Chapter 11

An Investigation of the Effects of Temperature on the Genetic Organization of Life History Indices in Three Populations of Drosophila melanogaster

JAMES T. GIESEL, PATRICIA MURPHY, and MICHAEL MANLOVE*

Introduction

Since its conception in a paper by Lamont Cole some 25 years ago, life history theory has developed into a complex field with many hypotheses, approaches, models, and assumptions. The basic question embodied in this set of theory concerns the evolution of life history schedules, including the expected relationships between early life fecundity and late life fecundity or age of reproductive senescence and death. The predicted relationships between these parameters may well depend on the theoreticians' assumptions about the genetic correlation structure of life history traits. For instance, Lewontin (1965) asked how colonizing species might best maximize their intrinsic rate of increase and concluded that they should evolve to reproduce heavily early in life. His analysis was based on the implicit assumption of little or no genetic correlation between life history traits since each trait was considered separately. Murphy (1968) suggested that the distribution of reproductive output over several age classes might be advantageous in situations in which the probability of successful reproduction was temporally variable and unpredictable. Mertz (1971) suggested that the variance in reproductive output about the age of peak reproduction should match environmental uncertainty for successful reproduction. Demetrius (1975) expanded this idea to include matching the entropy of the fecundity schedule to the entropy of the environment. These approaches seem to assume positive genetic correlation between early and late life fitness traits and fecundities.

All of these approaches to the problem are relatively free of any assumptions concerning the cost of reproduction or reproductive effort in terms of reduction in the probability of future reproductive ability. However, Gadgil and Bossert (1970) suggested that genotypes that reproduced heavily early in life might have to pay for this in terms of reduced longevity or subsequent ability to reproduce. Their paper introduced the concept of reproductive effort to the life history theoretician. Heavy reproductive effort early in life was assumed to entail some cost that prevented concurrent maximization of late life fecundity or of longevity. This trade-off assumption, which

*Department of Zoology, University of Florida, Gainesville, Florida 32611 U.S.A.
implies a negative genetic correlation between early and late life fitness traits, has become an entrenched paradigm.

Schaffer (1974), assuming the validity of this concept, introduced the idea that life histories might be molded by the relative extents to which mortality applied to prereproductive individuals vs. those which were already reproductively competent, concluding that when juveniles suffered unpredictably high death rates natural selection would lead to the evolution of many ages of reproduction. Conversely, in those populations in which mortality falls most heavily on reproductive adults, there should be selection for early reproduction at the expense of future reproductive potential. Earlier, Williams (1957), advancing one of the many theories of the evolution of senescence, had hypothesized that natural selection would favor the accumulation of genes that enhanced early life fitness (survivorship and fecundity) and that these might be imagined to have negative serial pleiotropic effects on longevity, resulting in cessation of life soon after the end of reproductive life.

Dobzhansky (1958) suggested that, like the construction of a cheap watch, selection should result in the accumulation of sufficient fitness early in life to guarantee reproduction sufficient for the persistence of the population and individual's genotype, with senescence amounting to gradual failure following the guarantee period.

Most existing evidence purporting to test the assumptions and conclusions of life history theory is based on phenotypic correlations between characters. For example, Snell and King (1977) reported a negative phenotypic correlation between fecundity and longevity in *Asplanchnia brightwelli*, a rotifer, but this could have resulted from intragenotypic or environmental effects. Many studies, such as those by Tinkle (1969), Tinkle and Ballinger (1972), Tinkle et al. (1970) and Murphy (1968), have involved measurement of pertinent variables in the field and may simply reflect environmental effects on life history organization. Hickman (1974) demonstrated the strength of such environmental effects when he showed that several populations of an alpine plant that differed in terms of apparent response to r and K selection in situ were identical when grown in the greenhouse. As Stearns (1977) notes, the papers of Solbrig and Simpson (1974, 1977) stand alone in indicating real genotypic interpopulational differences in life history organization. They refer only to differences in growth form and devotion of energy to seed production. Mertz (1975) showed that high early reproduction could be selected for in *Tribolium* but was unable to demonstrate correlated reduction in either survivorship or late life reproduction in the selected lines.

In *Drosophila*, positive genetic correlations between life history components have been shown in several studies. Temin (1966) found positive genetic correlation between viability and fertility, and Mukai and Yamazaki (1971) found positive correlation between developmental rate and viability in studies based on hundreds of lines of *Drosophila melanogaster*. In two sets of data Giesel (1979) and Giesel and Zettler (1980) have found positive genetic correlation between early and late life fitness traits to be the rule, using flies raised at 25°C which were derived from a natural population from the Palm Beach, Florida area. Yet, Hiraizumi (1960) found that developmental rates and female fertilities in more fit lines were negatively correlated in this species; and Simmons et al. (1980) presented data suggesting that negative pleiotropy might exist between viability and a measure of competitive ability, using flies taken from a cage that had been seeded from a collection made several years previously in Madison, Wisconsin. The differences among these various results may be caused either by the