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DENSITY DEPENDENCE, EVOLUTIONARY OPTIMIZATION, AND THE DIVERSIFICATION OF AVIAN LIFE HISTORIES[1]

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Abstract. Although we have learned much about avian life histories during the 50 years since the seminal publications of David Lack, Alexander Skutch, and Reginald Moreau, we still do not have adequate explanations for some of the basic patterns of variation in life-history traits among birds. In part, this reflects two consequences of the predominance of evolutionary ecology thinking during the past three decades. First, by blurring the distinction between life-history traits and life-table variables, we have tended to divorce life histories from their environmental context, which forms the link between the life history and the life table. Second, by emphasizing constrained evolutionary responses to selective factors, we have set aside alternative explanations for observed correlations among life-history traits and life-table variables. Density-dependent feedback and independent evolutionary response to correlated aspects of the environment also may link traits through different mechanisms. Additionally, in some cases we have failed to evaluate quantitatively ideas that are compelling qualitatively, ignored or explained away relevant empirical data, and neglected logical implications of certain compelling ideas. Comparative analysis of avian life histories shows that species are distributed along a dominant slow-fast axis. Furthermore, among birds, annual reproductive rate and adult mortality are directly proportional to each other, requiring that pre-reproductive survival is approximately constant. This further implies that age at maturity increases dramatically with increasing adult survival rate. The significance of these correlations is obscure, particularly because survival and reproductive rates at each age include the effects of many life-history traits. For example, reproductive rate is determined by clutch size, nesting success, season length, and nest-cycle length, each of which represents the outcome of many different interactions of an individual's life-history traits with its environment. Resolution of the most basic issues raised by patterns of life histories clearly will require innovative empirical, modeling, and experimental approaches. However, the most fundamental change required at this time is a broadening of the evolutionary ecology paradigm to include a variety of alternative mechanisms for generating patterns of life-history variation.

Key words: age at maturity, clutch size, density dependence, life history evolution, reproductive rate, survival.

INTRODUCTION

Birds vary in many aspects of their lives. Reproductive rate, age at maturity, and adult life span differ more than 10-fold between species with extreme life histories. Avian biologists have long appreciated general patterns in the relationships of organism and population attributes to variation in the environment, and correlations of these attributes among themselves. In one of the earliest scientific studies of life-history variation, Moreau (1944) described in detail the different number of eggs laid by birds in tropical and temperate latitudes. Lack (1947) developed the idea that clutch size evolved by natural selection to maximize individual reproductive success, and he explained the latitudinal trend in clutch size by the greater capacity afforded parents by the longer daylight periods in temperate zones to gather food for their offspring. From these early beginnings, a broad scientific investigation into the life histories of animals and plants, including basic issues of evolution and regulation of population size, sprang to life. A wealth of new insights, new hypotheses, and new empirical and experimental observation show convincingly that this research program has been an outstanding success and has maintained its vigor to the present. Ironically, how-

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ever, the oldest and most basic issue of the life-history research program—the latitudinal gradient in clutch size in birds—remains an unsolved problem. This reminds us that we understand life histories incompletely, and it should leave some doubt in our minds about the comprehensiveness of the central paradigms of life-history theory.

A BRIEF HISTORY OF LIFE-HISTORY THINKING

The study of life histories can be divided into two periods: the first extended from 1944 to 1966; the second began in 1966 and continues to the present. The early period is dominated by the seminal contributions of Moreau (1944), Lack (1947, 1948, 1949, 1954, 1966, 1968), Skutch (1949), and Ashmole (1963). Its major accomplishments were to establish natural selection of individuals as the primary formative mechanism of life-history evolution and to identify density-dependence in population processes as the primary mechanism of population regulation. The period was highlighted by Andrewartha and Birch's (1954) spirited challenge to density dependence, met effectively by Lack (1954, 1966). It culminated in the debate over group selection, which was championed by V. C. Wynne-Edwards (1962, 1963) and devastated by proponents of individual selection (Hamilton 1964, Maynard Smith 1964, Lack 1966, Williams 1966a). However, neither selection nor population regulation is a monolithic issue. Modern concepts allow selection at many levels of organization, as long as there is heritable variation in fitness among the units of selection (Lewontin 1970, Wade 1978, Wilson 1980, 1983). Modern concepts of population biology encompass many influences on population size, including various forms of density-independence and the finite probability of population extinction featured in metapopulation models (Hanski and Gilpin 1997, Hanski 1998). Nonetheless, by 1966 a general consensus had been reached that the diversification of life histories should be understood in the context of selection on the traits of individuals and that density-dependent processes balanced the tendency of evolutionary responses to increase population growth rate.

These principles set the stage for the second phase of investigation of life histories. This phase was dominated by the idea that evolutionary response to selection provided the basis for understanding variation in life-history traits among organisms. In resolving the problem of altruism by kin selection and inclusive fitness, and by developing game theory approaches to the evolution of behavior, Hamilton (1964) and Maynard Smith (1964, 1974, 1982) focused attention on the fates of genes in populations and wed life-history theory to population genetics. In suggesting that parents must balance a trade-off between current and future reproduction, Williams (1966b) articulated the idea of constrained evolutionary response. In the same eventful year, Cody (1966) formally introduced the concept of allocation of limited resources, drawing on Levins' (1962) invention of the constrained fitness set, and Hamilton (1966) showed quantitatively how changes in age-specific fecundity and mortality influenced population growth rate, which could be interpreted as individual fitness (see also Cole 1954, Lewontin 1965, Emlen 1970, Charlesworth 1994). Further elaboration of the theme of life-history evolution encompassed the optimization of the sex ratio (Hamilton 1967, Charnov 1982), parental investment (Trivers 1972), parent-offspring conflict (Trivers 1974), optimization in a variable environment (Schaffer 1974, Hastings and Caswell 1979), multivariate response of evolution to selection through the genetic variance–covariance matrix (Lande 1979), sexual selection (Zahavi 1975, Hamilton and Zuk 1982), and phylogenetic comparison (Felsenstein 1985, Harvey and Pagel 1991, Garland et al. 1992).

