DIVERSIFICATION OF LIFE HISTORIES IN NEW WORLD BIRDS

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LIFE HISTORIES ARE sets of adaptations that improve the match between an organism and its environment. The adaptations are genetic and interact with environmental factors that influence the fitness of the individual and, by extension, the demography of the population to which that individual belongs (Stearns 1992, Roff 2002). Thus, physiological and behavioral attributes of an individual influence the demographic rates of its population. These demographic rates can, in turn, influence the selective advantage of different combinations of attributes, for example through density-dependent feedback mechanisms (Ricklefs 2000a). These feedback mechanisms are then another component of the environment that applies selective pressure on the behavioral and physiological attributes of life histories. Gaining an understanding of how and why life histories vary among populations and species and across environmental gradients has attracted ornithologists for many decades, but significant methodological limitations have focused most of our efforts on a small number of issues, such as the importance of nest predation in shaping life-history strategies (Martin et al. 2000a, b; Ghalambor and Martin 2001).

Ornithologists were among the first to recognize geographic patterns in life-history attributes (Lack 1947). Perhaps the most famous example is latitudinal variation in clutch size of songbirds: birds that nest at lower latitudes tend to lay fewer eggs per nest than birds that nest at higher latitudes (Moreau 1944, Skutch 1949). The search for explanations of these interesting patterns led to many studies that evaluated possible mechanisms such as variation in food availability, adult survival rates, and rates of reproductive failure as a function of latitude (Ricklefs 1969, 1977; Martin 1987, 1996). In the process, we identified contrasts between temperate and tropical living, such as greater average longevity and apparently lower investment in single reproductive attempts in tropical areas, compared with shorter lifespans and higher contributions to individual reproductive events in temperate areas. These contrasting strategies are now generally referred to as "pace-of-life" strategies (Ricklefs and Wikelski 2002). Many tropical birds are on the slow end of an axis of continual variation, and many temperate birds tend to be on the fast end.

The occurrence of this slow–fast life-history axis might suggest constraints on patterns of variation (Charnov 1993). Indeed, certain combinations of traits frequently co-occur, whereas other combinations are rarely or never observed in nature. For example, species on the slow end of the axis often exhibit lower metabolic rates, slower growth and development, lower nesting success, and longer life spans, whereas those on the fast end tend to show opposite patterns (Martin 1996, Magrath et al. 2000). Examples of attributes that rarely co-occur include species that simultaneously maximize offspring number and adult longevity or offspring number and offspring size. The latter patterns have revealed important tradeoffs in life-history strategies, because multiple energetically expensive activities cannot all be maximized at once (Reznick 1985, Stearns 1989). Investigations into the mechanisms that control these tradeoffs have historically focused on constraints, because the underlying physiological or hormonal components that transduce environmental information into behavioral action were

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thought to form complexes that restricted the range of possible outcomes available to selection (Finch and Rose 1995). Recently, however, it has been suggested that selection may influence linkages between components that have been considered inseparable (Hau 2007). These connections between the environment and how individuals can respond to environmental information will shape our understanding of life histories in the coming years.

Because organismal functions are broadly interconnected, understanding the evolution of life histories requires measurement of key attributes of many different systems. Until recently, we have lacked sufficient data for multispecies comparisons of energy metabolism, immune function, endocrine control mechanisms, stress responses, and some behavioral components of parental investment. Over the past 10 years, new data that describe these attributes have accumulated rapidly. Many of these contributions have been achieved by focusing on a common set of species matched across sites to reduce the effects of phylogenetic differences and then bringing together a group of scientists with multidisciplinary expertise. Our life history–physiology nexus group, which includes all the authors of this paper and other colleagues, is one such group. Here, we summarize recent advances by some of these collaborations in studies of life-history attributes, as well as current information on variation in adult survival across latitudes, before briefly summarizing what studies of avian life histories may tell us about life histories in general. We conclude by charting some promising future directions in studies of avian life histories.

HORMONES: SIGNALS THAT MEDIATE LIFE-HISTORY TRADEOFFS

The finding that vertebrate life histories can readily be mapped on a one-dimensional slow–fast continuum implies the existence of general constraints that prevent the diversification of life histories in other dimensions (Ricklefs 2000a, Ricklefs and Wikelski 2002). What are the physiological mechanisms that underlie life-history tradeoffs? Hormones are internal signaling molecules that are involved in regulating (1) life-history traits such as fecundity, for example by regulation of clutch and egg size (Sinervo and Licht 1991, Sinervo and Svensson 1998), courtship, and parental behavior (Ketterson et al. 1992, Angelier et al. 2009); and (2) processes that determine survival rate, such as immune function, stress and fight-or-flight responses, and many others (Sapolsky et al. 2000, Romero 2004).

