TEMPERATURE HETEROGENEITY AND GEOGRAPHIC VARIATION
IN LIFE HISTORY PATTERNS OF Drosophila melanogaster

By

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They are legion.

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A crucial problem in evolutionary biology is the development of a general theory for the evolution of adaptive life histories in environments that differ in degree of fluctuation and predictability of sequential conditions. Resolution of this problem requires examination of the phenotypic and genetic structure of life history components in populations that differ in environmental heterogeneity. I examined variation in viability, development time, age-specific fecundity, longevity and rate of metabolism for populations of Drosophila melanogaster from sites representing three points on the stable-fluctuating continuum for temperature variation.

The observed differences in population means, phenotypic and genetic correlation structure, and phenotypic plasticity indicate that different selective pressures operate in stable as opposed to fluctuating environments. Flies from the thermally stable population were characteristically highly sensitive to environmental change and

displayed many attributes of a K-selected population. The ecologically marginal site engendered more r-selected life history patterns. The flies showed marked plasticity in response to an environmental shift from 22°C to 25°C, but were homeostatic in response to warmer temperatures. Flies from variable environments exhibited higher rates of metabolism. These data suggest that in variable environments, responsiveness to conditions conducive to reproductive success may be at a selective premium, while in more stable regimes specialist genotypes with lower reproductive rates may be favored. Potential differences in mode and timing of selective action are discussed.

Phenotypic correlation structure was markedly different for the three populations and appeared to reflect temperature specific constraints. Tradeoffs between early and late life components were especially severe at low temperatures, but the form of the cost differed by population. The presence of considerable genetic variability for early life traits could not be explained by the variable pleiotropy hypothesis, since genetic correlation structure did not show the expected negative relationships between early and late life traits. The marked changes in genetic variance-covariance structure with minor shifts in environmental temperature suggest that current quantitative genetic models of life history evolution will not be adequate for heterogeneous environments. Other approaches to resolving the life history dilemma are addressed.

INTRODUCTION

It would be instructive to know not only by what physiological means a just apportionment is made between nutriment devoted to the gonads and that devoted to the rest of the parental organism, but also what circumstances in the life history and the environment would render profitable the diversion of a greater or lesser share of the available resources to reproduction.

R. A. Fisher (1958, p. 47)

Most organisms reproduce in environments that are spatially and temporally heterogenous in both abiotic and biotic components. One of the most complex problems confronting evolutionary biology is the development of a general theory for the evolution of adaptive life histories in environments that differ in the degree of fluctuation and the predictability of sequential conditions. The perceivable life history syndrome of an organism can be described, in part, by its age-specific survivorship and fecundity distribution, which is a complex function of its genetic potential, and the developmental and environmental conversions of that potential. The degree of fluctuation and predictability of the physical environment may have multiple direct and indirect influences on the expression of an organism's life history.

Adaptation to the innumerable exigencies imposed by environmental variation can occur in many ways. An organism may adapt to variable environmental regimes by synchronizing development, growth, and reproduction to coincide with the most favorable environmental conditions when predictive cues are available (Giesel, 1976; Tauber and Tauber, 1981, 1982). They may adapt behaviorally by choosing

microhabitats where favorable conditions prevail. An individual may respond to deviations from optimum conditions physiologically by modulating energetic demands (e.g. acclimation) or by conversion to systems operative under the new conditions (e.g. switching enzyme production). Organisms can adapt to fluctuating environments through phenotypic plasticity (Bradshaw, 1965; Giesel, 1976; Jain, 1979); populations may adapt through genetic polymorphism (Giesel, 1974, 1976; McLeod et al., 1981). Since the life history is a composite of all physiological, behavioral and developmental factors that contribute to the expression of the genetic program for fecundity and longevity, the course of adaptation to a variable environment will depend on available genetic variability (Fisher, 1958), and on the duration and predictability of favorable conditions.

How Is Fitness Defined?

One critical issue in the development of a comprehensive life history theory is the impact of environmental variation on fitness. Stearns (1976) defined fitness as "something everyone understands but noone can define precisely" (p. 4). Relative representation in future generations will be in part determined by the organism's innate ability to survive and reproduce, but will also be modulated by all the biotic and abiotic constraints encountered across time. Thus the fitness of an individual (or population) is relative not only to other individuals (populations), but also relative to a particular set of circumstances encountered over a specified time period. Such difficulties led Thoday (1958) to propose that a true measure of fitness would require knowledge of persistence of evolutionary lineages over long periods of time. Operationally defined, fitness must be viewed as some composite of

survivorship and reproduction. Since Lotka (1913) derived the characteristic equation, which relates age specific fecundity and survivorship to population growth rate, a considerable body of theory uses population growth rate (r_m) under unrestricted conditions as the primary index of fitness (Fisher, 1958; MacArthur and Wilson, 1967). Many indices of fitness have been employed, such as reproductive value, net reproductive rate, and population size. Lewontin and Cohen (1969) suggest that selection might act to maximize the geometric mean rate of increase. Demetrius (1975a, b) used information theory to relate entropy and reproductive potential to the Malthusian parameter for age-structured populations. He suggested that entropy is a better measure of fitness because iteroparous and semelparous strategies can be discriminated. Tuljapurkar and Orzak (1980) emphasize that extinction probability is an essential component. As Thoday (1958) and Tuljapurkar and Orzak (1980) state no single measure of fitness is possible.

Many models of life history evolution are based on the assumption that natural selection acts to maximize or optimize some measure of fitness. Due to phylogenetic inertia and other design constraints, there are no guarantees that predicted optima or maxima are attainable (Levins and MacArthur, 1966; Schaffer, 1974a, b; Schaffer and Rosenzweig, 1977; Stearns, 1977 and McLeod et al., 1981). In fluctuating environments, particularly, the population may be genetically tracking environmental change, which implies that additive genetic variance for fitness traits is present and, therefore, some distribution around the optimum or optima. Levins (1965) suggested that environmental change must be autocorrelated and predictable to a degree for net fitness to increase.

Since fitness itself is difficult to define and measure, fitness components are the usual measures of a life history. Stearns' (1976) review identified the key traits as brood size, size of young, age distribution of reproductive effort, interaction of reproductive effort with adult mortality and variation in the above traits. Theoretical predictions are reviewed for traits considered singly and for reproductive tactics, which he defined as a "set of coadapted traits designed to solve a particular ecological problem" (p. 4). Wilbur et al. (1974) similarly suggested that a life history pattern represents "a series of selective compromises to environmental variation" (p. 805). The most important traits in their analysis are age specific juvenile and adult mortality, age at first reproduction, length of the reproductive span, age specific fecundity, egg size and degree of parental care. They also suggest that the trophic level of the organism and the degree of environmental predictability must be considered. Stearns (1980) suggests that the implicit assumption that component fitness traits, such as age at maturity, survivorship and fecundity, are free to evolve or co-evolve under demographic influences is violated when there are developmental or allometric constraints. Since the relationship of component traits to fitness and their interrelationships with each other (both genetic and phenotypic) may also limit the effect of natural selection on a single trait, these associations must also be incorporated into predictive theory. Clearly, most traits considered as fitness traits display continuous variation rather than discrete character states. The impact of natural selection on such traits requires the merger of population and quantitative genetic treatments. Kempthorne (1983) in an analysis of the success of the merger to date

suggested that fitness can never be characterized as a single scalar variable which remains constant through a dynamic selection process. He suggested that survivorship and fecundity must be viewed as functions that are both genotypically and environmentally determined and that partitioning the effects of genotype and environment on variance and covariance of such traits will be an important but complex addition to general theory.

The crucial questions of life history evolution appear to revolve around the impact of environmental variation. A brief review of requisite ideas concerning environmental variation and its impact on the demography, phenotypic flexibility and genetic variation follows.

Environmental Variation and Life History

Since Dobzhansky (1950) proposed that selection operates differently in stable tropical habitats than in more variable temperate habitats, the impact of environmental variation has been a central focus of life history theory. Dobzhansky proposed that in temperate environments, density-independent mortality from environmental fluctuation would select for high, early reproduction. In more stable tropical areas, density-dependent competition and predation would be more important. His tropical-temperate dichotomy not only focused attention on the effects of environmental variation, but also influenced the development the stable-fluctuating dichotomy that forms the basis for the central-marginal model and the r/K selection model of life history evolution.

Levins (1962, 1963, 1968a, b) used the term environmental grain as an indicator of spatial and temporal variability of a particular habitat, measuring how rapidly environmental conditions change relative

to the lifespan of the organism. Temporal environmental variation can be perceived as fine-grained if the period of oscillation is shorter than the lifespan of the organism. Temporary, reversible physiological or behavioral adjustments might be expected in response to fine-grained variation. Conversely, coarse-grained environments, with periods of oscillation longer than an individual lifespan, may generate genetic polymorphism or more long term physiological or developmental conversions. Spatial variation can be considered analogously. If an organism spends its entire life in one habitat patch, the environment is perceived as coarse-grained. Where the organism is subjected to many patches in a lifetime, the environment is viewed as fine-grained. Templeton and Rothman (1974) generalized this approach by including alternatives to fitness maximization and by modelling continuous grain. When populations maximize minimum fitness over all environments, fitness homeostasis may result and can also generate polymorphisms in a fine-grained environment.

Adaptations which counter deleterious effects of environmental variation can encompass demographic, energetic or genetic strategies, although it is quite conceivable that all may be employed by the same population. The majority of theoretical treatments on the effect of environmental variation have focused on demographic tactics with little consideration of genetic variability (see reviews, Giesel, 1976; Stearns, 1976, 1977) or on simple two locus genetic alterations (Levins, 1968; Selander and Kauffman, 1973; Gillespie, 1974; and Johnson, 1974). The major genetical models, although they provide a useful beginning, are unlikely to characterize life history evolution, since life history traits are undoubtedly under predominantly polygenic control and because

the interaction between loci controlling any one component trait may be decidedly non-linear (Stearns, 1977). Emlen (1970) began to incorporate quantitative genetics into demographic models. Lande (1979, 1982) has formally incorporated quantitative genetic considerations of fitness traits and their association structure into demography.

One serious drawback to most life history models is that the pattern of fluctuation of even one environmental variable may be both coarse- and fine-grained with respect to the organism. For instance temperature has diurnal variation overlaid by seasonal variation as well as longer term changes. In response to temperature change an organism may employ several concurrent responses. If the environmental variability is smaller than the tolerance range of the organism, Levins (1968a) predicts a single phenotype of intermediate fitness. When the environmental range exceeds the tolerance of the organism, he predicts a single phenotype adapted to the most frequent environment if the environment is fine-grained, but a mix of phenotypes which parallel environmental variability in coarse-grained environments. These adaptive phenotypes may be produced through a number of pathways. A highly canalized trait may show little or no environmentally induced variation, which may be an optimum solution if no predictive information is available. The organism may respond by acclimation to prevailing conditions. Complete phenotypic stability in the face of environmental change is rarely seen in life history traits, but may be important in terms of modulating energy demands or may reflect phylogenetic constraints. Life history traits may display a "norm of reaction" in response to environmental change, which may result from a continuous developmental response to environmental conditions or a developmental

switch from one phenotype to another at a given threshold (Gupta and Lewontin, 1982; Parker, 1984). Levins has suggested that a developmental switch strategy would be most appropriate in fine-grained environments when the tolerance range is exceeded by environmental variation. He predicts continuous responses in coarse-grained environments. Stearns (1980) suggests that developmental plasticity protects the gene pool from short term selective pressures imposed by spatial and temporal heterogeneity.

The appropriate choice of critical environmental variables also complicates interpretation of much life history data. Climatic factors such as temperature tend to be correlated with other important variables such as food availability, but the pattern of correlation is not necessarily simple. Interactions between important environmental factors may generate complex response patterns in immediate and long term responses to environmental variation. In short, environments can rarely be classified discretely into stable or fluctuating, predictable or unpredictable categories. Selective regimes are difficult to classify exclusively into density-dependent or density-independent categories. In fact, density-independent selection can be an important component at any density. An environment may fall into one category with respect to temperature, another with respect to humidity, and yet another with respect to resource availability.

Central versus Marginal Populations

Selection pressures in peripheral populations may be different from the selective pressures operative in the center of a species range. Ecologically marginal populations are usually smaller and subject to the challenges of a stressful environment, while at the core favorable

conditions permit large, contiguous populations in which the primary selective agent may be inter- and intraspecific competition (Lewontin, 1974a; Brussard, 1984). Central populations may be less resistant to physical stressors. As physical environmental conditions deteriorate toward the range periphery, more energy may be diverted to maintenance and energetic partitioning may differ. Genetic variation has been predicted to be lower for ecologically marginal populations of a species relative to the more central populations (Mayr, 1963). Data on inversion polymorphisms in many Drosophila species essentially support this view (see reviews: Lewontin, 1974a; and Parsons, 1973, 1983a, b). Dobzhansky (1950) suggested that different inversions were adapted to different environmental conditions such that central populations with more spatial variation in resources may be expected to have many inversions when compared with marginal populations. Carson (1965) has suggested that the lower incidence of inversions in marginal populations allows a more open genetic system, with greater flexibility to adapt to new conditions through recombination. Markow (1975) demonstrated that the presence of inversions reduced the effect of selection for negative phototaxis in Drosophila melanogaster. Central populations are generally considered to be spatially more diverse in microhabitats leading to microgeographic genetic differentiation (da Cunha and Dobzhansky, 1954).

Lewontin (1974) suggested that temporal variation may be more important in marginal populations. He added that inversion polymorphisms would tie up available genetic variance for adaptation to environmental extremes and thus would not be favored in marginal habitats. High enzymatic variability is not precluded by this approach.

High levels of isozyme variability may be maintained by general hitchhiking effects (Maynard-Smith and Haig, 1974) or by gene flow between populations. North-South inversion clines have been documented for 20 populations of Drosophila melanogaster in the United States (Mettler et al., 1977). Southern populations in more temporally stable habitats (which may, however, be more spatially diverse) display much higher inversion frequencies.

The data for genic heterozygosity do not follow this pattern. Evidence from natural populations (Band, 1975; Prakash et al., 1969; Ayala et al., 1971; and Marinkovic et al., 1978) suggests high levels of heterozygosity in marginal and central populations. Laboratory studies indicate that environmental heterogeneity may be the main determinant of heterozygosity. Lewontin (1974a) suggested that high levels of heterozygosity in marginal populations may primarily be due to temporal instability in relevant ecological parameters and consequent changes in the direction of selection. Intermediate ranges of fluctuation appear to generate more genetic variability than either extreme fluctuations or constant conditions. Extremely stressful conditions may reduce genetic variation. Band and Ives (1968) showed that frequency of lethals was correlated with dry conditions in Drosophila melanogaster. The lower variance in very dry years may indicate population crashes resulting from extreme selection. Lethal and semilethal data also indicate lower genetic variance at ecological margins (Parsons, 1973, 1983a, b). In contrast, Langley et al. (1977) showed that gene frequencies for a number of allozymes were relatively stable over seasons and that linkage disequilibria were small for a large North Carolina population of Drosophila melanogaster.

Brussard (1984) in a review of the central-marginal model for Drosophila populations suggests that niche breadth, heterosis, and historical accidents are insufficient to account for the observed trends in reduction of inversion heterozygosity as one moves from central populations to those which occupy marginal habitats. He suggests that environmental favorability and predictability decline as one approaches the periphery of a species range, and that concurrently the primary selective mode changes from one which favors high average fitness in central populations to selection favoring flexibility at the periphery. As a consequence in the center of the species range selection is predominantly stabilizing and may even favor linkage disequilibria to minimize extreme phenotypes, which eventually can result in the coagulation of the genome into rigid supergene complexes. At the periphery selection is viewed to favor extreme phenotypes which can survive stressful conditions and free recombination is likely to become increasingly important as conditions become more stressful. He thus predicts that marginal populations will be chromosomally monomorphic, highly resistant to the appropriate environmental stressor and have on the whole a higher level of expressed variation.

Brussard concluded that population size for Drosophila species will depend primarily on availability of resources for feeding and breeding and on the prevailing annual temperature regime. Of course, population growth rate and the seasonal duration of positive population growth will be strongly influenced by the variation in environmental temperature. His conclusion that "once the temperature dependence of life history characteristics are known for a species, it should be possible to predict average levels of abundance along this gradient" (p. 52) may be

an oversimplification. The central-marginal hypothesis was developed for species that originated in the tropics and later colonized temperate areas. The predictions may not apply to species of temperate origin that expanded their range into more ecologically favorable tropical areas. In some senses, central populations would be marginal for such species. Even in species with tropical origins, central populations may experience episodic bouts of severe selection, when they become for a time ecologically marginal. For example, since the widespread eradication efforts, directed at the medfly in 1982, many drosophilids are difficult to collect in habitats that formerly supported high population densities.

Demographic Models

Early demographic models attempted to assess which life history traits were most important by considering the sensitivity of some composite measure of fitness to changes in single traits (Cole, 1954; Lewontin, 1965; Meats, 1971). Cole (1954) showed that age of first reproduction and birth rate could be expected to be strongly selected for in rapidly growing populations. Lewontin (1965) demonstrated that an iteroparous organism can raise its intrinsic rate of increase most effectively by increasing net fecundity per female or by decreasing age at first reproduction. In terms of caloric costs, he suggested that lowering the age of first reproduction may be more efficient than increasing the number of offspring. He predicted that colonizing species would have lowered genetic variance for age of first reproduction relative to variance for fecundity. Meats (1971) extended Lewontin's models to populations with low growth rates. He showed that if intrinsic rate of increase falls below 0.05, it becomes less

sensitive to factors affecting timing of reproduction and relatively more sensitive to fecundity changes. Hamilton (1966) and Mertz (1971) suggested that reproduction should be delayed in declining populations.

Demographic models that attempt to accommodate associations of life history traits in specific environments have been divided into stochastic and deterministic approaches (Stearns, 1976, 1977). Deterministic models predict associations of traits such as early maturity, large reproductive effort and short life will evolve in response to high density-independent mortality or wide fluctuations in population density. Density-dependent mortality and relatively constant population densities result in lowered reproductive effort and long life. These alternatives have been termed *r*- and *K*-selection respectively (MacArthur and Wilson, 1967). Pianka (1970) presented a table of life history correlates of *r*- and *K*-selection, based on his assumption of an inverse relationship between population density and juvenile survivorship, which suggested that reproductive effort should decrease in dense populations. An extensive literature subsequent to Pianka's paper employs the *r/k* dichotomy as a label for associated life history traits and as an explanation for the evolution of trait associations. In this dissertation, *r*-tactic and *K*-tactic will be used when referring to the trait associations suggested by Pianka. *K*-selection and *r*-selection will be reserved for situations where density-dependent selection may operate.

Stochastic models, which have been called "bet hedging", may produce similar trait associations in response to environmental variation, but the primary selective factor is the relative importance

of variability in juvenile mortality relative to variable adult mortality (Cohen, 1967; Murphy, 1968; Schaffer, 1974b). In predictable environmental regimes, r -maximization strategies might be expected (Holgate, 1967). Murphy's (1968) model showed that when the survival of juveniles is uncertain relative to the survival of reproductive adults increased iteroparity would be advantageous. The causes for fluctuations in juvenile survivorship could be density-independent factors such as weather conditions or density-dependent competition between juveniles for food, space or other resources. Murphy developed a simple genetic model and with computer simulations showed that long life and repeated reproduction could predominate under such conditions. His genetic model assumes that high fecundity and short life are closely linked and can be treated as facets of a single trait. Schaffer (1974 a, b) suggested that populations in which the young face high mortality rates and/or the adults have low probability of reproductive success should evolve a strategy of extended iteroparity. High adult mortality was predicted to generate early ages of first reproduction and thus relatively " r " strategies. Istock (1977, 1980, 1981, 1982) emphasized mortality differences between stages of a complex life cycle and predicted decreases in egg production and development time where larval mortality was of primary importance, but increased reproductive effort and development time where adult mortality was high. Goodman (1984) generalized bet hedging models to incorporate age structured populations using autoregressive time series models. He found that predicted growth rate was lower than that predicted by previous models, and that the degree of discrepancy increased with environmental variability and decreased with degree of iteroparity. Stenseth's (1980) models assert

that as reproductive rate increases, variance of population size increases. As spatial heterogeneity decreases, reproductive rate increases. As the apparent contradictions in the above hypotheses suggest, the evolutionary path taken by a given organism may depend on the duration, predictability, and density-dependent or density-independent nature of the primary selective agent.

Parry (1981) suggests that associating habitat stability and duration with r and K trait associations may obscure the specific selective forces that predominate in different habitats. This point reiterates the conclusions of Wilbur et al. (1974) who suggested that the r/K model does not include sufficient parameters to explain natural variation in life history patterns. They suggested that trophic position of the organism and degree of environmental predictability are essential parameters to include. Attempts to test the predictions of the various demographic models have met with limited success (Stearns, 1977). Some studies support r/K predictions (e.g. Gadgil and Solbrig, 1972); others support bet hedging models (e.g. Legett and Carscadden, 1978). Barclay and Gregory (1981), in an experimental study of stage specific-mortality in Drosophila melanogaster, showed that some life history traits followed the predictions of r/K models, while others more closely resembled bet hedging predictions.

Application of r/K models to populations subjected to fluctuating environments frequently assumes that environmental perturbations impose density-independent mortality that is age- and genotype-independent (MacArthur and Wilson, 1967; Planka, 1976). Boyce's (1984) review suggested that such assumptions rarely hold for natural populations. Caswell (1982) traced the historical background of the connection

between r/K selection models and the equilibrium status of populations. He contrasted the relevant selective pressures on r and K for equilibrium and nonequilibrium populations. The predictions of the standard r/K models assume that the selective pressure on r declines to zero as the population size approaches carrying capacity. In nonequilibrium populations selective pressures may change dependent on whether the population is increasing or decreasing and on the relative duration of the increasing phase. The patterns predicted in equilibrium situations would be intensified in nonequilibrium populations which have spent a large proportion of time in decline. Declining populations show trait combinations usually associated with K -tactics, such as slow development time, delayed reproduction and longer lives. Populations that have predominantly been in the increasing phase may show r -tactics. Caswell's model depends in part on a presumed equivalence between selective intensity in the increasing and decreasing phases (Boyce, 1984). Boyce suggested that the specific selective forces operational in the two phases may actually reverse Caswell's predictions, especially in cases where the density-independent mortality is age-specific.

Boyce (1984) explicitly states that the r/K model is useful for life history evolution problems only if applied as originally intended, that is, as a model of density-dependent selection. He attributes much of the difficulty in interpretation to confusion of realized population growth rate with r_{max} or the logistic growth rate. The maximum growth rate (r_{max}) is the amount of growth that could be attained in a totally unlimited environment. The logistic growth rate measures population growth under a particular environmental regime still unconstrained by density effects. It may be maximized by emphasis on early reproduction

or by extending longevity dependent on demographic conditions (Schaeffer, 1974b). Boyce states that high r "does not necessarily mean a high birth rate and it certainly cannot be equated with the birth rate" (p. 429). In addition, Hairston et al. (1970) suggested that much confusion stems from equating the logistic growth rate of a population with the genotypic character, m . In their view high m will always be favored by natural selection under a given set of constraints, but that the populations growth rate may be reduced from maximum under density-dependent mortality.

Strictly speaking the r/K model is only valid where mortality and fecundity rates are age-independent. But Boyce (1984) in reviewing the arguments for and against applying the logistic model to age-structured populations with overlapping generations suggests that deviations from the stable age distribution "do not invalidate long term population growth rates as one measure of fitness" (p.430). He concludes that although r - and K -selection may be important in shaping life histories, the effects of r - and K -selection may be totally independent of the selective impact of environmental variation.

Cost of Reproduction and the Tradeoff Assumption

Bell (1980) stated that "if reproduction is not costly then fitness is maximized by maximizing reproduction to the physiological limit . . . if reproduction is costly, there comes a point where the cost exceed the benefit" (p. 45). Although Pearl (1922, 1925, 1928) may have introduced the concept of cost of reproduction, Fisher's (1958, original edition, 1930) seminal work defined the problem of reproductive allocation in graphic terms. Anecdotal natural history data began to accumulate that suggested that reproduction at a particular point in

time entailed a cost in decreased future survivorship of the parent or decreased future reproductive potential (see Stearns, 1976). Cody (1966) suggested that observed tradeoffs might reflect energy partitioning when environmental resources are limited. He suggested that available energy must be allocated to competition, predator avoidance and reproduction causing tradeoffs to occur. Williams (1966a, b) incorporated these tradeoffs into demographic theory. He partitioned the reproductive value (Fisher, 1958) of an organism of a particular age into current reproduction and future reproduction, which he called residual reproductive value. The central idea of William's paper was the tradeoff between current reproduction and future survival (or reproduction). Charnov and Krebs (1973) agreed that the act of reproduction implies a mortality risk to the parental organism and reviewed examples. Stearns (1976) added other observations that suggest such a tradeoff. A plethora of models incorporating linear and curvilinear tradeoff functions were developed (Gadgil and Bossert, 1970; Fagen, 1972; Schaffer, 1974 a, b; Taylor et al., 1974; Charlesworth and Leon, 1976; Schaffer and Rosenzweig, 1977; and others).

Williams' formulation rests somewhat on the assumption that maximizing mean fitness is equivalent to maximizing age specific reproductive value. Schaffer (1974) and Taylor (1974) established proofs of that assertion, but Caswell (1982b) showed that this assumed equivalence holds only for cost constraints that operate within age classes. His review of the available evidence suggests that most costs are incurred well after reproductive investment.

Schaffer (1974a), Hirschfield and Tinkle (1975), Pianka and Parker (1975), Schaffer and Rosenzweig (1977) and others have developed this

assumption of the equivalence of maximizing fitness and maximizing reproductive value at each age to develop optimality models for age-structured populations (but see Caswell, 1980). Schaffer's (1974a) model suggested that multiple optima can occur as a result of tradeoff between current reproduction and future survivorship. This idea was developed further in Schaffer and Rosenzweig (1977), where they detailed the circumstances where particular cost curves might be expected to apply. Caswell (1982) extends the consideration of age specific costs of reproduction, separating clearly what different implications are generated if the reproductive cost is paid predominantly in the currency of future survivorship from the implications when the cost is measured in future reproductive output. He suggested that survival costs increase with age as the inverse of the reproductive value function, but that costs paid in future fecundity are relatively age-invariant. These predictions are operative only where the life history is optimal. Caswell (1984) added the joint consideration of costs in survivorship and fecundity which can be used to predict tradeoffs between demographic parameters given an optimal life history.

Optimality models have been criticized for a variety of reasons (see Stearns, 1977; and Charlesworth, 1980, among others). As Charlesworth (1980) suggested, since organisms live in changing environments, the appropriate genetic potential may not occur to produce an optimal life history. He suggested that since natural selection is usually more effective early in life, closer agreement with the predictions of optimality models may be expected for traits assessed early in life relative to late life traits.

The cost of reproduction at a particular point in time, whether paid in the currency of lessened survivorship or decreased future reproductive output, may play an important part in constraining life history structure. The cost of reproduction is intimately related to the organism's ability to procure and assimilate food resources. Resource variation in space and time may then represent major constraints on an organism's fitness. The energy budget approach to life history evolution focuses on optimal partitioning of available energy to maintenance, reproduction and growth (Calow, 1973; Gadgil and Bossert, 1970). If total energy available is limited, then a tradeoff between early reproduction and subsequent survivorship is assumed to exist. In general the theoretical predictions of cost-benefit models parallel those of Schaffer (1974b). When the profit gained from reproductive expenditure is low, the organism will gain more from delayed maturity and increased iteroparity. Delayed maturity may be expected where fecundity increases with age. The proportion of resources devoted to reproduction, i.e. reproductive effort, is expected to increase with age; however, Charlesworth and Leon (1976) showed theoretically that if the intrinsic rate of increase is high, reproductive effort may decrease with age or remain constant. In essence, costly reproduction may impose constraints on what age-specific fecundity and mortality curves are possible for an organism.

Inverse correlations between early life fecundity and later reproduction have been demonstrated in Tribolium (Boyer, 1976, 1978) which may have a genetic basis (Mertz, 1975). Selection experiments on chickens (Morris, 1963) on mice (Wallinga and Baker, 1978) and on Drosophila melanogaster (Luckenbill et al., 1984) indicate that

selection for increased early fecundity led to decreases in late life production. Maynard-Smith (1958) showed that reproductive females had shorter lives than nonreproductives in Drosophila sudobscura. Gowen and Johnson (1946) and Rose and Charlesworth (1981a) observed negative phenotypic correlations between longevity and rate of egg laying in Drosophila melanogaster. Snell and King (1977) reported negative phenotypic correlations between fecundity and longevity in the rotifer, Asplanchnia brightwelli, but such associations may result from intergenomic or environmental effects. Giesel (1979) and his coworkers (Giesel and Zettler, 1980; Geisel et al., 1982a, b; Murphy et al., 1983) have observed significant positive associations between early fecundity and duration of life and between early and late life fecundity in some environmental conditions for Drosophila melanogaster and Drosophila simulans. Positive correlations between early reproduction and late reproduction or longevity have been observed (Bell, 1984a, b; Hegmann and Dingle, 1982).

The relationship between current reproduction and future survivorship or fecundity deserves further investigation. Few critical measures of the tradeoff function under controlled conditions have been made. Tuomi et al. (1983) suggest alternatives to tradeoff models for life history evolution. Compensation and threshold hypotheses that they advanced allow weaker correlation between reproduction and later survivorship. They suggested that the allocation system must be considered as the basis for the cost of a given absolute reproductive effort. When reproductives and nonreproductives have the same amount of available energy, the cost may be high. Where reproductive individuals garner a greater amount of energy relative to nonreproductive

individuals (or less reproductive), the cost depends on the allotment of increased energy to acquire these resources and on what proportion of the excess is devoted to reproduction. Their compensation hypothesis suggests that increased intake during the reproductive period or growth prior to the reproductive period can negate or reduce the cost of reproduction. The threshold hypothesis implies that physiological resistance may be great enough so that the cost becomes important only after a certain proportion of somatic investment. Tuomi et al. (1983) also suggest that tactics are not molded by demographic forces alone but by structural and physiological interrelationships between traits that act as constraints on life history evolution.

Boyce (1984) suggested that K-selection might result in lowered metabolic rate. Bennett (1983) stated that low rates of metabolism in ectothermic vertebrates may be advantageous because of lower food intake requirements and higher conversion efficiencies. McNab (1980) suggested that when sufficient resources were available, high metabolic rates might be favored because of a positive association with intrinsic rate of increase. The predicted association between metabolic rate and intrinsic rate of increase has been demonstrated for mammals (Hennemann, 1983). Marsteller (1984) presented an allometric model that considers the joint interaction of food and temperature on reproduction and survivorship for eutherian mammals. This model allows quantitative consideration of the energetic constraints on life history evolution.

Genetic Predictions in Heterogenous Environments

Consideration of the genetic basis of fitness and its component traits adds complexity to theories of life history evolution. Early population genetic theory emphasized the genetic determination of

fitness to such an extent that the only conceivable explanation for polymorphisms in fitness traits, as well as other traits less closely related to fitness, was heterosis. The discovery of nearly ubiquitous polymorphism in natural populations for enzymes led to reconsideration of mechanisms for the maintenance of genetic variation. One school of thought attributes genetic variation to some form of balancing selection (e.g. Selander et al., 1971; Ayala, 1972), while another considers electrophoretic variation to be essentially neutral (e.g. Kimura, 1968; King and Jukes, 1969) and maintained by stochastic processes such as drift. Since gene frequency clines are frequently highly correlated with environmental factors (see Parsons, 1983a, for review, and Mitton and Grant, 1984), most life history theorists fall into the selectionist school.