THE EVOLUTIONARY ECOLOGY PARADIGM

The paradigm of evolutionary ecology that developed during this second phase built upon Lack's principle that life histories reflected evolutionary responses to selection. Selective factors in the environment broadly included individuals of other species (coevolution) and of the same species (kin selection, parent-offspring relationships, sexual selection), as well as physical factors. However, the rise of the "evolutionary ecology" paradigm has had two consequences that made the interpretation of differences in life histories among populations more difficult. The first of these was confusion about the definition of life history, which variously includes both adaptations of individuals and life-table variables of populations. Adaptations express the evolutionary modification of the gene pool of the population in response to changes in the environ-

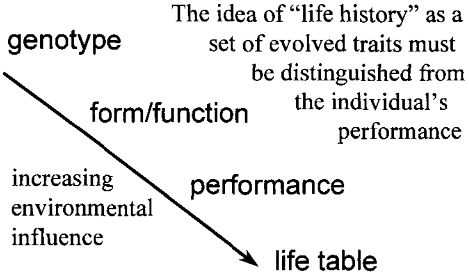

FIGURE 1. The genotypes of individuals are expressed in the life table of a population through the performance of the organism (phenotype) in its particular environment. The genotype is the singular intrinsic property of the individual. The form and function of the individual expressed in the phenotype are sensitive to the environment through its influence on development [epigenetics (Waddington 1957); canalization (Møller and Swaddle 1997); the reaction norm (Stearns and Koella 1986, Stearns 1992)]. The performance of the individual has meaning only in the context of the environment (Arnold 1983, Ricklefs 1991). This performance ultimately can be summarized in terms of components of evolutionary fitness by the survival and fecundity of individuals over their life spans, that is, by the life table (Caswell 1989, Charlesworth 1994).

ment. The life table, however, represents interactions of an individual's adaptations and its environment (Fig. 1). Evolutionary interpretation of life-history variation requires a link between attributes of morphology, physiology, and behavior, on one hand, and evolutionary fitness, on the other. The life-table variables of age-specific fecundity and mortality are related to evolutionary fitness directly, and have often been considered as, or in the place of, adaptations, which they are not. This confusion has blurred the distinction between organism and environment and tended to lift life-history evolution out of its environmental context. When a life-table entry such as fecundity is taken to be a measure of adaptation, then variation in the adapted property assumes a fitness consequence independently of the environment.

DENSITY DEPENDENCE AND LIFE HISTORIES

A second consequence of the evolutionary ecology paradigm for studying life-history variation has been to diminish the perception of density-dependent feedback as an influence on life-history patterns. Changes in the environment and adaptive responses to these changes both influence population processes and tend to vary the density and age structure of a population. These changes may stimulate further evolutionary responses, but they also induce population responses that restore an equilibrium state. The role of density-dependence in the regulation of population size, perceived in the early 1900s (Howard and Fiske 1911, Nicholson 1933), was integrated into the development of life-history theory by Moreau, Lack, and Skutch in the 1940s, and especially by Ashmole (1963). Population and evolutionary responses connect the three fundamental components of life histories: the environment, the life-history attributes of the organism, and the life table (Fig. 2). The environment directly influences the form and function of individuals, and their survival and reproductive rates. The environment also affects the gene pool of a population indirectly over generations by promoting evolutionary response.

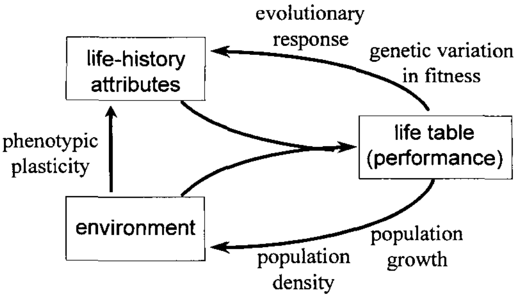

FIGURE 2. The life table of the population reflects the performance of individuals in a particular environment. Genetic variation in fitness establishes the potential for evolutionary response in the gene pool of the population to variation in the environment. Variation in the environment also affects population processes and stimulates density-dependent feedback to restore the population equilibrium by modifying the phenotypes and performance of individuals.

For David Lack (1947), variations in the life histories of birds were driven by the influence of differences in the food supply on reproductive rate. Accordingly, natural selection and evolutionary response adjusted clutch size to the maximum number of young that parents could nourish adequately. The resulting reproductive rate influenced population density through the recruitment of young individuals into the breeding population. Lack (1949) felt that "population density is determined primarily by the operation of density-dependent mortality factors (i.e., factors whose proportionate effect increases as the population density rises) and that such factors

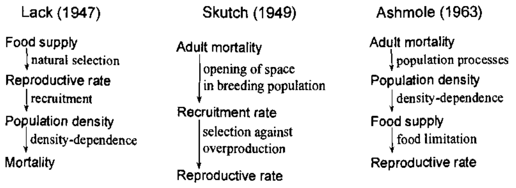

FIGURE 3. Three different views of the relationship between population density and reproductive rate: (a) Lack (1947), (b) Skutch (1949), (c) Ashmole (1963).