Recent studies in birds have indicated that the two steroid hormones testosterone and corticosterone are involved in mediating tradeoffs, especially those between fecundity and survival. Testosterone is a steroid hormone found at elevated concentrations in male vertebrates during the breeding season (Knobil and Neill 1988; female vertebrates also produce it, but at lower levels). During the breeding season, increased testosterone concentrations are known to support male reproductive functions and behaviors. Indeed, a long-term study of free-living Dark-eyed Juncos (*Junco hyemalis*) showed that males with experimentally increased testosterone concentrations had larger home ranges and more extrapair fertilizations than controls (Ketterson et al. 1996). However, testosterone administration in this species decreased the male survival rate (Ketterson et al. 1996, Reed et al. 2006; see also

Dufty 1989), which is a classic life-history tradeoff. Impaired survival rate could result from various processes, for example from immune suppression (Folstad and Karter 1992) or an inhibition of molt by testosterone (e.g., Schleussner et al. 1985). Supporting the relationship between testosterone and fecundity traits found in intraspecific studies, several recent large-scale comparative analyses showed that the length of the breeding season was the factor that best explained interspecific variation in male testosterone concentrations during the breeding season (Goymann et al. 2004; Garamszegi et al. 2005, 2008). However, whether and in what way testosterone affects processes related to survival rate on an interspecific level is still unclear.

Corticosterone has important regulatory functions on metabolism, behavior, and the immune system (Sapolsky et al. 2000). At baseline concentrations (in an undisturbed animal), corticosterone participates in regulating blood carbohydrate levels and energy stores (Sapolsky et al. 2000). Additionally, when an individual experiences acute adverse disturbances (e.g., a predator attack), corticosterone is released into the bloodstream at greatly increased concentrations. The function of such stress-induced corticosterone concentrations is to redirect behavioral and physiological processes away from other tasks (digestion, reproduction, etc.) and toward processes that aid in surviving the disturbance (increased locomotor activity, increased immune function, etc.; Wingfield et al. 1998, Sapolsky et al. 2000, Martin 2009). Indeed, increased corticosterone concentrations typically lead to increased locomotor activity (Breuner et al. 1998), energy mobilization (Sapolsky et al. 2000), and inhibition of reproduction (Wingfield and Sapolsky 2003). Acute increases in corticosterone also boost immune function (Dhabhar 2009) and have been suggested to enhance fitness in most but not all studies (Breuner et al. 2008).

In light of these actions, corticosterone has been hypothesized to be involved in regulating the tradeoff between current versus future reproductive investment (e.g., Wingfield et al. 1995). Indeed, detailed intraspecific studies support a quantitative relationship between corticosterone concentrations (mostly stress-induced concentrations, but also baseline levels) and reproductive investment (e.g., in House Sparrows [*Passer domesticus*]; Lendvai et al. 2007, Lendvai and Chastel 2008). In interspecific studies, brood value (i.e., the value of the current brood in relation to future broods) has been found to explain a large part of the variation in stress-induced corticosterone concentrations (Wingfield et al. 1995, O'Reilly and Wingfield 2001, Holberton and Wingfield 2003) and in baseline corticosterone levels (Bókony et al. 2009).

Until now, studies that explicitly link variations in testosterone and corticosterone concentrations among species to the pace of life in avian species have been lacking. Because procedures both in the field and laboratory can vary dramatically between studies and result in much unwanted variation, we conducted an original study on a set of temperate and tropical species to collect baseline corticosterone, stress-induced corticosterone, and testosterone concentrations in males during the breeding season. All samples were taken using identical procedures and were analyzed in the same laboratory (Hau et al., unpubl. data). Hormone concentrations were then related to key life-history traits such as fecundity and longevity. Following the physiology–life history concept (Ricklefs and Wikelski 2002), we predicted that species

that adopt slow life histories (low reproductive rate, high survival rate) should reach higher stress-induced corticosterone concentrations if those function to increase processes related to survival and self-maintenance. Species with slow life histories should also reach lower testosterone concentrations during the breeding season, given that they typically show lower reproductive rates. Species on the fast end of the continuum were predicted to display opposite hormonal traits.

