ON BEING THE RIGHT SIZE

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One of the most obvious features of an organism is its size. Equally obvious is the range in size between taxa. What is not obvious are the factors that determine the size of a particular species. Explanations based on metabolic arguments stem from observations such as those of Bergmann (1847), while Lack (1947, 1954) and Hutchinson and MacArthur (1959) have stressed the importance of predation and competition. Most papers concentrate on one of these three phenomena in their examination of the causes of inter- and intraspecific variation in body size. Metabolic arguments are commonly advanced for homeotherms (Hamilton 1961; Kendeigh 1970, 1976; James 1970; Brown and Lasiewski 1972; Tracy 1977) though such explanations are not unknown for poikilotherms (Nevo 1973; Sweeney and Vannote 1978). Character displacement through competition has been invoked for a wide range of organisms, from snails (Fenchel 1975) to salamanders (Frazer 1976). Predation is less often called upon but the range of organisms in which it is suggested to be important is equally large, from zooplankton (Sprules 1972) to mammals (McNab 1971).

Mayr (1956, p. 107), arguing against the generality of the physiological interpretation of ecogeographical rules, such as Bergmann's Rule, advocated that a more holistic approach be taken since there is "a multiplicity of selection pressures to which an organ is exposed and of which the final phenotype is a compromise." The importance of several factors interacting to produce a particular size spectrum has been well demostrated in studies on zooplankton communities (Brooks and Dodson 1965; Brooks 1968; Dodson 1974). Although there may be circumstances in which body size or variation in body size is caused by a single agent the more general condition is likely to be one in which these are determined by an interplay of several factors operating at different points in the life history of an organism. Any attempt to explain the evolution of body size should, therefore, take a holistic viewpoint.

When only a single factor is considered it may be possible to assess its effect on body size qualitatively without explicitly invoking some mathematical model. When several factors are involved, the possible opposing effects of some and interactions of others make the construction of a mathematical analogue essential. Allan (1974) used a general graphical model to examine the importance of preda-

tion and competition in the size spectrum of cladoceran communities. While this approach is important in developing a conceptual framework within which to organize general observations its lack of precision makes the application of the model to a specific circumstance difficult, if not impossible. In this paper I examine an approach to the understanding of the evolution of body size that lies at the other end of the scale, viz., a model that sacrifices broad generality for precision.

To attain this precision I consider the simplest possible analysis, that in which intra- and interspecific interactions are assumed to be relatively unimportant in determining the optimal body size. With this assumption we may adopt the Malthusian parameter, r, as a measure of fitness. Each life history component determining r is specified as a function of body size and the relationship between r and body size then derived. That body size which maximizes r is that which has the highest fitness. If for a particular case the optimum does not correspond with the observed size we may conclude either that one or more of the components has been incorrectly specified or that density-dependent or interspecific interactions are important. More importantly if prediction corresponds to observation we have a strong case for arguing that those factors not considered are of no great consequence in determining the optimal body size. This approach thus permits us to introduce factors sequentially, beginning with the most fundamental, and complexity is only increased as much as required to bring prediction and observation into line.

To obtain the necessary relationships between life history components and body size requires a relatively large amount of data on the life history of an organism. In this respect *Drosophila melanogaster* is a suitable candidate since it has been reasonably well studied, at least under laboratory conditions. Different geographic strains of *D. melanogaster* differ in body size when reared under identical conditions, indicating a genetic basis for these differences (Robertson and Reeve 1952; David et al. 1977). The range in thorax length is, however, rather small, from 0.90 mm to 1.15 mm. Thus we might expect a priori that *D. melanogaster* selects very similar habitats and is subjected to similar environmental regimes throughout its range and/or body size is robust to variation in life history components. The purpose of the analysis is thus to see if the integration of an a priori defined set of life history components predicts an optimum thorax length that falls within the observed range and then to test its sensitivity to variation in parameter values.

During the spring in the temperate zones *D. melanogaster* colonize their habitat, expanding in numbers from a small overwintering population (Lewontin 1965). A similar pattern is followed in the tropics where population growth is interrupted by the seasonal change in food supplies (Pipkin 1965). Birch and Battaglia (1957) found that in a tropical situation food supplies during the breeding season always remained far in excess of requirements for the species *D. willistoni* and that the number of species (including *D. simulans* the sibling species of *D. melanogaster*) emerging from fruit collected in the field was far below that at which competition for food could be expected to occur. Differing requirements

between species may also act to decrease the potential for competition and in this regard it is noteworthy that even species as close as *D. melanogaster* and *D. simulans* show distinct differences in resource utilization (McKenzie and McKechnie 1979). Recent studies by Atkinson (1979b) indicate that in vegetable markets populations of *D. melanogaster* may increase to levels at which density-dependent effects are measurable, though it is debatable whether these conditions are "natural." As a working hypothesis, I shall assume that the genus *Drosophila* and the species *D. melanogaster* in particular do not commonly encounter situations in which intra- or interspecific competition is significant. If competition is a significant determinant of body size then this should be apparent by a failure of the model to correctly predict the optimal size. However, these considerations aside, the choice of *D. melanogaster* as an illustrative example of the methodology is appropriate because the data base available will at least keep us from deviating too far from reality.