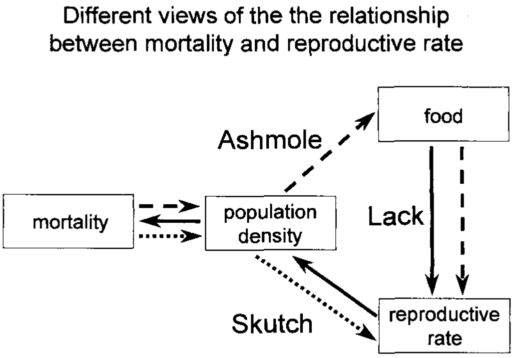

FIGURE 4. A diagram of the different views of Lack (1947), Skutch (1949), and Ashmole (1963) of the relationship between mortality and reproductive rate in populations. Arrows indicate the direction of influence. For Lack, food supply for reproduction drove variation in life histories; for Skutch and Ashmole, adult mortality took on this primary role. The only points of agreement were between Lack and Ashmole over the determination of reproductive rate by the food supply and between Ashmole and Skutch over adult mortality driving variation in population density.

produce the apparent stability of many bird populations" (Fig. 3a). Skutch (1949) argued that the influence of density ran in the opposite direction. In his view, reproductive rate is adjusted to match the rate at which breeding opportunities become available in the population through the deaths of adults (Fig. 3b). The problem with Skutch's idea is the mechanism by which this feedback is achieved. Skutch suggested that overproduction of offspring is wasteful, but he did not explicitly link waste to evolutionary mechanisms, except through selection of populations. Natural selection, argued Lack, is incapable of restraining individual reproductive performance to match mortality rate; the waste produced by density-dependent mortality is inevitable. This impasse was resolved by Ashmole (1963), but not in a manner to rationalize Skutch's predilection against waste. Ashmole suggested that population density, determined by mortality rate, could influence reproductive rate through its effect on the food supply (Fig. 3c). To the extent that population density depresses breeding success, the influence of reproductive rate on mortality was diminished.

The different perspectives of Lack, Skutch, and Ashmole are diagrammed in Figure 4, which shows points of similarity and difference among these authors. For Lack, food availability was the driving force in life history; for Skutch and Ashmole it was adult mortality. Lack emphasized the evolutionary response of reproductive rate to food supply, however evolution was merely the mechanism that brought clutch size (an attribute of the individual, that is, form and function) into line with the availability of resources for rearing offspring. Thus, variation in reproductive rate (performance), and the pattern of the life history more generally, was driven largely by variation in the food supply. One of the ironies of the development of life-history theory is that the major debate centered primarily over the mechanisms of natural selection and evolutionary response, while the phenomenon of life-history variation was seen as driven primarily by variation in one or more aspects of the environment. With respect to generating variation in life histories, Lack, Skutch, and Ashmole agreed that variation in the environment was primary and that correlations among life-history traits or life-table variables were the secondary result of density-dependent feedback. One of the unfortunate consequences of the second phase of the development of life-history theory was that evolutionary adjustment largely replaced both direct environmental determination in explaining variations in life histories and density-dependent feedback in explaining correlations among life-history attributes. In his review of life-histories, Cody (1971) illustrated this shift when he said, "The variation in clutch size with latitude seems to be no more than a particular case of reduced reproductive commitment with the increased "stability" of the conditions under which the populations exist" (p. 492).

By the early 1990s, the paradigm of evolutionary ecology was so firmly established that two important books (Roff 1992, Stearns 1992), which provided major overviews of life-history thinking, together had only a single entry for "density-dependence" in their indices.

VARIATION IN LIFE HISTORIES

In the more than 50 years since the seminal publications of Moreau (1944) and Lack (1947) on variation in clutch size in birds, our understanding of the forces that mold the life-history attributes of individuals and life-tables of populations has developed to a high level. Yet we still lack compelling explanations for many empirical patterns in life-history variation, including the latitudinal gradient in clutch size that provided the initial motivation for life-history studies. That evolutionary responses and density-dependent responses are both important features of populations should no longer be an issue. However, the extent to which each of these is responsible for variations in the attributes of individuals and populations is not resolved. Nor is there a clear research agenda for approaching this problem.

My reading of the literature suggests that many factors together explain the current muddle in life-history thinking. Several of these already have been mentioned: (a) confusion over what constitutes a life history, (b) de-emphasis of density-dependent influences, and (c) divorcing life-history from its environmental context. To these factors might be added (d) ignoring or explaining away relevant empirical data, (e) failing to pursue the logical implications of certain plausible ideas, and (f) not evaluating quantitatively ideas that are compelling qualitatively. For example, density dependence is one idea that has hardly been pursued in the development of life-history thinking, and yet provides a powerful paradigm for understanding correlations among life-history traits and life-table variables (Ricklefs 1980). Empirical observations indicating that birds do not provide as much food to their broods as they can (time-activity budgets, brood enlargement experiments) have accumulated in the literature since Skutch (1949), yet these data were often ignored because they were associated with untenable theory or ran counter to accepted theory (see, for example, the discussion in Ydenberg and Bertram 1989). The idea that increased environmental variation might select for increased parental investment and higher reproductive rates is compelling (Schaffer 1974, Hastings and Caswell 1979) but has received little rigorous quantitative scrutiny (Sibly et al. 1991, Cooch and Ricklefs 1994). In general, theory has been used to develop qualitative rather than quantitative tests, but these often have little power to reject hypotheses.