Since Levene (1953) suggested the importance of spatial heterogeneity to the maintenance of genetic polymorphisms, theorists have advanced a number of models implicating spatial heterogeneity (see Felsenstein, 1976, for review). Basically, these models can be classified as habitat choice models or random distribution, variable fitness models. Temporal and spatial heterogeneity have been proposed as major selective agents in life history evolution. Levins (1965, 1968a) and Gillespie (1974, 1977) have predicted that populations living in spatially fine-grained habitats will show increased genetic variability in comparison with populations from relatively coarse-grained habitats. Gillespie and Langley (1974) suggest that the conditions for polymorphism in temporally varying habitats are more stringent than for spatial variation. Ayala et al. (1971) and Valentine and Ayala (1974) have proposed an adaptive strategy model

which suggests that species with food resources which vary temporally in quantity and quality might evolve a number of specialized genotypes each exhibiting high fitness in specific trophic conditions. On the other hand, temporally coarse-grained trophic resources might accentuate a spatially fine-grained adaptive response. The species might then evolve a flexible genotype which has high fitness over a range of conditions. Giesel (1974) in a simulation study showed that populations polymorphic for net fecundity distributions had higher fitness in a varying environment. Bryant (1976) has pointed out the difficulty of separating spatial and temporal components of variation, but a few laboratory experiments have suggested that indeed spatial and temporal heterogeneity do increase additive genetic variation (MacKay, 1981).

Evidence from many natural populations showing positive correlations between environmental variance and genetic variance suggests that some form of balancing selection may be important (Nevo, 1978; Powell and Taylor, 1974; Hedrick et al., 1976). Caution is necessary in interpreting data from natural populations, since our knowledge of breeding history is generally limited and does not allow exclusion of stochastic processes. In addition the degree of variation in relevant environmental parameters is difficult to assess. In laboratory experiments, MacKay demonstrated that both temporal and spatial heterogeneity increased genetic variation for sternopleural bristle number and body weight in Drosophila melanogaster, relative to control populations which were held in constant environments. In these experiments the absence of genotype-environmental interactions indicated that the increased genetic variance was due primarily to heterosis. Temporal variability was at least as effective as spatial heterogeneity

in inducing increased genetic variance, contrary to the predictions of most models (Felsenstein, 1976).

However, spatial heterogeneity can be viewed as more predictable than temporal variation (Bryant, 1976). Stenseth (1980) suggested that increased spatial heterogeneity led to more stability in population size than would be found in more homogenous habitats. Laboratory experiments (Powell, 1971; Powell and Taylor, 1979; and Powell and Wistrand, 1978) demonstrated positive correlations between the degree of enzyme polymorphism and environmental variability in Drosophila willistoni and D. pseudoobscura. Band (1963) found that the frequency of lethals and semilethals was higher in populations subjected to an 8oC diurnal temperature range than it was for populations raised at constant temperature or with a 14oC range of variation. Beardmore (1961) demonstrated increases in additive genetic variance in fluctuating temperature environments compared with stable temperature environments for Drosophila melanogaster. Beardmore and Levene (1963) compared offspring of populations raised at constant temperature with offspring of populations reared with a 17 to 27oC oscillation in temperature. Higher viability was reported for the offspring of the population exposed to variable temperatures. Long (1970) reported that Drosophila melanogaster populations exposed to fluctuating temperature conditions in the laboratory had higher competitive ability and lower NaCl tolerance than stable populations. Overall population fitness was related to the frequency of the temperature oscillation, and the population from a constant temperature environment had the lowest overall fitness.

Since fitness may be subdivided into component metric traits, a quantitative genetic approach may allow some resolution of the tangle of models and predictions. Quantitative genetics allows the partitioning of observable variation into phenotypic, genetic and environmental components. Under restricted conditions, measurement of genotype by environment interactions which may maintain genetic variance in a population are possible. Measurement of heritabilities of traits may indicate past selection on those traits and assessment of genetic correlations which may constrain response to selection are possible. The application of quantitative genetic principles to life history is yet in its infancy, and the data so far collected do not present a clear picture. Most models employing the quantitative genetic approach (Lande, 1979, 1982a, b) and much of the empirical data (Dingle et al., 1982 and other papers in that volume) interpret genetic variance-covariance structures according to Robertson's (1955) analysis of Fisher's Fundamental Theorem. Robertson suggested that additive genetic variance would be depleted for traits closely related to fitness, and that genetic correlations between fitness traits would become negative. However, Robertson's analysis may only apply under very restrictive assumptions, which may never hold for natural populations.

Rose (1983) classified life history theories according to their characterization of the genetic association between life history traits. He identified a unitary hypothesis which suggests that all life history traits should be positively correlated components of fitness, evolving as fitness evolves. The test implication of this view would be that fitness traits would display low additive genetic variance and

covariance, as a result of constant directional selection to maximize fitness, which of course may not characterize all evolutionary events. Rose suggested that the unitary hypothesis must be rejected because of evidence for abundant genetic variation in fitness components. Another hypothesis, which he termed the "particulate" hypothesis, includes as its major premise the age-specific intensity of selection. The test implications were that additive genetic variance should increase with age for life history traits such as fecundity, and that late life characters and early life characters should exhibit low genetic correlations. His own view is embodied in the variable pleiotropy hypothesis which suggests that antagonistic pleiotropy is the rule for fitness components. Although life history parameters surely display complex developmental interactions and therefore may not be expected to behave autonomously or in a unitary fashion with respect to natural selection, as yet no clear picture emerges that suggests that natural selection always acts through variable pleiotropy.

As Parsons (1982) indicates, the critical issue may not be the variability of the genome as a whole, but the nature of the variability controlling ecologically important phenotypes. He suggests that the genetic architecture of Drosophila melanogaster in marginal populations might be primarily controlled by a few additive genes with large effects. Parsons also suggests that in ecologically marginal situations adaptive strategies will shift to the "r" end of the r/K continuum. In Drosophila melanogaster desiccation resistance is high, and development time is not only fast but nearly invariant, in southern Australia populations. Toward the equator, low desiccation resistance and slow, variable, development times are the rule. Spatial variability toward

the equator appears to favor more variability in such traits as ethanol tolerance and larval ethanol preference. Parsons implies that temporal variability in ecologically important variables is the primary determinant of genetic variability in marginal habitats while spatial variability is more crucial in central populations. The type of environmental heterogeneity, as well as the predictability and the degree of fluctuation relative to the general tolerance range, may determine the variability available for further selection.

Problem Statement

Since as yet no coherent synthetic model has emerged that adequately treats demographic, energetic, and genetic strategies in varying environments, sensible resolution of which model may apply to a given organism is quite difficult. Testable hypotheses require knowledge of which abiotic factors are important and how they vary in space and time. It requires knowledge of biotic influences, energetic constraints and the genetic and phenotypic architecture of fitness traits. The measureable life history reflects the underlying genetic system, epigenetic systems which translate genotype into phenotype and the environmental system. This dissertation is a preliminary attempt to resolve some of these difficulties. I have chosen to measure life history variation in three populations of a widely distributed cosmopolitan species, Drosophila melanogaster, under different temperature conditions.

A primary consideration in the choice of environmental temperature as the critical variable was that timing and quantity of reproduction are known to vary with temperature. Environmental variance of the habitats could be approximated from weather data. Measuring life

history variation under several temperature regimes may allow dissection of gene-environment interactions and in concert with measures of metabolic rate under the same conditions may indicate evolution of physiological responses to changed conditions.

I shall address the following questions:

1. Do the populations from habitats differing in degree of fluctuation and predictability of environmental temperature differ in life history phenotypes?
2. Is each population adapted to a characteristic temperature optimum?
3. Does temperature affect the expression of life history traits in a similar fashion?
4. Are the components of fitness as measured by cohort intrinsic rate of increase similarly weighted at all temperatures and in each population?
5. Do tradeoffs exist in these populations between current reproduction and future survivorship or reproduction? If so, are they more severe in a particular population or environment?
6. Does metabolic rate differ for these populations? If so, do the changes in metabolic rate explain the differences in life history parameters?
7. Does a cosmopolitan species have a globally coadapted life history pattern or has selection modified the correlation pattern of life history traits?
8. What does the genetic architecture of fitness traits in these populations indicate about the nature of selection in these habitats and the potential for further life history evolution?

CHAPTER I GEOGRAPHIC VARIATION IN LIFE HISTORY PATTERNS

Introduction

Drosophila melanogaster is perhaps the most cosmopolitan of the dipteran species with a worldwide synanthropic distribution. David and Toscas (1981) define a cosmopolitan species as one that is known from all six classical faunal regions. Drosophila melanogaster is not only known, it is populous and ubiquitous wherever man or a more natural disturbance disrupts the habitat. From a probable African origin (Wheeler, 1981; but see Okada, 1981) Drosophila melanogaster has hitchhiked with man nearly everywhere, even to Nearctic regions. Such reproductive success in the face of a multitude of environmental contingencies, and in competition with numerous endemic fruitflies, requires a remarkable degree of genetic, physiological or behavioral flexibility. Carson (1965) and Dobzhansky (1965) proposed that cosmopolitan drosophilids have greater genetic adaptability leading to ecological versatility relative to their endemic relatives. Parsons and Stanley (1981), in their review of the cosmopolitan drosophilids, suggest that they are characterized by temperature races and biogeographic clines associated with temperature. Comparisons of Drosophila species from different habitats suggest that widespread species are more tolerant of environmental stressors than endemic tropical species (Levins, 1969; Parsons and MacDonald, 1978; Parsons 1981a).

For a species like Drosophila melanogaster, which is basically a colonist, it may be instructive to consider that different selective pressures may be operative in central and marginal populations. Periods of hard selection (sensu Wallace, 1981) may predominate at the edge of a species range (Parsons, 1982). Marginal populations are more likely to be responding to environmental stressors, while core populations may be responding primarily to inter- and intraspecific competition. Temporal variation is suggested to be the prime driving force at the periphery (Lewontin, 1974a), while in the center spatial heterogeneity may be more important. Temporal heterogeneity has been predicted to increase genetic variance if the pattern is fine-grained (Levins, 1965, 1968; Gillespie, 1974, 1977). Giesel (1974) in a simulation study showed that populations polymorphic for fecundity distributions had higher net fitness in temporally varying environments. Temporal variation has been shown to increase genetic variance for sternopleural bristle number and body weight in Drosophila melanogaster (MacKay, 1981). However, when the range of fluctuation is extreme, genetic variance may be reduced (Band, 1963; Long, 1970).

Brussard (1984) in a review of the central-marginal theory for Drosophila populations suggests that niche breadth, heterosis and historical accidents are insufficient to account for the observed trends in reduction of inversion heterozygosity in marginal habitats. He concludes that as environmental favorability and predictability decline toward the periphery of a species range, the predominant selective mode favors flexibility. At the more predictable and suitable central part of the range, high average fitness is favored. As a consequence selection on central populations may be primarily stabilizing and may

even result in linkage disequilibria to minimize extreme phenotypes. At the periphery extreme phenotypes that can survive the particular stressors are favored and free recombination is likely to become more important as conditions become more stressful. He thus predicts that marginal populations will be chromosomally monomorphic, highly resistant to the appropriate environmental stressor and have a higher level of expressed variation.

As Parsons (1982) suggests, the critical issue may not be the variability of the genome as a whole, but the nature of variation controlling ecologically important phenotypes. Parsons suggests that ecologically marginal habitats will favor adaptive strategies toward the r end of the r/K continuum. Parsons implies that temporal variation is more important at the periphery while spatial heterogeneity predominates as a selective agent in the center of a species range. Temporal heterogeneity favoring r-selection and flexibility of response to environmental stress may be the primary factor in the periphery, while spatial heterogeneity may cause K-selection, adaptation to the optimum environment and great susceptibility to stress in central populations. Brussard (1984) suggests that saturation selection (Whitaker and Goodman, 1979) may predominate in central populations and severe exploitation selection may occur in ecological margins.

Other life history models may explain intraspecific variation in life history patterns, but without prior knowledge of environmental variation and other aspects of the selective regime, predictions are uncertain. Since environmental variation is one key aspect of the selective regime, this analysis focuses on the mean life history and the phenotypic correlation structure in Drosophila melanogaster derived from

three sites that differed in temporal heterogeneity and uncertainty for environmental temperature.

Environmental Variation in the Habitats

Drosophila melanogaster used in this set of analyses were third generation descendants of field collected flies from three areas. The Gainesville population collection site was an abandoned orange grove near Melrose, Florida. The Palm Beach site was a backyard citrus grove. Michigan flies were collected from rotting cherries in a grove near Grayling, Michigan. The areas chosen for study were presumed to differ in selective regimes, varying in the degree of stability and predictability of important environmental parameters.

Gainesville, Florida, is located in the north-central portion of the Florida peninsula (Latitude 29°31'N; Longitude 82°21'W). The surrounding terrain is gently rolling with an average elevation of 50 m above sea level. The soils are generally sandy and of low natural fertility. The general climate is marine in summer due to prevailing winds and ocean proximity. Summers are long, warm, and relatively humid with little day-to-day temperature fluctuation. In winter the climate more closely approximates continental conditions. In general winter conditions are mild and relatively dry, but daily maximum and minimum temperatures show considerable day-to-day variation. During warm spells daytime highs may remain above 27°C for several consecutive days. During cold spells daytime highs may remain at 5°C for several days. Relative humidity ranges from an early morning average of 90% for all seasons to an average low of 40% in the afternoon of the late spring dry season or 60% in the June through September rainy season (NOAA, 1981c).

West Palm Beach is located on the coastal sand ridge of southeastern Florida (Latitude 26o41'N; Longitude 80o07'W). The average elevation is 5 m. The area is characterized by very fertile peatlike soils. Because of its southerly location and marine influences the weather conditions are least variable and the most predictable of the three areas studied. Temperatures in excess of 40o C can occur in all months of the year. The wet season is May through October but relative humidity rarely falls below 60% at any time of the day or month of the year (NOAA, 1981d).

Grayling, Michigan (Latitude 44o40'N; Longitude 84o42'W) is much cooler and drier than either Florida area. The elevation averages 348 m and the soils are sandy supporting little agricultural production. The daily temperature range is quite extreme and variable from day to day even in the summer. Precipitation is slightly higher in the April to September period, but always less on a monthly basis than either Florida site. The average growing season is 90 days. Temperatures below 0o C have been reported every month of the year although they are rare in July and August (NOAA, 1978).

Table 1.1 presents the average monthly mean, minimum, maximum and min-max range for the three populations. Data have been converted to C from National Oceanic and Atmospheric Administration (NOAA) data for a thirty year period (NOAA 1979a, b; 1980a, b; 1981a, b, c, d). The three sites can be ranked in terms of mean annual temperature. Palm Beach is the warmest (23.6o); Gainesville is slightly cooler (21.3o); and Michigan is much colder with an annual mean of 6.7oC. Temperature variation was assessed by calculating the variance for the thirty years of temperature data. Variance in month-to-month temperature over the year is lowest in

Table 1.1 Temperature Variation in the Three Collection Sites

Month	Mean monthly temp			Minimum		
	GV	PB	MI	GV	PB	MI
Jan	14.7	18.6	-7.6	8.5	13.3	-12.1
Feb	15.7	18.9	-7.3	9.3	13.4	-12.8
Mar	17.8	21.0	-2.4	11.4	15.7	- 8.3
Apr	20.9	23.3	5.8	14.4	18.3	-0.8
May	24.4	25.3	12.4	17.8	19.4	4.9
Jun	26.7	26.9	17.7	20.8	22.6	10.3
Jul	27.2	27.7	19.8	21.6	23.4	12.5
Aug	27.3	27.9	19.0	21.8	23.6	11.9
Sep	26.2	27.5	14.5	20.9	23.7	8.0
Oct	22.3	25.1	9.3	16.4	21.2	3.4
Nov	17.6	21.7	2.1	11.3	16.9	-2.1
Dec	14.8	19.3	-4.6	8.7	14.3	-8.6
Annual	21.3	23.6	6.6	15.3	18.9	0.5

Month	Maximum			Average daily fluctuation		
	GV	PB	MI	GV	PB	MI
Jan	20.7	23.8	-3.0	12.2	10.5	9.1
Feb	21.9	24.4	-1.7	12.6	11.0	10.1
Mar	24.3	26.3	3.4	12.9	10.6	11.7
Apr	27.4	28.3	12.3	13.0	10.0	7.4
May	31.1	30.1	19.9	13.3	10.7	15.0
Jun	32.6	31.3	25.0	11.8	8.7	15.3
Jul	32.7	32.0	27.1	11.1	8.6	14.6
Aug	32.8	32.3	26.0	11.0	7.7	14.1
Sep	31.5	31.3	20.9	10.6	7.6	12.9
Oct	28.3	29.1	15.2	11.9	7.9	11.8
Nov	23.8	26.4	6.2	12.5	9.5	8.3
Dec	20.8	24.5	-0.7	12.1	10.2	7.1
Annual	27.3	28.3	12.6	12.0	9.4	12.1

GV= Gainesville, PB= Palm Beach, MI= Michigan

Palm Beach. The Gainesville area is 2.3 times as variable as Palm Beach in average monthly maximum, 1.7 times as variable in average monthly minimum and 1.9 times as variable in average month-to-month variation. Michigan is 13 times as variable in average monthly maximum, 5.2 times as variable in the minimum and 8.2 times as variable in month-to-month variation. The average degree of diurnal variation as approximated from the max-min fluctuation for this thirty year period shows that Palm Beach is the most stable on a short term basis, followed by Gainesville. The Michigan site is the most fluctuating and least predictable with the exception of the November-March period when it is quite stable but below temperatures required for Drosophila activity.

Crude estimates of temporal and spatial heterogeneity of larval food resources are indicated by USDA market data (Florida Department of Agriculture, 1984). Citrus is available in the Palm Beach market in every month but August. In the November to March period at least six varieties are in production. In the Gainesville area, citrus availability is limited to the hardiest oranges and quite localized. Probable resource bases include secondary vegetable foods, such as cucumber and the varied resources of human refuse dumps. The Michigan site is perhaps the most limited seasonally. Small localized cherry orchards and individual vegetable gardens are the only concentrated resources available (Michigan Department of Agriculture, 1983a, b;1984).

Methods

Drosophila melanogaster used in this set of analyses were third generation descendants of field collected flies from the three sites described in detail above. To initiate these experiments one pair of offspring from each putatively unrelated wild female was used to

initiate each isofemale line in half pint milk bottles at 25o. The isofemale lines were cultured on a 14 day turnover schedule for two generations. To initiate the study virgin females were either sib-mated or mated with a male from another line within the population. Twenty sib-mated isofemale lines and 20 outcrossed lines were set up for the Gainesville and Michigan populations; 31 inbred lines and 20 outcrossed lines were initiated for the Palm Beach population. Each mated female was allowed to oviposit for 24 hrs on a paper strip containing a large drop of standard Drosophila medium which was lightly innoculated with live yeast. After approximately 24 hrs, larvae judged to be in the first instar were picked from the laying strip and seeded in groups of 20 into plastic pill vials containing approximately 5 ml of fresh medium. At least three cultures of sibling larva were established and assigned randomly to developmental temperature regimes of 22o, 25o, or 28oC. The relative humidity was approximately 80% and the light cycle was 12L:12D for all treatments.

The cultures were monitored daily until eclosion began at which time emerging flies were removed twice daily. Females of known development time were individually pair mated, usually with siblings. From five to seven replicate cultures were initiated for each original mating. The experimental flies were transferred to a vial containing fresh medium supplemented with a drop of live yeast suspension each day. The number of eggs laid in the previous 24 hour period was recorded daily for each individual in the experiment. Males from lab cultures were added if the original male died or escaped in the course of the experiment. Complete records of development time, age-specific fecundity and longevity were attained for a total of 1232 flies in the

course of the experiments. Equipment failure resulted in the loss of data for a large number of 250 Palm Beach flies.

The analyses reported in this paper are based on a subset of the total data set for which life history data and metabolic rates were available at all temperature treatments (Table 1.2). Age specific fecundity data were reduced for analysis to several measures of early, late and total fecundity. Reproduction on day 2 (RD2) was recorded as the number of eggs laid on the second day after emergence. First five days fecundity (FFD) was recorded as the total number of eggs laid in the first five days after emergence. First third fecundity (FTF) was the average number of eggs laid per day by an individual female in the first third of her life. Amount of peak reproduction (PK) was the number of eggs laid on the day when the largest amount of reproduction occurred. Late reproduction was indexed by last third of life average daily fecundity (LTF). Average daily fecundity (AVF) was recorded as the total number of eggs laid during life divided by the length of life post eclosion. Net reproductive rate (R_0) was calculated for each cohort as the sum of the $l_x m_x$ distribution (l_x and m_x represent age-specific survivorship and age-specific fecundity, respectively). Reproductive timing was assessed by several measures. Development time (DT) was recorded to the nearest 0.5 days for each individual female in the analysis as the time from first instar larva to adult emergence. Age of peak reproduction (AOP) was recorded as the day of life post-eclosion when the largest number of eggs was laid. Age of death or longevity (AOD) was recorded as the number of days of adult life. Cohort generation time (GT) was calculated from the formula $\ln(R_0)/rc = GT$.

Table 1.2 Sample Sizes in the Total Data Set and Cohort Analysis

TOTAL DATA SET

Pop	Temp	Inbreds		Crosses	
		#lines	#flies	#lines	#flies
GV	22	19	67	15	53
	25	19	79	16	58
	28	18	69	15	76
PB	22	31	116	14	69
	25	14	42	5	21
	28	28	136	15	48
MI	22	16	58	18	80
	25	15	58	19	83
	28	15	45	18	76
TOTAL			670		564

COHORT DATA SET

Pop	# Inbred lines	# Outcrossed lines	# Females
GV	10	11	269
PB	12	5	284
MI	11	13	295
TOTAL 848			

Intrinsic rate of increase (r_c) was calculated for each cohort by iteration from the Lotka-Euler equation, assuming a sex ratio of 1:1 and that maternal cohort viability would be characteristic of offspring cohorts. Larval to adult viability was recorded for each cohort as the percentage of larvae seeded that emerged within three days of the first fly to emerge in that cohort. Complete survivorship curves are plotted for each population at the three temperature treatments.

Rates of metabolism were estimated at all three temperatures on full sibs of the females from Gainesville and Michigan. Palm Beach metabolic rates were estimated using third generation descendants of the original field collected females. Oxygen consumption was estimated by Gilson respirometer at three temperatures. Seven to ten females from each line were transferred to 7 ml respirometer flasks and equilibrated in a 22°C water bath for 1.5 hours. Readings were taken at 15-20 minute intervals for 2 hours or until 3 sequential readings were essentially equal. Environmental temperature was then raised to 25 °C and following a 1 hour equilibration period the measurements were repeated. The same process was repeated at 28°. Each group of females was then etherized and weighed to the nearest 0.01 mg. All oxygen consumption data were converted to standard temperature and pressure prior to analysis. All experiments were initiated at the same time of day to prevent differences due to circadian rhythmicity, and flies were kept in the dark to inhibit activity. These data will be discussed in a separate chapter. If either metabolic rate data or life history data on at least three females were not available for a particular line, it was excluded from the cohort analysis.

Data Analysis

Before the analysis of variance was conducted, the data were partitioned by temperature and examined for normality of distribution and heterogeneity of variance across temperature treatments both within and across population groups. A series of transformations was applied as suggested by Sokal and Rohlf (1981). Rather bizarre transformations were required to reduce the heterogeneity of variance in the data (Table 1.3). Since the data set was inherently expected to display some heterogeneity, I decided to apply the full model to both transformed and untransformed data. The very minor differences between the analyses will be noted in the results section. In general the results of ANOVA on transformed data did not differ from untransformed data. Since untransformed data are more readily interpretable for population mean differences, this report will focus on the untransformed data. Some caution in interpreting marginal levels of significance is therefore required.

Analysis of Variance

Mixed model analysis of variance was conducted using SAS general linear model procedures (Freund and Littell, 1981). The model employed in the overall analysis was

$$\begin{aligned}
 Y_{ijklm} = & u + T_i + P_j + G_k + L(PG)_{jk1} + \\
 & (P \times T)_{ij} + (G \times T)_{jk} + \\
 & (P \times G)_{jk} + (P \times G \times T)_{ijk} + \text{error}
 \end{aligned}$$

Table 1.3 Transformations that Reduced the Heteogeneity of Variance

Character	Transformation
Metabolic Rate	Log [arcsine 1/square root (MR)]
Cohort Intrinsic Rate	Arcsine (r)
Age of Death	Square root (AOD)
Vaibility	Arcsine (viability)
Development Time	Log [log (DT)]
Generation Time	Arcsine [1/square root (GT)]
Average Fecundity	Square root (AVF)

where T_i represents the mean effect of the i th temperature

P_j represents the mean effect of the j th population

G_k represents the mean effect of the k th group

L_{jk} represents the mean effect of lines within a
population-group.

The lines effect was a random effect; all others were fixed effects. The population and group effects were tested with the lines mean square, since lines was nested within population-group. The two and three way interactions comprise the rest of the model. Partial correlations between metric traits were estimated from the error sum of squares and cross products matrix. Phenotypic correlations between metric traits were estimated by Pearson product-moment correlation. Statistical significance of correlations depends on sample size, and was determined from standard tables (Dixon and Massey, 1957). Spearman rank correlations were also calculated but did not give results which differed from the Pearson correlations.

Results

Quantity Variables

Table 1.4 summarizes the ANOVA for fecundity variables. Interpretation of the main effects for this data is complicated by the presence of two and three-way interactions for several of the quantity variables. Populations differed significantly for all quantity variables except net fecundity and total lifetime fecundity. However, since the $P \times G \times T$ interaction is significant for net fecundity and total, the lack of significance for population effect may indicate that population differences occur. Group and temperature effects are highly significant for all quantity variables. The line component is

Table 1.4 F Values for the Cohort Analysis of Variance for Fecundity Traits

Effect	df	RD2	FFD	PK	FTF	LTF	Ro	TOT
Pop	2	5.96**	6.53**	9.89**	3.70*	10.24***	0.98	2.92
Group	1	5.67*	7.45**	8.18**	9.10**	4.17*	20.32***	16.44
Temp	2	33.06***	33.73***	9.01**	32.85***	3.24*	6.71**	6.92
L (PG)	67	3.98**	1.75**	1.87**	3.01***	2.07**	1.52*	1.16
PxG	2	.04	.28	.41	1.55	2.56	.09	.48
PxT	4	4.36**	3.35*	.23	1.35	.56	1.16	1.54
GxT	2	.24	2.05	.32	.27	.15	.36	2.54
PxGxT	4	1.32	2.35*	.91	.75	.22	2.12+	2.46
Error	148							

+ = .05 < p < .10

* = .01 < p < .05

** = .001 < p < .01

*** = p < .001

significant for all traits except total fecundity, indicating a genetic basis for these traits. Since interaction effects were significant for several quantity traits, population differences may be best assessed by examining differences in mean values for each population at a particular temperature.

Mean values for fecundity characters are presented in Tables 1.5 and 1.6. At 22oC the inbred samples display significant differences between population means for reproduction on day 2, peak fecundity, last third fecundity, total and net fecundity. These differences are primarily due to much lower values in the Palm Beach population. This population also displays much lower values for first five days fecundity and average fecundity although the values are not significantly different. The pattern displayed by the outcrossed flies is quite different with most significant differences resulting from low values in the Gainesville population. At 25o there are no significant differences in inbred flies or crosses in total or net fecundity, but early reproduction is significantly lower in the Palm Beach population, intermediate in the Gainesville flies and highest in Michigan flies. Amount of peak reproduction is significantly higher in Michigan than in either Florida population. Late fecundity and average fecundity are higher in the Michigan population, but only in inbred flies. At 28o Michigan flies have significantly higher fecundity relative to Palm Beach flies at all phases of the life cycle, and they are significantly higher than the Gainesville flies for all traits but reproduction on day 2 and total fecundity among inbred flies. Fewer means differ significantly in the crosses, but the pattern is essentially the same. These results suggest a pattern of relatively stronger r-selection as

Table 1.5 Arithmetical Means for Fecundity Variables (S.D.)
in Inbred Flies

Trait	Gainesville		Palm Beach		Michigan	
-----22o-----						
RD2	18.33	(1.15)	16.54	(1.10)	26.44	(1.70)
FFD	144.6	(26.1)	135.2	(20.6)	148.4	(23.6)
AVF	44.1	(4.22)	34.9	(3.34)	41.7	(3.86)
PK	89.44	(2.07)	67.82	(2.90)	87.67	(1.13)
LTF	34.50	(1.15)	25.90	(0.96)	40.50	(0.87)
TOT	1183	(138)	792	(109)	895	(126)
Ro	401.1	(59.0)	232.6	(46.6)	298.2	(53.8)
-----25o-----						
RD2	31.70	(4.47)	13.90	(6.40)	41.70	(5.20)
FFD	171.0	(22)	157.5	(23.7)	228.3	(23.8)
AVF	39.6	(3.6)	40.0	(3.8)	53.4	(3.8)
PK	87.3	(4.9)	89.5	(7.0)	104.1	(5.8)
LTF	35.5	(2.7)	34.6	(3.9)	45.5	(3.2)
TOT	1021	(116)	1092	(126)	1017	(125)
Ro	338.7	(49.8)	388.6	(53.8)	334.1	(53.7)
-----28o-----						
RD2	31.90	(4.80)	43.6	(3.80)	44.3	(5.80)
FFD	226.1	(20.0)	240.3	(20.5)	299.3	(24.8)
AVF	42.1	(3.2)	37.4	(3.4)	62.1	(4.0)
PK	90.1	(5.3)	95.6	(4.3)	107.4	(6.5)
LTF	29.9	(2.9)	28.6	(2.3)	39.9	(3.6)
TOT	939.1	(106)	731.6	(112)	1140.1	(131)
Ro	236.2	(45.1)	216.1	(48.4)	338.1	(56.2)

Table 1.6 Mean Values of Fecundity Traits in Crosses (S.D.)

Trait	Gainesville		Palm Beach		Michigan	
22o						
RD2	20.67	(2.20)	32.00	(3.01)	26.40	(1.38)
FFD	125.6	(26.1)	205.6	(26.0)	178.6	(22.0)
AVF	37.0	(4.2)	46.3	(4.2)	46.2	(3.6)
PK	85.67	(2.40)	98.20	(4.09)	103.10	(1.61)
LTF	34.10	(1.01)	40.50	(1.80)	54.7	(1.64)
TOT	1036	(138)	1195	(137)	1205	(116)
Ro	377.8	(59.0)	499.2	(59.0)	426.5	(49.8)
25o						
RD2	34.90	(4.6)	20.5	(7.6)	55.80	(3.9)
FFD	247.6	(26.1)	190.0	(29.0)	293.2	(22.0)
AVF	55.4	(4.2)	53.0	(4.7)	62.8	(3.6)
PK	112.7	(4.4)	96.6	(7.3)	125.7	(3.8)
LTF	41.3	(2.9)	41.0	(5.0)	47.6	(2.4)
TOT	1417	(138)	1604	(154)	1425	(116)
Ro	486.8	(59.0)	529.5	(65.9)	547.8	(49.8)
28o						
RD2	53.90	(4.4)	58.60	(5.1)	55.5	(4.1)
FFD	280.3	(24.3)	232.4	(31.1)	301.2	(22.9)
AVF	51.04	(3.8)	51.59	(5.0)	57.28	(3.7)
PK	111.0	(4.2)	108.8	(4.9)	124.6	(5.8)
LTF	38.2	(3.1)	36.9	(3.4)	40.1	(2.6)
TOT	1274.6	(126)	806.0	(164)	1147.1	(121)
Ro	448.0	(54)	271.1	(70)	431.0	(51.7)

environmental conditions become less predictable. The only contraindication is the relatively high early reproduction in the Palm Beach flies at 22o.

The effects of temperature on population means are more clearly displayed in Figures 1.1 to 1.6. A change in temperature from 22o to 25o causes a sharp increase in all fecundity traits in the Michigan population. However a further increase in rearing temperature to 28o gives slight increases in early fecundity measures but declines in late fecundity, total and net fecundity. The Gainesville flies display a similar pattern but all fecundity traits are lower than those for Michigan flies at 25o and most are lower at 28o. The Palm Beach population displays an entirely different temperature response pattern. Early fecundity measures such as reproduction on day 2, first five days fecundity and peak fecundity show slight decreases as temperature is changed from 22o to 25o, but large increases in these variables result when temperature is increased to 28o. Average fecundity shows no significant response to temperature. Late fecundity decreases with increases in temperature, while total and net fecundity are highest at 25o falling off at either extreme. These response patterns contraindicate a simple physiological response to increasing temperature. A clear temperature optimum for each population following the environmental gradient is not indicated, since early fecundity in Palm Beach flies is higher at 22o and 28o, while Gainesville and Michigan flies perform better at 25o and 28o. These results may suggest that flies from the more variable and unpredictable habitats are less sensitive to environmental variation, as has been predicted for marginal populations.