THE RELATIONSHIP BETWEEN r AND LIFE HISTORY COMPONENTS

The rate of increase, r, here used as a measure of fitness, is obtained by solving the Euler equation,

$$\sum_t e^{-rt} l_t m_t = 1, \tag{1}$$

where t is age, l_t is the age schedule of survival probabilities and m_t the age schedule of female births. For there to be an optimum body size one or both of the terms l_t, m_t must be a function of size. Another factor to be considered is the time taken to reach maturity, r diminishing with delayed maturity. The relationship between development time and body size is thus an important consideration. Except where stated I shall confine the following analysis of the relationship between body size and the life history components to data obtained under optimal conditions. The consequences of deviations from these conditions shall be examined in a later section.

Fecundity and Body Size

In *D. melanogaster,* as with most poikilotherms, fecundity increases with size. This increase is described by the equation,

$$\text{Fecundity} = aL^\gamma \tag{2}$$

where fecundity is measured over a number of days (Chiang and Hodson 1950; Robertson 1957), L is some metric such as wing length or thorax length, and a and γ are constants. The actual time course of egg production is triangular in shape, production beginning on the second day after eclosion, rising fairly rapidly until about the tenth day and then declining at a slower rate. A mathematical description of this process has been developed by McMillan et al. (1970a, 1970b),

$$m_t = 1/2\, M[1 - e^{-\beta(t-t_0)}]\, e^{-\alpha t} \tag{3}$$

where $t_0 + 1$ is the first day eggs are laid and M, α, and β are constants characteristic of the strain (the factor 1/2 is added to the original formulation to take into account only female births).

To satisfy (2) one or more of the parameters M, α, β or t_0 must be functions of size. Changes in α or β alter the shape of the egg production curve, a change in t_0 shifts the curve to the right or left along the time axis and a change in M changes the vertical axis, magnifying or diminishing daily production. That the relationship between fecundity and size is qualitatively independent of the period over which fecundity is measured (Chiang and Hodson measured it over the first 10 days whereas Robertson over the 4 days of maximum production) suggests that flies of different sizes differ primarily with respect to the value of M. The assumption that fecundity changes operate through a change in M is intuitively appealing since it is understandable on an argument of space; larger flies have more space for eggs and hence are potentially capable of producing more (assuming that they can ingest food at a sufficient rate and egg size is independent of body size. Evidence for the latter is given by Warren [1924]). Changes in any of the other parameters imply physiological changes with size: They may occur, but in the absence of evidence to the contrary the simplest assumption of no effect is preferable, at least as a working hypothesis. Thus the effect of size may be incorporated into (3) by replacing M with $F(L) = KL^\gamma$, where K is a constant.

Development Time and Body Size

An increase in fecundity increases r and hence an increase in body size is favored. If an increase in size, however, is accomplished by an increase in development time the advantages of increased egg production may be offset by the delay in reproduction and probably by increased prereproductive mortality. As might be intuitively expected, body size in $D.$ $melanogaster$ is positively related to development time (Robertson 1960; David and Bocquet 1974), the observed relationship being of the form,

$$D(L) = \text{Development time (egg to adult)} = bL^\delta + c \tag{4}$$

where b, c, and δ are constants and L is as previously defined.

Survival and Body Size

It is reasonable to suppose that an increased larval period will be accompanied by an increased larval mortality. This mortality might be directly related to size, if, for example, larger larvae experience difficulties in obtaining rations, or it may be indirectly related as when survival depends on time not size. In the absence of data concerning the former possibility I shall assume a constant instantaneous rate of mortality, m_1. Under this assumption the probability of surviving the larval period is

$$p(L) = e^{-m_l D(L)} \tag{5}$$

The final parameter required is the adult mortality rate. Under optimal labora-

tory conditions the survival curve of *D. melanogaster* is a type 1 curve, with most flies surviving to at least day 40 (Pearl and Parker 1924). It seems unlikely that such a long life would be realized in the field, the available data indicating a span of only a few days (Boesiger 1968; Boulétreau 1978). The factors causing this relatively high mortality rate are unknown, though the laboratory data suggest that it is probably not physiological aging: I therefore adopted the simplest realistic model and assumed a constant adult instantaneous rate of mortality, m_a.

THE RELATIONSHIP BETWEEN r AND BODY SIZE

Using the above information the Euler equation can be rewritten as

$$\sum_{t=1}^{\infty} e^{-r[t+D(L)+t_0]-m_l D(L)-m_a(t+t_0)-\alpha t_0} 1/2 F(L) e^{-\alpha t}(1 - e^{-\beta t}) = 1. \qquad (6)$$

For mathematical convenience time has been rescaled to begin at the first day of egg laying. Values for the various parameters are given in table 1. As a first estimate of the parameter values I used laboratory data. The one exception to this is the adult mortality rate for which I used a guess based on the field observations mentioned above because there appears to be a large difference between the survival rates of laboratory and field populations.

