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LACK, SKUTCH, AND MOREAU: THE EARLY DEVELOPMENT OF LIFE-HISTORY THINKING[1]

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Abstract. Papers by Reginald Moreau, David Lack, and Alexander Skutch published during the 1940s set the stage for the development of thinking about life histories over the following decades. Lack was concerned about the fundamental issue of individual vs. group selection and turned life-history evolution into a battleground for this debate. His monolithic focus on nesting success as a measure of fitness and on food availability as the principal determinant of nesting success obscured the rich empirical background brought to the debate by Skutch and the diverse evolutionary forces envisioned by Moreau. Lack's strong convictions, single-mindedness, and eloquence forced biologists to confront several important problems but also held back the full development of life-history theory until the mid-1960s. Retrospective consideration of these early life-history studies shows how science can progress through a balance of conviction and reflection.

Key words: Alexander Skutch, clutch size, David Lack, history of biology, life-history theory, Reginald Moreau.

The study of life histories today is an active, multifaceted program of research that unites behavior, ecology, population biology, and evolution into a broad concept of the responses of organisms and populations to the conditions of their environments. This endeavor can be traced to three articles, published in *Ibis* during the 1940s, which established the basic issues of life-history theory and determined the directions of thinking and research for decades. After 50 years, consideration of these three articles allows us to glimpse the beginnings of a discipline from within the security of its accomplishments and provides some insights into the workings of science more generally.

In the first of these articles, Reginald Moreau (1944) established scientifically that birds lay more eggs per clutch at high latitudes than in the tropics. He also outlined most of the mechanisms that might account for this pattern. David Lack (1947) argued the narrower but more fundamental point that clutch size should be interpreted in the context of natural selection and individual fitness. In doing so, Lack formally integrated evolution and population biology in a theory that encompassed the life-history traits of individual organisms as evolutionary adaptations. Alexander Skutch (1949) challenged Lack's belief that selection and evolutionary response maximize individual fitness. The ensuing debate, which continued into the 1960s with Lack's active involvement, sharpened evolutionary thinking but at the same time narrowed perceptions about the fundamental issues related to variation in life histories.

Because Lack was the dominant personality in the development of life-history thinking, it is appropriate to begin with his central idea that evolutionary responses to natural selection maximize individual fitness. Accordingly, reproductive rates observed in a population were the highest possible given the resources available; differences in reproductive rate between populations therefore reflected differences in the availability of food or ability of parents to gather food. In Lack's own words (Lack 1947, p. 331), "... clutch size is considered to be ultimately determined by the average maximum number of young for which the parents can find enough food. ... Clutch size increases with increasing latitude and daylength because, in general, a longer day enables the parents to find more food per day, and so to raise more young at one time."

Lack raised two issues. One was the role of natural selection in molding life histories. Lack

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argued that selection favored parents that reared as many offspring as possible and that the average clutch size in a population was adjusted through natural selection so as to maximize individual reproductive success. The second issue concerned the diversification of life histories, specifically the underlying causes of differences among species. In Lack's view, these causes were the different ecological conditions experienced by each species, including the time available for gathering food, which placed different constraints on evolutionary responses to selection on reproductive rate. J. R. Baker cleared the way for this type of evolutionary thinking 10 years earlier in his writings on the evolution of breeding seasons (Baker 1938). It was Baker who distinguished between "proximate" factors that birds used as cues to initiate breeding and "ultimate" factors that influenced survival and reproductive success.

The idea that clutch size might be adjusted to food supply also was not new. For example, in their text *Ecological Animal Geography,* Hesse, Allee, and Schmidt (1937) said that "longer feeding hours [at higher latitudes] make possible the production of a greater number of eggs and the maintenance of a larger brood." Rather, Lack crusaded against unorthodox Darwinian interpretations based on the survival of populations and species, as set forth, for example, in the widely read ecology text by Allee et al. (1949, p. 685): "Birds that are subjected to a greater mortality rate tend to have larger clutch-sizes. . . . These balanced interrelationships of a whole population to its environment are best understood as the result of evolutionary adaptation through natural selection of population units." Allee and his co-authors had introduced this line of thinking when they said (p. 684) "The more integrated the population, the more it takes on supraorganismic aspects, and the greater is the tendency for inherited and adaptive density control."