Figure 1.1 The effect of temperature on reproduction on day two.
 (least squares means)
 (a) inbred isofemale lines
 (b) intrapopulation crosses

Figure 1.2 The effect of temperature on first five days fecundity.
 (least squares means)
 (a) inbred isofemale lines
 (b) intrapopulation crosses

Figure 1.3 The effect of temperature on peak fecundity.
(least squares means)
(a) inbred isofemale lines
(b) intrapopulation crosses

Figure 1.4 The effect of temperature on last third fecundity
 (least squares means)
 (a) inbred isofemale lines
 (b) intrapopulation crosses

Figure 1.5 The effect of temperature on average fecundity.
(least squares means)
(a) inbred isofemale lines
(b) intrapopulation crosses

Figure 1.6 The effect of temperature on total fecundity.
 (least squares means)
 (a) inbred isofemale lines
 (b) intrapopulation crosses

The patterns are fairly similar for inbred flies and crosses. The main differences in pattern are seen between Michigan inbred and outcrossed flies for first five days fecundity, net fecundity, average and total fecundity. Inbred flies show more nearly linear temperature response patterns for these variables, while crosses tend to have much higher fecundity at the intermediate temperature. In all populations the outcrossed flies have higher mean fecundity as expected due to heterosis, with the exception of the Gainesville flies at 22o. The measured degree of difference between outcrossed and inbred flies is presented in Table 1.7. The Gainesville population displays no heterotic effects at 22o; significant heterosis for all traits except reproduction on day 2 and last third fecundity at 25o and large differences for all traits at 28o. Palm Beach flies, however, display the highest heterosis for all traits at 22o, while only reproduction on day 2, average fecundity and last third fecundity remain significant at 28o. Michigan flies display significant heterosis for all traits except last third fecundity at 25o, but only reproduction on day 2 and peak fecundity are significantly higher at 28o. At 22o peak fecundity, last third fecundity, net fecundity, and total show heterosis.

Phenotypic correlations between fecundity measures are presented in Table 1.8 for the crosses. If the correlation patterns are similar for the three populations when reared under identical conditions in the laboratory, a common basis for the pattern or coadaptation of fecundity traits is inferred. These data illustrate that correlation patterns are not the same in these three populations. The correlation between first five days fecundity and average fecundity is positive in the flies from both Florida populations, but there is no apparent correlation between

Table 1.7 Heterosis for Fecundity Traits, Indexed by Percent
Difference Between Means of Inbreds and Crosses

Trait	22o			25o			28o		
	GV	PB	MI	GV	PB	MI	GV	PB	MI
RD2	13	93	0	10	47	34	69	34	25
FFD	-15	34	17	31	17	22	19	-3	.6
AVF	-11	25	10	29	25	15	17	28	-9
PK	-4	45	18	30	8	21	23	15	16
LTF	-1	56	35	16	19	5	30	35	1
TOT	-14	34	26	28	32	29	26	9	1
Ro	-6	54	30	30	27	39	47	20	22

Table 1.8 Phenotypic Correlations between Fecundity Traits in Crosses

Trait	Gainesville			Palm Beach			Michigan		
	22	25	28	22	25	28	22	25	28
FFD with									
AVF	.73*	.58*	.52*	.49*	.94*	.12	.00	.42	.62*
Ro	.20	.35	.56*	-.26	.21	.61*	.43+	.25	.70*
TOT	.52+	.53*	.65*	-.03	.64*	.65*	-.03	.37+	.64*
AVF with									
Ro	.46+	.47+	.78*	.48+	.38	.59+	.48*	.39+	.88*
TOT	.80*	.84*	.70*	.38	.70*	.71*	.52*	.73*	.78*
Ro with									
TOT	.76*	.80*	.77*	.95*	.61*	.97*	.74*	.55*	.87*
RD2 with									
PK	.26	.73*	.80*	.78*	.75*	.72*	-.06	.11	.47+
LTF	.27	-.14	-.44*	.13	.27	.66*	-.57*	.31	.44+
Peak with									
LTF	.59*	.14	-.02	.56*	.45*	.87*	.42+	-.22	.92*

* = $p < .05$ + = $p < .10$

early fecundity and average fecundity in the Michigan flies. Net fecundity is not significantly correlated with first five days fecundity in Florida flies, but it is significantly positive in the Michigan flies. Correlations between average fecundity and total or net fecundity appear to have a common basis at 22o. This may indicate that essentially the same trait is indexed by these variables. Early fecundity and late fecundity are not significantly associated in the Florida flies at 22o, but are negatively associated in the Michigan flies, which may indicate some phenotypic costs are incurred due to high early reproduction. At 25o the correlation patterns for the three population are much more similar. At 28o, however, many differences emerge. Correlations between early and average fecundity are similar in the Gainesville and Michigan flies. The correlation between early and late fecundity is negative in the Gainesville flies but positive in Palm Beach and Michigan flies. The response to temperature in correlation between traits within populations suggests that changing temperature conditions impact the three populations differently. Some correlations (average with total or net fecundity) behave similarly with shifts in temperature in all populations, but early fecundity measures have different patterns of association with each other and with late fecundity measures in each population.

Timing Variables

Traits that relate to the timing of reproduction provide additional information on differences in life history patterns for these populations. The analysis of variance indicates clear population, temperature, and population by temperature interaction effects for age of peak reproduction, age of death (duration of reproductive life),

and generation time (Table 1.9). There are no significant differences between the populations for development time, which is essentially equivalent to age of first reproduction. In addition, the lines component is not significant for development time indicating little or no genetic variance for this trait.

Temperature response patterns for timing variables follow similar patterns in the Gainesville and Michigan populations (Figures 1.7 to 1.10). Development time and age of death are highest at 22o and decrease somewhat linearly with increasing temperature in both inbred and outcrossed flies. This may essentially indicate a linear physiological response to increasing temperature. Michigan flies nearly always have lower values than Gainesville flies for timing variables but the mean differences are not significantly different (Table 1.10). Age of peak fecundity and generation time show a similar decline from 22o to 25o, but the effect is modulated at 28o which may indicate tolerance to extreme conditions as might be expected of flies from marginal habitats. The low age of peak reproduction, short life and short generation time in the Michigan flies supports stronger r-selection in this peripheral population. The Palm Beach flies present a different picture. They have the highest value for age of peak reproduction and age of death at 25o for both inbreds and outcrossed flies. Generation time is also highest at the intermediate temperature for the crosses. These data may indicate that the significant P x T interaction in the ANOVA reflects a

Table 1.9 F Values from Analysis of Variance for Timing Traits

Effect	df	DT	AOP	AOD	GT
Pop	2	.49	19.10***	7.51**	3.12*
Group	1	7.65**	.29	4.96*	.89
Temp	2	206.49***	37.18***	15.34***	163.47***
Line (PG)	67	.89	2.58*	1.09+	.98
PxG	2	.80	1.46	.20	.21
PxT	4	1.36	3.46*	4.09**	4.50**
GxT	2	.32	.07	.61	.10
PxGxT	4	.77	.68	1.64	.55
Error	148				
model r2		.95	.91	.90	.95

* = .01 < p < .05

** = .001 < p < .01

*** = p < .001

Figure 1.7 The effect of temperature on development time (least squares means)
 (a) inbred isofemale lines
 (b) intrapopulation crosses

Figure 1.8 The effect of temperature on age at peak fecundity (least squares means)

(a) inbred isofemale lines

(b) intrapopulation crosses

Figure 1.9 The effect of temperature on age of death
(least squares means)
(a) inbred isofemale lines
(b) intrapopulation crosses

Figure 1.10 The effect of temperature on generation time
 (least squares means)
 (a) inbred isofemale lines
 (b) intrapopulation crosses

Table 1.10 Mean Values for Timing Traits with Standard Error
in Parentheses

Inbreds			
Trait	Gainesville	Palm Beach	Michigan
22o			
DT	9.50 (.26)	10.19 (.21)	9.92 (.24)
AOP	10.24 (.15)	6.83 (.21)	10.21 (.26)
AOD	28.65 (2.2)	21.14 (1.7)	21.38 (1.9)
GT	18.17 (.50)	17.94 (0.4)	17.93 (.50)
25o			
DT	8.57 (.22)	8.50 (.26)	8.50 (.24)
AOP	7.77 (.40)	9.20 (.25)	7.97 (.23)
AOD	23.80 (1.81)	26.60 (1.96)	18.70 (1.90)
GT	15.91 (.44)	16.78 (.48)	14.99 (.47)
28o			
DT	6.82 (.20)	6.80 (.29)	7.18 (.25)
AOP	6.91 (.21)	3.80 (.09)	6.27 (.15)
AOD	21.97 (1.6)	18.24 (1.7)	18.25 (2.0)
GT	13.19 (.40)	12.35 (.42)	12.90 (.49)

Table 1.10 (continued)

Crosses			
Trait	Gainesville	Palm Beach	Michigan
22o			
DT	9.30 (.26)	9.40 (.26)	9.79 (.22)
AOP	11.75 (.46)	8.40 (.30)	9.14 (.19)
AOD	27.71 (2.1)	26.35 (2.1)	26.05 (1.8)
GT	17.87 (.51)	16.88 (.51)	17.85 (.44)
25o			
DT	8.50 (.26)	8.50 (.29)	7.93 (.22)
AOP	8.21 (.28)	11.20 (.27)	7.86 (.09)
AOD	25.32 (2.1)	30.34 (2.4)	22.93 (1.8)
GT	16.08 (.52)	17.31 (.58)	14.28 (.44)
28o			
DT	6.75 (.24)	6.57 (.31)	6.77 (.23)
AOP	6.77 (.25)	4.56 (.32)	6.25 (.12)
AOD	24.96 (1.9)	15.08 (2.5)	20.04 (1.9)
GT	12.88 (.47)	11.57 (.62)	12.49 (.45)

different strategy for temperature adaptation for timing of reproduction in the Palm Beach population. These data do not clearly indicate a high temperature optimum for Palm Beach population since the 22o and 28o flies have lower development time and age at peak reproduction and shorter generation times.

Correlation patterns between timing variables illustrate further population differences. Although mean development times did not differ by population, the correlation of development time with other timing variables did differ (Table 1.11). In the Gainesville flies development time is not correlated with any other timing trait. In the Palm Beach flies development time is negatively correlated with age of death and generation time at 28o and positively correlated with generation time at 25o. The negative correlations imply that flies that develop fastest and have a lower age of first reproduction have longer lives. The same kind of relationship is seen in Michigan flies at 22o, but not at the higher temperatures. Positive correlations between development time and generation time were expected. The negative correlation between these two timing factors in the Palm Beach 28o flies means that those flies with the lowest age of first reproduction had longer generation times. This implies a high negative correlation between development time and fecundity traits at 28o. This is confirmed in Table 1.11. The positive correlation between age of death and age of peak reproduction implies that flies who delay maximum reproduction until late in life survive longer. This association is significant in Gainesville flies at 22o and in Palm Beach and Michigan flies at 28o. Age of death and generation time are positively correlated at 22o in all populations.

Table 1.11 Phenotypic Correlations between Timing Variables for Crosses.

	Gainesville			Palm Beach			Michigan		
	22	25	28	22	25	28	22	25	28
DT and									
AOP	.28	.25	.16	-.30	.15	.36*	.19*	-.17	.05
AOD	-.24	-.12 ⁺	.26	-.27	-.09*	-.85*	-.62	-.26*	.16*
GT	.17	.49*	.38	.36	.53	-.64	.06	.69	.62
ACD and									
AOP	.60*	.20	-.05	.37*	.37	.90*	.05*	.06	.57*
GT	.69*	.35	.32	.71*	.31	.41 ⁺	.56	-.03	.13

* = $p < .05$ + = $.05 < p < .10$

Correlation patterns between timing variables and quantity variables are presented in Table 1.12. Development time is negatively correlated with all quantity variable at 28o in Palm Beach flies and in Michigan flies at 22o. This implies that for those flies and those temperature conditions lowered age of first reproduction is associated with higher early, average, and total fecundity. The positive DT-FFD correlation in the 28o Gainesville flies suggests that lowered development time has a cost in terms of amount of reproduction. Although age of death can be expected to be positively associated with net fecundity and total fecundity, one might anticipate tradeoffs between amount of early reproduction and duration of life, especially under stressful or limiting conditions. However, age of death has a significant positive association with early fecundity at 25o and 28o in Gainesville flies and at 28o in Palm Beach flies. The expected negative correlation only appears in 22o Palm Beach flies.

Temperature effects on the correlation patterns are particularly apparent for age of death and generation time. The association of early fecundity with longevity changes from no significant correlation at 22o to significant positive correlations at 25o and 28o in Gainesville flies, but the pattern in Palm Beach flies is negative at 22o, insignificant at 25, and positive at 28o. Average and peak fecundity are positively associated with age of death at 25o, but uncorrelated at both extreme temperatures in the Gainesville flies. In Palm Beach average fecundity is positively correlated at 22o and uncorrelated at 25o and 28o while peak fecundity is uncorrelated with age of death at 22o and 25o but positively associated at 28o. Michigan flies display no significant associations between age of death and first five days

Table 1.12 Phenotypic Correlations between Timing and Quantity Variables for Crosses

	Gainesville			Palm Beach			Michigan		
	22	25	28	22	25	28	22	25	28
DT and									
FFD	-.14	-.07	.42 ⁺	.26	.32	-.65*	-.30	-.16	.25
AV	.00	-.11	.30	.38	.21	-.60*	-.13	.29 ⁺	-.03
Ro	-.17	.04	.02	-.07	-.46 ⁺	-.90*	-.47*	.41 ⁺	.14
TOT	-.17	-.11	.37	-.03	.07	-.95	-.60	.11	.11
ACD and									
FFD	.01	.45 ⁺	.45 ⁺	-.68*	-.04	.89*	-.01	-.08 ⁺	.27
AV	.18*	.68*	.08	.71*	-.06 ⁺	.18*	.04*	-.37 ⁺	-.04
Ro	.75*	.88*	.38*	.61*	.49*	.84*	.61*	.15	.24*
TOT	.72*	.97*	.77*	.76*	.66*	.80*	.87*	.35*	.59
LTF	.35	.41	-.73	.27	.23	.84	-.11	-.52	.18
GT and									
FFD	-.47 ⁺	-.27	-.20	-.59*	-.54*	.84*	-.62*	-.56*	-.41
AV	-.05	.29	.10	-.03	-.58	.77*	.11	.30	-.03
Ro	.35	.35	.04	.43*	-.46	.76*	.19*	.19	.06
TOT	.34	.35	.30	.62	-.22	.68	.53	.26	.11

fecundity or average fecundity or peak fecundity. There were no significant correlations with age of peak reproduction in any population.

Viability and Survivorship

The ANOVA for larva-adult viability shows highly significant group, temperature, and line effects. The PxGxT interaction is significant at 0.02 level (Table 1.13). The mean temperature response patterns for the populations (Figure 1.11) suggest that Palm Beach flies survive to eclosion best at 22o, decreasing the proportion surviving when the temperature is raised. Gainesville inbred flies show a similar pattern, but outcrossed flies have higher viability at 28o than they have at 25o. Michigan flies perform slightly better at 25o but essentially have the same average viability at all temperatures. These results follow the pattern of lowered environmental sensitivity in populations from the most unpredictable environment and higher response to environmental change in populations from stable habitats.

The strongest phenotypic correlates of viability in all populations are with net fecundity (Table 1.14). This correlation is expected to be very strong because of the intimate relationship of age specific survivorship in the formula for calculating net fecundity. In the Gainesville population, early fecundity and average fecundity showed weak negative correlations with viability at 22o, no correlation at 25o and significant positive correlations at 28o. If 22o is viewed as a limited or stressful environment for Gainesville flies, a tradeoff between energy allocation to successful larval development and residual energy for early reproduction may be indicated. Palm Beach flies display a weak negative correlation between viability and age of death

Table 1.13 F Values from Analysis of Variance for First Instar to Adult Viability

Effect	df	F
Population	2	.24
Group	1	7.21**
Temperature	2	3.48*
Line (PG)	67	2.29***
PxG	2	.02
PxT	4	.92
GxT	2	1.64
PxGxT	4	2.56*
Error	148	

* = .01 < p < .05

** = .001 < p < .01

*** = p < .001

Figure 1.11 The effect of temperature on viability
(least squares means)
(a) inbred isofemale lines
(b) intrapopulation crosses

Table 1.14 Phenotypic correlations of Viability in Crosses

	Gainesville			Palm Beach			Michigan		
	22	25	28	22	25	28	22	25	28
Ro	.27	.75*	.74*	.03	.71*	.85*	.49 ⁺	.70*	.93*
TOT	-.38	.22	.20	-.28 ⁺	-.10	.80*	-.19	-.18	.65
ACD	-.05	.38	-.21	-.50 ⁺	.05	.80*	.26	.17	.00
DT	-.25 ⁺	.14	-.31	-.25	-.60 ⁺	-.78*	.04*	.34	.19*
FFD	-.43 ⁺	.04	.23	.23*	-.29	.62	.67 ⁺	.00	.56*
GT	-.16 ⁺	.19	-.30*	-.71*	-.34	.54 ⁺	-.48 ⁺	-.01	.03*
AV	-.48 ⁺	-.14	.59	.18	-.14	.48 ⁺	.11	-.11	.82*

* = $p < .05$ + = $.05 < p < .10$

at 22o; development time also is negatively related at 22o. Both generation time and age of death are positively correlated with viability at 28o. This may indicate a penalty for high viability in the Palm Beach population, but the cost appears to be paid in the currency of reduced late life survivorship. The associated negative relationship with development time suggests that to attain superior viability extracts a penalty in age of peak reproduction as well. In the Michigan flies, early, average and late fecundity display strong positive correlations with viability at 28o, which should be the most stressful temperature. This population (Figure 1.11) displays essentially the same mean viability at all temperatures, while the Gainesville and Palm Beach populations achieve very high viability at 22o which falls off as temperature rises. Phenotypic correlation for inbred flies follow similar patterns.

Another measure of survivorship is length of life after eclosion. Combining the two survivorship measures results in population survivorship curves for the total lifespan except for egg to first instar period (Figure 1.12 to 1.14). Palm Beach flies display higher survivorship early in life at 22o but there appears to be no real differences between the populations late in life at that temperature. At 25o outcrossed Michigan flies have higher survivorship early in life but reduced survivorship late in life relative to the Gainesville and Palm Beach flies. Gainesville flies show appreciably greater late life survivorship at the intermediate temperature. Palm Beach flies have slightly higher mid-life survivorship than Gainesville flies, but a few Gainesville flies live extremely long lives at 25o. At 28o Michigan flies display somewhat higher early life survivorship but at a cost in

Figure 1.12 Survivorship curves from first larval instar
in the three populations at 22°C

Figure 1.13 Survivorship curves from first larval instar
in the three populations at 25°C

Figure 1.14 Survivorship curves from first larval instar
in the three populations at 28°C

terms of late life survivorship. Gainesville flies display much higher mid- and late-life survivorship than either of the other populations.

Differences Between Inbreds and Crosses

Inbred lines in general have lower mean values than crosses for quantity variables (Table 1.6, 1.7), with the exception of the Gainesville flies at 22o. If the differences we observed for timing variables result primarily from heterosis, inbreds would develop slower, have delayed age of peak reproduction and longer generation time, but lifespan would be reduced. These expectations hold for development time, although the differences are small. The pattern for generation time also is as expected. Inbred flies have higher age of peak reproduction in the Michigan flies and in the Gainesville flies at 28o, but Palm Beach flies at all temperatures, and Gainesville flies at lower temperatures, show earlier age of peak reproduction in inbred lines. Longevity follows the expected pattern in the Michigan flies at all temperatures, but at 22o Gainesville inbreds live longer than outcrossed Gainesville flies and at 28o Palm Beach inbreds live longer.

Since inbreds differ from crosses in mean values, the coefficient of variation can be used to address the question of whether inbreds are more variable than crosses as expected if they are less homeostatic for these traits. In addition the relationship of variation to temperature within populations may suggest which temperatures may be considered stressful for each population. Inbreds are more variable than crosses for all life history traits except development time and generation time (Table 1.15). If the coefficient of variation is used as an index of stress, net fecundity and total fecundity are little affected by temperature stress in the Gainesville or Michigan population. Palm

Beach flies, on the other hand, are quite variable at 28o. Lifespan is most variable at 22o for Gainesville and Michigan flies and at 22o and 28o for the Palm Beach flies. Viability is especially variable in response to temperature in the Palm Beach flies. Development time is most variable at 28o in Gainesville flies and at 25o in the other populations. No clear pattern emerges in terms of the relation between environmental variation and phenotypic variation in these life history parameters. In the next chapter variation in fitness, as indexed by cohort intrinsic rate of increase, will be addressed.

Inbreds also differ from crosses in the effect of temperature on the sex ratio of emerging flies (Table 1.16). Outcrossed flies do not show any significant departure from a 1:1 sex ratio, although a higher proportion of females is seen at 25o and 28o in all populations. In inbred flies female proportion increases with temperature in the Gainesville and Palm Beach flies, and the differences are significant at 28o in both populations. At 25o a significantly greater number of females emerges in the Palm Beach and Michigan populations. Stenseth (1980) has suggested that female biased sex ratios may be anticipated in spatially heterogenous environments, as a result of inbreeding in subdivided populations, but it is also conceivable that the differences between crosses and inbreds indicates that differential larval mortality of males may be responsible. Differences in female bias in sex ratio between populations may indicate differences in the degree of inbreeding in the original populations. Bengtsson's (1978) model predicts that inbreeding can be favored if the cost of migrating to a new habitat patch to find an unrelated female exceeds $2/3$ of the cost of inbreeding depression from sib mating. Such conditions might occur in

Table 1.15 Coefficients of Variation for Life History Traits.

Inbreds								
Pop	Temp	Ro	Tot	Aod	V	DT	FFD	GT
Gainesville	22	59.1	45.1	30.1	29.7	4.8	28.2	5.2
	25	63.1	60.3	29.6	34.1	8.9	50.2	8.9
	28	62.0	44.4	32.3	40.4	10.9	40.6	15.0
Palm Beach	22	79.8	68.5	42.0	70.9	16.0	68.1	19.2
	25	59.7	48.9	25.4	34.5	11.5	68.7	15.4
	28	83.9	60.8	34.7	45.5	9.5	62.2	14.7
Michigan	22	66.3	46.2	42.6	28.3	3.3	42.6	8.9
	25	51.2	42.8	33.6	30.8	7.2	36.3	8.0
	28	64.0	45.6	31.4	40.1	5.7	33.9	8.7
Crosses								
Pop	Temp	Ro	Tot	Aod	V	DT	FFD	GT
Gainesville	22	42.2	39.4	27.2	22.7	5.6	38.7	7.0
	25	40.0	27.7	20.3	24.5	5.3	25.9	4.9
	28	41.8	27.6	19.4	26.4	7.4	28.1	3.8
Palm Beach	22	34.4	33.7	34.5	11.2	10.4	26.2	12.6
	25	51.5	33.4	23.0	45.6	12.2	57.4	6.0
	28	76.7	58.3	44.7	46.3	10.2	30.4	7.5
Michigan	22	31.7	26.9	24.3	21.6	3.3	23.4	5.5
	25	30.2	20.0	13.7	23.8	6.3	17.7	5.2
	28	39.2	19.1	13.1	24.9	4.7	24.8	4.5

Table 1.16 Sex Ratio in the Three Populations

Inbreds				Crosses		
	Females	Males	Chi Sq	Females	Males	Chi S
Gainesville						
22	143	135	.12	129	126	.02
25	162	136	2.27	139	123	1.00
28	155	106	9.20***	166	149	1.03
Palm Beach						
22	159	170	.18	146	150	.05
25	175	137	4.63*	113	85	3.96*
28	149	101	9.23***	81	60	3.13+
Michigan						
22	106	106	0.00	157	169	.44
25	108	79	4.50*	162	136	2.27
28	88	84	0.09	156	132	2.60
<hr/>						
Chi Sq >	p					
7.88	.005					
6.64	.010					
3.84	.050					

the Michigan and Gainesville populations where suitable habitat is more patchily distributed, if the conclusions of Stenseth for spatial heterogeneity apply to temporal heterogeneity as well.

Discussion

The phenotypic values presented here could be considered as support for several models of life history evolution. The intraspecific patterns fit the tenets of the central-marginal hypothesis. The Michigan population, which is relatively peripheral in location, has high early fecundity, early age of peak reproduction, short life and short generation time compared to the other populations. Michigan flies on average have lower sensitivity to environmental change, especially to the 25o to 28o shift. The intermediately fluctuating environment of the Gainesville flies show similar patterns, but the effect is less strong. Palm Beach flies are characteristically very sensitive to changes in temperature. They also display the lower, broader fecundity distribution which is expected in a central population. As a result of inter- and intraspecific competition or variance in recruitment, central populations may be expected to show more K type strategies (Parsons, 1982, 1983). These data do not suggest that selection has operated primarily to optimize reproduction at the characteristic mean environmental temperature, which would predict that Michigan flies would achieve better reproductive success at cooler temperatures and the two Florida populations would be more successful at warmer temperatures. Variation would also be minimal at the temperature optimum. Quantity measures are least variable at 22o in Palm Beach flies. Lifespan is least variable at 25o and development time and generation time are least

variable at 28o. Michigan flies are most variable at cooler temperatures for total fecundity and age of death and generation time.

If juvenile survivorship is relatively uncertain in the Palm Beach population, Murphy's (1968) model could apply, although his assumption of a negative phenotypic correlation between high early fecundity and lifespan is not supported by these data. Schaffer's (1974a, b) models could explain if a lower probability of reproductive success characterizes Palm Beach flies, or high adult mortality is characteristic of the Michigan population. Stenseth's model could also explain these patterns, if spatial heterogeneity is low in northern populations and high in southern populations. Since Drosophila melanogaster is almost certainly a nonequilibrium species, Caswell's (1982) predictions would fit if the northern population spends relatively more time in the increasing phase of population growth. Boyce (1984) suggested that Caswell's predictions would be reversed if the selective mortality was age-specific. No indication of a stage-specific effect of environmental temperature is seen in these data, but environmental temperature may be only one component of the selection vector. Boyce's (1984) review of r and K selection concludes that the r/K model may only be validly applied as a density-dependent model. He suggests that density-dependent resource availability favors genotypes with high r when resources are abundant, but favors more efficient genotypes, or those with lower reproductive output when resources are scarce. Such patterns are opposite of the trait associations seen in my data, so r/K selection are probably not important for these populations.

Tantaway and Mallah (1961) suggested that different populations of Drosophila melanogaster exhibited characteristic temperature optima for traits such as fecundity and % emergence and that variation increased as rearing temperature deviated from that population specific optimum. Their data suggest that Drosophila melanogaster from more variable temperature environments were less susceptible to changed temperature regimes. Bateman's (1967) data on Dacus tryoni suggested that populations from more seasonal environments display greater tolerance to temperature variation and have relatively "r" tactics compared to tropical populations. Data on Oncopeltus fasciatus (Dingle, 1981; Dingle et al., 1982) suggest that for clutch size, number of clutches and total fecundity the population from the most fluctuating environment (Iowa) is less sensitive to changes in environmental rearing temperature, when compared to a stable tropical population (Puerto Rico). Age at first reproduction and duration of life were more sensitive in this population and also had relatively high means, but this may be due to photoperiodically induced diapause in the Iowa population. Mean size at metamorphosis was slightly less sensitive to rearing temperature in a presumptively more variable tundra population of Rana sylvatica relative to a lowland site of relatively stable temperatures. However, larval development rate showed an opposite trend across populations (Berven and Gill, 1983). They suggested that population differences for these frogs are related to physiological constraints inherent in development and the degree of compromise between timing and size at metamorphosis that is possible in each environment.

Similar patterns of geographic variation in mean values for life history traits could reflect selective action on rate of metabolism. A

higher metabolic rate could produce the higher age specific fecundity, early reproduction, and relatively short life that characterizes Michigan flies. This proposition will be explored in the third chapter.

When the correlation data in Tables 1.11 to 1.12 are considered as a whole, one observes that at 22o Gainesville flies display positively correlated fecundity traits which have little or no correlation with timing traits. However, longer lived flies tend to delay age of peak reproduction, but not amount. At 25o quantity traits are still positively associated, but longer lived flies are the best early reproducers. At 28o the flies that develop fastest have high early, average and total fecundity, but lower late life fecundity. They also have a longer reproductive life. Palm Beach flies at 22o that display high early fecundity also have high peak and late fecundity, but relatively short lives. At 25o there is no significant penalty in lifespan for the positive association between fecundity traits. At 28o the most highly productive flies actually live longer lives, but they tend to develop slower and to delay age of peak reproduction. The Michigan flies at 22o have a negative association between early and late fecundity, which appears to counteract association between these quantities and longevity. At higher temperatures high early reproduction does not appear to be associated with lifespan, although the 25o flies that have high last third fecundity tend to live shorter lives.

Phenotypic correlations do not necessarily reflect the underlying genetic association structure. They may, however, reflect constraints that limit the usefulness of quantitative genetic models of life history evolution developed thus far, since these models assume that phenotypic

correlation structure is relatively invariant in time (Lande, 1982a, b). These data suggest that small environmental changes can effect large changes on the correlation structure between traits within populations and that populations of the same species may differ markedly in their response under the same regime.

Ecological tradeoff arguments only apply under conditions of resource limitation. In these laboratory experiments, the primary constraint would be environmental temperature stress. Since the Michigan population is rarely exposed to 28°C in the wild, I anticipated that phenotypic tradeoffs would be stronger at higher temperatures. The constraints implied by tradeoff argument appear to be relatively more important at 22°C in all the populations, although the form of the tradeoff differs for the populations. Gainesville flies that achieve an early peak of reproductive activity pay a cost in reduced lifespan. Palm Beach flies with high early reproduction have shorter lives, whereas in Michigan flies the cost of high early reproduction at 22°C appears to be paid in the currency of reduced late life fecundity. Phenotypic correlations are the net result of genetic correlations caused by pleiotropy and/or linkage and environmental variation that influences traits simultaneously. Measurements of phenotypic correlations in the field are subject to the criticisms leveled by Stearns (1976, 1980) and Giesel et al. (1982a,b) when evolutionary trends are inferred. Stearns (1980) demonstrated, for instance, that growth and survivorship were strongly influenced by osmoregulatory problems and that offspring weight was influenced by early maternal environment in Fundulus. As Stearns suggested, phenotypic correlations under one set of controlled laboratory conditions may reflect

differential adaptation to the laboratory environment. To be relevant to assess evolutionary responses, measurements of correlation made under laboratory conditions must be made in an appropriate series of environments for the population under study. Although it could be argued that the 28°C regime was essentially outside the selective range for the Michigan population, drastic reductions in fitness components and perhaps strong tradeoffs would be expected. This is not the case.

Phenotypic correlations may either reduce or augment the intensity of selection on a series of traits (Doyle and Myers, 1982). In a study of laboratory adaptation in Gammarus lawrencianus, that originated in a variable estuarine environment, Doyle and Myers showed that age at maturity decreased, fecundity and intrinsic rate of increase were higher when unlimited resources and constant environment were provided, and no density constraints were permitted. They presented a method for measuring immediate selection intensities, which considers direct and indirect effects of correlated life history characters, and which is appropriate where selection is directional and the characters have been shown to be linearly related to fitness. In their experiment selection intensity was reduced by correlation between reproductive effort and growth rate. Reproductive effort was linked to fitness by a direct negative relationship and an indirect link through fecundity. Similar constraints are apparent in our data.

Crosses between partially inbred lines display the expected heterosis for fitness components under most temperature treatments. Since the pattern of mean temperature response is essentially similar in inbreds and crosses, inbred lines do not appear to display the expected increase in sensitivity to environmental change that would be implied

if they were generally less homeostatic than crosses on average. Variance in fitness components is in general greater for the inbred lines. Fitness differences between heterozygotes or heterokaryotypes and homozygotes or homokaryotypes are often maximal under stress (Parsons, 1983). Parsons (1971) suggested that extreme environment heterosis results from greater flexibility or efficiency which is required to adapt to marginal habitats. Homozygotes could also show lower fitness due to general disruption of coadaptation or reduced homeostatic ability. In a study of Liatris cylindracea, a perennial herb, Schaal and Levin (1976) suggested that in extreme environments heterozygosity was directly favored and could buffer the population against demographic events that might reduce polymorphism.