As predicted, we found that stress-induced corticosterone concentrations were correlated with the survival rates of species, when we controlled for body mass (Hau et al., unpubl. data). Likewise, testosterone concentrations were related to the reproductive intensity of species. Hence, both corticosterone and testosterone concentrations covary with the slow–fast life-history continuum, which suggests that these two hormones may be causally involved in mediating the pace of life in birds. Although our data are only correlative, together with the existing experimental data reviewed above, they point to the existence of an endocrine system that underlies the regulation of life histories in avian species and probably in vertebrates in general. These findings open exciting new research questions on the causality of these hormone–life history relationships and their potential to evolve in populations or species from particular environments (e.g., Hau 2007, Ketterson et al. 2009).

ENERGY

Passerine birds of the lowland tropical forests have long been expected to have a more "leisurely" lifestyle, including lower activity rates (Martin 1996, Weathers 1997, Wikelski and Ricklefs 2001), lower resting metabolic rates (Vleck and Vleck 1979, Hails 1983, Bennett and Harvey 1987, Klaassen 1995, Lindström and Klaassen 2003, Tieleman et al. 2006, Wiersma et al. 2007b), and possibly lower daily energy expenditures (Bennett and Harvey 1987). Recently, tropical birds have also been shown to have a 39% lower peak metabolic rate than temperate species (Wiersma et al. 2007a), a difference that is perhaps not surprising given the general relationship between resting and peak metabolic rate (Ricklefs et al. 1996).

What is still poorly known is the use of energy by birds in the wild, largely because field studies on the physiology of tropical birds are difficult to conduct and methods to quantify energy expenditure in the field are hard to employ. Individual understory birds can hardly be recaptured in the daily intervals needed for use of the doubly-labeled-water method (Nagy 1980). An alternative, the heart-rate method (Butler et al. 2004), was recently applied by Steiger et al. (2009) for the first time to estimate all components of the daily energy budget of a tropical understory passerine, the Spotted Antbird (*Hylophylax naevioides*). The birds were much less active than expected: they made only about 1.5 locomotory movements per minute in their natural habitat and were inactive for 35% of the day. At night, the energy expenditure of males approximately matched their expected resting metabolic rate based on laboratory studies in the thermoneutral zone. However, ambient temperatures in the wild were below thermoneutrality, which suggests that the birds may have lowered their body temperature regularly in the wild. Overall, this energy allocation strategy resulted in a daily energy expenditure that was only half the value expected for a bird this size (Steiger et al. 2009).

Although torpor has been found in other bird species, such as the 6-g Puerto Rican Tody (*Todus mexicanus*; Merola-Zwartjes and Ligon 2000), pigeons (Schleucher 2001), nightjars (McNab and Bonaccorso 1995), mousebirds (McKechnie et al. 2004), and White-throated Sparrows (*Zonotrichia albicollis*; Dolby et al. 2004), it was unknown that tropical lowland birds may regularly revert to this energy-saving mechanism. However, it is still unclear why Spotted Antbirds did not lower their body temperature and energy expenditure even more at night. Possible explanations for the maintenance of energy expenditure at expected resting metabolic levels at night are that Spotted Antbirds either need to be alert to predators or need to keep somatic repair processes running at high levels throughout the long tropical nights. For example, we found that more long-lived tropical understory bird species spend more energy on acute-phase immune responses than less-long-lived or temperate-zone species (Lee et al. 2008, K. Lee et al. unpubl. data).

Using automated telemetry methods (Crofoot et al. 2008), we also confirmed the overall prediction that tropical birds generally have a less active lifestyle than their temperate-zone relatives (M. Wikelski et al. unpubl. data). All tropical species show lower daily activity rates than their northern counterparts (as low as 20% active periods during the day in tropical birds, as compared with 92% active periods in temperate-zone birds; Ricklefs 1971). These data support a general syndrome of energetic leisure in tropical lowland birds compared with their busy northern relatives.