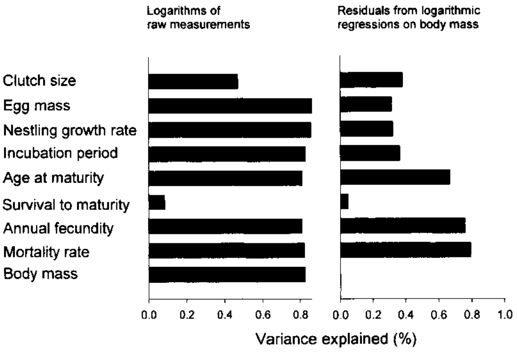

FIGURE 5. Amount of variation in life-history traits and life-table variables associated with the first principal component derived from the correlation matrix among the logarithms of these values (a) with all variables included and (b) among residuals from the logarithmic regression of each variable on body mass. The first principal component explained 71% of the total variance in (a) and 46% in (b). In the first factor analysis, the second component represented variation in survival to maturity. The remaining components did not represent significant axes of variation.

It would be overly optimistic to hope that we can resolve the life-history problem at this time. The issues are complex. Many mechanisms mold life histories. These mechanisms are expressed under the unique environmental circumstances of each population, thereby producing the tremendous variety of life histories and life-table patterns observed in nature. However, a useful point from which to begin to organize our thinking about life histories is that of empirical observation. To this end I have compiled values for 34 species of birds for several variables that are often included in studies of avian life histories. These variables include six attributes of individuals (body mass, clutch size, egg mass, incubation period, nestling growth rate, and age at maturity) and three life-table variables (survival to maturity, annual fecundity, and annual adult mortality). A principal components analysis of the logarithms of these measurements shows that most of the variation among species constitutes a single "life-history" dimension explaining 71% of the total variation in the data (Fig. 5). Only survival to maturity is unrelated to this axis of variation, and it will be shown below that this value is relatively invariant among populations of birds. Much of the variation among species is related to body mass, with larger species tending to slower development, delayed maturity, lower fecundity, and higher survival. Even with body mass removed statistically, however, the other variables continue to be interrelated along a single dimension of life-history variation (Sæther 1988, Promislow and Harvey 1990). In particular, the life-table variables and age at maturity remain highly intercorrelated, whereas individual components of the life-table variables (e.g., clutch size, incubation period, nestling growth rate) exhibit unique variation not related to the predominant life-history continuum.

CORRELATION AND FUNCTIONAL CONSTRAINTS AMONG LIFE-HISTORY ATTRIBUTES

Correlations among life-history attributes have provided a foundation for many ideas about the mechanisms responsible for life-history patterns. Many of these mechanisms are firmly embedded in the paradigm of evolutionary ecology. For example, the direct relationship between reproductive rate and adult mortality is consistent with the idea that where extrinsic factors cause little mortality, evolution reduces parental investment to reduce reproduction-related mortality and preserve the potentially long life spans of individuals. The result would be low fecundity and high adult survival. According to this idea, evolutionary adjustment of the life history with respect to adult survival rate would be responsible for much of the correlation between the resulting life-table variables.

The idea that two life-history attributes are functionally constrained and that evolution optimizes the allocation of resources between the two provides a compelling explanation for the inverse relationship between fecundity and adult mortality, or the relationships between any other set of life-history or life-table variables. This idea was developed by Cody (1966) and Gadgil and Bossert (1970), who postulated that limited time, energy, and other resources must be allocated among competing demands. Evolution optimizes the point of allocation. In the example just mentioned, survival by adults of the potential risks of reproduction should decrease as parental investment increases because time and resources that could be allocated to adult maintenance and avoidance of predation are instead devoted to offspring. The bounded area in Figure 6 represents the "fitness set" of all possible phenotypes with respect to realized fecundity and reproductive survival of parents. Because fitness increases as one moves away from the origin of the graph (a combination of higher fecundity *and* higher survival), all internal points in the area represent less fit phenotypes. Therefore, selection leads to an optimum phenotype that resides somewhere on the perimeter of the fitness set. The optimum point depends on the demography of the population. I will not go into the mathematics here, but one can show that this point is tangent to a line (the "adaptive function") whose slope is determined by the annual adult survival rate (see Ricklefs 1977b, 1983a). Thus, when adult survival of factors other than reproductive risk is higher, the adaptive function has a shallower slope and is tangent to the adaptive function at a lower fecundity but higher adult survival rate (Fig. 6).

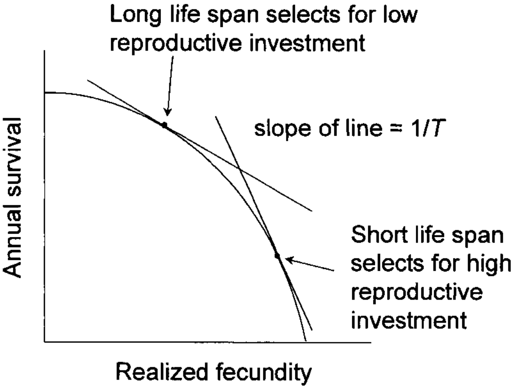

FIGURE 6. A diagram of the optimization of the trade-off between annual adult survival and annual fecundity. The bounded area within the curve represents the set of possible phenotypes, among which those potentially having maximum fitness are represented on the periphery. The adaptive function is a line running through combinations of fecundity and survival having equal fitness and just tangent to the fitness set. The tangent point is the phenotype that maximizes evolutionary fitness. The slope of the line ($-1/T$) is the negative value of the inverse of the average age (T) of a female at the birth of her offspring. Thus, the slope is related to the negative of the adult mortality rate.