Lack's most troublesome critic on the subject of clutch size was Alexander Skutch (1949), who rejected Lack's idea that parents produce as many offspring as they possibly can. Instead, Skutch sided with those who believed that selection acted to maximize the efficiency with which individuals were replaced within populations, which contributed to long-term population persistence. Like Allee and many others, he believed that reproductive rate was adjusted to balance adult mortality and thereby maintain the size of the population. This idea was nourished in part by Skutch's detailed observations of the lives of tropical birds and in part by a deeply felt conviction that nature cannot be so wasteful as would result from the maximization of reproductive rate by individual selection. Skutch argued that tropical birds lay smaller clutches of eggs because adults had longer lives and fewer offspring were required to replace adults that died each year. In his words (p. 451), ". . . in the humid Tropics conditions are fairly uniform from year to year, and the population density of the birds tends to be constant over long periods. Let us examine the effects of an increase in rate of reproduction, arising as a mutation, in a steady, nonexpanding "saturated" population. The increase in fecundity . . . is of no advantage to any individual—it affects no bird's ability to escape its enemies nor increases its skill in finding food." Skutch's concept of individual fitness in this instance clearly excluded the contribution of reproduction to the future gene pool of the population. Instead, he argued that overproduction of offspring places a population at a disadvantage relative to other, competing species. "Thus we would have the spectacle of all organisms enslaved to a terrific murine fecundity, dedicating all their available strength to the production of offspring, even though the great majority of these progeny are not needed to preserve the population of the species at a constant level, and are destined merely to fill the maws of predators or to starve in the lean seasons" (p. 432).

At stake was nothing less than the principle of evolution by individual selection, and Lack (1949) was quick to respond to Skutch's challenge: ". . . I consider that tropical birds (as well as others) raise not only all the offspring that they need, but also all that they *can.*" Resolution of such differences of opinion should come from empirical and experimental evidence. Skutch offered observations that parents normally did not search for food continuously and that they increased food delivery to the nest in response to increased demand. Lack countered by pointing out that the rapid recovery of the population of the Gray Heron *Ardea cinerea* after a severe winter "shows that [the normal] clutch-size is sufficiently high for a rapid increase to be possible" (Lack 1947, p. 317). How could this be true if birds did not normally produce an excess of young? "Ultimately," Lack said (1949, p. 458), "one comes back to the question of what really controls bird population density, but to attempt to answer this point one must write a book." In 1954, Lack published his classic book, *The Natural Regulation of Animal Numbers,* which further explained his ideas on the evolutionary maximization of clutch size in birds and the density-dependent response of mortality to reproductive rate.

Moreau (1944) had also clearly seen the relationship of reproductive rate to population regulation: ". . . on the long view, the local population of a species is, relatively, so stable it seems certain that clutch-size and the local complex of lethal factors are in mutual adjustment." But in seeming contradiction to the principle that Lack developed three years later, Moreau went on to say that "The availability of food for nestlings is almost irrelevant; at most it would fix an upper limit to the brood that could be reared and, conceivably, by adaptation, an upper limit to the size of the clutch. But within this limit the food factor could not by itself determine the size of the clutch" (p. 30). It is evident from Moreau's paper that he understood not only the principle of evolutionary optimization of clutch size to maximize individual fitness, but also that many considerations might lead to an optimum clutch size smaller than that set by the food supply. Not unexpectedly, Lack (1949, p. 319) considered Moreau's position contrary to the principle of evolution by natural selection based on individual fitness: "In my view, the part of this [Moreau's] quotation beyond the semi-colon, so far from being irrelevant, is the essence of the whole matter. Only the upper limit of clutch-size requires serious discussion. As remarked before, if clutch-size is inherited and if other things are equal, those individuals laying larger clutches will come to predominate in the population over those laying smaller clutches. . . . [That is,] *in nidiculous species, the average clutch-size is ultimately determined by the average maximum number of young which the parents can successfully raise in the region and at the season in question. . .*"

According to Lack, Moreau had implied that clutch size, or more generally reproductive rate, was adjusted to balance the adult mortality of the population. In fact, Lack had misinterpreted Moreau's views, perhaps because of his own narrow perception of individual fitness. Moreau argued, as did Lack and Skutch, that reproduction and adult mortality must be balanced in a population whose size remained constant. Where Moreau and Lack differed is summed up in Lack's words "and if other things are equal." Lack felt they were; Moreau suggested that populations might differ in many ways beyond food availability that could result in reduced clutch size in response to selection on attributes of individuals.

From Lack's narrower viewpoint, Moreau's ideas were contrary to Darwinian principles, which were based on the maximization of individual fitness. Again, in Lack's words (1947, p. 318), "Another strong argument against the view advocated by Stresemann, Rensch, and Moreau, is the extreme difficulty of seeing how natural selection could act on clutch-size so as to bring about its alleged adjustment to total mortality." (An alternative, that food availability, and thus clutch size, is adjusted to adult mortality through population density feedbacks was formalized by N. Philip Ashmole [1963].)