Other evidence for increased heterozygosity in fluctuating environments is reviewed by Parsons (1982, 1983) for Drosophila robusta and Drosophila melanogaster. Critical interpretation is difficult since small population sizes and founder effects could counter the expected increase in heterozygosity in marginal populations. If heterosis is more pronounced under conditions of environmental stress as Parsons suggested, all three populations of Drosophila melanogaster in this study show stress responses at cooler temperatures.

Central populations have been suggested to be less resistant to physical stress and to have higher average fitness than more ecologically marginal populations. The more central Palm Beach population does appear to be less resistant to temperature change than the more ecologically marginal Michigan population for most life history traits. The marginal Michigan population also exhibits the predicted shift to the r end of the r/K continuum in a temporally variable

environment. Marginal populations have also been predicted to display higher levels of expressed variation, but under these conditions, the most central population is the most phenotypically variable. This may suggest that temperature is not as important as some other environmental component for the Palm Beach flies.

In summary, the three sites described here differ in the nature of the fluctuation and the predictability of environmental temperature. Palm Beach is relatively stable and predictable; the Gainesville site is intermediate in variability and predictability, and the Michigan site is the most variable and unpredictable. The three populations differ significantly in their phenotypic life history pattern. The Michigan population displays a typical "colonizing" pattern under most conditions, while the Palm Beach population displays a lower, broader fecundity distribution and longer life under 22o and 25o temperatures. The patterns of environmental sensitivity differ for the three populations, with the Michigan population displaying reduced sensitivity to environmental change and the central Palm Beach population showing marked response to small changes in environmental conditions. These data basically support the differences one would expect in comparing central and marginal populations, but data on relative juvenile/adult mortality, spatial heterogeneity, and timing and nature of selective action in these populations are necessary before unambiguous support for any life history model is justified.

CHAPTER II FITNESS DIFFERENCES BETWEEN POPULATIONS

Introduction

Stearns (1976) defined fitness as "something everyone understands but noone can define precisely"(p. 4). Although the most fit organisms are those that are better represented in future generations than their less fit competitors, fitness in that sense can only be assessed post hoc. Individual and population fitness are inherently difficult to define because they are relative concepts. Relative representation in future generations will be in part determined by the organisms innate ability to survive and reproduce, but will also be influenced by all the biotic and abiotic constraints imposed by the environments encountered across time. Thus fitness is not only relative with respect to other individuals (or populations), but relative to a particular set of environmental circumstances encountered over a specified period of time. Such difficulties led Thoday (1958) to postulate that a true measure of fitness would require knowledge of persistence of evolutionary lineages over extended time periods.

Operationally defined, fitness must be considered as a composite of survivorship and reproduction. Since Lotka (1913) derived the characteristic equation, which relates age specific survivorship and reproduction to population growth rate, a considerable body of theory has been developed that proposes that the population growth rate is the primary quantity that is maximized by selection (Fisher, 1958; MacArthur

and Wilson, 1967; Stearns, 1976). Many other fitness indices have been proposed, such as reproductive value, net reproductive rate and population size (Charlesworth, 1980; Lande, 1982a, b). Lewontin and Cohen (1969) suggested that selection might act to maximize the geometric mean rate of increase. Demetrius (1975a) used information theory to relate entropy and reproductive potential to the intrinsic rate of increase for age structured populations. He suggested that entropy is a better measure of fitness since iteroparous and semelparous strategies can be more readily discriminated. Tuljapurkar and Orzak (1980) emphasize that extinction probability is an essential component of fitness.

Since fitness itself is difficult to define and measure, fitness components are the usual measures of a life history. Stearns' (1976) review identified the key traits as brood size, size of young, age distribution of reproductive effort, interaction of reproductive effort with adult mortality and variation in the above traits. Theoretical predictions are reviewed for traits considered singly and for reproductive tactics, which he defined as a "set of coadapted traits designed to solve a particular ecological problem" (p. 4). Wilbur et al. (1974) similarly suggested that a life history pattern represents a series of selective compromises to a suite of environmental variables. The most important traits in their analysis are age specific juvenile and adult mortality, age at first reproduction, length of the reproductive span, age specific fecundity, egg size and degree of parental care. They suggest that the trophic level of the organism and the degree of environmental predictability must be considered to predict which of these traits will be the primary focus of selection. Stearns

(1980) suggests that the implicit assumption that component fitness traits, such as age at maturity, survivorship and fecundity, are free to evolve or co-evolve under demographic influences is violated when there are developmental or allometric constraints. Since the relationship of component traits to fitness and their interrelationships with each other (both genetic and phenotypic) may also limit the effect of natural selection on a single trait, these associations must also be incorporated into predictive theory.

Comparative demography and observations of associations of fitness components can perhaps be traced to Pearl (1922, 1925, 1928). In developing his "rate of living" hypothesis for observed interspecific differences in lifespans, he contrasted species that displayed high fecundity, small size and short lives with longer lived, larger species that were more restrained in their reproduction. His suggestion of a critical choice between a live fast, love hard, die young lifestyle and one characterized by more temperance perhaps formed the initial basis for the tradeoff assumptions that permeate current demographic theory. Clearly, most traits considered as fitness traits display continuous variation rather than discrete character states. The impact of natural selection on such traits requires the merger of population and quantitative genetic treatments. Kempthorne (1983) in an analysis of the success of the merger to date suggested that fitness can never be characterized as a single scalar variable that remains constant through a dynamic selection process. He suggested that survivorship and fecundity must be viewed as functions that are both genotypically and environmentally determined and that partitioning the effects of genotype and environment on variance and covariance of such traits will be an

important but complex addition to general theory.

Stearns' (1980) view that life histories are physiologically and developmentally constrained, and therefore not free to covary in response to selection, is not new. Most life historians have realized that organisms are genetically, physiologically, developmentally and ecologically constrained. However, it has not been possible as yet to incorporate all constraints into a mathematically tractable model (Caswell, 1983; Kempthorne, 1983). As Caswell (1983) re-emphasizes, real organisms can adapt by phenotypic plasticity, genetic change, or both. In addition organisms can maintain physiological, developmental or genetic homeostasis in response to environmental change.

This analysis addresses the relationship between fitness, as indexed by cohort intrinsic rate of increase, and fitness components. The response of intrinsic rate and its correlation structure is examined in three populations of Drosophila melanogaster from geographic areas representing different points on the stable-fluctuating continuum with respect to environmental temperature. The Palm Beach population occupies the most temporally stable thermal environment; the Michigan population is the most thermally variable and unpredictable in time (Chapter I). Biotic constraints probably also differ for the three populations, but no attempt has been made to quantify other ecological constraints in the original sites. The primary focus in this paper will be the temperature response of fitness and its correlation structure. Variance in fitness and its relationship to environmental variance will be addressed. The temperature responses of different cohorts within each population may allow some intimation of genetic polymorphism or phenotypic plasticity, but the genetic architecture of selected fitness

components will be more fully explored in a separate paper (Chapter V).

Among the possible evolutionary options open to these populations are:

1. Each population could be adapted to a different temperature optimum.
2. The populations could display homeostasis for fitness, maintaining high fitness across temperature treatments.
3. The populations could evolve plasticity of response to temperature, either by matching variance of fitness with variance of environmental temperature or by physiological or developmental responses keyed to environmental conditions.
4. Coadaptation of fitness components may be reflected in similar patterns under each environmental condition and may limit plasticity of responses.
5. Correlation structure may differ for each population or by each treatment.

Finally, I shall present data on some indices of intrinsic rate of increase, which may permit further work in this area without the necessity of tedious iterative calculation, if the relationship is strong and predictable from population to population and environment to environment. Since calculation of intrinsic rate from the logistic equation requires quantifying age specific mortality and fecundity, it is tedious and time-consuming even for a short lived organism. Indices of intrinsic rate that are highly correlated may allow more critical experiments.

Methods

Drosophila melanogaster used in this set of analyses were third generation descendants of flies collected near Gainesville, Florida;

Palm Beach, Florida; or Grayling, Michigan. Details of line derivation and culture methods were presented in Chapter I. For each cohort included in this analysis, the following life history traits were recorded: viability (% of larva seeded that survived to eclosion), development time (mean number of days from first instar to eclosion), first five days fecundity (mean number of eggs laid in the first five days of life), and longevity (mean number of days from eclosion to death). Intrinsic rate of increase was calculated for each cohort by iteration from the Lotka-Euler equation. Three other derived fitness measures were calculated. B1 was calculated as log of the average fecundity adjusted for the viability of the line and corrected to females only, divided by the development time. B2 followed a similar formulation, based on first five days fecundity. B3 was calculated as the log of net fecundity divided by development time. Relative fitness of the lines in each population was calculated by considering the line at a particular temperature treatment with the highest cohort intrinsic rate to have a fitness of 1.0. The proportionate fitness of a particular cohort could then be calculated. Data were analyzed according to the methods described in Chapter I. Partial correlations were calculated from the simple correlations using the procedure in Sokal and Rohlf (1981). Multivariate regressions were calculated using SAS general linear models procedures and standard regression coefficients were determined as described in Sokal and Rohlf (1981).

Results

Environmental temperature data have been presented for the populations (Chapter I). To summarize the pertinent information, however, the Palm Beach encounters the warmest temperatures over the

year and the lowest month-to-month and year-to-year variability. The Gainesville population is slightly cooler overall and approximately twice as variable as the Palm Beach area. Michigan is much cooler at all times and 5-13 times as variable as the Palm Beach area, even when only months when flies are actively reproducing are considered. Therefore, if temperature optima exist for each population the Palm Beach population should show the highest optimum, followed by Gainesville, with Michigan reproducing best at the coolest temperatures.

Fitness Differences between Populations

The ANOVA for cohort intrinsic rate of increase displays highly significant population, group and temperature effects (Table 2.1). The arcsin transformation, which reduced heterogeneity of variance, did not affect the interpretation of the ANOVA results. The population by temperature interaction is significant at the .025 level. The lines effect is marginally significant. The mean values for cohort intrinsic rate of increase are presented in Table 2.2. Inbreds have lower fitness than crosses between inbred lines for all populations and temperature treatments. Cohort intrinsic rate of increase varies linearly with temperature in all populations in inbreds and crosses with the exception of a slight decrease from 22 to 25o in the Palm Beach population. Mean temperature responses for the populations show that the populations do not differ in mean fitness at 22o (Figure 2.1, Table 2.2). At 25o, Michigan clearly has higher fitness than the Palm Beach or Gainesville populations for inbreds and crosses; the two Florida populations differ significantly in mean fitness at 22o for inbreds and at 28o for crosses.

Table 2.1 F Values from Analysis of Variance for
Cohort Intrinsic Rate of Increase

Effect	df	F (arcsin)	F (untransformed)
Population	2	5.04*	5.91**
Group	1	18.65***	20.98***
PxG	2	.02	.06
Temperature	2	64.73***	59.99***
Line	67	1.34+	1.37+
P x T	4	2.10*	2.84*
G x T	2	.25	.20
P x G x T	4	1.61	1.37
Error	148		

+ = .05 < p < .10

* = .01 < p < .05

** = .001 < p < .0001

*** = p < .0001

Table 2.2 Least Square Mean Values for Cohort Intrinsic Rate of Increase.

	Gainesville		Palm Beach		Michigan	
	Mean	SE	Mean	SE	Mean	SE
Inbreds						
22	.322	.018	.285	.014	.309	.017
25	.343	.015	.342	.016	.378	.017
28	.400	.014	.408	.015	.436	.017
Crosses						
22	.328	.018	.368	.018	.337	.013
25	.380	.018	.354	.020	.440	.015
28	.468	.016	.431	.022	.480	.016

At 28o Michigan inbreds are significantly higher than Gainesville or Palm Beach flies, while in the crosses the Michigan flies have higher values than Palm Beach flies but do not differ significantly from the Gainesville flies. The analysis of variance results (Table 2.1) confirm the graphical interpretation, since the $P \times T$ interaction is significant.

One approach to assessing the fitness differences between populations is to examine the net fecundity distribution for the populations. Although mean cohort rate of increase was not significantly different between populations at 22o for crosses, similar fitness was achieved in different ways (Figure 2.2). The Palm Beach population is characterized by a lower, broader fecundity distribution. Both Palm Beach and Michigan flies had high early fecundity relative to Gainesville flies, but the Gainesville flies had relatively high late fecundity and longer lives. At 25o where Michigan flies achieve significantly higher intrinsic rates of increase, the entire fecundity distribution is shifted to the left (Figure 2.3). Similar mean fitness is achieved by Palm Beach and Gainesville flies but Gainesville flies emphasize early reproduction, whereas Palm Beach flies again display a lower, broader fecundity distribution which emphasizes reproduction late in life. Mean fitness at 28o is higher in Gainesville and Michigan relative to Palm Beach (Figure 2.4). All three populations have relatively high early fecundity; however, the low amount of peak reproduction and very short life in Palm Beach flies contribute to their lower values. Palm Beach flies appear to pay a penalty for high early fecundity in both survivorship and late reproduction. Gainesville flies

Figure 2.1 The effect of temperature on cohort intrinsic rate of increase in the three populations
 (a) inbred isofemale lines
 (b) intrapopulation crosses

22°C

Figure 2.2 Net fecundity distributions at 22°C for the intrapopulation crosses

25°C

Figure 2.3 Net fecundity distributions at 25°C for the intrapopulation crosses

Figure 2.4 Net fecundity distributions at 28°C for the intrapopulation crosses

have a lower amount of peak reproduction relative to the Michigan flies but they achieve essentially the same average fitness due to high late reproduction and longer lives.

Although the populations differ in fitness and temperature response of fitness, there is no evidence that fitness is optimized at the characteristic mean temperature of the population. Instead the Michigan population has intermediate intrinsic rate of increase at 22o and much higher rates at high temperature. Relative fitness calculated on the cohort data also do not support a clear temperature optimum for each population (Table 2.3). Relative fitness is clearly lower for the inbred lines in all populations, except for Gainesville flies at 22o (Table 2.3). The temperature response of relative fitness shows low, but stable values in the Palm Beach flies, which are derived from a stable thermal habitat. In Gainesville crosses, relative fitness increases with increasing temperature. In Michigan crosses, there is little change in relative fitness from 22 to 25o, but a large increase when the temperature is shifted to 28o. The impact of inbreeding is especially severe in Michigan flies at high temperature. Environmental variation appears to produce not only higher relative fitness but also fitness responses to the temperature shift.

Phenotypic Plasticity and Genetic Differentiation in Cohort r

Temperature responses of individual cohorts may indicate differences in populations in genetic polymorphism or phenotypic plasticity for intrinsic rate of increase. Temperature response patterns (Figure 2.5) are quite different for the populations. Generally inbreds are more variable than crosses as is expected due to reduced homeostatic ability or lowered buffering capacity. A general

Table 2.3 Mean Relative Fitness (W)

	Gainesville	Palm Beach	Michigan
Inbreds			
22	.902	.741	.851
25	.818	.736	.878
28	.825	.740	.773
Crosses			
22	.885	.856	.898
25	.906	.857	.880
28	.932	.816	.910

Figure 2.5 "Norms of reaction" for cohort intrinsic rate

Figure 2.6 The effect of temperature on the relationship between cohort intrinsic rate of increase and viability for all populations

Early Fecundity with Intrinsic Rate

Figure 2.7 The effect of temperature on the relationship between cohort intrinsic rate of increase and early fecundity for all populations

Figure 2.8 The effect of temperature on the relationship between cohort intrinsic rate of increase and development time for all populations

Figure 2.9 The effect of temperature on the relationship between cohort intrinsic rate of increase and longevity for all populations

physiological response should give the same patterns in each population. The Gainesville population has several cohorts that change very little from 22 to 25o, but have a marked response to higher temperatures. Several cohorts reverse that trend and show some homeostasis over the 25-28o shift, but respond greatly to the lower temperature shift. Palm Beach flies as a whole show more marked plasticity and genetic differentiation than the other populations. Michigan flies show less cohort differentiation, although they appear to have two separate types of responses. One set of cohorts exhibits linear temperature responses and one set show a marked response as temperature is shifted from 22 to 25o, but are essentially homeostatic to the high temperature shift. This response may indicate also that some costs incurred at 28o limit intrinsic rate of increase that can be achieved.

The strong temperature effect on the interrelationships of life history components can be seen in Figures 2.6 to 2.9. Increasing temperature appears to raise not only the intercept, but also the slope of the relationship between cohort intrinsic rate and viability, when the crosses from all populations are included in the analysis. The relationship between early fecundity and cohort intrinsic rate and between development time and intrinsic rate are primarily due to the impact of temperature (Figure 2.6 and 2.7). Early fecundity has the predicted residual positive relationship within temperatures with cohort intrinsic rate. Longevity has no residual relationship at 22 or 25o and a slightly positive residual relationship at 28o.

There is no indication that variation in fitness, whether assessed as absolute variation or by the coefficient of variation, matches environmental variance as has often been suggested (Table 2.4). In

fact, these data indicate an inverse relationship, since the thermally stable Palm Beach site has the highest fitness variance at all temperatures.

Phenotypic Correlations of Cohort Intrinsic Rate

Phenotypic correlations with intrinsic rate of increase do not differ in pattern in the three populations for net fecundity, viability, development time, or early fecundity (Table 2.5), by the Bartlett's chi square, which distinguishes whether a set of correlations can be viewed as samples of a common correlation. Net fecundity, viability and development time are positively correlated with intrinsic rate of increase in all treatments. The pooled correlation is 0.71 for net fecundity, 0.59 for viability and 0.63 for early fecundity. Development time is negatively correlated (-0.38). The pattern of correlation changes for total fecundity ($X^2 = 30.11$, $p < 0.025$). Among crosses, cohorts from Gainesville show positive correlations at all temperature, while the Palm Beach flies display positive correlations at 25 and 28o and the Michigan flies only at 28o. The phenotypic correlation with age of death differ at the $p < .055$ level. There are no significant correlations between age of death and intrinsic rate of increase in Michigan flies. Palm Beach flies display negative correlation at 22o and positive correlation at 28o in the crosses, but all correlations are positive in the Palm Beach inbreds. Gainesville flies have a positive association at 25o for inbreds and crossed cohorts. The Palm Beach results are somewhat puzzling in view of the net fecundity distribution for the population, but suggest that flies contributing most to the population mean fitness may be short lived at 22o and relatively long

Table 2.4 Variance and Coefficient of Variation in Cohort Intrinsic Rate of Increase in the Three Populations

	Inbreds		Crosses	
	V	CV	V	CV
Gainesville				
22	.0010	10.1	.0009	9.1
25	.0034	16.9	.0007	6.9
28	.0033	14.5	.0017	8.7
Palm Beach				
22	.0048	24.4	.0015	10.6
25	.0081	27.5	.0030	15.5
28	.0148	31.0	.0130	27.4
Michigan				
22	.0010	10.6	.0005	6.8
25	.0027	11.3	.0008	6.6
28	.0042	14.4	.0014	7.8

Table 2.5 Phenotypic Correlations of Fitness Components with Cohort Intrinsic Rate

Inbreds							
Pop	Temp	Ro	Tot	ADD	V	DT	FFD
Gainesville	22	.65*	.59 ⁺	-.01*	.64*	.01	.51 ⁺
	25	.92*	.78*	.84*	.49*	-.42	.75 ⁺
	28	.49	-.10	.16	.61	-.06	.41
Palm Beach	22	.72*	.68*	.46*	.22*	-.45*	.78*
	25	.89*	.86*	.41 ⁺	.64*	-.78	.78
	28	.83	.71	.73	.53	-.61	.73
Michigan	22	.57*	.51 ⁺	.38	.60*	-.13	.67*
	25	.73*	.35	.06	.72*	-.25	.52 ⁺
	28	.71	.22	.27	.58	-.08	.45
Crosses							
Gainesville	22	.64*	.47 ⁺	.11*	.31*	-.34	.62*
	25	.76*	.56*	.64	.64*	-.37	.57*
	28	.84	.56	.22	.82	-.15	.57
Palm Beach	22	.12*	-.09	-.30	.73*	-.57 ⁺	.42 ⁺
	25	.89*	.47*	.14*	.71*	-.56*	.38*
	28	.81	.83	.83	.93	-.90	.79
Michigan	22	.68*	.23	.11	.75*	-.45 ⁺	.84*
	25	.52*	.13*	.10	.54*	-.37	.61*
	28	.82	.71	.19	.79	-.18	.84
Pooled r		.71	.50	.34	.59	-.38	.63
Chi squared		23.18	30.11	27.26	15.12	18.98	13.71
Significance level		.11	.03	.055	.60	.31	.67

lived at 28o. The Palm Beach crosses represent a very small sample, however, which may be biased by a single cohort with a very low age of death. A closer examination of cohort norms of reaction for life history traits may allow further assessment of this pattern. Norms of reaction for fitness components and metabolic rate will be examined in Chapter IV.

Intercorrelations between fitness components may affect the simple phenotypic correlations. The correlations between fitness components that display differences in pattern by the Bartlett's chi square are first five days fecundity with net fecundity, total, age of death and development time; development time with net fecundity, total and viability and viability with net fecundity (Table 2.6). For the Gainesville flies at 22o, intrinsic rate of increase is positively related to first five days fecundity and with viability; but viability and first five days fecundity are negatively correlated, which may reduce the correlation between intrinsic rate of increase and viability. The partial correlation of intrinsic rate of increase with viability with first five days fecundity held at its mean value, is much higher than the simple correlation (Table 2.7). Similarly, the correlation of intrinsic rate of increase with first five days fecundity, with viability held at its mean value, is much stronger. At 25o Gainesville flies do not show a relationship between viability and first five days fecundity and viability is strongly correlated with intrinsic rate of increase. The partial correlations are not different from the simple correlation in this case. Age of death is positively associated with r_m at 25o and this effect does not result from the positive correlation between first five days fecundity and age of death, since the partial

Table 2.6 Phenotypic Correlations between Several Life History Components in Crosses

Gainesville				Palm Beach			Michigan		
	22	25	28	22	25	28	22	25	28
FFD with									
AOD	.01	.45	.45	-.68	-.04	.89	.00	-.08	.26
V	-.43	.04	.23	.23	-.30	.62	.67	.01	.66
DT	-.14	-.07	.42	.26	.32	-.83	-.30	-.16	.05
DT with									
AOD	-.24	-.12	.26	-.27	-.09	-.85	-.62	-.26	.16
V	-.25	.14	-.31	-.25	-.60	-.78	.05	.34	.19
V with									
AOD	-.05	.38	-.21	-.50	.05	.80	-.26	-.17	.00

Table 2.7 Selected Partial Correlations for the Intrapopulation Crosses

Gainesville					
22		25		28	
R-FFD:V	.878	R-AOD:FFD	.523	R-AOD:FFD	.049
R-V:FFD	.814	R-V:FFD	.752	R-DT:FFD	.523
		AOD-V:FFD	.406	AOD-DT:FFD	.087
		R-AOD:V,FFD	.353	R-AOD:FFD,DT	.103
		FFD-AOD:V	.472	FFD-AOD:DT	.382
				FFD-AOD:V	.522
				FFD-DT:V	.530
				AOD-DT:V	.209
				FFD-AOD:V,DT	.504
Palm Beach					
22		25		28	
R-AOD:FFD	-.022	R-FFD:V	.882	R-AOD:DT	.341
R-AOD:V	.110	R-FFD	.380	R-V:DT	.840
R-AOD:DT	-.183			R-AOD:V	.416
R-DT:V	-.581			R-AOD:V,DT	.026
AOD-DT:V	-.123			FFD-AOD:DT	.627
R-AOD:V,DT	.050			FFD-AOD:V	.849
FFD-AOD:V	-.669			FFD-V:DT	-.076
R-FFD:V,AOD	.611			V-AOD:DT	.391
R-FFD:V	.379			FFD-AOD:V,DT	.719
R-FFD	.421			R-AOD:FFD	.470
Michigan					
22		25		28	
R-V:FFD	.464	R-V:FFD	.676	R-V:FFD	.548
R-V	.75	R-V	.54	R-V	.79

correlation with first five days fecundity held at its mean value is similarly high. At 28o the correlation of first five days fecundity with age of death is similarly high and the positive correlation between development time and age of death and development time and first five days fecundity do not reduce the impact on intrinsic rate of increase. When the correlation between intrinsic rate of increase and age of death is partialled for viability and first five days fecundity, it is somewhat reduced. Some unmeasured factor may be affecting the Gainesville flies at this temperature.

Palm Beach flies at 22o have a low correlation between rc and early fecundity, which may indicate that the high negative correlations between first five days fecundity and age of death and viability and age of death have a significant impact. Energy devoted to highly viable, early reproducing offspring seems to shorten life. This is confirmed by the increase in the correlation between intrinsic rate of increase and first five days fecundity when partialled for viability and age of death (Table 2.6). At 28o there is a positive first five days fecundity with age of death correlation, which results in age of death being correlated with intrinsic rate of increase. Development time is also negatively related with both age of death and first five days fecundity and thus development time may be the driving force at this temperature, since it is strongly negatively associated with intrinsic rate of increase. The partial correlation between intrinsic rate of increase and age of death when both viability and development time are held at their mean values is near zero, but the correlation between first five days fecundity and age of death remains strong when similarly adjusted. This suggests that first five days fecundity has a direct relationship with longevity.

Michigan flies display strong positive correlations between viability and first five days fecundity at 22 and 28o which directly impact intrinsic rate of increase. The absence of a correlation between viability and first five days fecundity at 25o suggests that viability has a direct effect on intrinsic rate of increase , but its effect is mediated through first five days fecundity at 22 and 28o. Development time has a negative relationship with intrinsic rate of increase at 28o which primarily seems to act through a large negative correlation with age of death, although there is a slight negative association between development time and first five days fecundity. The phenotypic correlations of fitness components with intrinsic rate of increase, and their interrelationships with each other, suggest not only different organizations of the life history in the three populations, but also different suites of trait contributing to the intrinsic rate of increase at different temperatures.

Multiple regression analysis confirms that different traits are emphasized in the determination of cohort intrinsic rate of increase in the populations and also that temperature effects differ (Table 2.8). Standard regression coefficients, which express the relationship in units of standard deviation of intrinsic rate of increase with units of standard deviation of the relevant variable, indicate that in the Gainesville population the relative importance of first five days fecundity declines with increasing temperature, while the importance of viability increases with temperature. Age of death only enters the model at 28o. In Palm Beach crosses first five days fecundity is very important at 22 and 25o, but is less heavily weighted at 28o. In Michigan flies, first five days fecundity is weighted very heavily at

Table 2.8 Standard Regression Coefficients for Best Three Variable Multiple Regression Models in Outcrossed Flies.

Gainesville			r ²
22	.8065 FFD + .5478 V - .3961 DT		.91
25	.5309 FFD + .7516 V - .2693 DT		.88
28	.2768 FFD + .8375 V + .2749 AOD		.87
Palm Beach			
22	.5024 FFD + .4077 V - .6679 DT		.93
25	.5741 FFD - .3230 DT + .7278 AV		.96
28	.2528 FFD + .4937 V - .3067 DT		.99
Michigan			
22	.2379 MR + .9079 FFD + .2808 AV		.94
25	.4927 FFD + .6623 V - .5691 DT		.91
28	.5615 FFD + .4572 V - .2819 DT		.95

22o and less at 25 and 28o where viability and development time are more important. The 22o Michigan flies show a significant effect of rate of metabolism. The relationship between metabolic rate and fitness characters will be explored in chapter III.

Indices of Cohort Intrinsic Rate of Increase

Four indices of cohort intrinsic rate of increase were assessed with the idea of simplifying the calculations necessary for future work in this area. Pearson product-moment correlations indicate that b_2 , an index calculated as $\log (FFD \times V \times 0.5) / DT$, was more highly correlated with intrinsic rate of increase than the other indices (Table 2.9). The prediction equations for the regression of intrinsic rate of increase on b_2 (Table 2.10) show that the populations differ somewhat in the slope of the relationship with the Palm Beach flies having higher slopes. As expected the intercept differs by temperature and population. Michigan flies have higher intercepts at 25o and Gainesville and Michigan flies have high intercepts at 28o. Although the slope and intercept differences imply that this index would not be useful without a preliminary assessment of the slope and intercept of the relationship under specific conditions, it may still permit calculation of intrinsic rate of increase on only a sample of cohorts in a large experiment and reduce time investment in calculations.

Discussion

One central problem of life history theory is the impact of natural selection on intrinsic rate of increase in environments that differ in degree of stability and predictability. This analysis demonstrates that cohorts from more temperature variable environments have higher mean fitness at 25o and 28o relative to cohorts from more thermally stable

Table 2.9 Correlations of Fitness Indices with Cohort Intrinsic Rate

	P1G1	P1G2	P2G1	P2G2	P3G1	P3G2
22o						
R with						
Ro	.65	.63	.71	.12	.59	.68
B1	.95	.81	.87	.85	.78	.82
B2	.90	.91	.92	.94	.90	.95
B3	.87	.70	.88	.23	.69	.65
25oC						
R with						
Ro	.92	.76	.90	.90	.73	.52
B1	.93	.70	.95	.89	.94	.77
B2	.97	.86	.93	.98	.94	.95
B3	.94	.79	.93	.95	.77	.69
28oC						
R with						
Ro	.49	.84	.83	.81	.71	.82
B1	.66	.77	.91	.92	.79	.87
B2	.91	.81	.97	.99	.93	.94
B3	.61	.80	.96	.97	.76	.86

Table 2.10 Regression Relationships for Cohort Intrinsic Rate and the Index B2 for the Three Population at each Temperature (+/-S. E.)

Pop	Temp	Intercept	Slope	r ²
Gainesville	22	.078 (.043)	.062 (.011)	.81
	25	.055 (.021)	.064 (.005)	.94
	28	.136 (.031)	.046 (.005)	.83
Palm Beach	22	.103 (.019)	.054 (.005)	.84
	25	.138 (.022)	.047 (.005)	.87
	28	.077 (.023)	.058 (.004)	.94
Michigan	22	.116 (.030)	.051 (.008)	.80
	25	.102 (.032)	.056 (.006)	.88
	28	.006 (.055)	.071 (.009)	.87
Crosses				
Gainesville	22	.093 (.037)	.059 (.009)	.83
	25	.126 (.051)	.050 (.009)	.74
	28	.162 (.069)	.046 (.010)	.65
Palm Beach	22	.095 (.035)	.057 (.007)	.89
	25	.110 (.020)	.053 (.004)	.96
	28	.050 (.017)	.061 (.003)	.99
Michigan	22	.132 (.019)	.049 (.004)	.91
	25	.143 (.030)	.050 (.005)	.89
	28	.182 (.033)	.043 (.005)	.88

environments, when measured under controlled conditions. At 22o the populations were indistinguishable in average fitness. Bateman (1967) calculated r_m for four populations of the Queensland fruit fly, Dacus tryoni in the laboratory at 20, 25 and 30o. For these populations the rank of intrinsic rate of increase at 30o agreed with the average temperatures of the original sites. At 20o, the ranking reversed, with the population from the highest average temperature having the lowest intrinsic rate of increase. At the intermediate temperature, the populations were indistinguishable. Another population, from the most variable temperature environment sampled, performed well at both extremes. My results do not support the Bateman hypothesis that each population will perform relatively best at its average temperature. At 22o the population from the coolest environmental temperature had an intermediate rank in cohort intrinsic rate of increase. At 28o the population from the coolest environmental regime had the highest intrinsic rate of increase.

