Introduction

In 1954, Lamont Cole stated the basic tenet of life history pattern analysis and in so doing established a new branch of evolutionary ecology. According to Cole, “The total life history pattern of a species has meaning in terms of its ability to survive and ecologists should attempt to interpret these meanings.” The interpretational method he proposed and used was “to compute the characteristics of the future hypothetical population by assuming an unvarying pattern of the life history features which govern natality and mortality.”

Although Cole’s study attracted considerable attention, the interpretation of life history patterns languished until the publication of R. C. Lewontin’s paper in *The Genetics of Colonizing Species* (1965). Lewontin’s contribution was to introduce classical population dynamics to the analysis. He also brought the problem to the attention of individuals in the nascent field of population biology who were schooled in the interpretation of ecological patterns in an evolutionary context. These developments have stimulated, either directly or indirectly, most of the dominant conceptual movements in ecology over the past 15 years, including r and K selection, age-specific selection, selection for competitive ability, and most recently the analyses associated with life history “strategies” and “tactics.”

When considering a constant environment, the usual procedure has been to define two or more alternative life history patterns. These patterns are then examined for their effects on fitness, commonly r, the instantaneous rate of population growth. With simple patterns, the assumption is made that the life history maximizing r will be the superior adaptation and will therefore be favored by natural selection. Analyses of this type have led to the conclusion that selection should minimize the age of first reproduction, and maximize both fecundity rates and survival to reproductive maturity. A corollary suggestion is that age-specific reproductive value is maximized by the superior life history pattern (Schaffer 1974, Taylor *et al.* 1974), but a recent analysis by Caswell (1980) casts doubt on the generality of this assertion.

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In other studies the focus has been on optimization of the components of fitness. For instance, Lack (1947) proposed that clutch size in certain birds is adjusted by natural selection to maximize reproductive success consistent with the expected availability of food for nestlings and the ability of the parents to exploit the food resources. In birds or other organisms in which the clutch size is small, repeated (iteroparous) reproduction in successive years is an important component of fitness. Clutch size maximization in one year may produce physiological stress and lower parental survival in future years. Consequently, fitness may be highest when clutch sizes are optimized rather than maximized. This topic has been considered recently by Stearns (1976) and De Steven (1980).

Another example of life history optimization is derived from the work of my colleague, Peter S. Dawson. In laboratory populations of the flour beetle *Tribolium castaneum*, oviposition and pupation are frequently synchronized by culture techniques that impose discrete generations on the populations. Larval flour beetles are cannibalistic on pupae. In a dense, synchronized population of developing larvae, the first individuals to pupate have substantially higher probabilities of being cannibalized than individuals pupating later, when there are fewer larvae (and more pupae) in the experimental container. Thus, in spite of the general conclusion that fast development maximizes fitness, in this situation the timing of pupation appears to be determined by a stabilizing selection that results from countering forces favoring fast and slow developmental times (Dawson 1975).

Although there are many hypotheses on the causes of aging and senescence (see, for instance, reviews by Lamb 1977, Lints 1978), with the exception of an argument rooted in group selection by Wynne-Edwards (1962), none of these suggests that life span is a primary life history feature the duration of which is subject to the direct action of natural selection. The hypotheses on aging treat death as either a secondary (indirect) consequence of selection for optimal reproductive patterns, or as an environmental rather than a genetic event. In the former situation, postreproductive survival is not explained and in the latter situation, unless there is some genetic control over the effects of accidents, life span is simply a statistical happenstance. In this chapter I will argue that these views are too restrictive. I suggest that life span is, in fact, directly related to fitness and, moreover, that it can be subject to direct selection rather than just indirect selection operating through "trade-offs" between reproduction and survival during the reproductive period as discussed by Hamilton (1966) and many others.

### Materials and Methods

In response to appropriate environmental cues, monogonont rotifers have normal meiosis and sexual recombination. In the absence of these cues, reproduction occurs by diploid, ameiotic parthenogenesis and unless mutation occurs, the parthenogenetic descendents of a single female constitute a genetically homogeneous clone. Details of this life cycle are presented in Gilbert (1977) and King (1977, 1980). Reviews of studies of aging using rotifers are available in King (1969) and King and Miracle (1980).

Experimental data on which this chapter is based were obtained using parthenogenetic females of clone SP (King and Miracle 1980) of the marine rotifer *Brachionus plicatilis*. Because both survival and fecundity rates are strongly influenced by envi-