The relationship between thorax length and the rate of increase obtained using the values from table 1 is shown in figure 1. Also shown is the range in size of flies raised in the laboratory (data from Robertson and Reeve 1952; David et al. 1977; Atkinson 1979a) from stocks obtained at different geographic locations. There is very little difference in size between flies raised in the laboratory under optimal conditions and those obtained from the field (field specimens tend to be slightly smaller [Tantawy 1964]), and hence the range shown is a fair representation of the size range of the species. The inclusion of the predicted size of 0.95 mm in the

TABLE 1

PARAMETER VALUES USED IN OBTAINING FIGURE 1

Equation	Parameter	Value	Source
$1/2\ KL^{\gamma}(1 - e^{-\beta(t-t_0)})\ e^{-\alpha t}$	K	135	McMillan et al. (1970b)*
	β	.45	
	α	.12	
	t_0	2	
	γ	3	Robertson (1957)
$bL^{\delta} + c$	b	3.2	Robertson (1960)
	δ	3	
	c	5.1	Robertson (1960) and Prowsner (1935)
m_l	m_l	.1	Chiang & Hodson (1950) Sang (1950)
m_a	m_a	.2	See text

* Values based on "wild" strains A and D. Other strains examined by McMillan et al. are mutant strains and thus are not reliable data.
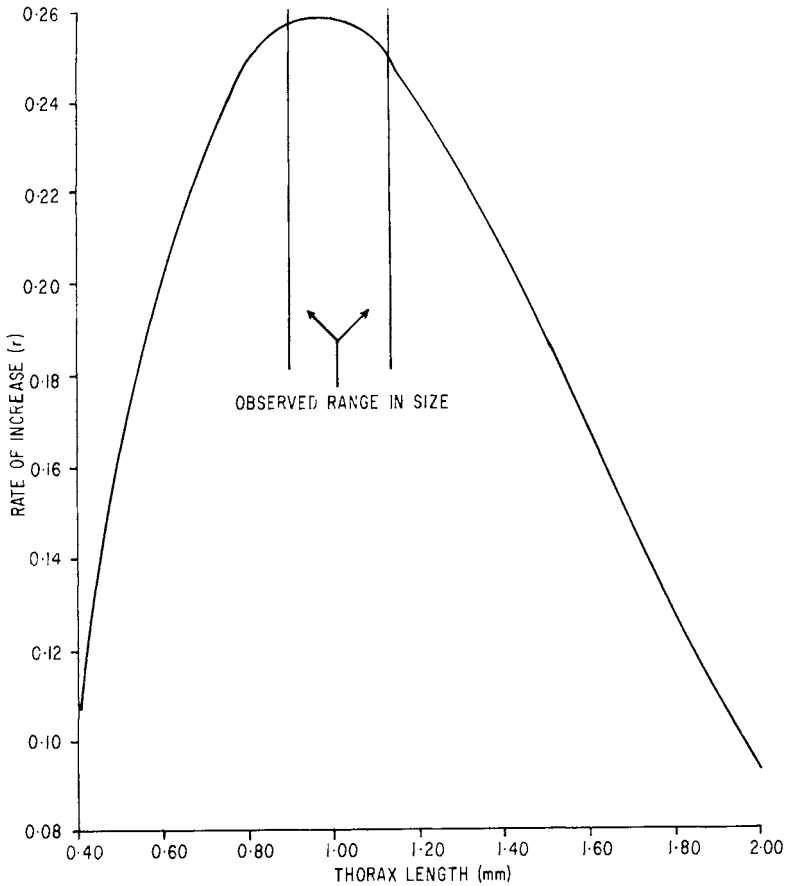
Fig. 1.—The rate of increase, r, as a function of thorax length using parameter values given in table 1.

observed range from 0.90 mm to 1.15 mm is encouraging, but there are two reasons why the correspondence between observation and prediction must be scrutinized carefully. Firstly, several parameters are at best only crudely estimated, larval mortality under field conditions being the most notable in this regard. Secondly, conditions in the field may vary depending on location in time and space. These factors will clearly influence the value of r but it is not a priori clear how the optimum thorax length might be affected; in some models, for example, r can be changed by a change in a parameter value but the optimum body size remains unchanged (Roff 1980). In the next section I examine the sensitivity of the optimal body size to changes in parameter values (the examination of eq. [6] is most easily undertaken after some algebraic manipulation, the algorithm for which is given in the Appendix).

The Fecundity Function

Boulétreau (1978) found that females captured in the wild contained one third as many mature eggs as wild females maintained under laboratory conditions. This reduction in fecundity may be the result of three factors: food quality, food quantity, and flight.

