die; they obviously cannot disperse any genes beyond that time. This definition will be modified later. Substituting $T = 14$ or 23 days into equation (8) at the observed average temperature of 23°: $L(14,23) = 2.60 \pm 0.50$ trap units; and $L(23,23) = 3.28 \pm 0.56$ trap units.
The 95% confidence limits were calculated from the regression in Table 1. Converting trap units to meters, using the average trap unit for all experiments (145 m) gives 377 ± 73 m and 476 ± 81 m. This yields neighborhood radii of 533–673 m, similar to the estimates of Powell, et al. (1976) and Crumpacker and Williams (1973). However, the trap unit of the various experiments ranged from 60 to 247 m, giving estimates of neighborhood radii from 221 to 1146 m. It is necessary to know the spacing of the natural egg-laying places in order to get a reliable estimate of the actual neighborhood size in meters.

The above estimate of $T$ may be inappropriate for estimating $l$; both mortality and fecundity change with time. A much better estimate for $T$ would be the time at which all or (say) 98% of the eggs were laid. Dispersal after reproduction is meaningless to the gene flow measure, and if most eggs are laid and most of the mortality occurs soon after leaving the birthplace, then the gene flow estimate will be too high. We will consider first the effects of the fecundity schedule.

**FECUNDITY AND DISPERSAL TIME**

Data on the number of eggs laid per female per day have been published by Matzke and Druger (1977), and unpublished data were provided by W. W. Anderson and T. Watanabe (personal communication, 1978). The data are for D. pseudoobscura populations maintained in the laboratory at 16°C and 25°C, and with AR/AR, AR/PP and PP/PP karyotypes. Matzke and Druger's flies actually came from one of the dispersal sites used by Dobzhansky (Piñon Flats, California), but were raised for many generations in the lab before testing. Anderson and Watanabe's flies were in the lab for only a few generations, but came from another location (Colorado). The data of Matzke and Druger (1977) were extracted from their Figure 2 by means of a computer operated "digitizer," and are shown in Figure 2 of this paper. The fecundity schedule of D. pseudoobscura shows an early peak soon after eclosion, followed by a gradual tailing off in daily fecundity. This is also found in the data of Dobzhansky (1935) and Tantawy and Vetukhiv (1960). D. persimilis, D. melanogaster, D. serrata, D. pachea, and D. mojavensis show a similar pattern (data from Dobzhansky 1935; Hanson and Ferris 1929; Kaliss and Graubard 1936; Shapiro 1932; Gown 1952; Birch, et al. 1963; Jefferson, Williams, personal communications 1977), as do many other insects; it seems to be a general phenomenon.

Because flies disperse at a rate proportional to the square-root of time, and may fly over unsuitable habitats between food and egg-laying places, it is possible that their fecundity schedule is adjusted to center the number of eggs at the average time it takes to reach new feeding and laying places over the geographical range of the species. Thus, it is reasonable to predict that the distribution of eggs per female per day will be normal in square-root time. Therefore, we expect the fecundity schedule to be approximated by:

$$E(t) = \frac{k}{\sigma} \exp\left[-\frac{(\sqrt{t}-\mu)^2}{2\sigma^2}\right],$$

(9)
Figure 2.—Eggs per female per day in laboratory populations of *D. pseudoobscura*, compared with the best-fit square-root normal distribution (equation 9); data from Matzke and Dlugosch (1977). a, raised at the same temperature at which they were kept for many generations in the lab (16° or 25°). b, kept at temperatures colder (16°) or warmer (25°) than that at which they were kept for many generations. The fit is excellent in each case; see Table 2.

where \( k \) is a constant such that \( \int_0^\infty E(t)\,dt = 1 \), \( \mu \) is the mean, and \( \sigma \) is the standard deviation in square-root days. The mean \( \mu \) may be favored by the average time it takes to get from one food place to another, and \( \sigma \) may be determined by the average density of food sites for the species as a whole. The reasons are speculative, but the fit to the square-root normal distribution (equation 9) is very good (Table 2; Figure 2). This is the first time this has been noted for any species.
GENE FLOW AND LIFE HISTORY