IMMUNE SYSTEMS

The immune system is an important component of self-maintenance and competes for nutrients with other systems to develop a robust capacity to recognize a plethora of potential pathogens, maintain immunity in a ready state, and marshal appropriate components during a disease challenge. The currency (energy, amino acids) and expense of operating the immune system have been appreciated in medical and agricultural disciplines for decades (Beisel 1977) and have more recently been integrated into life-history theory of animals, especially birds (Sheldon and Verhulst 1996, Tella et al. 2002). It has been suggested that animals with high reproductive rates should invest less in immune defense (Sheldon and Verhulst 1996). Testing of such predictions has been fraught with theoretical and technical shortcomings related to the extreme complexity of the immune system and the difficulty of measuring its functional capacity in free-living animals. Single blood-sample endpoints have been developed (Matson et al. 2005, Millet et al. 2007) and have catalyzed a burst of research that clearly shows that immune systems are strikingly different among species of New World birds and that life-history correlates can explain much of this variation.

Immunity is commonly divided into constitutive and inducible components. Constitutive immunity results from continual investment in protective cells and proteins, whereas inducible immunity is attributable to a burst in production of new cells and proteins in response to a pathogen challenge. Tieleman et al. (2005) examined the constitutive bactericidal activity of whole blood from 12 species of Neotropical birds and found a negative correlation with mass-adjusted basal metabolic rate, which suggests that species with a slower pace of life have evolved a more

robust constitutive immune capability. Lee et al. (2008) examined the relationship between life-history variables and natural antibodies in 70 species of Neotropical birds and found a strong positive relationship between incubation period and natural antibody levels in adult birds, which suggests that longer incubation times facilitate development of a more diverse adaptive immune system.

Inducible immunity, especially the acute-phase response, is especially costly to animals. The production of the acute-phase protein, mannan binding protein (MBP), in response to a vaccination with *Escherichia coli* was followed in 40 species of temperate and tropical New World birds (K. Klasing unpubl. data). Across locations, the magnitude of energy invested in the acute-phase response increased proportionally with body size. After differences in body size were accounted for, tropical species had higher levels of MBP than temperate species. Furthermore, species that produced more MBP had higher survival rates, and for a given survival rate temperate species had higher levels of MBP than tropical species.

Immunity can be passively transferred from mother to offspring via immunoglobulins in the egg yolk. In 23 species of small Neotropical birds, there was a strong relationship between body size and transfer of passive immunity, which suggests that larger species can invest more in the protection of their offspring (Addison et al. 2009). Interestingly, developmental period and the transfer of passive immunity were negatively related. This may reflect the value of microbial interaction with developing lymphocytes for avoidance of autoimmunity in species with a slower pace of life.

The immune system is a complex network of interacting cells and proteins, so it will take considerable effort to unravel its detailed relationship with life histories. However, a theme has emerged: the immune systems of New World species with a slow pace of life have a higher level of constitutive immunity, but they are also able to respond to a challenge with greater production of protective acute-phase proteins than those with a fast pace of life.

GROWTH AND DEVELOPMENT

Tremendous variation among species exists in growth rates, which ornithologists have historically characterized by placing species along the altricial–precocial continuum. Growth rates directly affect the fitness of individuals and are influenced by physiological and ecological factors (Ricklefs 1969, 1996; Stearns 1992; Blount et al. 2006). Growth happens within the egg, as well as after hatching, so variation in incubation periods has garnered attention as well. The primary correlate of incubation and post-hatch growth rate is body size; larger species grow more slowly both in and out of the egg (Ricklefs 1976, Ar and Rahn 1978). However, interesting variation remains after the effects of body size are controlled, and some of that variation is a function of geography. Incubation periods are ~9% longer in tropical than in temperate birds (Ricklefs 1969). Recent work has suggested that reduced attendance by tropical parents in response to higher levels of nest predation (Ricklefs 1969, Robinson et al. 2000, Martin 2002) can lengthen the duration of incubation (Martin 2002, Chalfoun and Martin 2007, Rompré and Robinson 2008). Those field studies suggested that behavioral responses of adults to perceived risks of predation on themselves or

their eggs extended incubation. However, a common garden experiment that controlled for effects of adult attendance by incubating eggs of temperate and tropical House Wrens (*Troglodytes aedon*) under constant temperature found that the tropical eggs still took longer to hatch (Robinson et al. 2008). This suggests that differences in nest attendance do not necessarily cause latitudinal differences in incubation period, but that intrinsic differences in how birds grow govern this variation across latitudes.