Drosophila melanogaster prefers to lay its eggs on fruit though it does not appear to be highly specialized on any particular variety (Atkinson and Shorrocks 1977). The potentially wide range of sites selected suggests that both the adults and larvae may encounter a wide range of yeasts upon which to feed. (Even *D. mulleri* which is relatively specialized on *Opuntia* encounters at least 9 types of yeast [Wagner 1944].) The oviposition rate of *D. melanogaster* is significantly affected by the type of yeast fed upon as an adult, although the total fecundity is apparently unaffected because those females with a lowered oviposition rate have an increased reproductive life (Robertson and Sang 1944). However, because of the high mortality rate of adults, this increase is unlikely to be of any consequence under field conditions. Over the first 10 days of egg production the change in reproductive output resulting from a change in yeast is largely one of scale and can be simulated by varying the fecundity coefficient, K, or the fecundity exponent, γ. In the former case the effect on fecundity is proportionally the same for all sizes whereas in the latter instance a size effect is introduced. Apart from food quality, food quantity affects egg production (Chiang and Hodson 1950), as also does flight (Roff 1977). In the former instance the effects are probably size specific, larger flies being less likely to obtain sufficient food. In the latter case the effect of size is unknown: Flight certainly causes a reduction in egg production but the importance of size remains to be examined experimentally. To examine the importance of these three factors I varied K from 40 to 140 and γ from 2 to 4, the latter range covering both negative effects (2–3) and positive effects (3–4) resulting from size. The results are shown in figure 2: A reduction in fecundity, caused by either decreasing γ or K, favors an increase in size. Significantly, the total variation is only from 0.85 mm to 1.10 mm.

Egg size varies between geographic strains (Oksengorn-Proust 1954; Cals-Usciati 1964; David and Legay 1977) but not within strains (Warren 1924; David and Legay 1977). The fecundity of strains laying larger eggs will be reduced if the volume of reproductive tissue remains constant for a fly of a given size. The result of an increase or decrease in egg size would thus be to decrease or increase the fecundity coefficient K by an amount corresponding to the change in egg volume. Thus, for example, an increase in egg volume of 50% would decrease K by 50%. As shown above such a decrease does not have a dramatic effect on the optimum body size. An even more striking prediction from the analysis, however, is that body size between strains should be positively correlated to egg volume. This is precisely what David and Legay (1977) found in their study of 42 different geographic strains. According to their data a 30% increase in egg volume, which represents the range over which their regression line extends, leads to a 60%
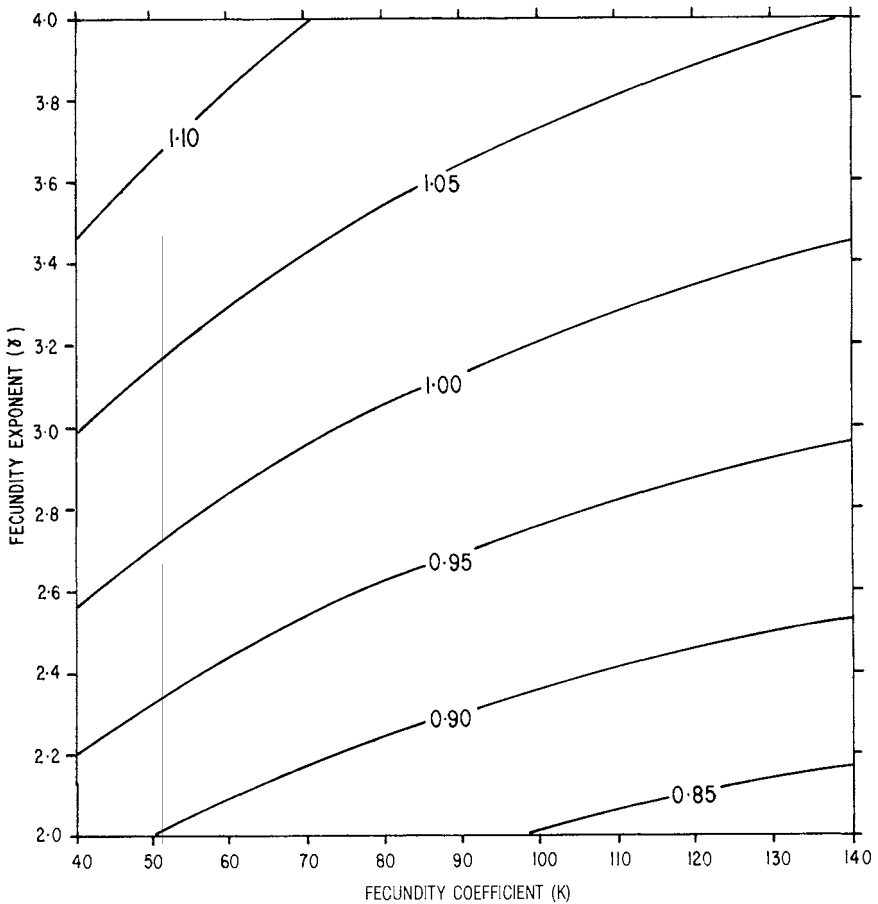
FIG. 2.—Response surface of the optimum thorax length on the fecundity coefficient, K, and the fecundity exponent, γ.

increase in body weight. Assuming a cubic relationship between body weight and thorax length this change in body weight represents approximately a 17% increase in thorax length. This is substantially more than predicted from figure 1, which would suggest a change of approximately 5%. However, this difference may be due to interstrain differences in other parameter values and the important point with regard to the present analysis is that the changes are relatively small and, most importantly, in the direction predicted.