TABLE 2

Square-root normal distribution of eggs per female per day

<table>
<thead>
<tr>
<th>Karyotype</th>
<th>Treatment</th>
<th>Test</th>
<th>Source*</th>
<th>Mean Normal</th>
<th>Variance Normal</th>
<th>Goodness of fit</th>
<th>C.V.</th>
<th>Days (T)†‡</th>
</tr>
</thead>
<tbody>
<tr>
<td>AR/AR</td>
<td>Cage 16°</td>
<td>Cold</td>
<td>M &amp; D</td>
<td>5.50</td>
<td>8.80</td>
<td>39.34</td>
<td>79</td>
<td>&gt;0.99</td>
</tr>
<tr>
<td>AR/AR</td>
<td>Bottle 16°</td>
<td>Normal</td>
<td>M &amp; D</td>
<td>5.40</td>
<td>5.65</td>
<td>40.83</td>
<td>69</td>
<td>&gt;0.99</td>
</tr>
<tr>
<td>AR/AR</td>
<td>Cage 25°</td>
<td>Normal</td>
<td>M &amp; D</td>
<td>3.40</td>
<td>2.45</td>
<td>10.09</td>
<td>26</td>
<td>&gt;0.99</td>
</tr>
<tr>
<td>AR/AR</td>
<td>Bottle 25°</td>
<td>Hot</td>
<td>M &amp; D</td>
<td>3.40</td>
<td>3.20</td>
<td>12.66</td>
<td>26</td>
<td>&gt;0.98</td>
</tr>
<tr>
<td>AR/AR</td>
<td>Bottle 25°</td>
<td>Normal</td>
<td>A &amp; W</td>
<td>3.55</td>
<td>2.55</td>
<td>20.49</td>
<td>14</td>
<td>&gt;0.10</td>
</tr>
<tr>
<td>AR/PP</td>
<td>Bottle 25°</td>
<td>Normal</td>
<td>A &amp; W</td>
<td>3.54</td>
<td>2.97</td>
<td>20.92</td>
<td>14</td>
<td>&gt;0.10</td>
</tr>
<tr>
<td>PP/PP</td>
<td>Bottle 25°</td>
<td>Normal</td>
<td>A &amp; W</td>
<td>3.50</td>
<td>2.93</td>
<td>22.17</td>
<td>14</td>
<td>&gt;0.05</td>
</tr>
</tbody>
</table>


† Parameters of the square-root normal fitted by iteration.

‡ Estimate of dispersal time from the time at which 98% eggs have been laid ($\mu + 2\sigma$).

Note that no matter what the karyotype, the means are similar for a given temperature. The coefficient of variation ($\sigma/\mu$), which is a measure of the spread of egg laying in time, is independent of temperature, except in experiments where the flies were tested at a warmer (Bottle 25°) or colder (Cage 16°) temperature than that at which they were raised for many generations, hence presumably genetically adapted (Table 2). We will use the data from the experiments with unchanged temperature to avoid artifacts.

From Table 2, we have the estimate of $T$, the time it takes for 98% of the eggs to be laid: $T = (\mu + 2\sigma)^2$. We do not take $T$ as the time when all eggs are laid, as this is extremely sensitive to sampling error, and usually only one or two individuals are laying sporadically by this time. The 98% time avoids these problems, while still using most of the data. Thus, at 25° virtually all eggs are laid by day 46, and at 16° by day 103.

An important point is that the egg-laying time is shorter at higher temperatures than at lower temperatures. This was also noted by Dobzhansky (1935), Tantawy and Vetukhiv (1960), Kaliss and Graubard (1936), Birch et al. (1963) and Roff (1977) for D. pseudoobscura, as well as D. persimilis, D. serrata and D. melanogaster. Using all the data from Matzke and Druger (1977), Anderson and Watanabe (personal communication, 1978), and the older data from Dobzhansky (1935) and Tantawy and Vetukhiv (1960), we can obtain the relationship between temperature and $T = (\mu + 2\sigma)^2$ for D. pseudoobscura. The relationship is $T = 234.8 - 7.68C$, and is highly significant ($P < 0.001$); the standard error of the slope (7.68) is 0.945.

