

Course Syllabus FW 893 Seminar (1 credit)
Mating Systems and Strategies and the Evolution of Life Histories

Instructor Kim Scribner
Office Rm 2E NR
Phone 3-3288
E-mail scribne3@msu.edu

Office Hours by appointment
Meeting Times One session per week of approximately 1½ hrs TBA

Required text Shuster, S., and M. Wade. 2003. Mating systems and strategies.
Princeton University Press. Princeton, NJ.

Supplemental Readings from the peer-review literature.
Readings Pdf files available at www.fw.msu.edu/people/ScribnerKim/teaching.htm

Expectations are that all students will come prepared to discuss the assigned readings each week. Students will take turns leading class discussions on the literature assigned for the week and for bringing additional background materials and examples to the attention of the group.

I. Historical literature that formed the basis for the field of life history

The role of natural selection in molding associations among life history traits

Natural Selection is the only acceptable explanation for the genesis and maintenance of adaptation (Williams 1966).

Hamilton, WD. (1966). The molding of senescence by natural selection. *J. Theoretical Biology*. 12:12-45.

Gadgil, M., and W. Bossert. 1970. Life history consequences of natural selection. *American Naturalist* 104: 1-24.

How demographic environments may influence life history traits

The strength of selection on genes affecting survival or fecundity depends on the ages at which they exert their effects (Medawar 1952).

Williams, G.C. 1957. Pleiotropy, natural selection, and the evolution of senescence. *Evolution* 11:398-411.

Schaffer, W.M. 1974. Selection for optimal life histories: the effects of age structure. *Ecology* 5: 291-303.

Broad overview of life history theory

Life history theory contributes to evolutionary thought by examining phenotypic causes of variation in fitness (Stearns 1992).

Stearns, S.C. 1976. Life history tactics: a review of the ideas. *Quarterly Reviews in Biology*. 51: 3-47.

Trade-offs

A trade-off exists when a benefit realized through a change in one trait is linked to a cost paid out through a change in another trait (Stearns 1992). Benefits and costs are reckoned in the currency of fitness.

Reznick, D. 1985. Costs of reproduction: an evaluation of the empirical evidence. *Oikos* 44: 257-267.

II. Historical Studies integrating life history and behavioral Ecology

Parental investment

Males and females use different tactics to maximize reproductive success (Trivers 1972) despite equal contribution to genotypes of offspring and the commonality of other life history traits.

Bateman, A.J. 1948. Intra-sexual selection in *Drosophila*. *Heredity* 2: 349-368.

Trivers, R.L. 1972. Parental investment and sexual selection. Pp. 136-179. in B.

Campbell ed.). *Sexual selection and the descent of man. 1871-1971*. Aldine, Publ. Chicago, IL.

Behavior viewed as part of an organism's life history

Sexually-selected traits are most appropriately viewed within a life history context as it is there that the costs of these traits are extracted (Hoglund and Sheldon 1998; Svensson and Sheldon, 1998).

Svensson, E., and B.C. Sheldon. 1998. The social context of life history evolution. *Oikos* 83: 466-477.

III. Mating Systems and Strategies (Shuster and Wade)

Chapter 1 – The opportunity for selection

Chapter 2 – The Ecology of Sexual Selection

Chapter 3 – The Phenology of Sexual Selection

Chapter 4 – Multiple Matings and Postcopulatory Prezygotic Sexual Selection

Chapter 5 – Female Life History and Sexual Selection

Chapter 6 – The Selection Surface

Chapter 7 - Conceptual Difficulties in Mating System Research

Chapter 8 – Behavioral Influences on the Selection Surface

Chapter 9 – A Classification of Mating Systems

Chapter 10 – A Darwinian Perspective on Alternative Mating Strategies

Chapter 11 – Sexual Selection and Alternative Mating Strategies

Chapter 12 – The Forms of Alternative Mating Strategies

BACKGROUND: LIFE HISTORIES

Organisms face common problems of acquiring and allocating finite resources to growth, reproduction, storage, and maintenance while avoiding death. It is the commonality of these problems, along with the recognition that suites of life history traits are adaptive, that provide unifying concepts for theories of life history evolution. Early contributions (Fisher, 1930; Cole, 1954; and Lack, 1954) were followed by contributions identifying resource environments (MacArthur, 1962) and demographic environments (Williams, 1966) as important factors

determining how natural selection influences the co-evolution of life history traits. Williams (1966), Murphy (1968), Charnov and Schaffer (1973) and Stearns (1977) developed and refined ideas about how the demographic environment influences the trade-off between age-specific reproductive effort (RE) and age-specific expectations of future reproduction. As the field of life history evolution developed, it became evident that predictions based on one factor were not adequate to account for the observed variation in suites of life history trait values.