The idea of functional constraint makes good sense, but it is not the only idea that explains the relationship among life-history variables. In Figure 6, the difference between two optimized points in the phenotype space represents a shift in the optimized point along the same fitness set. But it also could represent a shift in the fitness set itself without a change in the adaptive func-

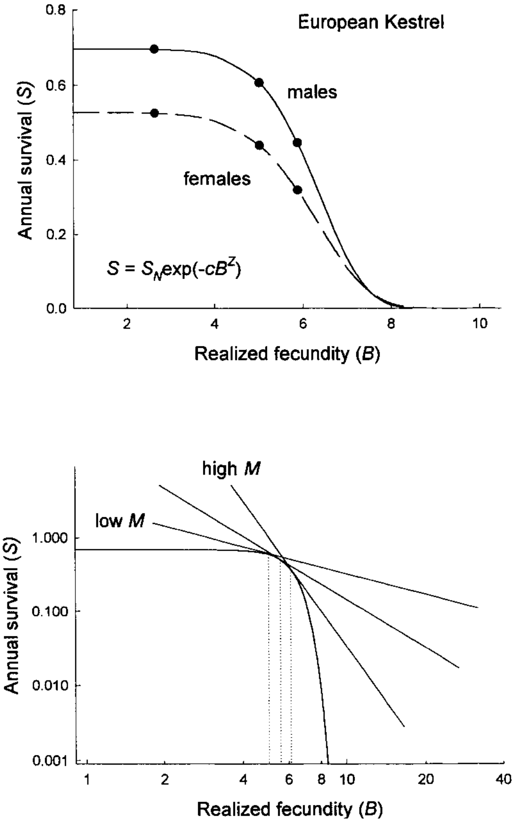

FIGURE 7. (Top) The relationship between adult survival of males and females and realized fecundity (number of young fledged) in experimental and control broods of European Kestrels (*Falco tinnunculus*) (Dijkstra, et al. 1990). The data points show the results of the field experiments. The points are fit by a curve relating survival to fecundity by the equation $S = S_N\exp(-cB^Z)$. This curve features a baseline survival (S_N) with minimal reproduction and an increase in mortality as a function of realized fecundity (B) controlled by the shape parameter Z. For the European kestrel, $Z = 6.4$ for females and 7.4 for males, indicating a rapidly accelerating mortality rate above a moderate level of fecundity. (Bottom) The survival-fecundity trade-off for males is log transformed to show the adaptive function at the optimized point (fecundity resulting from normal broods) and to show how little change in the optimized point results from major changes in the slope of the adaptive function.

tion. To distinguish between these possibilities it is necessary to measure the fitness set, which is problematic because most phenotypes far from the optimal point will have long been removed by natural selection. Experimentation by brood size manipulation offers one possibility. For example, Dijkstra et al. (1990) changed brood size in European Kestrels *Falco tinnunculus* and obtained values for annual adult survival and realized annual fecundity shown in Figure 7. Although only three data points are available (reduced, enlarged, and control broods), the results suggest that the decrease in adult survival accelerates very rapidly with increasing brood size. As a consequence of the sharp curvature of this "fitness set," large changes in the adaptive function result in rather small changes in realized fecundity, making it doubtful that large differences among life-table variables observed among species of birds could result from different adaptive functions applied to the same fitness set.

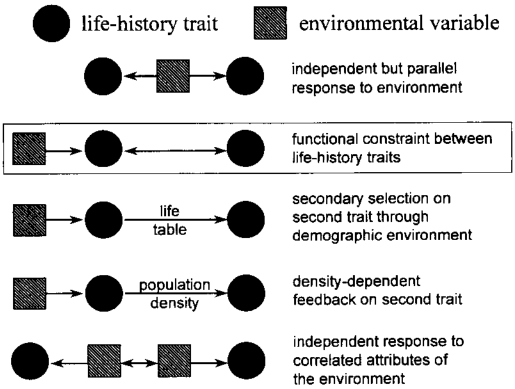

FIGURE 8. Five ways in which correlations may be generated between life-history traits or life-table variables in response to variation in the environment. The mechanisms stressed by the current evolutionary ecology paradigm are framed by a line-box. Of the other four mechanisms, density-dependent feedback was advocated by Ashmole (1963) and others, but is not now an important point of consideration in the literature. The other three possibilities, especially the last, are rarely discussed in the context of life-history variation. Arrows denote paths of influence.

ORIGINS OF CORRELATIONS AMONG TRAITS

Figure 8 illustrates five ways in which correlations between life-history traits can be generated in response to variation in features of the environment. First, variation in two traits could represent independent responses to variation in a single environmental variable. For example, a better food supply might promote both higher fecundity and higher adult survival, resulting in a positive correlation between the two. Second, variation in one environmental variable could influence a life-history trait or life-table variable, which through a functional relationship, or constraint, could cause a correlated response in a second trait. The constraint might take the form of a genetic correlation (for example, between brain and body mass: Lande 1979) or it might result from the allocation of resources among competing functions, as in the way the relationship between adult survival and fecundity often is conceived (Cody 1966). The third and fourth possibilities are similar to the second except in the way in which the correlated traits are interrelated. In the third case, adaptive response or other change in one trait selects change in another trait by changing the demography of the population. Optimization of character traits is sensitive to population demography, as illustrated in the case of the adaptive function for optimizing the survival-fecundity trade-off. Rather than being established by functional relationships among character traits of individual organisms, correlations between life-history traits arise over generations through evolutionary responses. For example, any environmental change that influences the component of adult mortality that is unrelated to reproduction will secondarily select for a shift in the optimized point in the survival-fecundity fitness set. Two traits also can be connected through density-dependent population processes. For example, when a change in adult mortality, regardless of the cause, results in a change in population density during the breeding season, then the food supply available to each adult for reproduction might be affected by density-dependence in the consumer-resource interaction. The consequence of this change will be a shift in the boundary of the fitness set, leading to a shift in the optimized point and generating a correlation between two life-history traits. The fifth possibility is that two life-history traits independently respond to different attributes of the environment, but that these environmental variables are correlated with one another. In this case, the correlation among the life-history traits is fortuitous. It is conceivable, for example, that pelagic seabirds have low adult mortality because of the absence of predators on the open ocean, but also have low fecundity because of the great distance between nesting colonies and the food supply (Ricklefs 1983b).