Population differentiation in intrinsic rate of increase has also been related to resource availability in interspecific competition. Dingle (1974) compared intrinsic rate of increase for three species of cotton stainer bugs. The estimates were consistent with resource fluctuation differences for the three species. The species most confined to a single seasonal resource had the highest intrinsic rate of increase. The species with broader resource availability but lower fluctuation in availability had the lowest intrinsic rate of increase. Dingle (1981) also reported that two non-migratory Dysdercus species had lower intrinsic rates than two other migratory species. For the mosquito, Aedes aegypti, feral strains have lower intrinsic rate of

increase than urban strains (Crovello and Hacker, 1972). Heron (1972) reported extremely high intrinsic rate of increase for the salp, Thalia democratica, which utilizes algal blooms, an ephemeral resource. My results supported the hypothesis that highly seasonal resource availability selects for higher intrinsic rate of increase. Higher r , achieved primarily by high early fecundity, has been reported in an introduced population of Chrysomelid beetles in British Columbia in comparison with their ancestral California population (Peschken, 1972).

The variance in fitness in these populations is not correlated with environmental temperature variance. The Palm Beach population which has the most stable thermal environment displays the greatest variance in fitness in all temperature environments. However, mean relative fitness is relatively invariant to temperature in Palm Beach. Palm Beach flies are more variable for components of fitness as well. High variance in fitness in the Palm Beach population may indicate that variance in environmental temperature is not an important component of the selective regime for this population. This population may be selected primarily for resistance to high temperature. Stephanou and Alahiotis (1983) showed that sensitivity or resistance to heat shock (40°C) in derived strains of Drosophila melanogaster is predominantly due to polygenic maternal factors. Some involvement of additive action located to chromosome II was indicated. Populations maintained at low temperature for seven years were more sensitive to heat shock than populations maintained at 25°. They suggested that temperature stress was an important component of natural selection maintaining protein polymorphisms through differential thermolability of protein synthesis. If a similar phenomenon is involved in the differentiation between these

populations, metabolic rates may differ between the cooler and warmer populations. Some strains in the Palm Beach population appear to be highly resistant to high temperatures in that they display much higher intrinsic rates of increase relative to their rates at 25o, but other cohorts are quite sensitive to 28o. The Michigan population appears to be quite sensitive to high temperature, since many cohorts do not show the expected increase in r_c when the temperature is shifted from 25o to 28o. The experimental design employed in these analyses can not distinguish maternal effects, but it is noteworthy that of the four Michigan crosses with the highest intrinsic rates of increase, three had maternal lines among the top four inbred cohorts for intrinsic rate of increase. The other two populations do not contain the appropriate cohorts to address this question. Murphy et al. (1983) indicated that dam effects, which may include a maternal component, were important for average fecundity at high temperature in Drosophila simulans, but an index of cohort intrinsic rate of increase only showed maternal influences at low temperature. Low (20o) and high (30o) temperatures are reported to increase the recombination rate in Drosophila melanogaster mutants in the laboratory, relative to lines reared at 25o (Tracey and Dempsey, 1981). The increased recombination rate at stressful temperatures may contribute to increase variation in cohort intrinsic rate of increase and its components at stressful temperatures in these experiments and in the wild. Such an increase could be viewed as adaptive in fluctuating environments.

The cool temperature regime of the Michigan population may select for resistance to cold temperatures in adult females. McKenzie (1975) showed that wild adult female Drosophila melanogaster underwent

reproductive quiescence at 9-13°C. He suggested that reproductive shutdown at low temperature was selected due to very low larval survivorship at low temperatures. Spring populations view may well be reconstituted from inseminated females that shut down reproduction to overwinter, but respond rapidly to increased environmental temperature in the spring. Inseminated females can reproduce viable offspring after six months at 6°C, when returned to warm temperatures (Anxolabehere and Periquet, 1970). The lower intrinsic rate of increase in Michigan flies at 22°C, and their much higher rates at higher temperature relative to the other populations, may suggest selection for overwintering through more rapid reproductive shutdown. The rapidity of the response to warming spring temperatures may also be favored in the Michigan population. The very steep response of early fecundity and viability to the 22-25°C shift also supports this idea.

The phenotypic correlation structure of cohort intrinsic rate of increase in these populations suggests that selection has acted differently in each population. Although viability, development time and early fecundity are the prime determinants of cohort intrinsic rate of increase, as might be expected from the formulation of r_m , they are weighted differently in each population and their temperature responses differ as well. No support for a globally coadapted life history in this colonizing species is seen, since the differences have a genetic basis and are not due entirely to phenotypic plasticity. Even at 22°C where very similar mean cohort intrinsic rate of increase is achieved in all populations, the populations differ in the components of fitness and the organization of fecundity patterns. Palm Beach has a low, broad net fecundity distribution, where high viability-high early reproducing

lines are penalized by shorter lives. This population is essentially polymorphic with some cohorts beginning to show reproductive quiescence at this temperature. Gainesville flies also appear to reduce early fecundity, but emphasize high late reproduction. Michigan flies are polymorphic for viability at this temperature, but have very steep responses in cohort intrinsic rate of increase and early fecundity when the temperature is shifted to 25o.

Correlations between components of intrinsic rate of increase in Drosophila melanogaster have been discussed as reviewed in Chapter I, but none of these reports address the total life history components of different populations in more than one environmental circumstance. The importance of genotype-environment interactions for fitness components (Giesel et al., 1982a,b; Murphy et al., 1983) suggest that high additive genetic variance for fitness components can be maintained in a variable environment without the necessity of postulating ubiquitous negative serial pleiotropy. The previous study on Drosophila simulans (Murphy et al., 1983) clearly showed high additive genetic variance for some fitness components under specific environmental conditions for a natural population.

The primary conclusion of this analysis is that Drosophila melanogaster from the most variable temperature environments achieve higher fitness under unrestricted laboratory conditions than those from more stable environmental regimes. More data are required to distinguish whether the fitness differences observed in these populations can primarily be attributed to differences in the temperature heterogeneity of their habitats or whether these differences reflect selective effects of differential intra- and inter-specific

competition or resource heterogeneity. Current application of quantitative genetic models to life history theory (Lande, 1982a, b) assume that phenotypic correlation structure is relatively invariant in time. This analysis shows that minor temperature changes strongly affect the correlation structure of fitness components. Although these data suggest that environmental heterogeneity may select for higher cohort intrinsic rate of increase under some conditions, there is no indication that the intrinsic rate of increase is maximal at the average temperature of a particular population relative to other populations. No indication of a correlation between variance in fitness and environmental heterogeneity was observed. Instead I must concur with Wilbur et al. (1974) that the life history patterns of these populations may represent a series of selective compromises to a suite of environmental variables. As Cohen (1985) suggests, no single measure of fitness is adequate for inferences regarding past selective history of a population. To understand selection on fitness attributes will require attention to multiple populations and multiple environments. Further work will be required to discern the importance of variation in competition and resource heterogeneity on these populations. The population differences in cohort intrinsic rate of increase and its components may be in part a result of selection for body size and metabolic rate resulting in different genetic and developmental constraints for the three populations. These possibilities will be addressed in the subsequent chapter.

CHAPTER III
THE INFLUENCE OF BODY SIZE AND RATE OF METABOLISM ON
INTRINSIC RATE OF INCREASE AND OTHER FITNESS COMPONENTS

The Allometry of Life History Components

Peters (1983) reviewed the allometric relationships of intrinsic rate of increase and other fitness components. Interspecific comparisons suggest that intrinsic rate of increase generally scales to body mass to the $-1/4$ power (Fenchel, 1974; Blueweiss et al., 1978; Peters, 1983). The allometry of life history traits in eutherian mammals is especially well studied (see Peters, 1983, for review). Ontogenetic timing of weaning, sexual maturity and lifespan scale to approximately $\text{mass}^{1/4}$, which suggests that each developmental phase requires approximately the same proportion of the mammalian lifespan (Peters, 1983). When the cost of reproductive growth is indexed as litter mass/gestation period, the allometric relation scales to $\text{mass}^{0.5-0.6}$ (Blueweiss et al., 1978; Payne and Wheeler, 1967a,b, 1968). If reproductive effort is defined as the proportion of available energy devoted to reproduction, then effort declines with increasing body size for mammals. Other measures of reproductive cost for mammals are reviewed by Peters (1983). Litter mass in mammals and clutch mass in birds increase to approximately $\text{mass}^{0.75}$ (Blueweiss et al., 1978). Mammalian gestation time is related to $\text{mass}^{0.25}$. Millar and Zammuto (1983) showed that age of maturation, generation time and lifespan all

scale to the 0.25 power, while litter size scaled to the -0.16 power for 29 mammalian species. Blueweiss et al. (1978) suggested that the combined consideration of these scaling relationships implied that intrinsic rate of increase is set by individual growth rates and that since larger animals invest proportionally less in reproduction, they will have a lower r_m . Fenchel (1974) had demonstrated such an allometry in a wide variety of taxa. He concluded that r_m can be interpreted as population productivity and thus must be correlated with weight-specific metabolism. He intimated that the evolution of homeothermy resulted not only in increased metabolic rate but in decreased production efficiency. Calder (1983) suggested that the attributes usually attributed to r and K selection are primarily a function of allometric relationships.

The coefficient of determination for these allometric relationships suggests good fit of this empirical model for mammals and birds, but the relationships appear to be less precise for poikilotherms (Banse and Mosher, 1980; Peters, 1983). Peters (1983) suggested that many poikilothermic animals differ from the eutherian mammal model because of indeterminate growth or growth for a longer proportion of the lifespan. Other critical considerations are that growth relations in poikilotherms are less well buffered from direct environmental influences, such as temperature, or that rate of metabolism scales differently in poikilotherms affecting other energetic considerations. The paucity of data for poikilotherms that include necessary statistical evaluation may also be, in part, responsible. The data on timing of maturity and lifespan are not in good agreement for poikilotherms. Fenchel (1974) suggested that maturation times for poikilotherms were

much greater than similarly-sized mammals. Blueweiss et al. (1978) reported very slight differences between the two groups. Reproductive investment appears to follow the mammalian model, but the coefficient of determination is much lower for poikilotherms in general and insects in particular. Fecundity appears to scale to $mass^{0.5}$ and generation time to the 0.25 power, as has been reported for mammals. However, in mammals mortality rate per unit time decreases with increasing body size, while in poikilotherms mortality rate rises with increasing body size. Body size in wild caught Drosophila melanogaster has been suggested to be an important component of adaptation to environmental temperature. Field collections indicate that larger size is favored in flies from cooler habitats, but it is not clear whether these differences are due to previous thermal history or whether genetically based differences in body size exist. Large body size has been shown to be genetically correlated with higher fecundity and longer lifespan in selection experiments (Robertson, 1957, 1966; Tantawy and El-Helw, 1966), although selection for fast development time has been shown to reduce body size as a correlated response (Cavener, 1983). The allometry of life history in Drosophila melanogaster thus may be an important constraint on life history evolution.

Metabolic Rate and Fitness Components

Peters (1983) reviewed the data on production, measured as rm or production to average biomass ratio, and suggested more data will be required to decide whether the same relationship is general for homeotherms and poikilotherms or whether the relationship is inherently variable. He suggested that the time available for maximum population growth rate for a species colonizing a new habitat would increase with

body size. McNab (1980) suggested that for mammals the most likely way to increase rm would be to increase metabolic rate given that the food resources were available to support increased maintenance costs. He suggested that for mammals rate of metabolism is set by body size and temporal and spatial variation in food quality or quantity. Growth rate, gestation period and number of offspring are then influenced by the interaction of body size and rate of metabolism. The components of intrinsic rate of increase were higher for mammals with high basal rates compared to similarly-sized mammals with low rates of metabolism. Hennemann (1983) reported that basal rate had the predicted positive correlation with intrinsic rate of increase when both were adjusted for the body size allometry. Body mass alone accounted for approximately 48% of the variation in rm ; rate of metabolism explained an additional 6% when adjusted for body size. He suggested that food habits and other lifestyle parameters may constrain the evolution of higher intrinsic rates of increase in some groups. Thermoregulatory constraints may also be important especially in energetically stressful environments. In contrast to the allometric relation of rate of metabolism to 0.75 power of body mass in mammals and other taxa, many insects show a direct proportionality between mass and rate of metabolism (Keister and Buck, 1974). Individual and interpopulation differences are usually attributed to differences in age, sex, reproductive condition, nutritional state, activity or thermal history.

Although allometric models are useful for interspecific predictions and possibly intraspecific predictions for equilibrium populations in stable habitats, they are less useful in predicting responses to temporal and spatial heterogeneity in less predictable environments.

Marsteller (1984) developed an allometric model which incorporated joint variation in temperature and food availability on potential for survivorship and reproduction in mammals. He reported synergistic effects of temperature and food availability and concluded that as size increased the effect of environmental variation declined. This bounded model approach should allow consideration of constraints that determine what life history may evolve for a given species.

Another useful approach taken in this analysis is to compare the relationships of body size and rate of metabolism in different populations of the same species. As McNab (1980) has suggested, if abundant resources are available or if reproductive expenditure is timed at peak resource availability, increased metabolic rate may be one way to achieve high fitness. This paper examines populations that fall at different points on the stable-fluctuating continuum with respect to environmental temperature (Chapter I). The intrinsic rate of increase is considerably higher in the population from the most variable habitat especially at warmer temperatures, as had been suggested previously in interspecific comparisons of Dysdercus by Dingle (1974). In this chapter the allometric relationships and rates of metabolism of the three populations will be analyzed with respect to the correlation structure with fitness components. I suggest that selection may act directly on rate of metabolism and on the correlation structure of life history components in relation to rate of metabolism in environments that differ in predictability and fluctuation of environmental temperature.

Methods

Flies used in this analysis were third generation descendants of wild caught females from three populations that differed in the degree of thermal stability and predictability. Details of derivation and culture methods were described in Chapter I.

Rates of metabolism were estimated at all three temperatures on full sibs of the females on which life history data was collected from Gainesville and Michigan and for crosses from the Palm Beach population. Metabolic rates for inbred Palm Beach cohorts were estimated using random sample of females from each isofemale line. Oxygen consumption was estimated by Gilson respirometer at three temperatures. 7 to 10 females from each line, reared at 25, were transferred to 7 ml respirometer flasks and equilibrated in a 22°C water bath for 1.5 hours. Readings were taken at 15-20 minute intervals for 2 hours or until 3 sequential readings were essentially equal. Environmental temperature was then raised to 25 °C and following a 1 hour equilibration period the measurements were repeated. The same process was repeated at 28°C. Each group of females was then etherized and weighed to the nearest 0.01 mg. All oxygen consumption data was converted to standard temperature and pressure prior to analysis. All experiments were initiated at the same time of day to prevent differences due to circadian rhythmicity, and flies were kept in the dark to inhibit activity. If either metabolic rate data or life history data on at least three females was not available for a particular line, it was excluded from the cohort analysis.

Data were analyzed according to the statistical techniques described in Chapter I. Phenotypic correlations between metabolic rate

and other life history components was estimated by Pearson product-moment correlation. Statistical significance of correlations was determined from standard tables (Dixon and Massey, 1957). Spearman rank correlations were also calculated but did not give results which differed from the Pearson correlations.

Body size was only estimated at 25o, so a simpler ANOVA model was employed. Regressions of life history characters on body size were employed using standard regression techniques. F tests were used to assess the significance of the regression and 95% confidence intervals were calculated for coefficients.

Results

Allometry of Life History

Body size did not differ significantly between populations or groups at 25o (Table 3.1). Mean values indicate that inbred flies were slightly larger than outcrossed flies in the Florida populations, but the outcrossed flies were relatively larger in Michigan, which explains the PxG interaction approaching significant levels. The phenotypic correlations of body mass with other life history traits at 25o suggests that body size is indirectly an important life history component in these populations (Table 3.2). The pattern of correlation differs between populations. Among crosses, the Palm Beach population displays significant positive associations of mass with development time and early fecundity and a significant negative association with viability. This suggests that larger flies take longer to develop and are less viable, but have higher fecundity when compared to cohorts of smaller body mass. Among inbred cohorts, larger flies develop significantly faster in the Drosophila simulans, population which may indicate that

Table 3.1 Analysis of Variance for Body Mass at 25o and Mean Values for the Three populations

Analysis of Variance				
Effect	df	F	significance	
Population	2	1.26	.28	
Group	1	.22	.63	
P $\times$ G	2	2.15	.12	
Line (P $\times$ G)	71	.58	.97	
Residual	42			

Mean Values (in mg) for Body Mass in the Populations				
Population	Inbreds		Crosses	
	Mean	S.D.	Mean	S.D.
Gainesville	1.24	.25	1.18	.19
Palm Beach	1.27	.15	1.25	.17
Michigan	1.21	.19	1.30	.22

Table 3.2 Phenotypic Correlations of Mass with other Life History Traits

Population	Mass with		Inbreds			
	MR	R	AOD	V	DT	FFD
Gainesville	.46+	.41+	.38	-.13	-.55	.29
Palm Beach	.35	-.01	-.05	.44+	.09	.17
Michigan	-.43+	.28	.25	.10	.38	.57*
Crosses						
Gainesville	.28	-.05	.10	.02	.04	.41
Palm Beach	.26	-.33	.22	-.53+	.79*	.48+
Michigan	.14	.01	.31	.10	.22	-.26

+ = .05 < p < .10

* = p < .05

development time in the first larval stage is speeded up (Robertson, 1963). Larger Michigan inbred flies have significantly higher early fecundity. The small sample sizes for body mass and the fact that they were measured on full sibs of the flies on which the life history data were collected suggest caution in interpreting these allometric data.

No significant allometric relationships were observed in either inbred or outcrossed flies when the data from all three populations were combined (Table 3.3). For inbred lines, development time scaled to $\text{Mass}^{-0.21}$ in Gainesville flies. This relationship was not significant in other populations. Cohort intrinsic rate also scaled to body size in the Gainesville population and had a positive slope (Table 3.4). Early fecundity scaled to body mass in the Michigan population, but the 95% confidence interval of the regression coefficient (-0.19 to 3.61) allows little assessment of the slope of this relationship. The relationship between body size and rate of metabolism was significant in the Gainesville and Michigan flies, although again the 95% confidence interval on the slope allows little comparative interpretation, although it does suggest that the relationship may be negative in the Michigan flies and positive in flies from Gainesville. Much larger sample sizes would be required to assess these relationships. In the crosses, only the Palm Beach flies displayed significant allometric associations at 25°C. Development time is positively associated with body size to approximately the 0.73 power. Body size explains about 55% of the variation in development time. Development time has been reported to scale to the 0.25 power in a number of species (Peters, 1983). Viability may have a negative relationship with size, but sample size limitations restrict interpretation of this relationship.

Table 3.3 Regression Relationships Between Mass and Other Life History Variables when The Data From All Populations are Combined (On Log Transformed Data)

Trait	Inbreds					
	a	b	SE (b)	r ²	F	95% CI
Viability	61.93	.032	.36	.0001	.003	
Development Time	8.91	-.071	.090	.0170	.98	-.25 to .11
Early Fecundity	132.66	.832	.599	.052	1.92	-.39 to 2.05
Longevity	19.45	.522	.363	.056	2.06	-.22 to 1.25
Trait	Crosses					
	a	b	SE (b)	r ²	F	95% CI
Viability	71.60	-.240	.453	.0081		
Development Time	8.37	.048	.094	.0083	.26	-.14 to .24
Early Fecundity	202.33	.523	.535	.030	.95	-.57 to 1.62
Longevity	24.66	.133	.095	.0096	.28	-.37 to .64

Table 3.4 Significant Regression Relationships for Each Population of Body Mass with other Life History Traits

		Inbreds					
Pop	Trait	a	b	SE(b)	r ²	F	95% CI
GV	Metabolism	4.008	.859	.302	.403	8.10	.20 to 1.52
	Imm Rate	.318	.315	.207	.161	2.31	-.14 to .76
	Dev Time	9.107	-.214	.093	.308	5.35	-.42 to -.01
MI	Early Fec	151.69	1.711	.562	.316	4.16	-.19 to 3.61
		Crosses					
PB	Dev Time	7.230	.725	.262	.559	7.63	.08 to 1.36
	Viability	122.61	-3.18	1.90	.318	2.81	-7.84 to 1.46

Rate of Metabolism

The ANOVA for metabolic rate shows highly significant population, temperature, $P \times T$, $P \times G \times T$ and line effects (Table 3.5). $G \times T$ is also significant at the 0.04 level. The presence of $G \times T$ and $P \times G \times T$ interactions suggests that inbreds differ from crosses in metabolic rate and temperature response also. This model explains 91.4% of the variance in metabolic rate. Mean values show that Michigan flies have much higher rates at all temperatures than the flies from Florida populations (Table 3.6). The two Florida populations do not differ significantly in mean rate of metabolism. The mean temperature response of the crosses shows similar patterns of response to temperature in all populations, with a steeper slope from 22° to 25° than for the shift from 25° to 28° (Figure 3.1). Q10's calculated over the low temperature range for each line averaged 4.51 and did not differ between populations. The high range Q10's averaged 2.37 and also did not differ significantly between populations or groups in the ANOVA. Michigan flies have more variable metabolic rates than either of the Florida populations. Examining the cohort reaction norms indicates that the inbred flies are more genetically divergent than crosses, at least in the Gainesville and Michigan populations (Figure 3.2). Similar shape of the temperature response lines in the Gainesville cohorts indicates no substantial differences in phenotypic plasticity between cohorts. However, the population appears to be comprised of two sets of lines with characteristic setpoints. Among the Palm Beach crosses, three cohorts display a pattern of large response to the low temperature

Table 3.5 Analysis of Variance for Rate of Standard Metabolism

Effect	df	F	signif
Population	2	10.78	.0001
Group	1	1.93	.1696
Temperature	2	117.78	.0001
PxG	2	1.01	.3692
PxT	4	8.30	.0001
GxT	2	3.12	.0474
Line (PG)	67	11.86	.0001
PxGxT	4	3.24	.0142
Residual	148		

Analysis of Variance by Temperature for Standard Metabolism

Effect	22		25		28	
	F	p	F	p	F	p
Population	5.16	.008	8.11	.0007	16.99	.00
Group	2.09	.152	2.20	.142	4.97	.02
PxG	.61	.543	1.25	.293	1.97	.14
Line	3.10	.0001	2.30	.0013	2.30	.00

Table 3.6 Mean Standard Metabolism in microliters /hour ($\pm$ S.D.)

Pop'n.	Temp.	Inbreds	Crosses	% Diff.
GV	22oC	3.57 (1.38)	3.33 (0.82)	7.2
	25oC	4.96 (1.50)	4.00 (0.75)	24.3
	28oC	4.99 (1.66)	4.44 (0.60)	12.6
PB	22oC	3.16 (0.56)	3.17 (0.62)	-0.3
	25oC	3.70 (0.45)	4.24 (0.93)	-12.9
	28oC	4.73 (0.96)	4.64 (0.79)	1.9
M	22oC	4.84 (2.17)	3.82 (1.36)	26.7
	25oC	6.07 (2.04)	5.54 (2.13)	9.6
	28oC	8.77 (3.73)	6.33 (1.65)	38.6

Figure 3.1 The effect of temperature on the rate of metabolism (microliters/hr) in the three populations

- a. inbred isofemale lines
- b. intrapopulation crosses

Figure 3.2 "Reaction norms" for rate of metabolism

range but are relatively homeostatic to the 25-28 shift. Several of the inbred lines are homeostatic to the full range of temperature tested. Michigan flies are by far the most genetically divergent as indicated by the variety of setpoints between cohorts. They display several forms of temperature response demonstrating plasticity. Among crosses, slightly less than half the cohorts respond directly to increasing temperature. A number of cohorts show some homeostasis over the high temperature range and three cohorts maintain similar rates of metabolism at all temperatures.

The higher rate of metabolism in the Michigan flies may explain some of the variation in cohort intrinsic rate of increase and other life history components. When rank correlations are calculated between life history traits and mean cohort rate of metabolism for the outcrossed cohorts, standard metabolism is strongly positively correlated with intrinsic rate of increase, and with early and peak fecundity (Table 3.7). Standard metabolism is strongly negatively correlated with timing variables, such as development time, age of peak fecundity and age of death. The correlations with viability and late fecundity are not significant. Inbred cohorts show similar correlation structure. These strong correlations between mean values are primarily due to the effects of temperature acting in a similar fashion on the life history traits (see Figures 3.4-3.6). The relationship between metabolic rate and life history components at a particular temperature are not nearly as strong.

Regression analysis on the combined data shows that only 6% of the variation in development time is explained by rate of metabolism in inbred flies (Table 3.8). The 95% confidence interval of the regression

Table 3.7 Rank Correlations of Means of Metabolic Rate with
Life History Traits in Crosses

Means

		MR	R	V	DT	AOP	FFD	AOD	PK	LTF
GV	22oC	3.33	.33	.77	9.3	11.8	126	27.7	87	34
	25oC	4.00	.38	.67	8.5	8.2	248	25.3	113	41
	28oC	4.44	.47	.71	6.8	6.8	280	25.0	111	58
PB	22oC	3.17	.37	.86	9.4	8.4	206	26.4	98	41
	25oC	4.24	.35	.67	8.5	11.2	190	30.3	97	41
	28oC	4.64	.43	.57	6.6	4.6	232	15.1	109	37
M	22oC	3.82	.34	.71	9.8	9.1	179	26.1	103	55
	25oC	5.54	.44	.78	7.9	7.9	293	22.9	125	48
	28oC	6.33	.48	.73	6.8	6.3	301	20.0	125	40

rS		.82*	-.23	-.81*	-.75*	-.80*	-.77*	.75*	-.05
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* $p < .01$.

Figure 3.3 The effect of temperature on the relationship between intrinsic rate of increase and rate of metabolism

Figure 3.4 The effect of temperature on the relationship between viability and rate of metabolism

Figure 3.5 The effect of temperature on the relationship between early fecundity and rate of metabolism

Figure 3.6 The effect of temperature on the relationship between development time and rate of metabolism

Table 3.8 Regression Relationships of Standard Metabolism and other Life History Traits

Crosses (n=98)						
Trait	a	b	SE(b)	r ²	F	95% CI
Viability	87.07	-.163	.104	.03	2.44	-.37 to .04
Devel. Time	10.94	-.194	.044	.17	19.75	-.28 to -.11
Early Fecundity	115.00	.433	.123	.12	12.43	.18 to .68
Longevity	30.16	-.179	.094	.04	3.64	-.36 to .008
Inbreds (n=101)						
Viability	72.70	-.168	.120	.03	1.97	-.40 to .07
Devel. Time	10.13	-.114	.045	.05	6.49	-.20 to -.02
Early Fecundity	111.06	.215	.161	.02	1.78ns	
Longevity	25.53	-.149	.104	.02	2.06ns	

coefficient is from -0.02 to -0.20. Among crosses, 17% of the variation in development time is attributable to rate of metabolism and the slope is also negative (-0.11 to -0.28). This is in the expected range from previous models. Among crosses, 11.5 % of the variation in early fecundity can be attributed to metabolic rate differences between cohorts. The positive slope has a 95% confidence interval of 0.19 to 0.68. Only about 3% of the variation in longevity and viability can be attributed to standard metabolism.

When within-temperature regressions are examined separately for each population, 23.9% of the variation in early fecundity at 22o and 48% of the early fecundity variation at 25o in Gainesville flies may be explained by rate of metabolism (Table 3.9). The slopes are positive, but the small sample sizes preclude serious comparisons with published relationships. In the Palm Beach population, approximately 30% of the variation in development time may be attributable to rate of metabolism. No other regressions are significant in this population. In Michigan crosses only viability has any significant relationship with standard metabolism.

Phenotypic correlations of standard metabolism within populations and within temperatures are reported in Table 3.10. The Bartlett's Chi Square indicates that these correlations do not differ significantly by population or temperature, although the correlations of metabolic rate with intrinsic rate of increase and early fecundity approach significance. Among crosses standard metabolism is significantly correlated with early fecundity at 22 and 25o in Gainesville, which may explain the slight positive correlation of metabolic rate with intrinsic rate of increase. In Palm Beach and Michigan flies the correlations of

Table 3.9 Significant Regression Relationships of Standard Metabolism separated by Population and Temperature (Crosses)

Temp	Trait	a	b	SE(b)	r ²	F	95% CI	n
22	FFD	43.04	.842	.53	.239	2.52	-.38 to 2.06	10
25	FFD	26.17	1.55	.61	.418	6.47	.17 to 2.95	11
28	DT	4.90	.229	.157	.174	2.10	-.12 to .58	12
25	DT	5.79	.276	.164	.320	2.82	-.13 to .678	8
28	DT	4.23	.305	.204	.308	2.23	-.22 to .83	7
28	V	135.72	.359	.235	.174	2.32	-.87 to .16	13

Table 3.10 Correlations between Standard Metabolism and other Life History Variables.

Inbreds								
		R	Ro	Tot	AOD	V	DT	FFD
GV	22oC	.26	-.19	-.31	-.59	.19	-.09	.15
	25oC	.41	.29	.36	.42	-.09	-.41	.32
	28oC	-.04	-.25	-.05	.00	-.12	-.29	-.34
PB	22oC	-.39	-.04	.06	-.05	.17	.11	.07
	25oC	.19	.27	.31	.30	.18	-.19	.15
	28oC	-.14	-.23	.14	.08	-.49	-.05*	.08
M	22oC	.02	.26	.39	.10	-.11	.50*	.04
	25oC	-.80*	-.38	-.18	.06	-.43*	.17	-.63
	28oC	.20	.39	.12	.20	.43*	.52*	.04
Crosses								
		R	Ro	Tot	AOD	V	DT	FFD
GV	22oC	.20	-.07	.07	.01	-.22	-.13	.63*
	25oC	.33	.21	.13	.05	.32	.18	.54*
	28oC	-.06	.11	.19	.35	-.15	.44*	.31
PB	22oC	-.26	.11	.09	.22	-.05	.24	.08
	25oC	-.09	-.14	-.21	-.34	-.04	.57*	.34
	28oC	-.46	-.39	-.57*	-.15	-.33	.57*	-.22
M	22oC	.00	.00	.02	.00	.00	.10	-.27
	25oC	-.06	-.08	.19	.07	-.25	-.24	-.18
	28oC	-.49*	-.55*	.62*	-.22	-.44*	-.20	-.34
Pooled r		-.03	-.03	.04	.07	-.07	.10	.10
Heterogeneity Chi-Squared		22.6	19.2	16.1	17.5	13.2	19.7	23.4

X_{2,10} = 24.77

metabolic rate with intrinsic rate of increase are usually negative. This correlation is significant in the Michigan flies at 28° and probably acts through a negative correlation with fecundity and viability. Indeed, the r -MR correlation drops to -0.31 when partialled for viability and to -0.39 when partialled for early fecundity. The negative correlation in the Palm Beach flies between MR and intrinsic rate of increase acts in a different way. The positive correlation between metabolic rate and development time (0.57) and the high negative correlation between intrinsic rate of increase and development time (-0.90) completely eliminate the negative correlation between intrinsic rate of increase and rate of metabolism when development time is held at its mean value (R -MR.DT=0.23). At 22 and 25 ° in Gainesville flies the residual correlation between intrinsic rate of increase and metabolic rate when adjusted for the positive MR-FFD correlation, actually becomes 0 or negative (R -MR.FFD=-0.31 at 22° and 0.03 at 25°).

Basically for these populations, there are no residual linear correlations between metabolic rate and life history traits once the common effects of temperature are taken into account. The graphic analysis described below shows that some of this lack of predicted effects of metabolic rate is due to curvilinear tradeoffs at high metabolic rate.

Intrinsic rate and standard metabolism

The relationship between intrinsic rate of increase and standard metabolism for the Gainesville population shows the temperature effect clearly (Figure 3.7). Little residual effect of rate of metabolism is seen within temperature treatments, although there appears to be some curvilinearity at warmer temperatures, causing cohorts with very high

Intrinsic Rate vs Standard Metabolism

Figure 3.7 The relationship between intrinsic rate of increase and standard metabolism for the three populations

rates of metabolism to have lower intrinsic rate of increase. The Palm Beach population does not show the temperature effect as clearly since intrinsic rates are roughly similar at 22 and 25°C. At 25°C there does appear to be some penalty for extremely high rates of metabolism. The Michigan population displays the temperature effect most clearly and extreme rates of metabolism at all temperatures appear to extract a premium in lowered intrinsic rate of increase.