Although there is a strong negative relationship between dispersal time $T$ and temperature, the dispersal rate is significantly higher at higher temperatures (Table 1 and equation 8), so that the effect of temperature on neighborhood size may not be large. Something similar was found by Roff (1977), using physiological arguments for Drosophila and called by him "the paradox of temperature-dependent dispersal."
Equation (8) gives the estimate of $L(t,C)$ as a function of time and temperature, so that we can substitute the estimates for $T$ at various temperatures to get estimates of $l_1$ as a function of temperature:

$$l_1(C) = -0.376 + 0.640\sqrt{234.8 - 7.68C} + 0.0255C.$$ (10)

Substituting in $16^\circ$ and $25^\circ$ we obtain:

$$l_1(25) = 4.46 \pm 0.74\text{ trap units}; \quad \text{and} \quad l_1(16) = 6.78 \pm 1.08\text{ trap units}.$$ (10a)

The 95% confidence limits are from equation (8) and Table 1 and do not include the error of estimating $T$ as a function of temperature ($C$). Without the error in estimating $T$, the 95% confidence limits come within one-half a trap unit of each other. With the error in $T$, the confidence limits overlap. This indicates that neighborhood size is independent of or decreases slightly with increasing temperature. For 145 m trap spacing $l_1$ is $647 \pm 107$ m at $25^\circ$ and $983 \pm 157$ m at $16^\circ$. The values in meters are speculative because we do not know the actual spacing of natural breeding sites. The differences in dispersal rates with temperature are more than offset by the differences in fecundity schedules. This fits well with the hypothesis that the behavior of the flies and their life history are adjusted to their ecology. It also explains Roff’s (1977) “paradox”; the average distance travelled should be adjusted to the geometry of the environment, and the geometry of feeding sites could be independent of temperature.

**Fecundity and Neighborhood Size**

There is a hidden assumption in using equation (8) and $T$ estimated from the fecundity schedule to estimate $l_1$, as above. This assumes that fecundity remains constant until the estimated time $T$ and then drops off rapidly. The actual distribution of fecundity in time has a peak soon after eclosion and then tails off (Figure 2). Most eggs will be laid before most of the flies have travelled very far; hence, the actual gene flow distance $l$ will be less than that estimated by $l_1$. We will now find the actual distribution of eggs with distance by combining the fecundity schedule with the dispersal function. The basic question is: how much smaller is $l$ than $l_1$?

Let $f(x,t)$ be normally distributed with respect to $x$, with a variance proportional to time as given by equation (4). Let $E(t)$ be normally distributed in square-root time as given by equation (9). Therefore the total fraction of eggs laid at a distance $x$ from the place of origin up to and including time $T$ will be:

$$f_f(x,T) = \frac{K}{Da} \int_0^T \frac{1}{\sqrt{t}} \exp \left\{-\frac{1}{2} \left( \frac{x^2}{D_2t} + \frac{(\sqrt{T} - \mu)^2}{\sigma^2} \right) \right\} dt , \quad (11)$$

where $K$ is a constant such that $\int f_f(x,T) dt = 1$, and $T$ is the dispersal time. For the model, let $T = (\mu + 2\sigma)^2$, the time by which 98% of the eggs have been laid. Then $l$ is obtained by substitution into equation (1), or:

$$l^2 = \frac{K}{Da} \int_0^\infty \int_0^T \frac{1}{\sqrt{t}} \exp \left\{-\frac{1}{2} \left( \frac{x^2}{D_2t} + \frac{(\sqrt{T} - \mu)^2}{\sigma^2} \right) \right\} dt dx . \quad (12)$$
This will be a closer approximation to $l$ than to $l_t$.

Equation (12) was solved numerically for various values of $D$, $\mu$ and $\sigma \left[ T = (\mu + 2\sigma)^2 \right]$. The most convenient way to present the results is to plot $l/l_t$ as a function of the coefficient of variation in fecundity, $\sigma/\mu$ (Figure 3). This is independent of $\mu$ because $T$ is a function of $\mu$. The curve is only slightly dependent on $D$, changing little from $D = 1$ to $D = 20$. The small change with $D$ is primarily due to the inaccuracy of the numerical integration at $D = 1$ and 2; only a few distance units are reached by individuals when $D$ is small. The measurement error of $g(x)$ in the field is larger than the theoretical differences with various $D$.

