

Life history evolution in tropical and south temperate birds: What do we really know?

Thomas E. Martin, U.S. National Biological Service, Montana Cooperative Wildlife Research Unit, Avian Studies Program, University of Montana, Missoula, Montana 59812, USA. E-mail: tmartin@seaway.umd.edu

Understanding why species differ in their life history traits is a central question of life history theory. Theory and evidence often focus on extrinsic sources of mortality in driving life history evolution (e.g., Cole 1954, Murphy 1968, Charlesworth 1980, Reznick and Bryga 1987, Curio 1989, Reznick et al. 1990). Yet, food is thought to be more important in birds (Lack 1948, 1968, Murphy and Haukioja 1986, Martin 1987). Nest predation is a theoretical alternative to food limitation (Slagsvold 1982, Lima 1987, Martin 1992) and recent evidence suggests that nest predation may exert a greater influence on life history evolution than previously thought (Slagsvold 1982, Martin 1993a, b, 1995, Martin and Clobert 1996, McCleery et al. 1996). However, nest predation may often interact with food limitation to influence life history traits (Lima 1987, Martin 1992, 1995). These contrasting and interacting roles of food limitation versus mortality (nest predation) make birds an intriguing system for examining ecological and evolutionary causes of life history variation.

Tropical and southern hemisphere birds represent a particularly interesting and apparently paradoxical system for studying life history evolution. These southern birds are thought to have life histories typified by small clutch sizes, high nest predation, many nesting attempts per year, long developmental periods, extended parental care of juveniles causing high juvenile survival, and high adult survival (e.g., see Skutch 1949, 1985, Lack 1954, 1968, Fogden 1972). These life history traits have been variously attributed to hypotheses related to nest predation, food limitation, and stable climates. Yet, many assumptions and predictions associated with these hypotheses have not been clearly delineated or tested and many general perceptions may be incorrect or misleading. Delineation of assumptions and predictions can help advance understanding of an issue by providing focus for future tests or to stimulate discussion of alternative views and clarify testable predictions. I will explore issues related to evolution of life history

traits of tropical and southern hemisphere birds, with special reference to the Neotropics, to illustrate discrepancies in many widely held perceptions and to outline assumptions and predictions for future tests. The following is not meant to be a comprehensive review of all possible alternatives and hypotheses but rather to highlight the weak state of knowledge surrounding several issues and to encourage further work on understanding why life histories differ among species both within and among continents.

An examination of hypotheses

Nest predation and small clutch sizes vs slow growth: A paradox?

Clutch sizes of most tropical and southern hemisphere birds in South America, Australia, and Africa are smaller than those of even phylogenetically related north temperate birds based on extensive documentation (Moreau 1944, Woinarski 1985, Yom-Tov 1987, 1994, Rowley and Russell 1991, Yom-Tov et al. 1994, Young 1994, Willson et al. 1996). These southern birds are thought to experience high nest predation which is argued to favor their small clutch sizes through selection for high numbers of re-nesting attempts, reduced parental activity near the nest, or small nest sizes that constrain numbers of eggs that will fit in the nest (Skutch 1949, Lack 1954, 1968, Lack and Moreau 1965, Cody 1966, Ricklefs 1969a, Fogden 1972, Foster 1974, Lill 1974, Snow 1978, Kulesza 1990, Robinson 1990, Major 1991). Indeed, this nest predation paradigm is presented in general textbooks (e.g., Welty and Baptista 1988, Gill 1990). Yet, developmental rates are generally thought to be slow, causing long nesting periods for birds in tropical and southern hemisphere areas compared to north temperate (e.g. Skutch 1949, 1985, Lack 1968, Ricklefs 1968, 1976, Mason 1985, Woinarski 1985, Yom-Tov 1987). For example, incubation and