Early fecundity and standard metabolism

The graphs of early fecundity and standard metabolism closely reflect the patterns seen in intrinsic rate (Figure 3.8). This is not surprising since they are highly correlated. The relationships with standard metabolism are stronger in the Gainesville and Michigan populations. At 22°C, Gainesville flies with higher rates of metabolism generally have higher cohort early fecundity. At 25 and 28°C, the relationship is less strong and there is some tendency for early fecundity to decline at high rates of metabolism. The Palm Beach flies are more variable in their responses and no clear residual effect of standard metabolism is apparent. Michigan flies again display the most curvilinear response within temperatures, paying a penalty for very high or very low rates of metabolism.

Development time and standard metabolism

Development time responds very strongly to temperature (Figure 3.9). Almost no residual relationship is explained by standard metabolism, although in the Palm Beach population development time appears to be slightly longer for flies with extremely high rates of metabolism.

Early Fecundity vs Standard Metabolism

Figure 3.8 The relationship between early fecundity and standard metabolism

Development Time vs Standard Metabolism

Figure 3.9 The relationship between development time and rate of metabolism

Viability vs Standard Metabolism

Figure 3.10 The relationship between viability and standard metabolism

Age of Death vs Standard Metabolism

Figure 3.11 The relationship between longevity and rate of metabolism

Viability and standard metabolism

Some temperature effects on viability-metabolism relationship can be distinguished in the Gainesville population (Figure 3.10). Within temperatures there is slight indication that higher rates of metabolism reduced viability. Michigan flies display similar effects at 22 and 28o, and the relationship is curvilinear at intermediate temperatures. Overall higher standard metabolism appears to reduce viability, whether it is due to increased temperature or to a more direct relationship.

Age of death and standard metabolism

The conjoint effect of temperature and rate of metabolism on longevity is not clear in the Gainesville population (Figure 3.11). Within temperatures, the effect of higher metabolism is highly variable, but most high rate of metabolism cohorts have shorter lives. In Palm Beach flies the primary effect is due to the temperature-metabolic rate response with little residual effect of metabolism on longevity. In Michigan flies the conjoint effect of temperature is quite strong, and there is a strong residual effect of metabolic rate at 28o, although it is essentially unimportant at lower temperatures.

Discussion

Allometry of Life History

These data show that body size as indexed by mean mass of a cohort does not differ significantly between populations when the flies are raised in common laboratory conditions. This may indicate that much of the size difference observed in field collected flies from different habitats is due to differences in thermal history, larval nutrition or other variables. The correlations of body size with other life history components does differ between populations indicating some divergence in

size constraints. The correlation between body size and development time is negative in the Gainesville population and positive in Michigan inbreds. The negative correlation may indicate that genes affecting the first larval stage (Robertson, 1963) are important in the Gainesville flies. Robertson (1964) has shown that the first stage is relatively canalized under most conditions, but flies reared on RNA-deficient media showed this negative correlation. Church and Robertson (1966) suggested that presence or absence of a correlation between development time and size reflected changes in DNA content if cell number was affected or protein/DNA ratio reflecting cell size differences. Cavener (1983) showed that selection for fast development time was correlated with increased frequencies of the fast allele at the 6GPCD locus, which suggests that energy flow through the pentose shunt is modified.

Warm temperature regimes have a strong selective effect on reducing body size as indexed by two wing size measures in Drosophila melanogaster (Cavicchi et al., 1985). Their results show that temperature-dependent selection operates in different ways on anterior and posterior wing segments. Population by temperature interactions accounted for much of the genetic divergence in wing area, cell number and cell size in the posterior segment but were unimportant for the anterior wing measures. Their data suggest that selection has acted to maintain as large a body size as possible under warm temperature conditions, even at the expense of decreased homeostasis of body size in fluctuating temperature conditions. My data suggest that flies from the least variable Florida population may have maintained body size by extending development time, but in the moderately variable Gainesville

population, body size may be maintained by faster growth in early larval stages.

Levins (1969) showed that under certain conditions, body size clines usually seen in field-caught flies, that is larger flies in north and cooler or higher altitude sites, can show countergradient variation when raised in identical laboratory conditions. His findings are counter to the cogradient variation seen in Tantawy and Mallah's (1961) transects. He attributed the difference to environmental differences between collection sites. Hot areas were also dry areas for the areas he surveyed, whereas in Tantawy and Mallah's sites hot areas were wet. He suggested that relative to other Drosophila species, Drosophila melanogaster had high heat tolerance by physiological mechanisms and that it has low levels of genetic variance for heat tolerance and little population differentiation.

In earlier selection studies, body size has been shown to be positively correlated with early fecundity in Drosophila melanogaster (Robertson, 1957). My results show a slight positive correlation in the Palm Beach flies, but a slight negative correlation in flies from more variable temperature habitats at 25o. Energetic costs imposed by higher metabolic rates in the flies from more variable regimes may explain this negative correlation. The correlation may also in part, reflect an upper limit to egg production. This explanation is also indicated by the relative homeostasis of early fecundity, especially in the Michigan flies at high temperature. In Florida populations where development time is lengthened to achieve high body size, the larger flies have lower viability. Robertson (1965) discussed the impact of the relationship between growth rate and critical pupation size for several

Drosophila species on response to nutritional stress. Drosophila funebris and Drosophila melanogaster had relatively good viability under suboptimal conditions that critically affected viability in Drosophila funebris. He suggested that an equivalent change in body size had differential fitness effects for the three species. My data suggest that different populations of the same species may show alternative fitness responses to equivalent changes in body mass.

Tantawy and El-Helw (1966) conducted bidirectional selection experiments on body size, indexed by wing length and thorax length in Drosophila melanogaster. In their base population thorax length was positively associated with longevity and egg production phenotypically. High egg production was also phenotypically associated with longevity. The genetic correlation was positive between thorax length and longevity. Two methods of selection, differing in the degree of inbreeding allowed, both generated direct responses of body size in the directions of selection. However, selection for larger or smaller wing size decreased early fecundity in the flies with more inbreeding. In the outbred regime, selection for larger size led to even higher egg production than was anticipated, while selection for smaller body size reduced fecundity. Genetic correlations between size and longevity increased in the outbred selected lines and decreased under inbreeding. Direction of selection had no impact on viability. All selection regimes had lower viability which may indicate the confounding effects of inbreeding with selection.

Since body size was only estimated at 25°C in this data set, it is not possible to explore the plasticity of body size in response to temperature change. Since considerable differences in fitness and

fitness components are evident in these populations at 25o, it is unlikely that body size selection has been a prime constraint on the life history organization of these populations. Calder (1983) has suggested that allometric constraints determine first order life history strategies and that second order strategies arise from adaptive modification for specific environmental conditions. No clear indication of such primary allometric constraints is indicated by these data.

Poikilothermic animals from continually fluctuating temperature environments have been predicted to develop temperature compensation in metabolic rate (Enright, 1967; Prosser, 1973). These results on Drosophila melanogaster do suggest temperature compensation. Although a few lines in the population from the most heterogenous environment display some compensation, the population from the most stable thermal regime displays the most temperature compensation. Nash (1979) did not observe such compensation in woodlice. Insects kept in oscillating temperature regimes appeared to acclimate to the median temperature. Fluctuating temperature appears to reduce development time relative to constant conditions in some insects (Messenger, 1964; Hagstrum and Leach, 1973). Although development time was slightly lower in the Michigan flies under some conditions, there were only significant population differences at 28o.

This analysis clearly shows that Michigan flies have much higher rates of standard metabolism at all temperatures than flies from Florida populations. The population differences have a genetic basis, but the small sample sizes preclude assessment of heritability in these populations. The higher rate of metabolism in the Michigan flies may explain, in part, their higher cohort intrinsic rate of increase, high

early fecundity and lowered development time and lifespan. However, within temperature treatments extremely high metabolic rate seems to entail a significantly higher cost for the Michigan flies. Since the temperature environment in Michigan is extremely variable and unpredictable, even in the summer, the high rate of standard metabolism may be an adaptation to facilitate rapid reproductive response when conditions are adequate for reproduction.

The intricate interrelationships between rate of metabolism and other life history traits, especially the constraints of body size, imply that rate of metabolism may be an important life history component. The data indicate that the pathway of action may differ when environmental uncertainty is an important component of the selective regime. I have suggested that environmental uncertainty may select for higher rates of metabolism in order to rapidly respond when good conditions are available. In flies from the most thermally variable environment, standard metabolism is negatively correlated with cohort intrinsic rate of increase within temperatures, especially under more stressful conditions. This correlation appears to act through a negative effect on early fecundity and viability. Flies with extreme rates of metabolism pay a penalty in lowered viability and decreased early reproduction, although they still attain a higher cohort intrinsic rate of increase than flies from a thermally more stable environment. In the most stable environment examined, high metabolic rate is associated with longer development times, causing a negative association with cohort intrinsic rate of increase. In flies from the intermediate environment, there is a positive association of metabolic rate and cohort intrinsic rate of increase, primarily due to the effects of

higher metabolic rate on increasing early fecundity in these animals. Taken together these results suggest that Michigan flies pay greater penalties for very high metabolic rates than their counterparts from less thermally variable environments, yet overall achieve higher rates of fitness when conditions are favorable and can respond more rapidly to good conditions.

These intraspecific data support in general McNab's contention that components of intrinsic rate of increase are higher for populations with higher standard metabolism. These metabolic rate differences between populations may represent a genotypic physiological adaptation to prevailing temperature conditions, since the average thermal sensitivity (Q_{10}) does not differ between populations, but the temperature response curves are displaced so that the cohort intrinsic rate of increase of cold acclimated Michigan flies is higher than warm acclimated Florida flies when they are assessed at the same temperature (Prosser, 1973). Similar temperature compensation patterns have been reported in anurans (Berven, 1982). Although the allometric relationships are not strong, it does appear that an interaction between size and rate of metabolism imposes a moderate constraint on life history evolution, but a constraint that may also evolve as an important component of the life history.

CHAPTER IV PHENOTYPIC PLASTICITY OF FITNESS COMPONENTS

I speculated whether a species very liable to repeated and great changes of conditions might not assume a fluctuating condition ready to be adapted to any condition.

C. Darwin (letter to K. Semper, 1881, p.391)

Introduction

Real organisms live and reproduce in environments that vary in space and time. To understand the selective importance of temporal and spatial environmental heterogeneity on fitness characters, a comprehensive life history theory will require integration of demographic, genetic, and developmental approaches (Lewontin, 1974a; Gupta and Lewontin, 1982; and Stearns, 1982; 1983a, b), since the fitness of an organism is an emergent property of the phenotypic and genetic interrelationships of component traits and the interplay of environments encountered through life on the expression of those traits. Although the need to incorporate epigenetic processes into evolutionary theory has been acknowledged (Waddington, 1952; 1957; Lewontin, 1957; 1974a; Bradshaw, 1965; Giesel, 1976; and Bonner, 1965; 1982), recently there has been a resurgence of interest in incorporating physiological and developmental components of plasticity into life history theory (Bradley, 1982; Caswell, 1983; Smith-Gill, 1983 and Stearns, 1983).

As Lewontin (1974a, b) and Gupta and Lewontin (1982) demonstrated, the norms of reaction of the genotypes in a population determine the outcome of any analysis of phenotypic variation. Phenotypic plasticity

in response to environmental change has long been recognized as a potentially important factor in life history evolution (Dobzhansky and Spassky, 1944; Waddington, 1957; Bradshaw, 1965; Lewontin, 1974a; Bonner, 1982). Bradshaw's (1965) review focused on conditions favoring plasticity of specific traits. He defined plasticity as the amount of modification of expression of a genotype given by a specific environmental change. He proposed that the plasticity response was character-specific, environment-specific, under direct genetic control and capable of being radically altered by selection. He suggested that phenotypic plasticity may be particularly important in temporally fluctuating environments, where the environmental change is more rapid than the generation time of the organism. For longer and more predictable environmental change, he suggested that genetic polymorphism might be expected due to cyclic selection pressures. He also suggested that characters under strong directional selection, with resultant low genetic variability, may have relatively high plasticity in variable environments. Bradshaw indicated that plasticity would not be favored if the cost was too high or the plastic effect was not easily reversible.

While the sensitivity of a genotype to environmental change is its plasticity, the maintenance of the same phenotype in differing environments may be termed homeostasis. Ashby's (1956) analysis showed that plasticity in some traits may cause homeostasis in other essential variables. Caswell (1983) applies this type of analysis to demography by considering some measure of fitness, such as population growth rate, as the essential variable. Recent attempts to incorporate phenotypic plasticity into demographic models indicate that phenotypic plasticity

may exert positive effects by increasing fitness, by reducing the variance of fitness or by generating negative covariance between fitness components (Caswell, 1983). He suggested that, in changing environments, mean fitness may increase or variance in fitness may be minimized by plasticity in development time or plastic responses in successive characters that are negatively correlated. In addition he showed that plasticity in dormancy would be favored if it responds in the opposite direction of mortality responses to environmental change. A similar expectation may apply to reproductive quiescence, that is, plastic variation in reproductive shutdown might be favored if survivorship is enhanced.

Caswell stressed an important idea developed previously by Bateson (1963, 1979) that regulative plasticity might act on several time scales: shallow, easily reversible behavioral and physiological processes; deeper developmental changes that are irreversible in the organisms' lifespan, and genetic changes reversible only over generations. In Caswell's formulation the effect of temporal variation in fine-grained environments generates time-invariant demography, while coarse-grained environmental variation generates time-varying demography. Different choices of fitness measures under time-varying demographic conditions may lead to quite different predictions (Hastings and Caswell, 1979). Caswell's model suggests that different conditions are required for adaptive maintenance of phenotypic plasticity for different life history traits, but that plasticity may be favored whenever it modulates the effect of environmental variability. Plasticity in developmental rate is favored if reproductive value increases from one stage to the next. Plasticity of quantity variables

is favored when negative correlations between successive components generate lower variance of fitness.

Kaplan and Cooper (1984) employed decision theory to model the maintenance of intrapopulation variability in such reproductive characters as egg size and clutch size. They suggested that decanalization or unbuffering of developmental systems may have important evolutionary consequences by modifying norms of reaction and that developmentally plastic systems can evolve for fitness components in a fluctuating environment. Although Caswell correctly identifies several unresolved difficulties with incorporating phenotypic plasticity into demographic theory, the critical problems may reside in our levels of analysis. Some plasticity probably underlies every case of homeostasis. For example, maintenance of constant body temperatures in mammals may result from plasticity of thermogenerative responses or thermodispersive responses. A more formidable problem may be to clarify how the degree of fluctuation and predictability in the environment will impact relative plasticity or homeostasis of demographic traits. Gupta and Lewontin (1982) pointed out that the analysis of variance has limitations for understanding phenotypic variance in life history traits because it confounds genetic and environmental influences.

Giesel et al. (1982a, b) showed that strains of Drosophila melanogaster derived from geographic areas that differed in temporal variability and predictability with respect to environmental temperature, displayed phenotypic differences in mean life history traits such as survival, fecundity and timing of reproduction. The correlation patterns between traits also differed in the three populations. The strains from the most stable temperature regime had

some characteristics associated with "K" selection, such as relatively long life and lowered amount of fecundity. Strains from the most temporally heterogenous regime had very high early fecundity and short lives in some conditions. The northern population had higher cohort intrinsic rate of increase and higher rate of metabolism than the more thermally stable Florida populations. The significant line by temperature interactions previously shown in the flies from the more stable population (Geisel et al., 1982b) imply that phenetic strategies may of major importance in structuring life history patterns.

In this paper I present data on the cohort reaction norms of three populations of Drosophila melanogaster for intrinsic rate of increase, early fecundity, development time, viability, age of death and rate of metabolism. I shall address whether component life history traits display similar patterns of phenetic responsiveness in the three populations as might be expected of a coadapted life history syndrome. Differences in pattern between populations may indicate temperature optima for particular traits. Another possible pattern may indicate that each population has a number of specialized genotypes each with their own temperature optima. Examining the responsiveness of particular genotypes under a number of environmental conditions may permit clearer prediction of response to selection. The shape of the response curves and the degree of crossover between cohort response curves may clarify the nature of the selective forces that have been operative in these populations.

Methods

Drosophila melanogaster used in this analysis were third generation descendants of wild caught females from three populations that differed

in degree of fluctuation and predictability of their thermal environments. The Palm Beach site represented a relatively stable thermal environment with little diurnal or month-to-month temperature fluctuation. The Michigan site was highly variable and unpredictable even when only the ninety day growing season was considered. The Gainesville site was intermediate between these two extremes. Isofemale lines were established for each wild caught female in half-pint bottles. After two generation intervals of fourteen days (at 25o), the experiment was initiated by crosses within and between isofemale lines for each population. Details of the line derivation and culture methods were outlined in Chapter I. Briefly, each population is represented in this analysis by a set of isofemale lines and a set of intrapopulation crosses between isofemale lines. First instar larvae of each cross were introduced into culture vials containing 5 ml of standard Drosophila media (20 larvae/vial). The culture vials from each cross were then randomly assigned to three temperature treatments (22o, 25o and 28oC). Humidity was maintained at approximately 60% and a L:D cycle of 12L:12D was employed in all treatments. The vials were monitored daily until eclosion began. Development times were recorded for each emerging female fly and she was then mated individually and housed in a separate vial. Fecundity was recorded daily for the entire lifespan.

This report will focus on cohort temperature responses for the following traits. For each cohort, viability was recorded as the percentage of the initial 20 first instar larvae that emerged as adults. at a particular temperature. Development time was estimated as the mean time from first instar larvae to adult emergence (females only). The number of eggs laid in the first five days following emergence was

recorded for each cohort and each temperature treatment. The cohort intrinsic rate of increase was estimated by iteration from the survivorship and fecundity data using the Lotka-Euler equation. Age of death for each cohort represents the mean time from emergence to death. Females whose deaths were due to experimenter error, such as those trapped in the cotton during transfer, were totally excluded from the analysis. Metabolic rates at each temperature were measured on a set of full sibs from each cohort that were reared at 25°C, as previously described (Chapter 3).

Although the isofemale line procedures employed in these analyses may entail some inbreeding which may alter physiological or developmental homeostasis, and the intrapopulation crosses between isofemale lines may display some hybrid luxuriance effects (Lerner, 1954), comparisons of cohort average "norms of reaction" may indicate phenotypic plasticity present in natural populations of a sexual species more clearly than fully inbred lines subjected to generations of selection for adaptation to laboratory conditions. They may also come closer to representing natural populations than isochromosomal lines such as those employed in Gupta and Lewontin (1982). However, since the full sib groups employed in this analysis may also possess varying degrees of genetic variance, the cohort "norms of reaction" presented may represent only an index of the genotypic temperature response patterns of the original populations. Some caution is required in the evolutionary interpretation of the patterns here described.

The analysis of variance results for these traits have been previously discussed (Chapter I-III) and will be briefly summarized subsequently.

Results

Phenotypic variation in life history patterns can be examined in a number of different ways. The analysis of variance employed for this data set allows estimation of mean population differences, an assessment of the effect of temperature and estimation of mean differences between intra-isofemale and inter-isofemale line crosses. The population by temperature interaction can discern average differences in the plastic response to temperature, but the limitations of the ANOVA performed on cohort means precludes assessment of cohort by temperature interactions. The coefficient of variation is also useful as an index of intrapopulation plasticity. However, a more detailed picture of the relative degree of differentiation in plasticity of the temperature response and genetic divergence within and between populations may be possible if the norms of reaction for individual cohorts that share some genetic identity are examined.

The analysis of variance (Table 4.1) shows significant population differences for cohort intrinsic rate of increase, early fecundity, longevity and rate of metabolism for these three populations. As was previously discussed, the intra-line crosses (inbreds) had lower intrinsic rates, early fecundity, viability and longevity and longer development times than inter-line crosses, which is reflected in the significant group effect. Temperature, as expected, had a highly significant effect on all traits. The significant interaction effects hint that there may be differences in phenotypic plasticity in response to temperature; but this analysis does not allow differentiation between plastic responses and genetic polymorphism, nor does it distinguish the responses of the populations.

Table 4.1 Analysis of Variance for Selected Life History Traits

Effect	df	R	FFD	V	DT	AOD	MR
Pop	2	5.91**	6.53**	.24	.49	7.51**	10.78*
Group	1	20.98***	7.45**	7.21**	7.65*	4.96*	1.93
Temp	2	59.99***	33.73***	3.48*	206.49***	15.34***	117.78*
Line	67	1.37+	1.75**	2.29**	.89	1.09+	11.86*
PxG	2	.06	.28	.02	.80	.20	1.01
PxT	4	2.84*	3.35*	.92	1.36	4.09**	8.30*
GxT	2	.20	2.05	1.64	.32	.61	3.12*
PxGxT	4	1.37	2.35*	2.56*	.77	1.64	3.24*
Error	148						

+ = .05 < p < .10

* = .01 < p < .05

** = .001 < p < .01

*** = p < .0001

The coefficient of variation has also been used to characterize phenotypic variation in life history traits. The data were partitioned by temperature for each population (Table 4.2). Inbred flies were more variable than crosses between isofemale lines as might be expected if some of the genetic divergence represented fixation of recessives within lines. Clearly, for intrinsic rate of increase the Palm Beach population is more variable than either population representing fluctuating environments. Some differences in the plasticity of responses is indicated by the effect of temperature regime on variation. Among crosses the Gainesville population is more variable at extremes of temperature, the Palm Beach population becomes more variable at higher temperatures and the Michigan population has relatively similar variation at all temperatures. Similar kinds of patterns are apparent for the other traits studies. In general the Palm Beach population, which represents the most thermally stable environmental regime, displays the most variation in life history traits. Metabolic rate is an outstanding exception. The Michigan population, which is derived from a site of extremely fluctuating and unpredictable temperature, has the most variable rate of metabolism and the thermally stable site has the lowest variation. If the coefficient of variation is taken as an index of phenotypic plasticity, then the Palm Beach population would be considered to be more plastic for all traits except metabolic rate than the populations from more variable habitats.

Examining the norms of reaction for each trait may allow further clarification of these differences in variation. Divergence in temperature response patterns can be used as an index of genetic polymorphism in the populations, and the degree of response of a given

Table 4.2 Coefficients of Variation for Life History Traits

Inbreds							
Pop	Temp	R	FFD	V	DT	AOD	MR
GV	22	10.0	28.2	29.7	4.8	30.1	38.7
	25	16.9	50.2	34.1	8.9	29.6	30.1
	28	14.5	40.6	40.4	10.9	32.3	33.2
PB	22	24.4	68.1	70.9	16.0	42.0	17.8
	25	27.5	68.7	34.5	11.5	25.4	12.3
	28	31.0	62.2	45.5	9.5	34.7	20.4
MI	22	10.6	42.6	28.3	3.3	42.6	44.7
	25	11.3	36.3	30.8	7.2	33.6	33.7
	28	14.4	33.9	40.1	5.7	31.4	42.5
Crosses							
GV	22	9.1	38.7	22.7	5.6	27.2	24.8
	25	6.9	25.9	24.8	5.3	20.3	18.7
	28	8.7	28.1	26.4	7.4	19.4	13.6
PB	22	10.6	26.2	11.2	10.4	34.5	19.4
	25	15.5	57.4	45.6	12.2	23.0	22.0
	28	27.4	30.4	46.3	10.2	44.7	17.1
MI	22	6.8	23.4	21.5	3.3	24.3	35.5
	25	6.6	17.7	23.8	6.3	13.7	38.4
	28	7.8	24.8	24.9	4.7	13.1	26.0

cohort to a particular environmental change can indicate the degree of phenotypic plasticity. The shape of the norm of reaction curve can indicate the environmental condition where maximal performance occurs. For instance, an inverted V norm of reaction for early fecundity would indicate that optimal performance of a cohort is seen at 25o. Since faster development time is assumed to result in higher fitness, a V-shaped response curve would indicate a 25o optimum.

For intrinsic rate of increase population differences are stronger than the analysis of variance or coefficient of variation patterns suggest (Figure 4.1). The Gainesville population contains cohorts that are relatively unresponsive to the low temperature shift, but exhibit marked plasticity at the higher temperature. It also contains cohorts that reverse that trend and are relatively homeostatic over the 25-28o shift, but very responsive to low temperature. A few cohorts display a linear response to increasing temperature as might be expected from a simple rate-related physiological response. The norms of reaction are non-parallel and exhibit considerable intersection of response curves, indicating that a cohort with the highest fitness at one temperature may be among the lowest fitness in another environmental condition. The Palm Beach population appears to be characterized by non-parallel reaction norms, which suggests that a number of specialized genotypes may be present within the population. The Palm Beach population appears to have higher plasticity of response and greater genetic divergence

Figure 4.1 "Norms of reaction" for cohort intrinsic rate

between isofemale lines than the other populations. The Michigan population shows the least divergence between cohorts and is basically characterized by two response patterns. One set of cohorts responds basically linearly to increasing temperature indicating a rate limited process, while another group shows enhanced plasticity from 22 to 25o, but is relatively homeostatic to further temperature increases. This kind of response may indicate that some cost is incurred at higher temperature that limits attainable rates. These results do not indicate a purely physiological rate response that is the same for all populations. The amount of crossover between response patterns in all populations indicates that natural selection would favor different sets of isofemale lines in each regime. Thus, a minor shift in temperature could greatly impact the perceived genetic variability in these populations. The Michigan population is characterized by significantly higher cohort intrinsic rate of increase in warm temperature regimes than the Florida populations. If selection has primarily been directional for high population growth rates in this fluctuating environment, reduced genetic variance might be expected.

The correlation of early fecundity with intrinsic rate of increase was high in all populations and temperature treatments (Chapter II), so similar patterns of reaction norms might be expected. However, Gainesville flies display much the same pattern of response to temperature (Figure 4.2). Nearly all cohorts show a large plastic response at the low end of the temperature scale and relative homeostasis to further temperature increase. The more genetically divergent inbred lines display other temperature sensitive patterns, indicating that the population may contain hidden variation for

Figure 4.2 "Norms of reaction" for early fecundity

fecundity. Among the interline crosses, three Palm Beach cohorts have inverted-V response curves, which may indicate either that 25o is the optimum temperature for early fecundity or that some other costs are incurred at 22 and 28o. Two cohorts have a V-shaped response pattern, indicating higher fecundity at temperature extremes. The intersecting patterns in this population, as well as Michigan, show that different cohorts would be favored if selection for early fecundity was performed at 25o than would be favored at 28o. Michigan flies display greater genetic divergence and plasticity than would have been expected from the coefficient of variation analysis.

Development time is usually viewed as the least genetically variable fitness parameter, since it is assumed to have been subjected to strong directional selection for fast development time. Bradshaw (1965) suggested that for such a character variable environments may favor extreme plasticity, since there would be little genetic variance for polymorphic responses. The expected response to increasing temperature would be an essentially linear decline in development time, if a primarily growth related physiological response is the primary mechanism. This expectation holds fairly well for the Gainesville and Michigan populations (Figure 4.3), although a few cohorts maintain higher than expected development times as temperature is increased. Surprisingly, these include the fastest developing cohorts at low temperature, which suggests that development time is not at its physiological minimum. The coefficients of variation (Table 4.2) do indicate that development time is the least variable parameter studied, but the Palm Beach population clearly is more developmentally polymorphic than the other populations. The inbred isofemale lines in

Figure 4.3 "Norms of reaction" for development time

all populations show that some genetic divergence and plasticity are potentially available in all populations. The cohort norms of reaction indicate population differences in development time that were not indicated by the analysis of variance.

Birch et al. (1963) found large differences in longevity and fecundity in different geographic races of Drosophila serrata, but little differentiation in development time. Development time has been shown to respond asymmetrically to selection (Clarke et al., 1961) with a minimal response in the direction of lower development time, which may indicate that development time is near its physiological limit. However, Giesel (1974) showed that development time was shorter in populations of Drosophila melanogaster from shorter growing seasons. Taylor and Condra (1980) also showed that after 17 generations of selection for rapid generation time in uncrowded conditions, development time was significantly lower relative to a population selected for tolerance to crowded conditions. This experiment also indicated that egg-to-adult viability declined under "r" selection conditions. Istock et al. (1975) have shown considerable genetic variability for development time populations of the pitcher plant mosquito, Wyeomyia smithii. Gupta and Lewontin (1982) showed that real genetic differences in development time and its norm of reaction exist in isochromal lines from different populations of Drosophila pseudoobscura, which were not detected by analysis of variance. Variation in development time was consistently greater in a California population than in a high altitude population subjected to seriously fluctuating thermal regimes. Parker (1984) showed differences in norms of reaction of development time in geographic populations of the cockroach, Pycnoscelus surinamensis. The

clone derived from the most stable environmental regime appeared to have moderate variation and was more plastic than clones from a more variable geographic area.

The data on viability demonstrate different patterns than other traits studied (Figure 4.4). Although the analysis of variance indicated no population differences in mean viability, the cohort norm of reaction patterns show clear population differences. The Gainesville and Palm Beach populations are more variable at 25o, while the Michigan populations displays essentially the same variation at each temperature. Michigan cohorts appear to be more temperature specialist for viability, with some cohorts displaying maximum viability at each temperature. No Palm Beach cohort has the highest viability at high temperature. The coefficient of variation indicated similar levels of variation in viability as in early fecundity in the two populations from more unpredictable thermal regimes. Again the Palm Beach population is much more variable, with the exception of the very low CV in the 22o crosses. Tachida and Mukai (1985) suggested that additive genetic variation for viability was maintained by genotype-environment interactions in southern populations of Drosophila melanogaster, while the variation in northern populations could be attributed to a mutation-selection balance. These data indicate that genotype-environment interactions may be important in northern populations, as well.

Lifespan has been reported to decrease with increasing temperature in Drosophila melanogaster. The cohort data depicted in Figure 4.5 show that the response is not that simple. The populations from variable thermal regimes appear to be mixtures of cohorts with very

Figure 4.4 "Norms of reaction" for viability

Figure 4.5 "Norms of reaction" for age of death

different temperature responses. Some cohorts are characterized by an intermediate lifespan at all temperatures. Others show very plastic responses. Among the isofemale lines, the Palm Beach pattern is more cohesive. Nearly all cohorts have their longest lifespan at 25o, with considerably shorter lives at lower and higher temperatures, although a few show the expected inverse relationship. The Palm Beach crosses show more divergent patterns. The coefficients of variation showed relatively similar levels of plasticity in the Gainesville and Palm Beach populations. Clearly, the study of reaction norms gives a better idea of the relative amount of variation in the populations. The Michigan population shows inverted-V, V-shaped and relatively homeostatic reaction norms, but the degree of plasticity response appears somewhat lower than for the Florida populations.

Rate of metabolism is generally expected to increase with increasing temperature in poikilothermic animals. Although the analysis of variance and the coefficient of variation suggest differences between populations in the plasticity and genetic variation on metabolic rate (Tables 4.1 and 4.2), examining reaction norms more clearly suggests differences (Figure 4.6). The Palm Beach population shows very little cohort-to-cohort deviation in pattern, and also displays relatively strong homeostasis over the range of temperatures tested. The Gainesville population shows a much stronger response to temperature indicating some plasticity. The cohorts, especially the more inbred isofemale lines, show some genetic polymorphism. The Michigan population which is characterized by much higher average rates than the

Figure 4.6 "Norms of reaction" for rate of metabolism

other two populations, also clearly displays extreme plasticity and strong genetic divergence. Although the modal pattern appears to be a linear response to increasing temperature, there seems to be a number of different setpoints.

Intriguingly, several cohorts in each population display the inverted-V norm of reaction for early fecundity, age of death and viability, that might be expected if selection has acted to maximize performance at an optimum temperature of 25o. These performance patterns do not translate into a similar pattern for cohort intrinsic rate, however. For the Palm Beach flies, this may be due in part, to a tendency toward longer development times at 25o, which may counter the effects of enhanced viability and early fecundity. Similar tradeoffs may damp the optimization effects for other characters. For instance, cross 34/29 in the Palm Beach population has its highest early fecundity at 25o, but also has very low viability at that temperature.

The phenotypic correlation data, presented in Chapters I and III, indicated that temperature had a profound effect on the interrelationships of fitness components and that the impact was different for the three populations. Briefly, the Gainesville flies displayed positively correlated fecundity traits with little or no correlation with timing traits, at 22o. At 25o, the quantity traits were still positively associated, but high early reproduction was associated with longer life. At 28o, fast development time was associated with lower late reproduction. In Palm Beach flies, the 22o regime was characterized by positive association between fecundity traits, and negative association between high early reproduction and lifespan. At 28o, most high early reproducers lived longer lives, but

were penalized by slow development and delays in age of peak reproduction. Similar complex patterns of association were apparent in Michigan flies.