Figure 3 shows that $l_t$ consistently overestimates $l$ over a broad range of parameter values, but the overestimate decreases when $\sigma/\mu$ is very small. The coefficient of variation of *Drosophila pseudoobscura* is about 0.46 (Table 2), placing it on the flat part of the curve and indicating that the actual gene flow distance is about 62% of $l_t$. Figure 4 compares the distribution of flies and eggs, using the observed parameters for *D. pseudoobscura* of $\mu = 3.5$, $\sigma = 1.6$; and $T = 45 \left(25^\circ\right)$; this gives $l = 2.8$ compared to $l_t = 4.5$ trap units for this combination of parameters. This the neighborhood radius ($\lambda/2$) estimated from the distribution of the offspring of parents originating at a given place is 62% of the estimate from the parents' movements alone. A fecundity schedule that con-
centrates egg laying in the earlier part of the lifetime results in a neighborhood size ($l$) that can be as little as 60% of the characteristic distance traveled during the flies’ lifetime ($l_1$). Those species that lay their eggs all at once (small $\sigma/\mu$) will have a neighborhood size that is more closely related to the characteristic distance traveled by parents, but those species like *D. pseudoobscura* that can lay eggs over a long period of time will have a neighborhood size smaller than that expected from their movements alone. Note that $l$ will always be less than $l_1$ if more eggs are laid early in the dispersal period rather than later; the fecundity schedule does not have to follow equation (9) for the gene flow distance to be smaller than the dispersal distance.

**THE EFFECTS OF MORTALITY**

Not all individuals will be alive by the end of the egg-laying period. Mortality should reduce the neighborhood size because there are more flies alive at the earlier stages of dispersal than at the later stages. As a result, proportionally more eggs will be laid closer to the origin than at increasing distances. This reduces $l$ even further than the effects of fecundity patterns.

To get an idea of the magnitude of the effects of mortality, we can add a mortality parameter to the model. It is reasonable to assume that a constant

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**Figure 4.**—Distribution of dispersing adults (parents) and the cumulative total eggs laid using equations (4) and (9) and parameters similar to that of *D. pseudoobscura*: $\mu = 3.5$, $\sigma/\mu = 0.46$. This gives $l/l_1 = 0.62$. $X$ is in trap units.
fraction of the population will survive to the next day (type III survivorship curve; Slobodkin 1961). Other survivorship patterns will effect only the details of the reduction of \( I \) relative to \( I_i \). Let \( W \) be the probability of surviving from one day to the next; then, the probability of surviving to day \( t \) is \( W^t \). For example, Dobzhansky and Wright (1943, 1947) estimated that the San Jacinto flies survive at a rate of \( W = 0.908 \) per day. The fraction of eggs laid at distance \( x \) from the place of origin at time \( t \) will therefore be a function of the fecundity schedule and the number of individuals alive at that time, as determined by \( W \); equation (9) becomes:

\[
E(t) = \frac{k}{\sigma} W^t \exp\left[-\frac{(\sqrt{t}-\mu)^2}{2\sigma^2}\right],
\]

(13)
giving the new estimate of \( l \):

\[
l^2 = \frac{K}{D\sigma} \int_0^\infty x^2 \int_0^t W^t \exp\left\{ -\frac{1}{2} \left( \frac{x^2}{D\sigma^2} + \frac{(\sqrt{t}-\mu)^2}{\sigma^2} \right) \right\} dt dx .
\]

(14)

This was solved numerically for various values of \( W, D, \mu, \) and \( \sigma \). An example with \( D = 4, \mu = \sqrt{8} \) and various \( \sigma \) and \( W \) is shown in Figure 5. The effect of varying \( D \) is again very small. Figure 5 shows that mortality can have a major effect on the neighborhood size, and quite a small change in \( W \) can greatly reduce \( l \). For example, when \( \sigma/\mu = 0.5 \), a change from \( W = 0.99 \) to \( 0.90 \) reduces \( l/I_i \) from 0.604 to 0.490, and the effect is even greater for larger \( \sigma/\mu \).