The Development Function

Food quantity is important in determining development time (Sang 1950). A reduction in food quantity increases development time, decreases survival, and reduces the final body size. To what extent this reduction in body size is a phenotypic response and/or a genetic response as a result of differential mortality
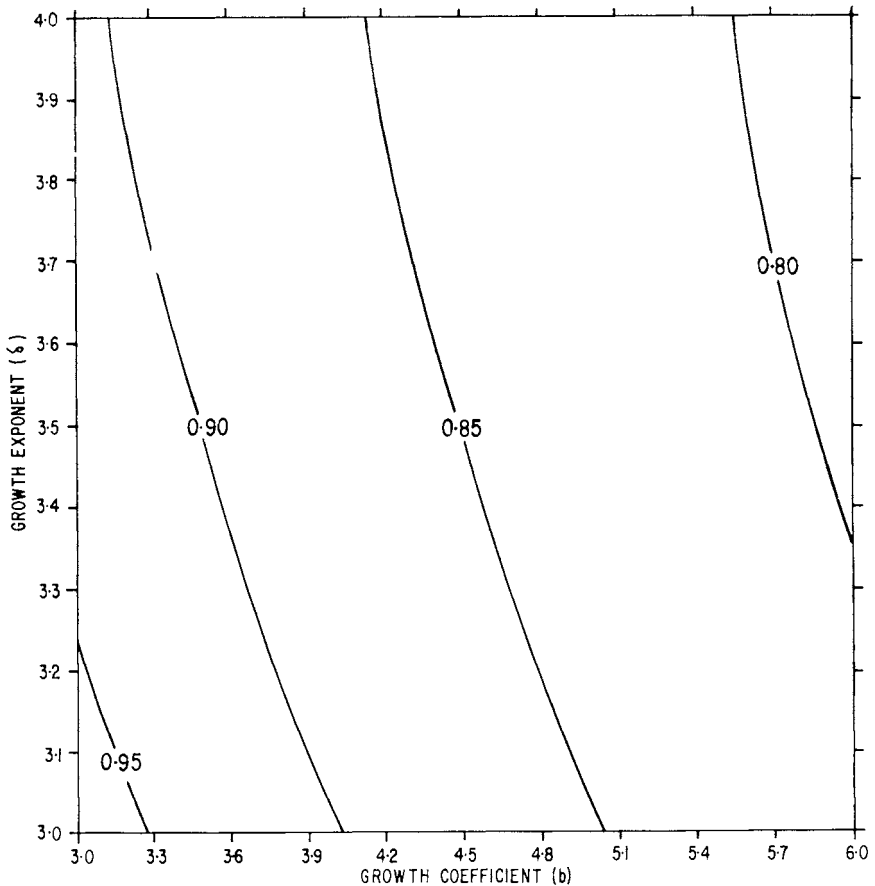
FIG. 3.—Response surface of the optimum thorax length on the growth coefficient, b, and the growth exponent, δ.

has not been adequately investigated. The data of Shorrocks (1970), although somewhat equivocal, suggest that the small size of flies raised under crowded conditions is a phenotypic response and not caused by an increased mortality of genetically large individuals. To assess the significance of increased development time I varied the "growth coefficient", b, from 3.0 to 6.0 and the "growth exponent", δ, from 3 to 4. The results are shown in figure 3. Any increase in development time selects for a reduced body size but the shift is rather small, from 0.95 mm to 0.80 mm. I have, in this analysis, ignored the phenomenon of phenotypic plasticity, evident in experiments such as Shorrock's (1970). This plasticity may increase the effective rate of increase of larger sized flies because they may pupate at a reduced size and hence have a smaller development time than predicted. However, the range in size of 0.15 mm is so small that ignoring phenotypic plasticity is of little consequence in this analysis.
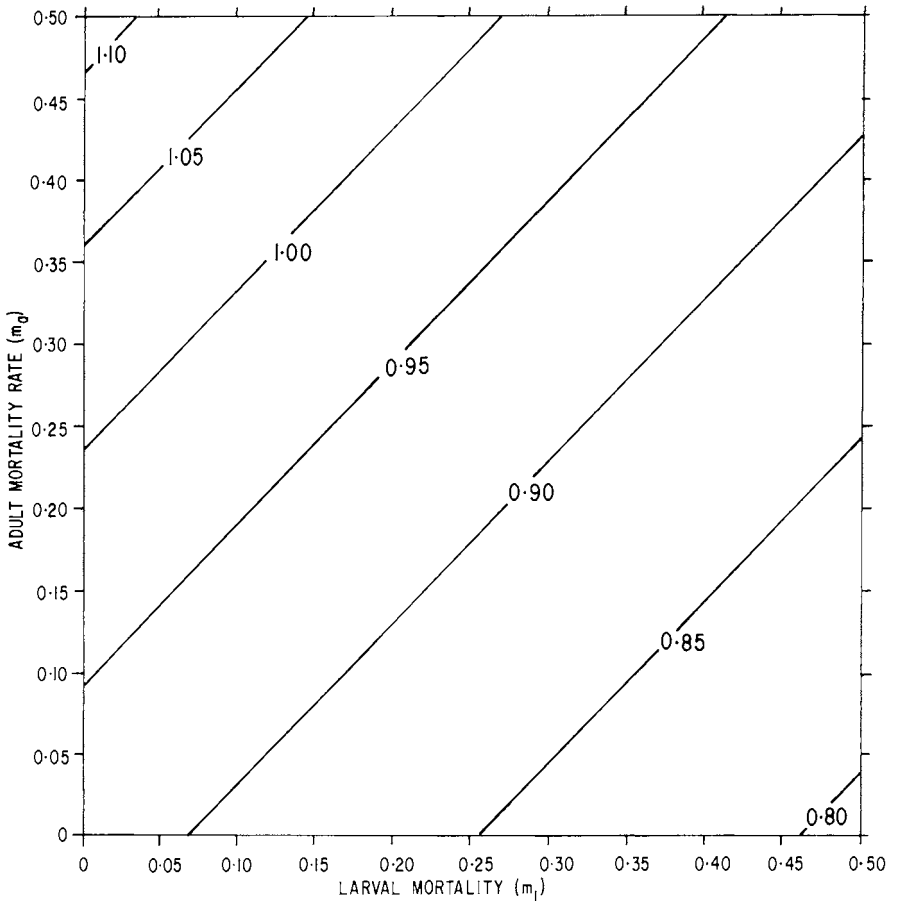
FIG. 4.—Response surface of the optimum thorax length on the larval m_l, and adult, m_a, mortality rates.