Intricate interrelationships between rate of metabolism and other life history variables suggested that, for flies from the thermally variable Michigan population, standard metabolism was negatively correlated with cohort intrinsic rate of increase and that this effect was primarily due to impacts of higher rate of metabolism on viability and early fecundity. The Michigan flies achieved higher population growth rates than the Florida populations, in spite of these constraints. In the most stable thermal population, high metabolic rate was associated with delayed development, which might have lowered the intrinsic rate of increase.

Taken together, these results do not clearly implicate environmental variation as the chief cause of phenotypic plasticity. On the contrary, for most traits the more thermally variable Michigan population appears less responsive to shifts in environmental temperature. Brussard (1984) has suggested that marginal populations might be characterized by resistance to appropriate environmental stressors, while more central populations would have more specialist genotypes, that were severely compromised by stressors. There is some support in these data for that hypothesis.

Discussion

Theoretical discussion (Caswell, 1983; Smith-Gill, 1983) and life history data (Berven et al., 1979; Berven and Gill, 1983; Parker, 1984) emphasize the importance of incorporating phenotypic plasticity into life history analysis. The data in this report provide further support

that phenotypic plasticity of fitness traits must be considered, but do not indicate that simple explanations based on the stable-fluctuating dichotomy will explain the whole picture. The observed differences in cohort polymorphism and phenotypic plasticity may reflect the nature of the selective action in each environment, as well as environmental constraints of the original environments. However, without more information on the timing of major selective episodes in each site and the type of selective action, interpretation of these patterns remains difficult. One alternative may be that the extreme fluctuating and unpredictable environment, coupled with a short growing season, in the Michigan population imposes a selective premium on fast development at low temperature acting through high rates of metabolism to attain fast development. The longer term and slower temperature variation in the Florida populations may permit genetic polymorphism for temperature specialists to predominate. Clearly, the analysis of geographic variation in genetic polymorphism and phenotypic plasticity is not so simple as most theoretical treatments suggest. Bradshaw's (1965) suggestion that phenotypic plasticity might predominate in variable habitats where the period of the environmental oscillation was less than the generation time of the organism, while genetic polymorphism was more likely for longer term fluctuation, is not unambiguously supported by these data. All three populations display plastic responses and retain considerable genetic polymorphism for fitness components. Tachida and Mukai's suggestion that diversifying selection for viability was of primary importance in southern populations of Drosophila melanogaster, but that mutation-selection balance explained the variation in northern populations does not appear to be general.

Individual life history traits are never free to evolve or coevolve under purely demographic selective forces, but are always constrained in some sense by historical, structural, physiological or developmental or behavioral constraints (Stearns, 1977, 1980; Tuomi et al., 1983). As Tuomi et al. indicated, we must consider an organismic theory of reproductive tactics that limits the action of selection to species-specific opportunity sets which consider physiological intercoupling between component traits and ecological conditions that limit potential trait combinations. Consideration of environmental sensitivity of fitness components by studying norms of reaction may further delimit these constraints.

These data confirm the major conclusions of Gupta and Lewontin's (1982) analysis of reaction norms in populations of Drosophila pseudoobscura. The ranking of different populations in terms of the amount of genetic variation they contain changes with environmental conditions and differs from trait to trait. These three populations appear to be composed of varying numbers of specialist genotypes that display no correlation between performances in different thermal environments. The results are somewhat counterintuitive in that the population from the most stable thermal environment exhibits the strongest plasticity for most traits. However, these Palm Beach flies are strongly homeostatic with respect to rate of metabolism. Perhaps, as Caswell (1983) suggested phenotypic plasticity is favored whenever it either increases mean fitness or decreases variance in fitness, but these results suggest that complex interactions between fitness component defy simple analyses that may be possible when only two traits are considered. Perhaps, as Turelli (1985) suggests the models of

selective action on polygenic traits oversimplify the consequences of unmeasured polygenic effects. He concludes that sorting the mechanisms responsible for variation in polygenic traits will be no simpler than explaining protein polymorphisms.

CHAPTER V GENETIC VARIATION IN LIFE HISTORY PATTERNS

The degree of deflection and rebound of r depends, of course, on the heritability of the life table parameters. Measurements of this heritability and estimates of its influence on evolution under various colonizing conditions remain to be made.

MacArthur and Wilson, 1967 (p. 157)

Introduction

Analysis of genetic variation in life history traits is crucial to understanding adaptation and evolution. The genetic architecture of fitness components can be described in terms of their variance and covariance structure. Biometrical methods developed for the analysis and exploitation of traits influenced by many genes with essentially additive effects have been developed (see Falconer, 1981 for review). These techniques, based on resemblance between relatives or responses to artificial or natural selection, may permit the estimation of parameters that can be used to make inferences regarding past selective history of the population and to evaluate the potential for subsequent adaptive change. Theoretical analyses of equilibrium populations under consistent directional selection for fitness predicts negligible additive genetic variance for major components of fitness and thus low heritabilities (Robertson, 1955).

The rate and direction of evolution may be constrained by genetic correlations between fitness characters (Lande, 1982a, b). The genetic correlation between two traits reflects the net effect of alleles contributing to additive genetic covariance between the traits. Genetic

correlations can reflect common biochemical or physiological pathways affecting both traits, caused by pleiotropic effects of single genes or by linkage disequilibria. Most mutations that affect quantitative traits have pleiotropic effects (Wright, 1968). Tightly linked genes of a coadapted complex may be produced by nonrandom allele combinations in gametes (i.e. linkage disequilibria). The effects of linkage and pleiotropy are similar, except that linkage becomes less important with recombination and as equilibrium is approached (Bohren et al., 1966).

If selection acts simultaneously to increase two traits, the additive genetic correlation between them is expected to become negative, since alleles contributing positively to both traits will be fixed. The remaining genetic covariance will be due to alleles that affect one trait positively and the other adversely (Robertson, 1955). Thus, if the structural relationship between the traits is strong, negative genetic correlations are predicted at equilibrium. However, if the structural relationship is weak, the correlation may be highly variable because of gene frequency changes caused by selection and by sampling variance if the population is small (Bohren et al., 1966).

Biometric analyses of domestic animals and laboratory adapted species confirmed the expectations of low additive genetic variance for major fitness components and negative genetic correlations between primary fitness traits, but more natural populations display higher additive genetic variance than theory would predict and sometimes appear to retain positive genetic correlations between major fitness components (Dingle et al., 1977; Rose and Charlesworth, 1981a; Giesel and Zettler, 1980; Giesel et al., 1982a, b; Hegmann and Dingle, 1982; Murphy et al., 1983). There are several potential explanations for the higher than

anticipated additive variance for fitness components. Rose (1983) suggested that the variable pleiotropy, where one allele may have positive effects at one age and negative effects at another, may be the best hypothesis. Rose (1982, 1983) has incorporated pleiotropic considerations into simple genetic models and concludes that variable pleiotropy favors the maintenance of polymorphisms and large genetic variance for fitness components, even where there is little remaining variance for fitness itself. Lande (1983) has proposed that additive variance in quantitative traits is maintained by mutation-selection balance. Giese et al. (1982a, b) suggested that in variable environments genotype-environment interactions may be responsible for high additive variance for fitness components under some environmental conditions. Lande (1982b) suggested that "developmental or energetic constraints must appear as lack of phenotypic and/or genetic variance for certain character combinations (i.e. negative correlation between the component traits, while functional ecological constraints are incorporated in the low fitness of certain phenotypes" (p. 608). He suggested that at evolutionary equilibrium major fitness components would have large negative genetic correlations with environmental correlations that are positive in good conditions and negative in limiting conditions.

Since most organisms live in variable environments, and their fitness may be environment dependent, I chose to examine the genetic architecture of three different populations subjected to differing degrees of environmental fluctuation. Genetic architecture was estimated under several temperature conditions to assess the degree of stability in the variance-covariance matrices and to address whether

habitat instability might be responsible for differential life history organization. I have previously shown that the populations differ in mean phenotypic life history patterns, and in their temperature responses. Populations from more variable environmental regimes had higher fitness, as indexed by cohort intrinsic rate of increase, in warm temperatures. Phenotypic correlation structures showed that the component fitness traits had complex interrelationships that differed for the three populations and seemed to indicate that selective pressures had emphasized different suites of traits in each population. The cohort norms of reaction, examined in Chapter IV, suggested that considerable genetic polymorphism was present in all populations and that phenotypic plasticity had been a focus of selection over different temperature ranges for the three populations. In this chapter, I examine the results of a full sib analysis, which may further elucidate the genetic architecture of fitness traits and permit preliminary assessment of the importance of genotype-environment interaction and variable pleiotropy in structuring the genetic architecture of these populations.

Methods

The flies included in this analysis represent the same populations described in Chapter I. Some of the Palm Beach data presented here have been previously reported (Giesel et al., 1982b). Details of the line derivation and environmental variation in the original collection sites were already presented. Complete records were attained for 1234 females. Sample sizes are shown in Table 5.1. This report will focus on traits that were measurable on each individual. Development rate was estimated as $1/\text{development time in hours from first larval instar to}$

eclosion. Age of peak reproduction (AOP) was assessed as the age post eclosion when the largest amount of reproduction occurred in one twenty-four hour period. Longevity (AOD) was recorded as the age in days that a female lived after eclosion. Three indices of the quantity of reproduction were employed. Reproduction on day two (RD2) was used as an index of early fecundity and represented the number of eggs laid by a female on her second day of life post eclosion. Peak fecundity (PK) was the largest number of eggs laid in a single day and late fecundity (LTF) was indexed as the average amount of daily reproduction that occurred in the last third of an individual's life.

The statistical analysis was performed by using the Harvey program for genetic data (Harvey, 1976). The potentially inbred isofemale lines were analyzed separately from the interline crosses because of differential variance expectations for the two groups. The general model employed in the overall analysis was

$$Y_{ijkl} = u + P_i + T_j + L(P)_{ik} + P \times T_{ij} + L(P) \times T_{ijk} + \text{residual}$$

where P_i represents the mean effect of the i th population, T_j represents the mean effect of the j th temperature and $L(P)$ represents the random effect of a given isofemale line or a given cross within the population. The line mean square was used to test the population effect. The interaction effects of population and temperature and cohort and temperature are also considered. The $L \times T$ interaction will be considered an index of genotype by environment interaction. Orthogonal contrasts for the population effects and linear and quadratic components of the temperature effect were estimated as described by Snedecor and Cochran (1980) and were evaluated by t -test. The $P \times T$ interactions were also examined by this method.

Table 5.1 Sample sizes in the full data set

Pop	Temp	Inbreds		Crosses	
		# lines	# flies	# lines	# flies
GV	22	19	67	15	53
	25	19	79	16	58
	28	18	69	15	76
PB	22	31	116	14	69
	25	14	42	5	21
	28	28	136	15	48
MI	22	16	58	18	80
	25	15	58	19	83
	28	15	45	18	76
Total			670		564

The data were then partitioned by population and temperature treatment and the Harvey analysis was applied separately for each cell in the overall analysis as described for the Palm Beach population in Giesel et al. (1982b). The Harvey program calculates heritabilities for each trait, and phenotypic, genetic and environmental correlation between each trait combination in the analysis. The "genetic correlations" reported here are more properly designated among lines correlations, since the full sib design employed in this study does not permit separation of additive and dominance genetic variation. The heritabilities also represent the broad sense heritability since neither dominance nor epistasis can be evaluated from this design. The standard errors for heritabilities and genetic correlations reported here were calculated by the method of Tallis (1959) and are based on a balanced experimental design. They may underestimate the true standard error. The significance level of the genetic correlations was evaluated as suggested by Falconer (1981). Significance level depends on sample size, the correlation itself and the heritability and variance in the two traits. For the small sample sizes employed in this analysis, genetic correlation estimates are subject to large sampling errors and are seldom precise. Nonetheless, gross changes in the correlation structure in these three populations and/or intrapopulation differences in genetic structure caused by changed environmental conditions may be discernable. Phenotypic and environmental correlations were estimated from the observed variances and covariances of the traits by the formulas in Harvey (1976) and evaluated from standard tables. The formulas used are presented in Giesel et al. (1982b).

Results

The populations differed significantly in peak fecundity and age of death in both outcrossed and inbred isofemale lines (Tables 5.2 and 5.3), and in last third fecundity in inbred flies. Linear contrasts on the population means demonstrate that the differences in peak fecundity in both analyses were predominantly due to differences between Florida and Michigan flies ($t=-4.63$, $p<.003$ for crosses; $t=-2.15$, $p<.01$ for inbreds). The differences in longevity reflect differentiation between the two Florida populations, as well as the combined Florida populations and Michigan in outcrossed flies (Table 5.2), but the inbred Florida populations were not different (Table 5.3). Late fecundity differences reflect the higher fecundity of Michigan flies.

Temperature effects were highly significant for all traits except late fecundity in both genetic groups. Most temperature effects were linear, but significant quadratic components were present for timing variables in outcrossed flies, while inbred lines displayed a quadratic component for late fecundity as well. Population by temperature interactions were highly significant for developmental rate, reproduction on day two and age of peak reproduction in the outcrossed flies. Orthogonal contrasts show no significant difference in the linear component of the crosses for development rate. The significant $P \times T$ interaction is primarily due to differences between Michigan and the combined Florida populations in quadratic components ($t=11.59$, $p<.001$), although there is a small difference between the Florida populations. Among inbreds, only the Florida vs Michigan quadratic component is significant. The population by temperature interactions can be more easily visualized by examining the graphs of mean responses (Figure

Table 5.2 F Values from Analysis of Variance and
Orthogonal Contrasts for Intrapopulation Crosses

Effect	df	DR	AOP	AOD	RD2	PK	LTF
Pop	2	1.39	2.02	6.96**	2.84+	10.76***	1.63
Line(P)	53	6.54***	3.08***	1.56**	3.21***	2.67***	1.61*
Temp	2	294.17***	44.07***	11.66***	36.85***	16.37***	1.64
PxT	4	7.31***	3.76**	2.38*	4.56**	1.53	.43
L(P)xT	74	4.80***	1.92***	1.01	2.02***	1.86***	1.28+
Error	428						

Orthogonal Contrasts (T Values)

Pop	DR	AOP	AOD	RD2	PK	LTF
GV vs PB	-1.65	-.63	2.22*	.77	.58	-.3
Fla vs M1	.09	1.99*	2.56*	-2.35	-4.63***	-1.6
Temp						
Linear	-23.88***	8.77***	4.16***	8.54***	-5.46***	.3
Quadratic	3.75***	-3.17***	-2.35*	.75	-1.81	-1.7
Pop x Temp						
Gv vs PB, lin	.52	.11	-1.75	.93	-1.82	-1.0
Fla vs M1, lin	.41	-.18	.75	.19	.83	.1
Gv vs PB, quad	-2.06*	4.72***	2.27*	-2.11*	-2.70**	-.3
Fla vs M1, quad	11.59***	-4.10***	-1.46	5.96***	1.74	1.0

* = .01 < p < .05

** = .001 < p < .01

*** = p < .001

Table 5.3 Analysis of Variance and Orthogonal Contrasts for Inbred Isofemale Lines

Effect	df	DR	ACP	ACD	FD2	FK	LTF
Pop	2	1.12***	.95***	4.49*	1.53***	2.86*	4.79**
Line	70	3.57***	2.75***	1.87***	4.14***	3.12***	2.34***
Temp	2	330.61	35.00	16.55	15.38**	5.96	3.25*
P x T	4	.97	2.13***	2.04***	3.53***	.70***	1.95***
L(P) x T	95	2.44	1.73	1.52	2.18	1.58	1.38
error	494						

Orthogonal Contrasts (T values)

Pop	DR	ACP	ACD	FD2	FK	LTF
Gv vs FB	.48	1.31	1.52**	.70	-1.08**	-.77***
Fla vs Ml	1.43	-.39	2.61	-1.59	-2.15*	-3.01
Temp						
Linear	-25.50***	8.06***	5.49***	-5.55***	-3.36***	-.01*
Quadratic	4.21	-2.51	-1.91	.15	-.69	-2.55
Pop x Temp						
Gv vs FB, 1in	-.02	-.61	.06	2.76**	-.59	-2.26*
Fla vs Ml, 1in	-1.39	-.77***	-1.56***	1.74***	1.52	1.65
Gv vs FB, quad	.76**	3.20**	3.06	-3.61**	-.68	-.99
Fla vs Ml, quad	2.58	-2.31	-1.07	-3.27	.98	.83

* = .01 < p < .05

** = .001 < p < .01

*** = p < .001

5.1). For developmental rate, the two Florida populations show the same pattern of response, while the Michigan population develops faster at 25o and slower at 28o relative to the other populations. Population by temperature effects for age of peak reproduction are attributable to differences among all three populations in both genetic groups for quadratic components of the response (Tables 5.2 and 5.3). The population response pattern (Figure 5.2) shows more clearly that the interaction effects result primarily from the Palm Beach flies, which display an exceptionally delayed age of peak reproduction at 25o. Although the PxT interaction is only marginally significant for age of death in outcrossed flies, the orthogonal contrasts show significant differences between the Florida populations in both genetic groups for quadratic components. Graphically, the effect appears to be primarily attributable to the different pattern for the Palm Beach flies, as it appeared for other timing variables (Figure 5.3).

Early reproduction is the only quantity variable with a significant PxT interaction in the overall models. Each population has its own pattern of response to changing temperature (Figure 5.4). The Gainesville population increases early reproduction approximately linearly with increasing temperature. The Palm Beach population shows little response to the 22-25o shift, but greatly increases RD2 at 28o. In contrast, Michigan flies show a rapid response to low temperature. Although the overall model did not show significant PxT interactions for peak or late fecundity, orthogonal contrasts suggest that peak fecundity responses differ between the Florida populations in crosses and and late fecundity may differ in inbred isofemale lines. The temperature response pattern for peak fecundity for Gainesville flies resembles the

Figure 5.1 Average development rate (least squares means)
 in the three populations
 a. inbred isofemale lines
 b. intrapopulation crosses

Figure 5.2 Age of peak reproduction (least squares means)
 in the three populations
 a. inbred isofemale lines
 b. intrapopulation crosses

Michigan pattern, with a sharp response to the cooler temperatures (Figure 5.5). Similar patterns are indicated for late fecundity (Figure 5.6). These significant line by temperature interactions provide additional support for our contention that these populations differ in degree of genetic polymorphism and phenotypic plasticity as suggested in the previous chapter.

In summary, the differences in average phenotypic life history pattern between these populations are predominantly due to Florida vs Michigan contrasts for RD2, peak fecundity and longevity. The temperature response patterns reflect differences in the shape of the Palm Beach response when compared to the populations from more variable thermal regimes. That is, the Michigan population has higher early and peak fecundity and a shorter lifespan than the average of the Florida populations, which do not significantly differ from each other. The Palm Beach response pattern suggests that the long life that characterizes these flies at 25o is achieved at the expense of reduced fecundity and delayed peak reproduction. The other two populations have more nearly linear average responses to temperature for fecundity and longevity with some overall damping at high temperature.

All traits have a significant degree of genetic determination as indicated by the line effects in the overall model (Table 5.2 and 5.3). Line by temperature effects are very strong for developmental rate, and all fecundity traits in both genetic groups. The strong genotype-environment interactions may indicate that genetic variability is maintained for these traits by microgeographic differentiation or habitat selection (MacKay, 1981).

Figure 5.3 Average age of death (least squares means) in the three populations

a. inbred isofemale lines

b. intrapopulation crosses

Figure 5.4 Average early reproduction (least squares means) in the three populations

- inbred isofemale lines
- intrapopulation crosses

Figure 5.5 Average amount of peak reproduction (least squares means) in the three populations
 a. inbred isofemale lines
 b. intrapopulation crosses

Figure 5.6 Average amount of late reproduction (least squares means) in the three populations
 a. inbred isofemale lines
 b. intrapopulation crosses

For natural selection to cause evolutionary change in life history patterns, phenotypic variation must be heritable. The response to selection of a particular trait will be determined by its heritability and the constraints imposed by the degree of genetic correlation with other life history traits. The highly significant line effects in the overall model indicate a substantial degree of genetic determination for life history traits. Estimates of the degree of genetic determination for this analysis are limited by the full sib design employed, which precludes partitioning genetic variance into additive and dominance components. However, preliminary indications of differential patterns of genetic determination and correlation may be detectable and may distinguish between some alternative models for life history evolution.

The genetic for life history traits is expected to be higher and more frequently significant in the inbred isofemale lines due to potential fixation of some alleles during inbreeding. Although small sample sizes and large standard errors limit the precision of the broad sense heritabilities, inbred lines have many more significant broad sense heritabilities than the crosses between lines (Table 5.4). Early life characters had a significant genetic variance in all three populations and in nearly every temperature treatment. The general expectation that characters most closely related to fitness would have the lowest genetic variance does not hold for these populations. The outcrossed flies, which may more closely approximate the variation in the original populations, have a high genetic variance for development rate at 22 and 25°. The heritability is lower at high temperature for the Gainesville and Michigan populations, where its relationship to fitness is weaker (Chapter II). Early reproduction presents a different pattern. Genetic

variance is high at extreme temperatures in Palm Beach flies, at low and intermediate temperatures in Gainesville flies and only at 25o in Michigan flies. The amount of peak reproduction has a significant genetic variance in outbred flies at 28o in Gainesville flies and at 25o in Michigan flies. Late life fecundity and longevity have no significant heritabilities in outbred flies, yet longevity is only significantly related to fitness in the Gainesville population at warm temperatures. The timing of the reproductive peak has a significant genetic variance for all populations at 22o, and for Michigan flies at 25o.

The high genetic variance for fitness traits is not without precedent (Jinks and Broadhurst, 1963; Perrins and Jones, 1974; Dingle et al., 1977; Istock, 1980; 1981; Rose and Charlesworth, 1981a; Berven and Gill, 1983; Murphy et al., 1983). Seasonally reversing selection, frequency dependent selection and antagonistic pleiotropy are among the mechanisms proffered for the maintenance of high level of genetic variation in life history traits. Since the Palm Beach population represents a relatively stable thermal environment, seasonally reversing selection models are unlikely, if temperature is an important selective agent for this population, although it may potentially be important in Michigan and Gainesville populations. Antagonistic pleiotropy may result from simultaneous directional selection on the traits, since the alleles that affect both traits in the direction of selection will be fixed or at least be in selection-mutation balance, while pleiotropic genes with antagonistic effects may be segregating at intermediate frequencies and be the primary determinants of covariance

Table 5.4 Degree of Genetic Determination for Life History Traits as Assessed by Broad Sense Heritabilities (S.E. under) Negative variance indicated by ---

Inbred Isofemale Lines									
Trait	Gainesville			Palm Beach			Michigan		
	22	25	28	22	25	28	22	25	28
DR	.584* .275	1.261* .201	.690* .271	1.354* .147	1.380* .255	1.199* .256	.441 .289	.925* .280	1.174* .278
RD2	—	.486* .244	.487* .269	1.035* .185	.106 .311	.911 .294	.683* .293	.986* .274	.528 .355
ACP	.836* .267	.179 .214	.884* .262	—	.787* .328	.604 .333	.599* .293	.727 .292	.884* .328
PK	.713* .273	1.204* .233	.453 .267	.398* .196	.539 .339	.529 .301	.308 .279	.320 .276	1.074* .298
LTF	.633* .275	.427 .241	.384 .263	.405* .197	.337 .333	.189 .264	.508 .292	.207 .262	.353 .354
ADD	.276 .261	—	.253 .252	.198 .182	—	.296 .173	.923* .279	.468 .288	.513 .355
Intrapopulation Crosses									
DR	.970* .289	.991* .272	.061 .182	1.059* .172	1.249* .426	1.199* .256	1.325* .174	1.835* .058	.550* .252
RD2	.744* .308	.864 .284	.223 .214	1.009* .263	.897 .512	.911* .294	.399 .241	1.131 .218	—
ACP	.709* .309	.148 .260	.273 .223	.625* .275	.746 .526	.504 .333	.751* .253	.356 .227	.497* .250
PK	—	.491 .291	.695* .258	.344 .253	.846 .518	.529 .301	.375 .239	.606* .243	.407 .244
LTF	.119 .277	—	.298 .226	.216 .233	.225 .473	.189 .264	.330 .234	.243 .214	.150 .213
ADD	.306 .299	.132 .258	.255 .220	.211 .232	—	.560 .302	—	—	—

between traits. A substantial amount of additive variation can be maintained by such antagonistic pleiotropy (Rose, 1982).

Although this data set does not allow estimation of true additive genetic correlations, the among lines correlations may indicate the degree of genetic correlation between traits (Table 5.5). The inbred lines correlation may be biased toward positive genetic correlations (Rose, 1984) due to potential fixation of rare recessives, but this effect should not be strong after only one generation of full sib mating. Nevertheless, the outbred lines may better indicate the genetic correlations in the original populations. Since all populations were subjected to the same breeding schemes, differences between the populations in correlation structure and the effects of temperature on the correlation structure should yield valid comparative assessments.

If selection has been consistently directional for high intrinsic rate of increase, negative genetic correlations between developmental rate and early reproduction might be expected, since these characters contribute more intensely to intrinsic rate. The correlation between these traits is negative at all temperatures in the Gainesville flies and at 28o in the Palm Beach flies, but it is not significant in any instance. Indeed, developmental rate is only significantly correlated with other life history traits in the Palm Beach flies, where it is primarily associated with another timing variable, age of peak fecundity. The association is negative at 22o and positive at warmer temperatures. Early fecundity is significantly associated with amount of peak fecundity in the Gainesville and Palm Beach flies at 25o.

Table 5.5 Among Lines Correlation for the Intrapopulation Crosses

Trait	Gainesville			Palm Beach			Michigan		
	22	25	28	22	25	28	22	25	28
DR and									
RD2	-.505 .389	-.079 .346	-1.098 2.198	.308 .292	.171 .610	-.198 .356	.355 .350	.157 .253	—
ACP	.528 .309	.120 .620	.046 .046	-.721* .312*	1.157* .184*	.934* .198	.185 .294	-.545 .341	-.508 .383
PK	—	.124 .402	-1.447 2.122	-.448 .414	-.333 .624	.304 .389	.199 .366	.413 .261	-.035 .442
LTF	-1.048 1.361	—	.277 .115	-1.033 .596	.119 .924	-.179 .576	-.230 .388	-.907 .479	-.332 .674
ACD	.667 .418	.331 .693	-1.454 2.310	-.500 .517	—	.708* .321	—	—	—
RD2 and									
ACP	-.789 .486	-.923 .987	-1.048 .971	.093 .372	.313 .660	-.699 .456	-.503 .446	.149 .218	—
PK	—	.636* .315	.383 .441	.009 .432	1.258* .309	.425 .352	-.114 .488	.268 .268	—
LTF	.981 1.029	—	-1.010 .681	.237 .512	1.069 1.626	-.463 .662	-.905 .478	.560 .377	—
ACD	1.284* .445	—	-.685 .649	-.465 .532	—	.578 .432	—	—	—

Table 5.5 continued

ACP and

PK	—	.148 .260	-.225 .501	-.019 .493	-.145 .707	.029 .479	.322 .400	.176 .414	-1.080* .405
LTF	-.624 1.054	-.704 .845	.054 .615	.257 .532	.279 .972	.231 .652	.127 .429	1.327* .515	.876 .756
ACD	1.284* .445	—	-.685 .649	.929* .448	—	.674 .360	—	—	—

PK and

LTF	—	—	.554 .381	.368 .590	1.467 .976	.984 .590	.542 .312	.047 .488	1.415 .712
ACD	—	.172 .792	.354 .354	-1.150 .626	—	1.039* .236	—	—	—

LTF and

ACD	.128 1.196	—	-.785 .802	-.337 .925	—	.488 .808	—	—	—
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Positive genetic correlations may indicate the degree to which joint variation in two traits is determined by the same physiological pathways. Nonsignificant negative correlations of early fecundity with age of peak fecundity were estimated at all temperatures in the Gainesville flies and at 22o in the Michigan flies and 28o in Palm Beach flies. Early and late fecundity are also negatively associated at 28o in Gainesville flies, at 22 and 28o in the Palm Beach flies and at 22o in the Michigan flies. If further experiments with larger sample sizes and more clearcut designs confirm these negative associations, a genetic basis for tradeoffs between early and late life characters may be indicated. The important point is that the tradeoff applies in different conditions for the three populations I studied. The only significant negative correlation for outcrossed flies is between age of peak fecundity and amount of peak fecundity at 28o in Michigan flies. This may indicate some energetic allocation constraints at this temperature. Longevity and late fecundity are significantly negatively associated in the Michigan flies at 22o. All other significant correlations are positive in both inbred and outcrossed flies.

In spite of the design limitations, these data indicate that the populations differ in the genetic constraints on life history evolution and perhaps more importantly, that the genetic variance-covariance structure is affected by minor changes in environmental conditions. For example, in Palm Beach flies, developmental rate is negatively associated with age of peak reproduction at 22o, but the association is positive at warmer temperatures. These data do not indicate the universal tradeoffs between early and late life characters implied by assuming negative serial pleiotropy (Rose, 1982). The two exceptions

are the positive association between age of peak fecundity and late fecundity in the 25o Michigan flies and the positive association between age of peak fecundity and longevity in the low temperature Palm Beach flies. A positive association between such traits indicates a tradeoff because one is inversely related to fitness and the other is directly related to fitness. Late life characters rarely display substantial heritability in this study, as has been previously observed (Rose and Charlesworth, 1981a,b), therefore limiting significant genetic correlations. Phenotypic correlation structure also differs for these populations (Table 5.6) and may reflect differing constraints on further evolution. Lande (1982a, b) implied that negative phenotypic correlations may represent developmental or energetic constraints. Population differences at a single temperature are readily apparent. At 22o, for instance, developmental rate is positively correlated with age of peak reproduction in the Gainesville flies, negatively correlated in the Palm Beach flies and uncorrelated in the Michigan population. This pattern is reflected in the genetic correlation. Early reproduction is negatively correlated with age of peak reproduction in the Gainesville and Michigan populations, and uncorrelated in Palm Beach flies. Similar differences in correlation pattern can be seen at other temperatures and have been more fully discussed in Chapter I. The effect of a small change in environmental temperature on the correlation pattern of each separate population suggests that energetic or developmental constraints may differ for these populations with respect to temperature. A constraint between early reproduction and age of peak reproduction is important at extreme temperature in Gainesville flies, only at high temperature in Palm Beach flies and only at low temperature in Michigan

Table 5.6 Phenotypic Correlations among Life History Traits for the Intrapopulation Crosses

Trait	Gainesville			Palm Beach			Michigan		
	22	25	28	22	25	28	22	25	28
DR and									
RD2	-.221*	-.068	-.218	.139*	-.012*	-.142*	-.024	.115	.066
AOP	.285	.258	.169	-.307	.661	.365	.188	-.173	.049
PK	.048	.039	-.125	-.188*	-.211	.068	-.033	.157*	-.043
LTF	-.135*	-.024	.128	-.265	.143	.057	-.107	-.333	-.074
AOD	.284	.056	-.076	-.160	-.053	.075	.082	.197	.073
RD2 and									
AOP	-.390*	-.145*	-.380*	.001	.031	-.429*	-.302*	-.005	-.124*
PK	.412	.316	.426	.132	.415	.452	.210	.208	.236
LTF	.249	-.030	-.014	.028	.350	-.075	.055	.183	-.123*
AOD	-.089	.041	.180	-.059	.083	.216	-.122	.083	.257
AOP and									
PK	-.013	.094	-.185	.191*	-.131	.064	.047	.214*	.026
LTF	-.053*	.218*	.024	.345*	.342	.236	.042*	.230*	.020*
AOD	.404	.331	-.019	.288	.169	.230	.398	.230	.278
PK and									
LTF	.402*	.129*	.275*	.399*	.610*	.317*	.375*	.166*	.407*
AOD	.272	.282	.213	.166	.334	.429	.207	.288	.383
LTF and									
AOD	-.222	-.346*	-.354*	-.249*	.009	-.177	-.328*	-.511*	-.235*

* = $p < .05$

flies. High late fecundity reduces lifespan at warmer temperature in Gainesville flies, at low temperatures in Palm Beach flies and operates at all temperatures in Michigan flies.