The magnitude of the reduction of \( l \) relative to \( l_i \) also changes with \( \mu \); as \( \mu \) increases (eggs are laid later on average), \( l/I_i \) decreases. We can reduce the number of parameters by considering the effects of the timing of mortality relative to the fecundity schedule. We can define the half-life of the population as the time taken for 50% of the individuals to die by solving \( 0.5 = W^\tau \) for \( \tau \):

\[
\tau = \frac{\ln(0.5)}{\ln(W)} .
\]

(15)

We can then plot \( \ln(\tau/\mu^2) \) for various \( \sigma/\mu \) to examine the effects of all the variables. The ratio \( \tau/\mu^2 \) relates the half-life to the age around which fecundity is centered. Figure 6 shows the general relationship for solutions to equation (14), using a wide variety of values of \( \mu, \sigma/\mu, \) and \( W \). The relationships hold true for many different \( D \). Figure 5 also gives \( \ln(\tau/\mu^2) \) for \( \mu = \sqrt{8} \). For \( D. pseudoobscura \), Dobzhansky and Wright (1943) estimated \( W = 0.908 \), so that \( \tau = 7.35 \) days.

The general result is that increasing \( \tau \) relative to \( \mu \) for a given \( \sigma \) increases \( l/I_i \). The effect is greatest when \( \tau < \mu^2 \); if a large fraction of individuals die before peak fecundity, then the neighborhood size can be quite small. If mortality is low or \( \tau/\mu^2 > 1 \), then \( l/I_i \) is larger and differences in mortality do not effect \( l \) very much. Finally, if the spread of egg-laying time is great (\( \sigma/\mu \) large), then the effects of mortality are larger than if the spread is small.

For \( Drosophila pseudoobscura \), \( W \) is about 0.91 (Dobzhansky and Wright 1943), and \( \sigma/\mu \) is about 0.46 (Table 2). At \( 25^\circ \), \( \mu \) is about 3.5 (Table 2), giving \( \ln(\tau/\mu^2) = -0.51 \). From Figure 6, this means that \( l/I_i \) is about 0.45, and \( l \) is
Figure 5.—Effect of mortality on gene flow for \( \mu = 2.83 \) using equation (12). Axes as in Figure 3. \( W \) = probability of surviving from one day to the next. \( \tau \) = half life, or day at which \( W = 0.5 \). \( \mu = \) mean of the square-root normal distribution; hence \( \mu^2 \) is the day around which egg laying is centered. The gene-flow distance is reduced for increasing and earlier mortality, and for increasing \( \sigma / \mu \). The curve for \( W = 1.0 \) is the same as in Figure 3.

moderately sensitive to changes in mortality. Including both the effects of fecundity and mortality schedules on \( D. \) pseudoobscura, we find that the gene-flow distance \( l \) is less than half the estimate from dispersal alone: 2.01 instead of 4.46 trap units at 25°. This gives \( l \approx 291 \pm 48 \) m, using 145 m as the trap unit, corresponding to a neighborhood radius of 411 ± 68 m. A neighborhood radius less than 0.5 km allows much geographic differentiation within small geographic areas.

GENE FLOW AND DIFFERENTIATION IN DROSOPHILA PSEUDOOBSCURA

There is no evidence for differences in dispersal rates among experiments, dates or places in \( Drosophila \) pseudoobscura, when the data are corrected for temperature and differences in average distance among traps. The later experiments (open symbols, Figure 1) appear no different from the earlier experiments (black symbols). This is expected if the trap spacing affects the dispersal rate because: (1) the earlier experiments had a 20 m spacing, while the later experiments were spaced at 40-m intervals, and (2) given the same trap spacing, as the
number of traps goes up in a cross or linear transect, the trap density falls, hence the average distance among traps increases; there is more empty space between traps when they cover a larger area. The later experiments extend over greater distances and have more empty space between transects than did the early experiments. Experiment I of Dobzhansky and Wright (1943) is at the other extreme, with virtually no empty space; hence, a short distance among traps. Both factors (1) and (2) mean that the flies in the early experiments can move shorter distances to travel to the same number of traps per square-root time than they would in the later experiments. By dividing $L_n(t)$ by $B(t)$ (equation 6), we correct for the differences in trap density.