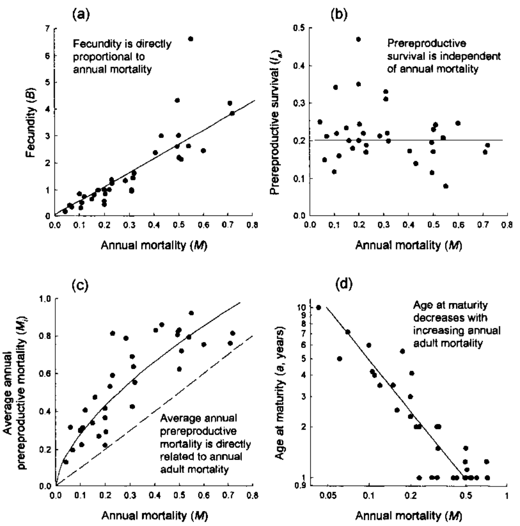

FIGURE 9. Empirical relationships among life-table variables of birds. Data compiled from the literature for 34 studies of 32 species, including 14 listed by Ricklefs (1977b). (a) Annual fecundity (number of fledglings per year) as a function of annual adult mortality: logarithmic regression, $F_{1,32} = 183$, $P < 0.001$, $R^2 = 0.85$, slope (*b*) = 1.08 (± 0.08). (b) Survival from fledging to maturity as a function of annual adult mortality: logarithmic regression, $F_{1,32} = 1.0$, $P = 0.34$, $R^2 = 0.03$. S_a was calculated as the ratio of annual mortality to fecundity, assuming constant population size. (c) The geometric mean of annual mortality of immatures M_i as a function of annual adult mortality. M_i was calculated as $1 - S_a^{1/a}$. The logarithmic regression, $F_{1,32} = 144$, $P < 0.001$, $R^2 = 0.82$, slope (*b*) = 0.62 (± 0.06). (d) Relationship of age at maturity (years) to annual adult mortality: logarithmic regression, $F_{1,32} = 76$, $P < 0.001$, $R^2 = 0.82$, slope (*b*) = −0.86 (± 0.07).

THE RELATIONSHIP BETWEEN FECUNDITY AND ADULT MORTALITY

The basic variables of the life tables of birds are annual fecundity (*B*), annual adult mortality (*M*), age at maturity (*a*), and pre-reproductive survival (S_a). Long-term studies of natural populations have shown that fecundity and survival vary with age (e.g., Newton 1989, Ricklefs 1998), however, these variations do not modify the basic patterns. The primary empirical relationships among the life-table variables of birds are summarized in Figure 9. The most striking pattern is that annual fecundity is directly proportional to annual adult mortality, that is, $B = kM$, a pattern shown quantitatively by Ricklefs (1977b). Charnov (1993) calls the ratio $k = B/M$ a life-history invariant (Fig. 9a). In a balanced population, the inverse of *k*, i.e., M/B, is equal to the survival of young to maturity, S_a. Thus, pre-reproductive survival tends to vary little among populations and, more importantly, it is insensitive to adult mortality and the turnover of breeding individuals in the population (Fig. 9b). We now define M_i as the geometric mean of the annual mortality fraction of immature individuals prior to reproduction. Therefore, $S_i = 1 - M_i$ is the mean annual survival fraction, and $S_a = S_i^a$, where a is the age at maturity. M_i may be estimated as $1 - S_a^{1/a}$. It seems reasonable that the average annual mortality rate of immature individuals should vary among populations in proportion to the annual mortality rate among adults, and this is indeed the case (Fig. 9c). As a consequence, to produce the relationship $S_a = M/B =$ constant, the age at maturity a must increase as M decreases, as shown in Figure 9d.

The implications of the direct relationship between annual adult mortality and annual fecundity ($M/B =$ constant) in terms of the possibilities outlined in Figure 8 are not clear. It has been suggested that fecundity may respond to variation in adult mortality through density dependence of the food supply for reproducing individuals. This may explain part of the relationship between M and B; however, the relationship between mortality (much of which occurs during the nonbreeding season), population density, and food supply for reproduction is not known. Furthermore, B has components, such as season length and rate of predation on nests, that may be unrelated to the food supply during the breeding period. Finally, not all components of fecundity contribute to its variation. For example, among the 32 species depicted in Figure 9, variation in annual fecundity is strongly correlated (log-transformed values) with variation in clutch size ($r = 0.73$, $P < 0.001$) and number of nesting attempts ($r = 0.48$, $P = 0.006$), but not with fledging success ($r = 0.27$, $P = 0.13$).

Although density-dependence may have a strong influence on the relationship between M and B, the inverse relationship between age at maturity and M also implies that density dependence strongly impacts the young, forcing immature individuals to delay their maturation.

In a balanced population, adult mortality equals recruitment of new breeders, that is, $M = BS_a$. Life history adjustments have resulted in constant pre-reproductive survival and a direct proportionality between adult mortality and fecundity. An extreme view of these relationships would hold that adult mortality rate is an intrinsic property of the biology and ecology of each species and is unaffected by the density of adults in the population. In this case, the parallel between fecundity and mortality could result from density-dependent effects of adult populations on their food supply through resource depletion or territory size (density-dependent establishment of life-history correlations). Alternatively, it may result from similar body-size scaling effects on mortality and fecundity or the independent influence on each of these traits of correlated aspects of the environment. That is, a life style with low mortality may only be possible physiologically and ecologically in conjunction with low fecundity. At present, the basis for proportionality between adult mortality and fecundity is not clear.