Moreau himself did not subscribe to the views of Stresemann and Rensch, which he referred to as "teleological explanations" and "unsupported speculations." Nevertheless, Moreau sometimes projected an appearance of non-Darwinian thinking with a number of ambiguous statements, such as ". . . it is far from certain that the bigger clutch is always more to the "good of the species"—which I take to be the maintenance or increase of the population" (p. 309) and "The fundamental assumption is made that natural selection ensures that clutch-size is adapted to provide the best brood-size with the minimum of wastage" (p. 310). Moreau did not specify whether the wastage is that of the individual or that of the population, but implied that it is somehow to be avoided. As Skutch (1949, p. 448) put it, "The principle of acquiring the greatest benefit through the least effort appears to hold in biology no less than in political economy." Lack, of course, felt that effort and wastage—overproduction of offspring—were natural consequences of selection to maximize individual fitness.

Lack and Moreau both clearly saw the intimate connection between life histories and population regulation. Lack viewed evolutionary forces as somehow predominant, with ecological forces secondarily taking care of population balance in the end. Lack (1949, p. 456): "I further consider that population density is primarily determined by the operation of density-dependent mortality factors (*i.e.,* factors whose proportionate effect increases as the population density rises) and that such factors produce the apparent stability of many bird populations." Thus, selection maximized reproductive rate, which then resulted in density-dependent feedback on survival to regulate population growth and balance population size.

Lack's publications in the 1940s, and subsequent books that developed these topics further (Lack 1954, 1966, 1968), firmly established two principles: the adaptive modification of life histories by natural selection and the role of density-dependence in the regulation of population size. Both principles were hotly contested at the time, the first by Skutch (1949) and later by Wynne-Edwards (1962), and the second by Andrewartha and Birch (1954). In spite of Lack's seminal contributions to many issues, these major battles appear to have made Lack dogmatic and inflexible on the issue of life-history evolution. Eventually, Lack's monolithic idea that the reproductive rate of the individual is maximized by natural selection was replaced during the 1960s by a broader concept of optimizing the allocation of time and resources among many attributes of life history that contribute to individual fitness.

What is remarkable about the papers of Lack, Moreau, and Skutch published during the 1940s is that they clearly stated most of the basic ideas about life-history evolution, albeit not in quantitative terms. It was not until the 1960s that ecologists, including, for example, Cody (1966), Williams (1966), Gadgil and Bossert (1970), and Pianka (1970), began to re-evaluate these ideas with new analytical techniques developed primarily by North American population biologists (e.g., Cole 1954, Levins 1962, MacArthur 1962, Lewontin 1965). Issues such as trade-offs involving fecundity and survival, predation-rate limitation of clutch size, the effects of environmental variability on life-history evolution, and r- vs. K-selection were articulated by Moreau and Skutch. For example, Moreau (1944, p. 309), referring to within- and between-season trade-offs between fecundity and survival, wrote: "It is possible, for example, that B/5 [a brood size of 5], at least in some circumstances, might put a significantly bigger strain on the parents than B/4, so that they were prevented from raising a larger total number [than] the product of the smaller broods in the same season; or that a succession of B/5 would so shorten the reproductive lives of the parents that their total of offspring, produced in smaller, less exacting broods, would be greater." Concerning the possibility that nest predation could select for smaller brood size, Moreau (1944, p. 309) stated, "Again, a greater abundance of helpless or inexperienced young may induce, not a proportionately, but a disproportionately, greater attention from predators." Skutch (1949, p. 434) later echoed the same idea when he said, "A possible advantage of small broods and infrequent parental visits to the nest is the smaller likelihood of betraying its position to enemies." Lack (1949) admitted the logic of this last idea, and suggested that it could be tested experimentally: "This point should be studied statistically. It would not be difficult, though it would be laborious, to compare the nesting success for broods of different sizes for various tropical species, to see whether Mr. Skutch's theory is correct" (p. 457). Lack saw no contradiction between this idea and his own. "My general theory is that the normal clutch-size is that which results in the maximum number of young surviving to become parents. Any mortality factor whose effect increases as brood-size rises will handicap larger broods and so will tend to reduce the average clutch size. The amount of food collected by the parents is an obvious factor leading to this result, but Mr. Skutch's suggestion shows that it is not the only possibility" (p. 457).