Powell et al. (1976: p. 503) try to counter the argument that dispersal rates are a function of trap spacing by pointing out that their displaced traps 7–20 did
not yield fewer flies when they were isolated from the rest of the traps (E-W) compared to when they were connected by traps 1–6 (N-S). However, if flies were dispersing over the study area when the traps were placed and if the flies travel to the nearest traps, then we expect that traps 7–20 should actually attract more flies when isolated (E-W) than when connected (N-S). An examination of their Table 3 shows that traps 7–20 attracted an average of 342 flies per day when connected (N-S) and 352 flies when isolated, supporting the hypothesis that dispersal rates are a function of trap spacing.

A third factor in the agreement among experiments is (3): the later experiments used alternate east-west and north-south transects on successive days. This has the effect of increasing the distance among traps, because flies in the vicinity of (say) the E-W transect, but not recaptured the first day, will be attracted by the N-S transect the following day. There is no reason why a fly at trap E-W-8 should fly to near the same trap (8) on the N-S transect; it could fly to any of the traps, increasing \( L_m(t) \). This is crudely corrected for by using the circumscribed circle around a single transect to obtain \( B(t) \). We may conclude that much of the variation in meters travelled per square-root day can be accounted for by differences in trap spacing, emphasizing the need to know the actual distribution of feeding and egg-laying sites in natural populations. Dobzhansky et al. (1979) found a great deal of heterogeneity in movement rates in different habitats; “unsuitable” habitats were associated with faster dispersal and greater distances travelled. This is what one would expect if the density of feeding and egg laying sites was lower in the “unsuitable habitats.” Yerington and Warner’s (1961) observations that *D. melanogaster* will fly up to four miles and Jones’ and Moore’s observations that *D. pseudoobscura* will fly up to nine miles over desert in 24 hours (J. S. Jones, personal communication, 1975; J. Moore in Wallace, personal communication, 1978) are extreme cases of long-distance travel over unsuitable habitats.

Taylor and Powell (1977) found fine-scale differentiation in allele frequencies in *D. persimilis*, a sibling species of *D. pseudoobscura*. Using their estimated gene flow distance of 581 meters (they mistakenly used \( r = \sqrt{d^2} \) in place of \( l \)), they found that the selection required to maintain the observed microgeographic differentiation was too strong to be believable, so that they postulated that the differences may be due to microhabitat choice by different genotypes. However, our estimate of \( l = 291 \) m makes a simple selective explanation much more likely; if \( l \) is small, then less selection is required to maintain the same degree of differentiation. This is not to belittle the possibility of microhabitat selecton maintaining differences in gene frequencies over small areas. This may explain the intriguing results of Makela and Richardson (1977) for *D. propachucha* and Richardson and Johnston’s (1975a,b) observations on *D. mimica*, *D. kamby-sellisi* and *D. imparisetae*. Taylor and Powell (1978) found that *D. persimilis* tend to return to the places where they are marked, indicating some site fidelity if not microhabitat preference. On the other hand, the site fidelity may simply be a result of flies moving more slowly in favorable microhabitats compared to unfavorable ones. However, the whole question becomes academic when we
remember that we do not know the geometry and spacing of the breeding sites; slight changes drastically affect our conclusions about gene flow and all aspects of genetic differentiation. We clearly need much more data on population structure and life history parameters.

DISCUSSION

Dispersal estimates of gene flow tend to overestimate the gene flow parameter $I$, because they do not take into consideration the shapes of the fecundity and mortality curves and their timing relative to the dispersal rate. If more eggs are laid early in dispersal than later, then more eggs will be laid closer to the origin than further away, reducing the gene-flow distance $l$ to about 60% of the dispersal distance $l_i$. The effect of mortality is a function of the ratio of the half-life of the mortality schedule ($\tau$) to the mean fecundity day ($\mu^2$), and decreases with decreasing relative mortality (increasing $\tau/\mu^2$). For low survivorship, the actual gene-flow distance $l$ can be as little as 20% of the distance estimated from dispersal alone (Figure 6). These results apply to any species with life tables similar (but not necessarily identical) to the model; early fecundity and mortality reduces the neighborhood size relative to the dispersal distances.