As with embryonic development, tropical songbirds also grow more slowly than temperate species. Ricklefs (1976) found a 23% slower rate of growth in mass of tropical birds (<100 g) as compared with temperate species. Using more species and a new method that accounted for bias associated with differences in phylogeny and size at fledging, Austin-Bythell (2006) also found that tropical songbirds grew in mass 23% more slowly than temperate passerines. The same pattern was true for growth of tarsi. Although it appears that tropical passerines grow more slowly than temperate species, it is interesting that nestling periods are not consistently longer in tropical passerines. This indicates that tropical birds fledge at a smaller relative size than temperate birds. One possible explanation for quicker fledging is an influence of nest predation pressure whereby species with higher rates of nest predation have offspring that leave their nests sooner (Ricklefs et al. 1998, Remeš and Martin 2002).

ADULT SURVIVAL

Much of life-history theory is based on variation in reproductive (parental) investment optimized with respect to adult survival rate (i.e., the expectation of future reproductive opportunities; Williams 1966a, Stearns 1992, Roff 2002). Many comparative studies of avian life histories have centered on differences between tropical and temperate birds, but it is important to have comparative data on survival rate as a function of latitude. Comparable estimates of adult survival rates for tropical and temperate birds have come primarily from local mark–recapture or resighting studies (e.g., Karr et al. 1990). Mark–recapture studies have expanded tremendously in the tropics since the 1980s and now provide parameter estimates and a broad empirical foundation for placing life histories in a demographic framework. Although unknown biases resulting from the dispersal of breeding adults out of a study area may differ systematically between tropical and temperate regions (Sandercock et al. 2000), the results of these studies have both corroborated and questioned assumptions about the architecture of avian life histories at tropical latitudes.

Building on a long tradition of estimating adult survival rates in Europe and North America, as well as in South Africa and Australia–New Zealand, estimates of survival for tropical species became increasingly available beginning with studies by David Snow in the 1960s, and continuing with long-term mark–recapture studies initiated in the 1970s (Karr et al. 1990, Johnston et al. 1997, Blake and Loiselle 2008). Early results pointed to systematically higher survival rates in tropical than in northern temperate birds, and this became the prevailing paradigm. With more extensive data and new or refined estimation methods, three patterns emerged: (1) annual survival is, on average, ~10% higher in tropical (and southern temperate) than in northern temperate regions (~65% vs. ~55%); (2) the distributions of annual survival overlap

greatly; and (3) even within tropical species or genera, annual survival varies geographically (Ricklefs 1997, Brawn et al. 1999, Ricklefs and Shea 2007). Thus, comparative statements on latitudinal variation in adult survival rates must be conditioned on factors such as body size and location.

Comparisons of adult survival have several implications for the evolution of life-history strategies. Because survival rates overlap broadly between tropical and northern temperate birds, adult survival cannot explain the more complete differentiation observed in the number of offspring reared per nesting attempt (Brawn et al. 1999). Furthermore, the theory that underlies the prediction that greater parental investment is associated with lower adult survival (Williams 1966b, Martin et al. 2000a, Ghalambor and Martin 2001) is incorrect in the sense that parents instead balance their own survival against the survival rate of their independent offspring in optimizing the level of parental investment (Ricklefs 2010). Current estimates of adult survival and the less-well-founded estimates of immature survival indicate that the expected level of parental investment (i.e., personal risk assumed in producing offspring) should be similar in tropical and temperate birds. That is, although adults in temperate regions do not survive particularly well, neither do their offspring, and so it is a toss-up whether to invest in self-maintenance or offspring production. Accordingly, differences in brood size between tropical and northern temperate birds are likely to reflect availability of, and competition for, food or other critical resources such as territories (Ashmole 1963, Lack 1968, Ricklefs 1980) rather than parental investment.

PARENTAL CARE

Since Moreau's (1944) paper on latitudinal variation in clutch size, studies that have dealt with the question of why clutch size increases with latitude have dominated the literature on avian life-history traits (Martin 1996, Ricklefs 2000b, Ricklefs and Wikelski 2002). Nevertheless, other aspects of parental care (and components of reproductive effort) influence offspring and adult survival, including feeding rates, food load, intervals between breeding attempts, duration of parental care, nest defense, nest attentiveness, and number of broods per year. A decade ago, few empirical studies, particularly of tropical birds, had been done and most comparative studies focused on clutch size or did not take phylogeny into account in the analyses (reviewed in Martin 1996). The results from these studies were equivocal, because differences in phylogeny, ecology, and location of the study obscured general patterns (Martin 1996). In the past 10 years, more empirical studies and comparative analyses that account for phylogeny have been conducted and a shift toward examining aspects of parental behavior other than clutch size has occurred. Recent comparative analyses have shown that tropical species tend to have extended postfledging parental care (Russell et al. 2004), delayed dispersal (Russell et al. 2004), lower nest attentiveness (Martin 2002), longer incubation periods (Martin et al. 2007), and greater egg mass (Martin et al. 2006) than temperate species. Furthermore, differences in feeding rates and food load are tied more closely to variation in nest predation (Martin et al. 2000b).