Age-specific traits related to reproduction and survivorship form the conceptual and theoretical focus of life history evolution (Williams, 1966). Life history theory and concepts are primarily age-based, and major differences have been consistently predicted to occur between short- and long-lived organisms (Stearns, 1992; Roff, 2002). A central goal of life history studies involves documenting changes in trait values associated with age and aging, as the strength of selection on genes affecting survival or fecundity depends on the ages at which they exert their effects relative to expectations of future reproduction. Lifetime fitness of a particular phenotype class may be represented as a weighted sum of age-specific fecundity and mortality (Lande, 1982).

The antagonistic pleiotropy concept (Williams, 1957) is the basis for invoking tradeoffs (Reznick, 1985) in many studies of life histories. In many organisms, old individuals are less fertile and have a higher probability of death than do younger ones. In contrast, for long-lived organisms, death rates appear not to vary over much of the life of an adult, and may actually decrease in the oldest age groups. Even in the absence of senescence, extrinsic causes of death (i.e., disease, accidents, and predation) still occur. Because mutations expressed at older ages only impact the few individuals that survive to old age, natural selection will be less effective at reducing the prevalence of these mutations. In addition, the frequency of mutations that increase fitness of young individuals can increase in frequency in a population even when they have negative effects on fitness at older ages.

Traits that increase the proportion of births late versus early in life promote the evolution of longevity (Williams, 1957) by allowing selection to favor modifiers that reduce, prevent, or postpone the expression of senescence traits (Medawar, 1952; Williams, 1957). Therefore, in populations of long-lived organisms, older individuals are expected to have phenotypic traits that enhance reproductive output or success (e.g., increased clutch size, reproductive frequency, egg size, or reproductive life span) compared to younger individuals (Williams, 1957). In contrast, the concept of senescence (aging in its negative sense; Williams 1957; Hamilton 1966) leads to the prediction that the oldest individuals will have traits that reduce reproductive output or survivorship compared to younger individuals.

Males and females use different tactics to maximize reproductive success (Trivers, 1972), despite equal contribution to genotypes of offspring and the commonality of other life history traits. Female reproductive output is primarily constrained by resources. Selection operates on female's ability to survive and produce the maximum number of offspring. Female traits of particular importance to reproductive success (particularly when those traits are positively correlated with body-size or age) include clutch size, clutch frequency, and offspring quality. Male reproductive success is thought to increase monotonically based on the number of females that they mate, by the timing of copulations, and by the traits of females mated.

The majority of life history concepts, theory, and data, are based on age-specific biology of females. However, some aspects of male reproductive ecology have been integrated into life history concepts (e.g., Bateman, 1948; Wade, 1979; Wade and Arnold, 1980; Arnold and Wade, 1984; Arnold and Duvall, 1994), but for many organisms, adequate documentation of male

reproductive success is inherently difficult. Differences in selection on males and females, non-random mating, sexual size dimorphism, adult sex ratios, and density dependence can all cause major deviations in evolutionary dynamics.

The relationship between mating success and fecundity has been an important component of theoretical and empirical studies of selection and mating systems. Previous studies have focused on components closely tied to fitness (fecundity and mortality), on those traits sexually selected, or on behaviors that are plastic with respect to variation in environmental conditions. There are differences in demographics among species (e.g., adult sex ratios, age structure, size and age at sexual maturity, and expected reproductive life span). Additional among-species differences in male and female attributes, including degree of sexual size dimorphism, female choice, and sperm competition, will result in differences in the intensity of intra-sexual competition that can influence the effective number of mates per male. Such competition can give rise to differences in the intensity of selection (Wade and Arnold, 1980).

Workers in the fields of life history and behavioural ecology are increasingly recognizing the importance of the interplay between disciplines. Sexually-selected traits are most appropriately viewed within a life history context as it is here that the costs of these traits are extracted. Similarly, life historians are profiting from studies of the social environment on life-history evolution (Hoglund and Sheldon 1998; Svensson and Sheldon, 1998).

In this seminar, we will review several early classical papers on life history theory. We will spend the remaining time reading and discussion chapters from a recent book on mating systems and strategies with the goal of better understanding how an organisms behavioral ecological and life history mold adaptive responses to environmental and anthropogenic pressures.

References

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