The effects of mortality may also apply to plants. Table 5–2 of STANLEY and LINSKENS (1974) shows a wide range in the amount of time pollen from various species remains viable; from one day to several thousand days. Simple estimates of the distance pollen can travel without regard to pollen mortality will over-estimate the neighborhood diameter.

The consequences of overestimating the neighborhood area are two-fold. First, for a constant density, a smaller neighborhood area means a smaller effective population size. This allows more genetic drift and hence greater random differentiation among neighborhoods than expected from the dispersal estimate alone (Wright 1943, 1969, 1978; ENDLER 1977). On the other hand, more genetic drift means differentiation of smaller areas or groups of neighborhoods, hence smaller patches with low within-patch differentiation (ENDLER 1977). Also, if the population size is small, selectively advantageous alleles may be fixed more rapidly. Additionally, if $l$ is smaller than that estimated from dispersal, then there is more potential for geographic differentiation by natural selection. There is more isolation by distance because more gene flow units ($l$) will fit on a given selection gradient. The amount of differentiation in a cline is proportional to the ratio of selection to gene flow (Fisher 1950; ENDLER 1973, 1977; SLATKIN 1973; MAY, ENDLER and McMURTRIE 1975). By overestimating $l$, we overestimate the amount of selection needed to maintain geographic differentiation.

If mortality increases towards the edge of the geographical distribution of a species, then, other factors being equal, we expect $l$ to decrease toward the edge of the range. The same is true in any part of the range where the habitat is sub-optimal. As a consequence, we expect to find more fine-scale differentiation at the edges of species ranges and in suboptimal zones than in the centers. This is extremely convenient for long-term evolution, as it allows more potential for genetic innovation in precisely those places where innovation is most badly
needed. In suboptimal areas where $W$ is decreased, $l$ is decreased; consequently, there is more isolation-by-distance from the main gene pool, and the local population can respond more quickly and fully to the local selection pressures than would be possible with larger $l$ (see also ROUGHGARDEN 1974; GILLESPIE 1975, 1976; SLATKIN 1973; ENDLER 1977). Peripheral populations also receive immigrants from fewer directions, and hence the gene frequency of the immigrants is less likely to be representative of the species as a whole. Thus, peripheral and suboptimal populations favor local differentiation for reasons additional to those given by CARSON (1955).

For similar reasons, a reduction of $W$ and $l$ near species boundaries will increase the probability of speciation there, by parapatric (ENDLER 1977) or any of a number of stasipatric means (WHITE 1978). Possible cases are found in some of the Hawaiian Drosophila (RICHARDSON 1974; RICHARDSON and JOHNSTON 1975a). For example, a new chromosomal rearrangement is less likely to be swamped in a locality with smaller $l$ because it is isolated from the main gene pool by more neighborhoods per unit distance than it would be in the center of the range, and the local effective population size is smaller (see WHITE 1978). Therefore, new adaptive peaks can be explored more easily near species boundaries and suboptimal habitats. This lends support for WRIGHT's (1940, 1969, 1978) shifting balance hypothesis.

It is likely that $I$ has an optimum value, which may be determined nearly independently of dispersal rate. If $l$ is too large, then too many genes will be moving from selectively favorable to unfavorable habitat patches; the scale of $l$ will be larger than the scale of microgeographic variation in fitness (SLATKIN 1973; NAGYLAKI 1975a,b; ENDLER 1977). In addition, if $l$ is too large, then too many gene complexes will be moving into selectively unfavorable habitat patches and recombining with the locally adapted complexes. This may result in co-adaptive breakdown. The effect of both co-adaptive breakdown and genotypes in wrong habitats will be to increase the mortality, decreasing $l$. The gene-flow distance will thus be reduced until mortality is decreased.