The Adult and Larval Mortality Rates

The final parameters to be examined are the larval and adult mortality rates. Since data are virtually nonexistent, for these two I selected a very large range for both, from 0 to 0.5, which is equivalent to a daily mortality rate of 0.0 to 0.6. Once again the effects are small, (fig. 4) the range in optimum size varying from 0.80 mm to 1.10 mm. Increasing larval mortality decreases body size, but as might be expected from the effect of K, increasing adult mortality increases size.

Temperature Effects

Laboratory stocks of flies are generally maintained at 25° C; but temperature fluctuations in the field may be quite large and it is therefore necessary to consider how this variation might affect body size. In practice any analysis of poikilotherm

life histories should use physiological rather than real time: This transformation (to degree days) results in development time being constant over all but the most extreme temperatures (David and Clavel 1967; and analysis of the data from Prowsner 1935). Although development time remains invariant with respect to temperature when a physiological time scale is used, mortality increases with deviations from the optimum (Tantawy and Mallah 1961; David and Clavel 1967) and phenotypic size increases with temperature (Eigenbrodt 1930; Stanley 1935; Tantawy and Mallah 1961; McKenzie 1978).

Over the range in temperature, 14° C to 30° C, a range that will encompass most environmental conditions, the total larval mortality varies between 12% and 22%. This, by itself, will have no significant effect on the optimal body size (see fig. 4). Although selection experiments and parent-offspring analysis clearly indicate that size is under genetic control (Robertson and Reeve 1952; Tantawy et al. 1964), the actual relationship between fecundity and size appears to be mediated most directly through phenotypic size rather than genotype. This suggestion is based on the observation that changes in size caused by crowding (Alpatov 1930; Chiang and Hodson 1950) or temperature (Alpatov 1932; Tantawy and Vetukhiv 1960) result in changes in fecundity that match those predicted by equation (2). In the latter study by Alpatov (1932) a change in the day of first egg laying was also observed, the larger flies beginning earlier. Thus changes in the phenotypic size of the adult will change the fitness of the genotype by altering the fecundity parameters. However, the maximum percentage increase or decrease in thorax or wing length is only of the order of 20% (Eigenbrodt 1930; Stanley 1935; Tantawy and Mallah 1961) and will have little effect on fitness and hence the optimum body size. Variation in the temperature encountered by the adult also changes the fecundity function. Much of this variation is a result of measuring on a real rather than physiological time scale (unpublished analysis of the data of Kaliss and Graubard 1936). In *D. pseudoobscura* total lifetime egg production is affected by temperature (Tantaway and Vetukhiv 1960) but this is only significantly altered in *D. melanogaster* when the temperature drops below 20° C (Kaliss and Graubard 1936). In both cases the magnitude of the change (at most a halving of production) is insufficient to greatly affect body size.

Although any one of the three effects of temperature discussed above will have little influence by itself, together they may be capable of producing a detectable shift in body size. An important caveat must be attached to this prediction: If flies are maintained at a particular temperature for any length of time it is likely that selection will favor physiological changes such as a shift in the temperature threshold for development and thus the relative fitness values may change. In this context it is interesting to examine the divergence of body size in M. Vetukhiv's experimental populations of *D. pseudoobscura* kept at different temperatures. Divergence was extremely slow, becoming evident only after 6 or 12 yr, depending on the temperature at which the stock was maintained (Anderson 1966, 1973). The pattern of change was for body size to be negatively correlated with temperature, though this is only clear when the flies were reared at 25° C (see table 1 of Anderson 1973). The total range in size was only of the order of 10%. This rather small change is predictable from the foregoing analysis and the slow rate of

divergence is not unexpected given the small change in r about the optimum body size. (For example, note the very small change in r for thorax lengths between .9 and 1.1 shown in fig. 1.) The direction of change, however, cannot be predicted satisfactorily because the opposing effects of an increase in larval mortality and a decrease in fecundity require the relevant functions to be precisely measured. Further, caution must be taken because the rates of development, as measured in real (daily) time, of the stocks changed, the flies maintained at 16° C developing faster than the other stocks, when raised at 19° C (Anderson 1966). This phenomenon may result from a decrease in the temperature threshold for development of the "cold" adapted stocks; such a decrease would make the rate of development appear faster when measured in real rather than physiological time. These results emphasize the extreme difficulty of adequately accounting for the "fine tuning" of body size unless a detailed examination of life history parameters is available.