AGE AT MATURITY

Having established a parallel between fecundity and mortality (Fig. 9a), it follows that pre-reproductive survival must be approximately invariant (Fig. 9b). Although the average annual mortality of immature individuals is consistently higher than that of adults, the two values maintain a relatively constant proportionality (Fig. 9c), in contrast to the inverse relationship of age at maturity to adult mortality rate (Fig. 9d). Clearly, density-dependent feedback may delay maturation when adult mortality rate is low. This simply requires that older birds control access to resources for breeding, with the implication that age and experience count for a lot (Curio 1983). An individual should delay breeding as long as its personal fitness increases as a result. Density-dependence would imply that social interactions have a strong impact on fitness, either directly, or through forcing younger birds into marginal habitats with poor prospects for successful breeding at low reproductive risk. Independently of density-dependent feedback, populations with low M might exhibit delayed maturity if food supplies for such populations required considerable experience to master. For example, it might take many years for pelagic seabirds to learn the vagaries of weather, ocean conditions, and shifting food supplies well enough to provide for even a single offspring. In this particular example, much of the correlation between mortality, fecundity, and pre-reproductive survival would result from the independent effects of correlated aspects of the environment, leaving direct feedback among the life-table variables to achieve the final population balance.

TABLE 1. Results of a multiple regression of log-transformed fledging success on log-transformed values of its six components as calculated by Ricklefs and Bloom (1977). The overall regression explained 96.3% of the variance in fledging success ($F_{6,25} = 110$, $P < 0.001$, residual variance = 0.0018).

Component	Variance in component	Slope	SE	Type III SS	Consistent?[a]
Fledging success	0.039			1.167	
Season length	0.017	1.09	0.08	0.295	no
Clutch size	0.016	0.93	0.09	0.214	yes
Nest cycle length	0.005	−1.42	0.13	0.208	yes
Nest failure rate	0.045	−0.60	0.05	0.232	yes
Renesting interval					
after success	0.030	−0.32	0.07	0.036	yes
after failure	0.028	−0.16	0.07	0.009	yes

[a] Is the regression consistent with the difference in fledging success between tropical and temperate regions?

COMPONENTS OF REPRODUCTIVE SUCCESS

Returning now to the life histories of temperate and tropical birds, an analysis of the components of annual fecundity in Nearctic and Neotropical passerines shows how difficult it is to understand the differences in life-history and life-table traits associated with contrasts between environments. For each of 32 species, Ricklefs and Bloom (1977) estimated annual fledging success from season length, clutch size, nest cycle length, nest failure rate, and renesting intervals after failures and successes. Multiple regression of the logarithm of fecundity on the logarithms of each of the independent variables showed significant contributions of all the independent variables except renesting interval after nest failure (Table 1). This result is not surprising in that the independent variables were used to calculate fecundity. What is striking, however, is that less than a quarter of the variation in annual fecundity is related to variation in clutch size. Season length, nest cycle length, and nest failure rate each explain similar amounts of the variation in annual fecundity. The statistical influence of each of independent variable is consistent with the lower fecundity of tropical compared to temperate songbirds, except for the length of the breeding season, which is generally longer at low latitudes. Among the independent variables in this analysis, season length, clutch size, and nest failure rate presumably have large environmental components, but nest cycle length is likely to reflect evolved attributes of individuals and exhibit less direct environmental influence.

The breakdown of fecundity into its several components distances fecundity even further from the direct influence of adult mortality through phenotypic constraint or density-dependent feedback on the food supply. Although components of fecundity other than clutch size may be related to parental investment or food supply, other explanations for variation in these components are equally plausible. For example, renesting interval may be determined by the nutritional state of the parent at the time of brood failure or fledging, thereby relating this component to food supply and parental investment. However, renesting following fledging also may be related to the fitness value of fledged offspring to a parent, which increases as rate of nest failure increases (Ricklefs 1969b). At present, we have very little understanding of the relationships among these variables.

PREDATION AND REPRODUCTIVE RATE

One hypothesis that has received attention since the 1940s is the idea that parents may rear fewer chicks than they can nourish because of the disproportionately higher risk of nest predation among larger, noisier broods (Moreau 1944, Skutch 1949). Lack (1949) agreed that this was a plausible mechanism and recommended that it be tested by brood-enlargement experiments. A question that comes to mind is whether clutch size-dependent predation sufficient to noticeably reduce optimal brood size could be detected by such an experiment. In this case, it is worth going through the mathematics to determine whether a qualitatively compelling idea makes quantitative sense. Consider a tropical species with a typical clutch size of 2 eggs. Assume that the instantaneous nest mortality rate (m) increases with brood size (C) according to a simple power relationship $m = bC^Y$, where Y indicates how fast the slope of m increases with respect to C. In this case, nest survival (S) over the nestling period t is $S = \exp(-btC^Y)$. The expected nesting success is S times C, which is maximized when

$$\hat{C} = \left(\frac{1}{btY}\right)^{1/Y}$$

at which point

$$\hat{m} = \frac{1}{tY}$$

(Ricklefs 1977a). When we evaluate these relationships, we find that the expected increase in nest mortality rate is substantial and should be detectable experimentally. For example, suppose that optimum clutch size is 2 and nest losses result only from clutch-size dependent predation. In this case, increasing the clutch from 2 to 3 would increase daily nest mortality rate by a factor of 1.5 for $Y = 1$, 2.25 for $Y = 2$, and 3.38 for $Y = 3$. The only direct test of the nest-predation hypothesis has been that of Young (1996), which failed to detect an increase in nest predation in enlarged broods of Tropical House Wrens *Troglodytes aedon* in a nest box colony in Costa Rica. Indirect evidence that predation is not important in regulating clutch size comes from the observation that the nest failure rate during the nestling period (high nest activity) does not increase over that during the incubation period (low nest activity) in most species of birds (Ricklefs 1969a, 1977a). Comparisons of nest loss during the day compared to the nighttime period of inactivity would also be revealing, if not conclusive (Lack 1949).