Despite these recent advances, how these different aspects of parental care are related to latitudinal variation in reproductive

effort and parental care strategies remains unresolved, partly because there have not been enough empirical studies to permit comparative analyses of renesting intervals, numbers of broods per year, and nest defense (Ricklefs 1977, Ricklefs and Bloom 1977). Moreover, understanding variation in reproductive effort requires understanding how hard parents work to provide care. Parental effort depends on a number of factors, including food availability. For example, for the same provisioning rate, parents work harder to feed offspring in an environment with low food availability than in an environment where food is readily available. Yet how such environmental factors differ with latitude remains elusive. Finally, although prolonged parental care and delayed dispersal are predicted to result in higher juvenile survival, estimates of survival until reproduction are largely unavailable, particularly in tropical species (Ricklefs 2010). Judging from the few currently available estimates of juvenile survival, tropical species appear to have greater survival during the period of dependence on adult care and equal or greater survival throughout the first year, compared with many temperate species (Russell 2000, C. Tarwater unpubl. data). If this pattern holds as more empirical studies are conducted, it will suggest that reproductive effort should be equal or greater in tropical species compared with temperate species because of the high value of the offspring of tropical birds.

Instead, for the same level of reproductive effort, tropical and northern-hemisphere species may use different strategies of parental care that favor offspring quality in tropical environments and offspring quantity in temperate environments. This fundamental tradeoff between the amount of parental care (influencing offspring quality) and offspring quantity (Smith and Fretwell 1974, Stearns 1992) is likely influenced by latitudinal variation in environmental factors. For example, in species in which offspring mortality is primarily influenced by winter conditions, increasing offspring quantity may increase parental fitness more than increasing offspring quality. Correspondingly, in less seasonal, tropical environments, stronger competition for breeding territories and lower food availability during the breeding season, owing to populations being near carrying capacity on a year-round basis (Ashmole 1963, Cody 1966, Ricklefs 1980, McNamara et al. 2008), may favor investment in offspring quality. Future work needs to examine how environmental conditions differ across latitudes, and more comparative analyses of parental care behaviors are needed. Nevertheless, current work suggests that tropical birds provide offspring with prolonged parental care and that variation in reproductive effort does not explain variation in clutch size.

WHAT STUDIES OF BIRDS MAY TELL US ABOUT LIFE HISTORIES IN GENERAL

Life-history analyses are important because they elucidate the relationships between a wide range of adaptations that have relatively clear associations with fitness and the conditions of the environment, thus exposing tradeoffs and constraints in evolution and adaptation (Ricklefs 2000a). Birds are excellent subjects for the comparative study of life-history traits, and of phenotypic diversification in general, because they have been well studied over a wide range of environments and are more accessible in some aspects of their behavior and demography than other groups of organisms. For instance, although model species, such as *Drosophila*

and other insects, which can be extensively manipulated in the laboratory, have provided many insights into the mechanisms that control expression of behavior and life histories (e.g., Nylin and Gotthard 1998, Zera and Harshman 2001, Partridge and Gems 2006), comparatively little is known about those organisms in their natural habitats. By contrast, because birds can be studied in the field, we have the chance to understand how real selection pressures influence fitness of different life-history attributes. The downside of birds as subjects for life-history research includes the relative difficulty of experimental studies and the dearth of information about genetic factors that underlie life-history traits. However, new technologies are quickly improving our understanding of avian genomes (Lerner and Fleischer 2010). Other taxonomic groups show strong patterns of life-history variation, but it is not clear that they parallel those of birds to the extent that general understanding will emerge by combining incomplete knowledge from several taxa. For example, plants, insects, amphibians, and reptiles exhibit more environmentally induced phenotypic flexibility than birds (Nylin and Gotthard 1998, Shine 2005). Even within birds, taxa that contradict the general pattern are perplexing, as in the case of the latitudinally invariant two-egg clutches of hummingbirds and most doves.