If $l$ is too small, then inbreeding and genetic drift will affect the population structure. Increased genetic drift when $l$ is very small will prevent or retard adaptation to local selective conditions, increasing mortality and decreasing $l$. Inbreeding may result in increased mortality, also tending to reduce $l$. GOWEN (1952) found that the egg-laying period ($T$) is shorter in inbred compared to normal populations of $D. melanogaster$; smaller $T$ means smaller $l_1$, hence smaller $l$. When $l$ is sufficiently small for the effects of drift and inbreeding to be appreciable, $l$ is reduced further, favoring more inbreeding and drift. However, the contraction of effective numbers at very small $l$ will mean that the effects of immigrating individuals from other neighborhoods will be proportionally greater. First, GOWEN (1952) found that "hybrids" between outbred or inbred populations had larger $T$ than the parental populations. This will increase $l_1$ and $l$. Second, if $l$ is heritable and because a large proportion of the neighborhood with very small $l$ will be immigrants who themselves traveled greater distances than the species as a whole, the alien genes will swamp the natives. Alien genes will
also have a disproportional effect if the rare-male effect operates (see Wallace 1970; Spiess 1970; Ehrman 1966). Third, if \( I \) becomes too small, then ecological as well as genetic factors favor greater dispersal (for examples, see Southwood 1962; Johnson 1969; Roff 1974a,b; Hamilton and May 1977). Hamilton and May (1977) showed that, even in a uniform or predictable environment, there is an advantage to more dispersal. If there is strong competition among genotypes, and competition is proportional to similarity, then dispersal reduces competition, as it ensures that dissimilar genotypes live together. Consequently, \( I \) will increase until the effects of inbreeding, drift and competition are reduced enough so that the aliens no longer have an advantage. Thus, \( I \) will increase when very small, but decrease when large compared to the scale of microgeographic variation in fitness, reaching some intermediate value depending upon local conditions.

Gene flow and dispersal can respond and result from differing selection pressures. Dispersal rates and fecundity schedules can be adjusted to the spacing and temporal pattern of food availability (Johnson 1969; Southwood 1962; Roff 1974a,b) or in the magnitude of fluctuation in fitness (Gillespie 1975, 1976), while gene flow can be adapted to the scale of microgeographic variation in fitness, the shape of the mortality schedule, and the effects of drift and inbreeding. Fecundity and mortality patterns are also subject to selection by purely ecological factors (Stearns 1976, 1977) secondarily affecting \( I \). Selection can favor large dispersal rates effectively to find and use breeding sites or avoid the consequences of temporal fluctuations, while favoring shorter gene flow to track smaller scale changes in selection coefficients. Note that selection is not specifically for smaller \( I \), but smaller \( I \) results from increased mortality, which is itself a function of \( I \), being too large for the selection scale. Gene flow and dispersal distances will be similar only if eggs are laid all at once, or if there is little spatial variation in fitness. In general, \( I \) will be adjusted to local conditions and may vary differently from dispersal rates.

If the gene-flow distance is adjusted to local conditions rather than remaining constant for a given species, then this affects the predictions about genetic heterozygosity and environmental heterogeneity (summarized in Hedrick, Ginevan and Ewing 1976). If \( I \) were invariant, then we would expect more genetic variation in areas with more environmental heterogeneity because there would be more gene flow among the different habitats or selective patches. The amount of heterozygosity is predicted to be maximal for intermediate levels of gene flow in this case (Spieth 1979). On the other hand, if \( I \) is adjusted to the scale of patches of particular selective values, then local adaptation can proceed further, more alleles will reach high frequencies or fixation, and heterozygosity per locality will be reduced. High heterozygosity would be found only in samples taken at or near the borders between adjacent but different patches. This may explain why there is disagreement in the literature about whether or not environmental heterogeneity is associated with genetic variability in natural populations (Hedrick, Ginevan and Ewing 1976). We clearly need to know much more about the ecology of species for which we wish to estimate the gene flow
distance; we need to estimate the dispersal rates, the geometry of breeding sites and the life history parameters.

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LITERATURE CITED


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