SOME UNRESOLVED PROBLEMS

In spite of the spectacular progress that has been made in understanding the diversification of life histories of birds and other organisms, some issues have been difficult to resolve. Among these issues is the relationship between the basic life-table variables of age-dependent survival and fecundity, which subsume age at maturity and pre-reproductive survival. Over a wide range of bird taxa, the basic patterns are outlined in Figure 9. Why annual fecundity (B) should vary in direct proportion to annual adult mortality (M), thereby forcing an inverse relationship between age at maturity (a) and M (aM approximately constant), is at present a complete mystery (Charnov 1993). To solve this mystery, we need to acquire a deeper appreciation of the life-table variables themselves. First, it is important to realize that each entry in the life table has many components, each of which represents the interaction between adaptations of the organism and various factors in the environment. Thus, fecundity is influenced by number of offspring per clutch, but also by number of clutches attempted per year, which in turn depends on length of the suitable season and length of the nesting cycle, and the proportion of nests that are successful. Annual adult survival can be decomposed, at the simplest level, into components associated with different phases of the annual cycle and with level of parental investment during the reproductive period. Each of these components likely represents different paths of environmental influence over the performance of the individual and different paths taken by evolutionary response to these environmental factors. Second, many mechanisms potentially connect life-history variables: internal constraints of the organism, correlated responses in evolutionary adaptation, density-dependent feedback of the population/environment system, and correlations among factors in the environment itself. Of course, characterizing the life history in a more complex manner will not necessarily make it easier to resolve its basic patterns. Indeed, complexity may have an opposite effect.

We may come closer to the essence of a particular pattern by trying to imagine alternatives. Constant fecundity would seem to contradict what we know about body mass scaling, that larger animals are generally slower and safer than smaller ones (Calder 1984). However, the relationships among life-history variables identified in this study apply equally when body mass is held constant, suggesting that a slow-safe/fast-perilous axis is an intrinsic property of the organization of living systems. If fecundity were approximately constant among species, populations would have to balance themselves through a direct proportionality between adult mortality rate and pre-reproductive survival. Because annual mortality rate of immature individuals is proportional to that of adults (Fig. 9c), this would require exceptionally early maturation of species with high adult mortality or exceptionally delayed maturation of species with low adult mortality. At one end of the spectrum, short breeding seasons might preclude maturation at an early age; at the other end, maturation may fail to outpace senescence. These considerations of the individual fitness consequences of age at maturation limit the expected range of values in this trait and require that variation in annual fecundity compensates variation in annual mortality, at least in part. That the relationship among these variables has settled on prereproductive survival being approximately constant may be completely fortuitous in the sense that it represents the realized balance between many factors, none of which by themselves dictates S_a = constant. One has to be impressed nonetheless with the tightness of the relationship between B and M ($r^2 = 0.85$), which suggests that the factors influencing the relationship are not entirely independent.

THE FUTURE

If adopting a more complex perspective on life-history variation is a first step, where do we go from there? Clearly, we need to strengthen our empirical foundation, finding ways to decompose pattern in the life table into components imposed by variation among phenotypes and variation among environments. This will require a much better understanding of both the environment and the performance of individuals, and how these two factors combine to yield life-table values. Perhaps the weakest part of our empirical foundation concerns the care of dependent offspring and the social context of attaining sexual maturation. I would also make a special plea for a better understanding of the physiological and biochemical mechanisms of life-history traits, as well as the endocrine mechanisms that control them. Undoubtedly, cognition also will figure prominently as a life-history variable in the near future.

Modeling should be integrated much more thoroughly into empirical and experimental life-history studies (e.g., Charnov 1993). This is often a humbling experience because models show the kinds of data that are needed to verify assumptions and to quantify constraints. Models should be explicit and developed to provide quantitative predictions of life-history variables (e.g., Konarzewski et al. 1998). Still, we should not shy away from exploring any possible relationship among aspects of the life history. For example, modeling provides a plausible scenario for a connection between the duration of embryonic development and the potential life span of the individual (Ricklefs 1993).

Experimental approaches hold tremendous potential for resolving relationships among life-history variables, but these must be applied with a full appreciation of the limitations of altering either the phenotype or the environment. Brood size manipulations have found the broadest application, but handicapping adults with weights or by trimming flight feathers, and hormone manipulations to change behavior more directly, also are finding fruitful applications.

It has been more than 50 years since the beginnings of modern studies of avian life histories. This has been a wonderfully productive field of study, having had a major role in the flowering of evolutionary ecology. Yet the task is not complete. In many ways the work of especially the past 20 years has given us a matured insight into the tremendous diversity of the lives of birds, a firm basis for a push to understand the origins, maintenance, and limitations on variation in life histories. However, to reach a consensus on how to interpret differences in the lives of any two species, will require a substantially higher level of integration of ideas and observations than we have been able to achieve to this point. Science is moving at a breathtaking pace nowadays, and so it would be foolish to hazard a guess at where we might be after five more decades of work, if the inheritors of our discipline will even find our concerns of interest. Clearly, at this time, the evolution and ecology of avian life histories is as exciting and challenging a problem as exists in biology.

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