FUTURE DIRECTIONS

A telling aspect of studies of life-history variation in birds is the recognition of how little we know, given the extent of work on the group over the past 60 years. Although many studies support the existence of tradeoffs, for example between reproductive success and adult survival (Bennett and Owens 2002), the shapes of such tradeoffs (e.g., how sharply they bend, which determines the evolutionary responsiveness of the optimized points) have not been quantified (Ricklefs 2000a). Many tropical species have long incubation periods and slow postnatal development, in spite of high nest predation (Ricklefs 1976), but no consensus has emerged concerning the meaning of this pattern (Ricklefs 1993, Martin et al. 2007). Lack (1947) and Ashmole (1963) emphasized the role of food resources in determining patterns of reproductive rate in birds, but food availability has not been quantified over a latitudinal gradient for any group of bird. In spite of the importance of disease in population dynamics, and notwithstanding the growing body of work in the area of ecological immunology (Norris and Evans 2000, Zuk and Stoehr 2002), we have little understanding of the pathogen environments of birds (Padilla et al. 2006, Soos et al. 2008). We tend to work on what is easy and what is fashionable. The lack of information on geographic trends in food supply, pathogens, and disease reflects the difficulty of the work contrasted with the attractiveness over the years of alternative explanations for reproductive rate, including brood-size-dependent nest predation (Skutch 1949) and parental-investment theory related to adult survival (Williams 1966b, Charnov 1993).

Much remains to be learned about the diversification of avian life histories, and it is an exciting time to be involved. Prominent among the unanswered questions is whether there is indeed a single dominant demography–physiology axis that characterizes the continuum of slow to fast life histories. Multiple important axes of variation will perhaps be revealed as we learn more about the mechanistic drivers that limit or facilitate expression of life-history syndromes. New techniques for quantifying endocrinological, physiological, and immunological parameters in the field will open new frontiers in our understanding of life-history evolution. The difficulty, for example, of examining immunity in the field— where one can usually capture a bird only once and take a single blood sample—has compelled research to focus on innate immunity. Understanding the relationship between life-history strategy and the adaptive immune system should be a future priority as new techniques emerge.

The multispecies comparative framework has been especially helpful for revealing evolutionary patterns in life histories and for generating new hypotheses. Many of our insights have come from studies that compare a small number of species chosen because sufficient sample sizes can be acquired and because comparisons can be phylogenetically controlled. In addition, most studies that have taken detailed looks at mechanisms have compared traits from one temperate and one tropical site, although general characterization of geographic patterns in life-history traits has been expanding recently (Jetz et al. 2008). Our nexus group has focused on one site in temperate North America (Michigan) and one in lowland rainforest (Panama). The temptation to take results from relatively small numbers of species and a couple of sites and then extend inference to global patterns has been difficult to resist. The ideas that nest predation and adult survival rates are generally greater in the tropics are commonly held, yet available data reveal plenty of overlap in those rates across latitudes (Karr et al. 1990; Brawn et al. 1999, 2010; Robinson et al. 2000). Many data on other aspects of life histories currently come from a relatively small number of passeriforms, and therefore from a relatively limited range of body sizes and associated life-history traits. Ornithologists should increase efforts to characterize patterns in additional songbird taxa as well as in taxonomic groups outside the passeriforms. Furthermore, to understand the associations of environmental gradients with life-history traits, sampling of additional sites between the well-studied temperate and tropical sites is needed. By adding more sampling, we can understand where shifts in life-history strategies and the pace of life occur. In addition, many of our insights come from a limited number of habitats, usually forests in temperate settings and lowland rainforest or submontane forest in tropical and subtropical locations. Do different strategies occur in species of montane forests, grasslands, or deserts?

Ornithologists should continue multispecies comparisons and focus on generating new data that have been difficult to obtain historically but that may provide new insights. Some of these data include quantification of renesting rates and interbrood intervals, juvenile mortality, and rates of recruitment to reproductive adulthood, which will help to fill in the remaining key unknowns in demographic models. At the mechanistic level, we still need to confirm the causality of relationships between hormones and life-history traits, including the processes by which stress-induced corticosterone may be linked with survival rate and testosterone may be linked with fecundity. The linkages of hormones with immune function also still need to be evaluated in wild birds. Although much remains to be learned, advances in the availability of techniques, clarity on appropriate field and laboratory experiments, and the availability of field data for comparative studies means that this is an exciting time in the study of avian life histories.

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