Lande (1982a, b) contends that in equilibrial or quasi-equilibrial populations major fitness components tend to be negatively correlated, with environmental correlations that are positive in good conditions and negative in harsh conditions. Environmental correlations from these data (Table 5.7) indicate that although the environmental correlation certainly may change in sign with different environmental conditions, no single environmental regime is characterized by predominantly negative correlations. On the contrary, 28o, which should represent harsh conditions for Michigan flies, shows predominantly positive environmental correlations. These populations may not represent genetic equilibrium, however.

Discussion

These experiments on the genetic and phenotypic variation in life history patterns in Drosophila melanogaster from different geographic populations lead to the following conclusions. First, a significant portion of the variation in timing and quantity of reproduction is genetically based. Secondly, some of the phenotypic variation within populations is heritable, given specific environmental conditions. Third, the pattern of phenotypic and genetic correlations between life history traits is different for the three populations if environmental temperature is the same. The populations exhibit different patterns at the appropriate mean temperature for their site of origin. The temperature response pattern of the correlation matrices also differs by

Table 5.7 Environmental Correlations for the Intrapopulation Crosses

Trait	Gainesville			Palm Beach			Michigan		
DR and	22	25	28	22	25	28	22	25	28
RD2	-.212*	.140*	-.100	-3.630*	.201*	-.482*	.641*	-.332*	—
AOP	.285	2.385*	.204*	-.904	.610	1.534*	-.011*	-.372*	.663*
PK	.048	-.691	.332	-.233	-.351	.572*	.382	.481*	-.052
LTF	-.135*	—	.111	-.512	.123	-.353*	-.104	-.343*	.031
AOD	.284	-.704	.131	-.192	—	1.713	—	—	—
RD2 and									
AOP	.672*	.543*	-.162*	1.283*	.217*	.473*	-.073*	.342	—
PK	—	-.371	.573*	-1.673*	.541	.773*	.411*	.062*	—
LTF	-.090*	—	.333	-1.682*	.417	.432*	.603	.351	—
AOD	1.133	-.192	.091	-1.884	—	-.990	—	—	—
ACP and									
PK	—	.432*	-.181	.400*	-.151	.111*	-.313*	.261*	.933*
LTF	.251*	—	.011*	.463	.317	.555*	-.052	-.231	.393*
AOD	-.431	.462	.222	-.092	—	-.390	—	—	—
PK and									
LTF	—	.363*	.041	.421*	.675*	.013*	.292*	.273*	.083
AOD	—	—	.133	.662	—	-.301	—	—	—
LTF and									
AOD	-.315*	—	-.191	-.222	—	-.562*	—	—	—

* = $p < .05$

population. These results strongly suggest that the patterns observed reflect local adaptation to differential selective pressures.

These populations exhibit high genetic variance for early life traits and lower proportion of genetic variance for late life traits under most treatments. Rose and Charlesworth (1981a) showed a moderately high heritability of rate of egg laying in early life and essentially zero heritability for late fecundity and longevity for their experimental population. Reported heritabilities for egg laying rate in Drosophila melanogaster range from 0.10 (Tantawy and El-Helw, 1970) to 0.68 (Tait and Prabhu, 1970). Rose and Charlesworth's results indicate heritabilities in the range of 0.3 to 0.4 for early reproduction, declining to 0.2 to 0.3 for late life reproduction. Their study indicated that early and late life reproduction were negatively genetically correlated, and they suggested that negative pleiotropy permits maintenance of substantial additive variance for early life characters. Egg laying from day 6 to day 10, however, was positively genetically correlated with late life fecundity and longevity.

Rose (1983) has suggested that high additive variance for early life traits is primarily due to variable pleiotropy with predominantly negative correlations between early and late life traits. Although this data set is limited by the full sib design and by the potential inbreeding fixation in the isofemale lines, there is little indication that Rose's conclusion is general. Hegmann and Dingle (1982) showed high heritabilities for development time and a reduction in the heritability of clutch size with age in Oncopeltus fasciatus. Their population retained considerable genetic variation for development time and body size, but progress in response to selection for either trait

would be limited by the large negative correlation between them. Body size was positively correlated with clutch size but negatively correlated with development time. Similar interrelationships between fitness components and between fitness components and metabolic rate are seen in my data. Complex interrelationships between fitness components may limit the generality of the variable pleiotropy hypothesis. Tachida and Mukai (1985) suggest that diversifying selection is responsible for the maintenance of considerable additive variance for viability in southern populations of Drosophila melanogaster, and my results suggest that it may be responsible for additive variation in other characters and other populations as well.

The line by temperature interactions in the present study were highly significant for all characters in the inbred isofemale lines, and for all traits but last third fecundity and age of death in the crosses between isofemale lines. Genotype-environment interactions may indicate an alternative to negative serial pleiotropy for the maintenance of genetic variation in life history traits even in the face of directional selection (Giesel et al., 1982a, b; Murphy et al., 1983). McKenzie (1978) showed similar genotype environment interactions in Drosophila melanogaster and Drosophila simulans for development time, longevity, % of females mating and fecundity. Gupta and Lewontin (1982) have illustrated the importance of such interactions to inferences regarding selective history and predictions of future adaptive patterns.

The negative indirect response of early fecundity to selection for high late fecundity in Rose and Charlesworth's (1981b) experiments supports their contention that antagonistic pleiotropy is characteristic of their population. The population they studied was maintained in the

laboratory for approximately 5 years, with a 13-15 day turnover time, which essentially results in directional selection favoring early life characters. Therefore, it is not surprising from a theoretical stance, to discover antagonistic pleiotropy. Natural populations may not be subjected to constant and consistent directional selection in a stable thermal environment.

Giesel (1979) and Giesel et al. (1982a, b) found some evidence of positive correlations between early life fecundity and late life traits in several populations of Drosophila melanogaster. Their studies were based on partially inbred isofemale lines and crosses between lines. Although Rose (1984) and Rose and Charlesworth (1981a) present valid objections to assuming such positive correlations would characterize the original populations if the lines were heavily inbred, since fitness components of heavily inbred lines may be biased by fixation of rare recessives, which may result in positive correlations. However, isofemale lines are not subject to the same criticism. Parsons (1980, 1983a) has suggested that isofemale lines can be employed to assess comparative genetic architectures as well as phenotypic variation in natural populations. Parsons emphasized that isofemale studies provide a powerful approach because line differences persist for many generations of laboratory culture. He suggested that isofemale lines are one of three valuable approaches to studying quantitative inheritance, along with the biometrical approach and the polygene location approach (Parsons, 1983a). He recommends the isofemale line approach because it permits rapid analysis of genetic architecture and phenotypic plasticity for species that can be cultured in the laboratory. He proposes that the inbreeding effect inherent in this

approach is of little consequence to interpreting the analysis for colonizing species, since the reduction in variability from the forced bottleneck depends on r (Nei et al., 1975), at least for genic heterozygosity. Thus if one assumes $N=2$, i.e. that the original female was not multiply inseminated and $r=0.5$, the reduction in heterozygosity is approximately 0.5. He calculated that 75% of the genetic variance remains after the bottleneck generation and that any further reduction depended on population size. Population size of the isofemale lines in this study was approximately 200 and thus the lines should retain approximately 74% of the variation characteristic of the original population until the one generation of full sib inbreeding. Because of the probability of multiple inseminations and heterozygote advantage for colonizing species, these may be minimum estimates. Although there are some drawbacks to the isofemale line approach, it may still preserve more of the genetic variation of natural populations than the use of fully inbred lines or chromosomal homozygotes for rapid assessment of phenotypic variation and its attendant genetic architecture.

Ives (1945) presents evidence from studies of lethals that suggests that inbreeding is a major factor in some populations of Drosophila melanogaster. Hirazumi (1961) has shown that chromosomes that depress fitness tend to exhibit positive correlations, while chromosomes that enhance fitness tend to display negative correlations. Rose and Charlesworth suggested that Giesel's results stem from surveying low fitness genotypes. Although the data from this analysis is also based on isofemale lines subjected to one generation of full sib inbreeding and crosses between isofemale lines, there is little indication that they represent low fitness genotypes, since the mean values for most

traits at 25o differ little from the Amherst population Rose studied, although the inbred lines do display some inbreeding depression relative to the crosses.

A number of studies that do not employ inbred material display significant positive genetic correlations between fitness traits in Drosophila melanogaster and other species (Rose and Charlesworth, 1981a; Hegmann and Dingle, 1982; Berven and Gill, 1983 and Murphy et al., 1983). Since the genetic correlation can represent the extent to which two measures are genetically the same character (Falconer, 1981) or controlled by the same physiological pathways, high positive correlations between such traits as milk yield in the first and second lactation ($r_a=0.75$; Barker and Robertson, 1966), clutch size in first and second clutch and second and third clutch ($r_a=1.0$ and 0.79 , respectively; Hegmann and Dingle, 1982), fecundity on days 6-10 and 11-15 ($r_a=0.51$; Rose and Charlesworth, 1981a) and instantaneous birth rate and average daily fecundity (Murphy et al., 1983) are not surprising. Although the full sib design and small sample size in this study limit the inferences that can be drawn, these data suggest that populations differ in the genetic correlations between life history traits and that the genetic correlation between two traits may shift from positive to negative with a small change in environmental conditions. If each population is comprised of a number of fitness genotypes, each with their own temperature optimum, positive or negative correlations would characterize a population in a specific environmental condition. Predictions concerning the impact of environmental variation on the selection response are less straightforward, since the genetic architecture, as well as phenotypic

correlation structure, changes radically with small changes in environment. Clearly, controlled selection experiments varying the degree of fluctuation and the period of oscillation will be necessary to generate realistic predictions of the future course of adaptation for populations with such genetic and phenotypic constraints.

Genetic correlations between two traits may also change in sign through ontogeny as Atchely et al. (1984) have demonstrated for brain and body size correlations. They suggest that brain size may be more closely related to the cell multiplication phase of growth, while body size is more closely linked to the cell enlargement phase. They suggested that genetic correlation between traits may arise from response to common stimuli such as embryonic somatomedin, but the receptors may vary with age (but see Ricklefs and Marks, 1984). Similar physiological connections may underlie correlation between life history parameters, but as yet have been little explored. Watt (1985) suggests that selection can modify energy flow patterns acting through genetic variation in metabolic parameters or on a syndrome that filters the effects of environmental variation. Further work along these lines may prove very useful to understanding life history variation.

Berven (1982) and Berven and Gill (1983) have shown that populations of wood frogs, Rana sylvatica, differ in heritability of larval development time and body size and that the genetic correlation between these traits differs by geographic area. Lowland populations had positive genetic correlations between these traits, while these traits were negatively correlated in high altitude populations. Their results suggested that larval size was relatively well canalized in lowland populations but that development time was plastic. They

suggested that in lowland populations, selection on body size has been more important than selection on development time. In mountain populations both traits were moderately well canalized, implying moderate selection on both traits. The negative genetic correlation between the traits would result from selection acting simultaneously on both traits. In this case, the high heritabilities might be explained by antagonistic pleiotropy, but other explanations are more likely in the lowland and tundra populations. They suggested that variable pleiotropy expectations were likely to be fulfilled only where selection had acted simultaneously and in a consistent direction on two traits that contribute equally to fitness.

Geographic populations may differ in coadapted gene complexes for life history traits. Mechanisms of coadaptation, such as epistatic interactions between homozygous loci (Wallace and Vetukhiv, 1955), chromosomal heterozygosity (Dobzhansky, 1970) or integration of gene pools based on heterozygote advantage, have been suggested. Life histories may show patterns of covarying traits with a number of different genetic structures, such that interpopulation hybrids display assorted phenotypes that are dependent on genetic and environmental influences (Dingle et al., 1982). Some life history traits, such as body size and development time, showed little population differentiation in populations of Lygaeus kalmii, but populations of another milkweed bug, Oncopeltus fasciatus were strongly differentiated. Since clines in inversion complexes have been reported for Drosophila melanogaster (Mettler et al., 1977), some of the geographic variation in genetic architecture in my populations may be explained by differences in coadapted gene complexes. Little is known about the

effect of linkage on metric characters (Falconer, 1981), although it may increase the covariance in full sibs.

This study, and others like it, raise more questions than they answer for life history theory. Theory suggests that past selective pressures can be inferred from knowledge of the proportion of additive genetic variance of fitness components and the genetic correlations between those traits. The populations under study may differ in the nature of selection and selection intensity. More variable environments might be expected to have periods of severe climatic stress (freezing spells, drought, resource limitation) and episodic hard selection that may result in population crashes, even extinction (Lewis, 1962; Wiens, 1977; Erlich et al., 1980). Parsons (1983a) suggests that for colonizing species frequency and density dependent selection can be ignored. Price (1975) suggests that parasites suffer little from competitive interactions because of such episodic hard selection. However, competitive interactions may be an important component of selective regime, especially in Palm Beach. Nonequilibrium populations, however, may more realistically be represented not only by episodes of directional selection, but also by intense inter- and intraspecific competition during population blooms.

Drosophila melanogaster may employ genetic heterogeneity, physiological plasticity and behavioral mechanisms for coping with environmental stressors. Levins (1969) showed that acclimation to dry heat was characteristic of Drosophila melanogaster, although the more narrow-niched Drosophila prosaltans showed no acclimation. Genetic variation in heat resistance and desiccation resistance has been shown in many Drosophila species. Genetic heterogeneity for high temperature

resistance in Drosophila melanogaster and other Drosophila species has been reported (Hosgood and Parsons, 1968; Parsons, 1969, 1983a). In Drosophila funebris (Timoffeff-Ressovsky, 1940) relative viability of northern races was more resistant to cold temperatures and southern races were more resistant to warm temperatures, while eastern races showed resistance to both temperature extremes. Inversion studies in Drosophila flavopilosa indicate that different inversion heterokaryotypes are favored at different temperatures in lab and field studies (Brncic, 1966, 1968). Levins (1969) concluded that a strong negative correlation might be expected between degree of behavioral avoidance of stressful environments and the plasticity of stress response. Stalker (1980) showed that frequency of an inversion complex related to cold temperature resistance was higher in northern populations. Geographic variation in life history patterns could result in part from differential selection for temperature resistance in northern and southern populations.

A general theory of life history evolution will require more complexity than the assumptions of antagonistic pleiotropy, infinite population size, genetic equilibrium, stable genetic variance-covariance matrices, and consistent directional selection will permit. Lande's (1982a, b) model for life history evolution is certainly a step in the right direction, but may be limited by the assumption that genetic and phenotypic correlation structure are relatively stable in time. Such expectations may not be justified under intense selection (Bohren et al., 1966), but may occur if selection intensity is quite low. A more serious problem may be that genetic correlation can change in direction with a minor shift in environmental conditions, as these data indicate.

Turelli (1985) suggested that theoretical analyses of mutation-selection balance for polygenic traits assume that all pleiotropic effects are known, and his models of the consequences of unknown pleiotropic effects suggest that mutation-selection balance is not the primary determinant of additive polygenic variation in natural populations. The assumption that increased intensity of pleiotropic selection will decrease equilibrium genetic variance also is suggested to depend critically on an underlying assumption that stabilizing selection acts on every aspect of the phenotype determined by the traits under study. Gillespie (1984) has shown that if pleiotropic effects involve balancing selection, pleiotropy can maintain genetic variance even under consistent selection.

The kinds of tradeoffs implied by Rose's variable pleiotropy hypothesis essentially only apply where reproductives and nonreproductives have similarly limited resources and where reproduction limits future survivorship or fecundity. Tuomi et al. (1983) point out that such conditions do not necessarily hold for natural populations, because they can compensate for reproductive effort by increasing resource input at the time of reproduction or in advance by storing energy and that adaptation for resistance to costs of reproduction can occur through increased efficiency of allocation. Although Rose concludes that "the hypothesis of antagonistic interaction between life history characters . . . is the most satisfactory theory of life history evolution available" (p. 15), no general agreement with his conclusions is apparent by theoreticians or the data.

Indeed, untangling the data and theory of life history evolution will require addressing the results of selection on correlated characters,

but I seriously doubt whether the assumptions of consistent directional selection on all fitness components will be part of a general theory. Negative genetic correlations are clearly expected when directional selection is simultaneously applied to two traits, but the unanticipated pleiotropic interactions may mediate the observed effects. The changes in gene frequency probable under such conditions may affect the genetic correlation since it can change in sign and magnitude with gene frequency changes (Bohren et al., 1966). The question of expectations of the sign of genetic correlation under other forms of selection and where selection intensity may fluctuate in direction is still at issue.

CONCLUSIONS AND PROSPECTUS

Complex patterns of factor interactions must be the major premise in serious discussion of population genetics and evolution...

S. Wright, 1968 (p. 105)

When this study was initiated, I was convinced that analysis of phenotypic and genetic correlation structure in geographic populations that differed in degree of environmental heterogeneity for an easily measureable factor constituted the best approach to resolving some of the theoretical questions and conflicting data on life history evolution. Although this data set, which contains records of complete life histories for members of three geographic populations, permits a broader analysis of the impact of environmental variation on life history pattern and correlation structure than most published studies, it raises more questions than it answers. Since most organisms reproduce in environments that are spatially and or temporally heterogenous to some degree, it seemed obvious that estimation of life history patterns and correlation structure in different geographic populations and observing differences in the underlying genetic architecture of age specific survivorship and fecundity patterns would permit inferences regarding past selective history of the populations and predictions regarding the future course of adaptation. Environmental temperature was the most reasonable choice of an index for environmental predictability and fluctuation, since it is closely correlated with resource availability and other seasonal factors, such

as photoperiod that might prove important for life history adaptation, and has been shown to affect such important traits as fecundity and longevity in Drosophila.

This study clearly shows that variation in environmental temperature is important in structuring the life history syndromes of Drosophila melanogaster populations. The three populations studied had different life history patterns when reared in the laboratory at a common environmental temperature. The population from the most variable site had a higher cohort intrinsic rate of increase than populations from more stable thermal sites. Even at 22°C, where mean fitness was not significantly different for the populations, similar cohort intrinsic rate of increase was achieved in different ways. The most stable environmental regime was characterized by lower, broader fecundity distributions at all temperatures assessed. The population derived from a site with intermediate level of temporal variation in thermal regime had moderate early fecundity and high late fecundity, while the most variable and unpredictable site generated fecundity distributions characterized by emphasis on fast development and high early fecundity. Since one major objective was to ascertain whether each population was adapted to perform optimally at its characteristic temperature, life history phenotypes were analyzed at three different temperatures. The three populations showed very different responses to temperature, not only in the average life history, but in phenotypic and genetic correlation structure.

Many of the results conformed to the predictions of the central-marginal hypothesis, but similar patterns could result from other life history models. Information on the nature and duration of

selective episodes in the three populations would be required to discern which model may apply. Central populations are presumed to have more predictable and more suitable environments than peripheral populations. Such conditions should lead to high relative fitness and as a consequence selection may be predominantly stabilizing in central populations and may result in a closed genetic system to minimize extreme phenotypes. As environmental favorability and predictability decline toward the periphery of a species range, the predominant selective mode favors flexibility and rapid response to favorable conditions. Extreme phenotypes may be favored and free recombination is likely to be increasingly important as the environment becomes more stressful. Ecologically marginal habitats are predicted to favor life history "strategies" near the r end of the r/K continuum and genotypes that are highly resistant to environmental stressors. The most thermally stable Palm Beach population was characteristically very sensitive to environmental temperature changes and displayed many attributes of a relatively K-selected population, exhibiting low, broad fecundity distributions and relatively long life under most temperature conditions. Mean relative fitness was relatively homeostatic to temperature in Palm Beach. The Michigan flies showed attributes of r-selection with an emphasis on fast development and high early fecundity. They were relatively insensitive to environmental temperature for many fitness components.

Tantawy and Mallah (1961) suggested that Drosophila melanogaster populations were characterized by specific temperature optima and that variation increased as rearing temperature deviated from the characteristic temperature. These data showed no evidence of a

characteristic optimum temperature for the populations. Instead, each life history component showed a particular pattern of temperature response. For example, in Palm Beach flies, quantity measures were least variable at low temperature, longevity was least variable at intermediate temperature and generation time was least variable at higher temperature.

Phenotypic correlations may not necessarily reflect underlying genetic architecture, but may reflect constraints on further adaptive change. These data show that the phenotypic correlation structure is organized differently in population representing stable and fluctuating environments, and more importantly that the impact of a minor (3°C) change in rearing temperature is different in the populations. Tradeoffs between life history traits that may indicate constraints on life history adaptation appear to be most severe at low temperatures in all populations, but the form of the tradeoff differs in each population. Gainesville flies that have an early peak of reproductive activity appear to pay a cost in reduced lifespan. In Palm Beach flies the cost takes the form of lowered longevity. Michigan flies pay the cost of high early fecundity in the currency of reduced late reproduction.

Some of the observed differences in phenotypic correlation structure may be due to energy allocation differences. The Michigan population from the most variable thermal regime shows a higher rate of metabolism than populations from more stable environments. The higher rate of metabolism in the Michigan flies may, in part explain their higher cohort intrinsic rate of increase, high early fecundity and lower development time. However, within temperature treatments, extreme rates

of metabolism appear to entail a significantly higher cost for Michigan flies. We suggest that much of the differentiation in the Michigan population may be attributable to selection to facilitate responsiveness to environmental conditions that are adequate for reproductive success. The population means for life history traits are highly correlated with rate of metabolism, but within populations linear correlations appear to be obscured by curvilinear tradeoffs at high metabolic rates. Intricate interrelationships between rate of metabolism and other life history traits and between fitness components suggest that each population has responded to different selective pressures and that environmental uncertainty may be an important component of the selective regime.

Phenotypic plasticity clearly differs for component fitness traits, although environmental variation does not appear to be the only determinant of differentiation between populations in responsiveness of fitness traits to environmental change. The most thermally variable Michigan population appears, on the whole to be less responsive to environmental change, which may be expected for a marginal population in which temperature is an important environmental stressor. However, Michigan flies do display very steep responses to a shift in temperature from 22 to 25°C, although they show considerable homeostasis to warmer temperatures. This may be another indication that selection has focused in this variable regime on rapid response to good conditions. The Palm Beach population shows considerable plasticity and genetic polymorphism, even though the stable environment does not conform to most predictions regarding the impact of environmental variation on plasticity. This more central population may be subject to more spatial heterogeneity or the population may have a number of specialist

genotypes adapted to different thermal microhabitats and that the plasticity responses essentially represent thermal environments outside their adaptive range. Perhaps, as Caswell (1982) suggested, phenotypic plasticity is favored whenever it increases mean fitness or decreases the variance of fitness, but certainly these results defy simple analysis.

Analysis of genetic architecture of life history traits is crucial to understanding evolution and adaptation. This experiment clearly shows that a considerable proportion of the variance in these populations for fitness components is genetic in origin. The genetic correlation structure differs for the three populations indicating that they have been subjected to different selective regimes; however, the patterns observed are not easily interpreted due to the complications engendered by genotype-environment interactions. Theoretical models suggest that past selective pressures can be inferred from knowledge of the proportion of additive variance of component traits and genetic correlations between them. The theoretical treatments focus on predictions for directional selection on fitness for populations at or near genetic equilibrium. These conditions may not hold for any real population. Consistent directional selection on fitness has been suggested to diminish additive genetic variance for fitness components and the additive variation that is maintained has been attributed to either a selection-mutation balance or negative serial pleiotropy. These data indicate that for natural population the complication of genotype-environment interaction must be considered. The most important general conclusion from this study may be that genetic and phenotypic correlation structures show drastic change in response to minor changes

in environmental conditions, but it certainly limits interpretation of life history studies and makes theoretical development more complicated.

One primary criticism of most life history models is their reliance on static optimization models, which depend on the assumption that critical genetic variation was available and sufficient time had elapsed for an optimum to be achieved. Optimization outcomes also depend on the identity of the trait presumptively optimized by evolution, and the constraints that may limit the outcome for the population under study. Even when some quantitative measure of fitness is maximized, multiple stable equilibria are possible (Wright, 1932, 1949; Simpson, 1953; Schaffer and Rosenzweig, 1977). The predictions of such optimization theory may apply reasonably well to equilibrial species who have occupied a relatively stable habitat for a long time, however may have little validity for non-equilibrium or colonizing species subjected to continual habitat variation and possibly fluctuating selection pressures.

Simple one or two locus genetic models primarily address Type II genetic architecture, where a major gene which has primary effects on fitness, and may reasonably describe some founder situations (Carson and Templeton, 1984); but such models are not likely to have general application to life histories. Biometrical quantitative genetic approaches (Lande, 1982a,b) that assume Type I genetic architectures with many small genes contributing essentially additively to fitness may be more satisfactory for life history modelling. Lande has demonstrated that the intrinsic rate of increase is maximized, but that rate and direction of evolutionary responses may be constrained by genetic correlation between characters. Such biometrical models are also

limited in applicability by assumptions of little or no linkage disequilibria, stable age distributions and weak selection that result in very slow change in the phenotypic and genetic variance-covariance structure.

Most of the questions raised by Stearns (1976) still require answers. Although adaptation to environmental variation can take many paths and a population can incorporate behavioral, physiological, and genetic strategies to cope with environmental variance, no clear answers emerge as to which mode of adaptation will prevail in particular environmental circumstances. In spite of the scope of the data reported here, many questions remain that might permit discrimination between life history models. One possible explanation for the population differentiation observed may be that stage specific mortality differs for the three populations. More importantly, no information exists on the timing of selective events or the type of selection that predominates. Selection intensity may vary seasonally for all three populations, but without data on when and how selection acts in different populations, past selective are difficult to infer pressures and future adaptive changes cannot be predicted. For a widespread species, such as Drosophila melanogaster, northern and southern populations may be differentially selected for cold resistance in the north and heat resistance in the south. Such selective action could have differential correlated effects on rate of metabolism and life history characters. Other potential factors that require more field data include levels of inbreeding differences in the three sites, assessment of time in increasing phase of population growth relative to decreasing phase, assessments of level of competition and parasite load

and resource availability. One major difficulty in interpreting life history variation in life history patterns for Drosophila melanogaster, is the scarcity of information on their natural history. Since they are difficult to track and observe in their natural habitat, details of their time and energy budgets are difficult to attain. Patterns of microhabitat utilization, food and oviposition site availability, and inter- and intraspecific competition may differentially affect the three sites studied.

To develop a comprehensive theory for the impact of environmental variation on life history adaptation, more research will be required from at least three directions. Perhaps the most useful first step would be to initiate selection experiments on a population with known genetic and phenotypic correlation structure. For example, selection for higher early fecundity or fast development time could be implemented in three environments, stable, fluctuating with a period of less than a generation interval and fluctuating with a period longer than a generation interval. Data on the direct response to selection of the index character and correlated response in other life history traits would provide useful information on selective modification of life histories. Changes in phenotypic and genetic correlation structure in the different selective regimes may resolve some of the difficulties regarding variable pleiotropy and selection-mutation balance for the maintenance of additive variation, and may clarify the role of genotype-environment interactions in structuring the genetic architecture of fitness traits.

Of course, selection may not always be consistent and directional. A series of experiments estimating changes in phenotypic and genetic

correlation structure under stabilizing and diversifying selection would be of great value. Another alternative that would be useful would be to experimentally and mathematically model seasonally reversing directional selection. Mather (1981), in reviewing response to selection studies, concludes that in general additive variance, phenotypic variance and developmental variance increase under disruptive or diversifying selection and decrease under stabilizing selection. Under stabilizing selection he suggested that one may in reality be selecting for reduction in additive variance or for genotypes less disturbed by environmental or genetic variation.

Information is needed on the effects of linkage on adaptive selection. Drosophila species with known inversion complexes could be very useful analytical tools for dissecting quantitative variation in the presence of linkage. Falconer (1981) suggested that linkage increases the covariance of full sibs predominantly when there is interaction between the linked genes, as might be expected if coadapted gene complexes characterize locally adaptive life history syndromes. The progress of the breakup of such complexes under different selective modes would provide a clearer basis for modelling life history evolution.

This study indicates that rate of metabolism may be an important pervading component of life history evolution. Selection experiments on rate of metabolism would be difficult to perform, at least for Drosophila, but experiments on an index variable such as body size, or measures of correlated response in metabolic rate to different modes of selection and in environments characterized by varying levels of environmental variation for another life history component might prove

very useful. This study considers the impact of variation in one environmental parameter. Experiments with other species have shown that interaction between such characteristics as resource availability and temperature and temperature and photoperiod can modulate the phenotypic life history pattern of organisms. Further consideration of joint effects of variation in more than one environmental variable may lead to more realistic models.

This study has clearly shown that the life history pattern of populations subjected to selective regimes that differ in degree of environmental uncertainty with respect to temperature show different mean life histories and different responses to temperature. We have shown that genotype-environment interactions may be very important in structuring life history patterns and that levels of genetic polymorphism and phenotypic plasticity differ for northern and southern population of Drosophila melanogaster. The conclusion that environmental heterogeneity is responsible for these patterns seems justified, but without more information on the timing and mode of selection in natural populations, and an experimental and mathematical modelling approach that considers, not only the effects of environmental variation, but also potential effects of unmeasured pleiotropic effects, no clearcut answers will emerge.

We must keep in mind that modelling dichotomies may allow mathematical tractability, but will never realistically describe nature, since theory is necessarily an abstraction and simplification of reality. We should not expect a perfect match between theoretical predictions and real populations. Life history theory and data still need the feedback loop Stearns has suggested, but as models begin to

include some of the considerations suggested here, they will become increasingly difficult to understand. Clearly, experimentalists will require a broader understanding of the assumptions of theoretical models and the difficulties of interpretation that result from violating those assumptions. Theorists and experimentalists alike may find that the search for a single cause for observed life history variation or a single genetic architecture for fitness components may not be productive. Perhaps the ultimate answer to why there are so many life history patterns will be a paraphrase of Hutchinson's answer to the Santa Rosalia question, --because there are so many environments, so many ways to achieve similar fitness and so much time. We may find that Wright's adaptive landscape model, with multiple selective peaks and valleys, will best approximate evolution of adaptive life histories in different geographic populations. The task then becomes discovering the phenotypic, environmental and genetic constraints that apply to the population of interest. Multiple causes for the patterns we observe may yield more complex answers to the life history problem, but the answers should be eminently more satisfying and realistic ones.

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BIOGRAPHICAL SKETCH

Patricia A. Marsteller was born in Waynesboro, Pennsylvania, many years ago. As the oldest of eleven children, and a member of a huge extended family, she learned a lot about people and responsibility. She began her college career as a pre-med at the University of Maryland, but volunteer work at St. Elizabeth's helped convince her that medicine was too distressing. During her senior year, she worked in the Beef Cattle Nutrition Branch of USDA and discovered the exciting world of research biology. For the next seven years, she experimented with biochemistry, genetics and ecology as a technician and research assistant. She played with alligators, snakes and humans. In 1971, her son was born and the real challenge began. In 1976 she returned to school at the University of South Carolina to study behavior and ecology. Her M. S. thesis concerned celestial orientation in alligators. Working with reptiles opened many new doors and caused some astonished looks. While at USC, she was introduced to life history theory and although there are days she wishes she'd never heard of theoretical biology, the struggle has expanded her vision of the complexity that is nature. She has always wanted to write books and be a synthesist; her mother wanted her to be a doctor. With some minor concessions on both sides, maybe she'll be both. If not, graduate school was worth it! While studying at the University of Florida, she met and married the joy of her life, Fred Marsteller. She made many new friends and learned a lot about life, the

universe and everything. The answer is 42. It's the question that's tough. Ms. Marsteller spent the last two years teaching human genetics, biology of aging, and ecology, among other subjects at New College of St. Edward's University in Austin, Texas. She recently moved to Columbia, South Carolina, where she is employed in the Physiology department of the medical school. She's happy and still sane after all the trials and tribulations of graduate school--what more can you ask?

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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Associate Professor of Zoology

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This dissertation was submitted to the Graduate Faculty of the Department of Zoology in the College of Liberal Arts and Sciences and to the Graduate School and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

December, 1985

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