Thus far, the sensitivity of the model has been examined by varying at most two parameters at a time. Some idea of the total variation possible can be obtained by selecting the set of extreme values that favor either an increase or decrease in body size. For the former this is $\delta = 3$, $A = 3.2$, $K = 40$, $\gamma = 4$, $m_l = 0$, $m_a = 0.5$ and for the latter, $\delta = 4$, $A = 6$, $K = 140$, $\gamma = 2$, $m_l = 0.5$, $m_a = 0$. The smallest optimum thorax length is 0.60 mm and the largest, 1.38 mm. Although this range is proportionally much wider than that observed (0.90–1.15) it is still surprisingly small given the large variation in parameter values. Under field conditions neither of the extreme sets of parameter values is likely to occur; conditions that are favorable for growth (small A, δ) are likely to be favorable for reproduction (high K, γ) and vice versa. Conditions probably change continuously and it is possible that the average conditions approximate the optimum conditions determined from laboratory experiments. This makes sense in that it is not unreasonable to expect development rates, survival rates, etc., to be adapted to average conditions, (although the fine tuning of body size may depend on environmental variability [Roff 1978]).

<div style="text-align:center">DISCUSSION</div>

The excellent fit between prediction and observation suggests that we do not need to invoke further factors to account for the general body size of *D. melanogaster*. The prediction that egg size variation between strains should be positively correlated to body size variation is also found to hold and gives added weight to the validity of the model. A significant finding of the sensitivity analysis is that wide variations in the life history parameters have relatively small effects on the optimum body size. This insensitivity is reassuring since *D. melanogaster*, being a cosmopolitan species, may encounter many different environmental regimes over its distribution, but the difference in size from the tropics to the temperate regions is only of the order of 10% (David et al. 1977).

The robustness of the model is important because if it were sensitive to parameter values then it would be possible to "tune it" to attain the appropriate thorax length. Under these circumstances we would have to have very accurate

measures of the parameters and have evidence that these were relatively invariable under natural conditions before we could say that the model predicted accurately. In the present case if thorax length in *D. melanogaster* were, say, 4.0 mm we would have to reject the model because its very robustness does not allow any reasonable parameter set that will give an optimum thorax length of 4.0 mm. The model predicts approximately 1.0 mm and that is the size actually observed. The robustness of the model to parameter estimation constrains and hence enhances the strength of the prediction.

The insensitivity of the optimum body size to variation in parameter values suggests that other *Drosophila* species having similar life histories to *D. melanogaster* should be approximately the same size. In this regard it is notable that the range in body length (which is approximately twice the thorax length) of the North American *Drosophila* species is only 1.4 mm to 3.00 mm, with a mean of 2.1 mm (data from Sturtevant 1921). The total variation likely from the sensitivity analysis was suggested to be 0.6 mm to 1.38 mm, or converting to body lengths, 1.2 mm to 2.76 mm. This range covers almost the full range observed for North American species and demonstrates that it is possible to account for this size variation with relatively minor parameter shifts while still maintaining the same structural model. Of the British *Drosophila* for which there are data *D. simulans* and *D. buskii* with thorax lengths of 1.02 and 1.05, respectively, lie within the observed range of variation of *D. melanogaster* while *D. subobscura* with a thorax length of 1.24 mm lies within the maximum range (Atkinson 1979a). *Drosophila immigrans, D. hydii,* and *D. funebris* lie outside this range, with thorax lengths of 1.59 mm, 1.51 mm, and 1.41 mm, respectively (Atkinson 1979a). It is still, however, possible to generate these optima by not unrealistic shifts in the parameters varied in this study and those held constant (t_0, α, β). A significant shift in body size can only be achieved by either gross shifts in a single parameter or lesser shifts in several parameters. The interaction of the life history components is such that body size tends to be buffered against variation. This buffering prevents the model from being infinitely flexible and it cannot give the relatively enormous sizes observed in some of the Hawaiian *Drosophila* species which may be three times as large as *D. melanogaster* (Hardy 1965). With changes in parameter values that seem reasonable for the Hawaiian *Drosophila* (for example, they have a much reduced fecundity implying a reduced K and/or γ [Kambysellis and Heed 1971]) it is possible to achieve an optimum body size of 1.8 mm. To increase the size to 3.0 mm would appear to require an additional component to the model. Given the enormous adaptive radiation of the Hawaiian *Drosophila* this finding is not unreasonable and demonstrates that the method of analysis can indicate both when sufficient factors have been considered and when there is a missing component.

In particular circumstances body size may be fine tuned by factors not considered thus far. For example, changes in the spatial distribution of oviposition sites may favor an increase in body size (Roff 1977). Similarly increased exposure to heat stress appears to favor large size (Levins 1969). Competition between larvae of *D. melanogaster* is a "scramble" rather than a "contest" (Bakker 1961) and hence under conditions of crowding selection should favor a reduction in size.

