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SPECIAL SECTION AVIAN LIFE HISTORIES

INTRODUCTION

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The papers in this special section of *The Condor* were presented as a plenary lecture by R. E. Ricklefs and in a symposium on life histories at the April 1998 meeting of the North American Ornithological Societies in St. Louis, Missouri. Both these events were sponsored by the Cooper Ornithological Society.

The analysis and interpretation of variation in life histories has played an important role in the development of ornithology as a scientific discipline during the past half century, since the landmark papers of Reginald Moreau, David Lack, and Alexander Skutch in the 1940s. Indeed, life history evolution, as well as evolutionary ecology more generally, is one of several disciplines in which studies of birds have had a critical, and in some cases, defining influence (Konishi et al. 1989, Gill 1995). The papers in this section address a variety of issues related to avian life histories. They were written to provide a platform, resting solidly on the legacy of the past 50 years, for looking into the future of life-history investigation. One point is quite clear. Although the study of life histories has developed into a mature discipline, it remains very active. Biologists continue to be confronted by fundamental questions concerning selective factors in the environment, constraints on evolutionary response, the direct role of the environment in shaping the phenotypes of organisms and the life tables of populations, and the history of evolutionary change (Harvey and Pagel 1991, Roff 1992, Stearns 1992, Charnov 1993, Gerhart and Kirschner 1997). The papers in this special section should stimulate discussion in the context of these larger issues.

The section begins with a review of the early development of thinking about avian life histories (R. E. Ricklefs). From the beginning, life history studies were linked to major problems of group versus individual selection and density-independent versus density-dependent regulation of populations. Ricklefs shows in the following paper how the flowering of population biology and evolutionary ecology during the 1960s captured life-history evolution as its principal focus. The evolutionary perspective has dominated consideration of life-history variation ever since, to the exclusion of more direct impacts of the environment on phenotypes through developmental plasticity and life tables through density-dependent feedback and other influences.

Forbes and Mock take up the observation that many birds produce more eggs than they can adequately nourish, seemingly in contradiction to the principle of matching established by Da-

vid Lack. Forbes and Mock emphasize that uncertainties often compel females to lay additional eggs as insurance against unpredictable losses. When the losses fail to materialize, this strategy of overproduction leads to family strife over the allocation of resources, often resolved through a variety of fratricidal behaviors. These situations underscore the basic conflict in life-history optimization between parents and their offspring.

Jacobs and Wingfield consider constraints on the evolutionary modification of life histories imposed by internal control mechanisms. They argue that endocrine control systems limit the number of simultaneous behavioral and physiological states—broadly, life-cycle stages—that an organism can assume at any one time. These limits arise owing to conflict over the mechanisms controlling breeding, molting, migration, and "quiescent" life-cycle stages, and also the development time required for change between one stage and another. The concept of life-cycle stages also allows one to predict how individuals should respond to different environmental cues depending on the annual course and predictability of environmental change.

Finally, Winkler shows how the phylogenetic concept of shared derived traits applies to understanding the evolution of life-history variables. One of the most promising advances in the study of life histories has been the development of comparative methods based on evolutionary relationships. Once a phylogenetic hypothesis has been established, analysis of character state changes within a phylogenetic tree can show the sequence of evolutionary changes leading to contemporary variation in life histories, such as nest construction, and relate those changes to shifts between environments.

The papers in this section emphasize the variety of ecological and evolutionary forces that shape the life histories of organisms and the life tables of populations. They also emphasize the importance of considering uncertainty in the environment and the constraining influence of physiological mechanisms that organisms use to adjust their internal states to external conditions. The general themes of sensitivity of individuals and populations to their environments and the constrained evolutionary responses of gene pools to selection are already firmly established in studies of avian life histories. Within this framework, the papers included in this special section show that much remains to be done. Indeed, one could argue that the legacy of the past fifty years has finally built an adequate foundation for a major synthesis of thinking about evolutionary diversification, one in which avian life histories should play a prominent role.

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