As in most insects, body size in *D. melanogaster* is strongly influenced by environmental conditions during development. It is not clear, however, to what extent the changes induced by the immediate environment are adaptive or simply unavoidable physiological responses. For example, is there any reason to suppose that a decrease in body size with temperatures above the optimum is advantageous? That the larva can survive and develop at all at elevated temperatures may be adaptive but the shift in body size may be, by itself, maladaptive. However, as described earlier such effects, even if maintained over a long period, do not have a major influence on the optimal body size. Variation in body size resulting from fluctuations in immediate environmental conditions may have insignificant influences on the fitness of particular genotypes for the following reasons. First, all genotypes may be affected so that flies of all sizes are smaller than if reared under optimal conditions. Second, there is considerable variability in fecundity, the life history component most directly affected by body size, even for highly inbred flies which are likely to be very similar in size (Robertson and Sang 1944). (Because major changes in fecundity are required to change r significantly this variation is expected [Lewontin 1965].) Third, effects on other life history components such as increased larval mortality may counterbalance the first effects on body size. For example, a decrease in the fecundity coefficient, K, favors an increase in body size but an increase in the larval mortality rate, m_l, favors a decrease.

Although the model presented in this paper applies specifically to *D. melanogaster*, the approach is not so limited and in principle could be applied to any situation. McLaren (1966), for example, used a model derived from similar considerations to explain the relatively large size of arctic marine zooplankters. In both this paper and McLaren's the assumption was made that density-dependent effects could be ignored. As a first approach such an assumption might be acceptable in most cases. For some, however, density-dependent phenomena could not be ignored. In these instances one approach that may pay dividends is to include in the Euler equation the relation between the life history component, density, and body size. The importance of density in determining the optimal body size can then be examined by varying density over the range observed in field populations. If it is found to produce substantial changes another approach such as simulation modeling may be required. In some cases both density and frequency effects might need to be considered. For example, in sockeye salmon, *Oncorhynchus nerka,* the probability of holding a mate depends on size (Hanson and Smith 1967) and it is probable that both the number of fish and the relative size are important in determining reproductive success.

SUMMARY

Most examinations of body size center on a single factor. However, because body size is directly or indirectly linked to many, if not most, life history characters a more holistic approach is advocated. In this paper I present such an approach in the analysis of the optimum body size of *Drosophila melanogaster*. The basic life history parameters determining r are shown to be related to body

size. Using these functions the relationship between r and body size is obtained. It is found that r is maximized within the observed range in size. A sensitivity analysis indicates that this result does not depend critically upon parameter estimation. This analysis also indicates that variation in egg size between geographic strains should be positively correlated to variation in body size. This prediction is shown to be correct. Reasonable variation in parameter values can account for much of the size range observed in the genus *Drosophila*. It does not appear to be possible to account for the very large size of certain Hawaiian species.

ACKNOWLEDGMENTS

APPENDIX

$$\sum_{t=1}^{\infty} e^{-r[t+D(L)+t_0]-m_l D(L)-m_a(t+t_0)-\alpha t_0} 1/2 F(L) e^{-\alpha t}(1 - e^{-\beta t}) = 1. \tag{1}$$

To obtain the optimum value of L in (1) we proceed as follows.

Let $A = r + m_a + \alpha$ and

$B = 1/2\, F(L)/\exp[D(L)(r + m_l) + t_0(r + m_a + \alpha)]$.

Substituting A and B in (1) and rearranging,

$$\sum_{t=1}^{\infty} [e^{-tA} - e^{-t(A+\beta)}]B = 1. \tag{2}$$

Now

$$\sum_{t=1}^{\infty} e^{-tA} = \frac{e^{-A}}{1 - e^{-A}}$$

and hence (1) and (2) can be solved to yield

$$e^r = \frac{B(1 - e^{-\beta}) + 1 + e^{-\beta} - e^{-(A+\beta)}}{e^{(m_a+\alpha)}}. \tag{3}$$

The optimum value of L is obtained by implicit differentiation of (3),

$$\frac{dr}{dl} K_1 = \frac{(1 - e^{-\beta})\,[F'(L) - F(L)D'(L)(m_l + r)]}{2e^{(m_a+\alpha+k_2)}} \tag{4}$$

where

$$k_1 = \frac{e^r + B(1 - e^{-\beta}) - e^{-(A+\beta)}}{e^{(m_a+\alpha)}}$$

$$k_2 = D(L)(r + m_l) + t_0(r + m_a)$$

and $F'(L)$, $D'(L)$ denote the differentials of $F(L)$ and $D(L)$, respectively. The rate of increase, r, is maximized when $dr/dL = 0$, i.e., when

$$F'(L) - F(L)\, d'(L)(m_l + r) = 0, \qquad k_1 \neq 0. \tag{5}$$

Hence the optimum size is that at which

$$r = \frac{F'(L)}{F(L)D'(L)} - m_l. \tag{6}$$

To obtain L (6) is substituted in (3) and a solution found numerically.

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