Moreau showed an appreciation for the challenges of a variable environment when he said (1944, p. 310), ". . . in a climate that is uncertain the effects of a bad season might be more disastrous on bigger broods that were adapted in size to the food supply of the best seasons." In Moreau's mind, these were factors that could, and most likely would, reduce clutch size to an optimum below the maximum that the parents could feed at any one time and "make the availability of food for nestlings . . . almost irrelevant."

Skutch also was flexible enough to see that many factors contributed to the diversification of reproductive rates among species. In one passage, he outlined a basic proposition of r- and K-selection theory: "These years of greatly reduced population furnish the key to our problem [of larger clutches at higher latitudes]. After each such catastrophic reduction, the survivors form an expanding population. . . . Under these circumstances a unusually high proportion of all the young survive to reproduce their kind, and the largest families make the greatest permanent contribution to the population" (Skutch 1949, p. 449). This passage also reveals an understanding of evolution in response to individual selection, but in other writings Skutch shows that this was not a cornerstone of his thinking.

If we accept that many of the seeds of modern life-history theory were sown by Lack, Skutch, and, especially, Moreau during the 1940s, it is worth asking why these did not grow better in the intellectual soil of the time. Why was it that most of these ideas had to be rediscovered, particularly in North America, more than 20 years later before life-history thinking began to flower? I do not pretend to have a definitive answer to this question, but several considerations come to mind. Above all, we must realize that understanding variation in life-history attributes among populations is an inherently difficult problem. Experiments that control all but a single variable are difficult to design and execute; comparisons are complicated by multiple correlations of independent variables and life-history traits and by phylogenetic relationships among sampled populations; empirical data are lacking for key aspects of life histories, such as relative adult survival rates of tropical and temperate birds and the nature of post-fledging parental care.

The concept of life history also has been poorly circumscribed. So-called "life-history" traits include a heterogeneous mixture of adaptations and life-table entries (survival and fecundity rates), which reflect the interaction between adaptations and the environment. During the 1940s, biologists were only dimly aware of the quantitative relationships between life-history attributes and individual fitness and so it was not possible to evaluate qualitative statements concerning the consequences of particular adaptations for individual fitness. These technical issues were accompanied by deeper scientific considerations, as well. The development of life-history thinking was imbedded in the contexts of other important issues. During the 1940s, biologists were struggling with the fundamental idea that evolutionary responses were driven by selection on individual traits. Even as late as 1961, the paleontologist George Gaylord Simpson was compelled to write an article entitled, "One hundred years without Darwin are enough" (Simpson 1961). For Lack, the idea that clutch size evolved to maximize individual fitness was more important than the connections between reproductive rate and other life-history traits. The opposing arguments of Skutch, and later Wynne-Edwards (1962), focussed the debate on basic issues of evolution rather than life history. Similarly, during the 1950s, Andrewartha and Birch's ideas about the regulation of populations shifted attention away from the role of density-dependence in shaping life histories and stimulated a strong defense of density-dependence as an intrinsic property of population processes (e.g., see Smith 1961).

Perhaps the most important consideration in the early development of life-history thinking is connected with the human side of scientific endeavors. Lack was a visionary who held his beliefs strongly and argued them effectively. For the most part his insights were brilliant and, projected through his strong advocacy and productivity, fostered the most influential work in ecology in the middle third of the twentieth century. By contrast, Moreau's work shows a more reflective approach to science in which alternatives are considered and ideas take on the weight of supporting evidence rather than logical status. Referring to the several means by which clutch size might be influenced, Moreau (1944, p. 310) said, "The foregoing arguments are hypothetical. Of course they do not exhaust the possibilities, and in our present state of knowledge they are no better than specimens of the inconclusive discussion that can take place around this problem; but they do serve to emphasize its complexity, to show that the availability of food for the nestlings is not likely to be a prime factor in determining the size of the brood that may be standardized by natural selection as the normal, and to show how brood-size and mortality rate may interact with each other."

Until the mid 1960s, however, Lack's influence was so pervasive that the insights of Moreau and Skutch had largely been obscured. In the introduction to a 1966 paper on clutch size, the first to challenge the dogma largely created by Lack, Cody (p. 174) said, "Lack (1954) discusses the validity of several hypotheses . . . all of which were rejected in favor of his now widely accepted theory that clutch size is adapted to a limited food supply. This paper is an attempt to show that this and other existing hypotheses when taken singly are inadequate in some respect to account for all the data . . ."

The study of life histories is at present a complex and sophisticated field of endeavor, with a wealth of ideas, empirical natural history, and experimental approaches. The tremendous energy of this discipline is sufficient indication of the strength of the central paradigm of evolutionary optimization of constrained phenotypes. Hindsight, however, offers a sobering view of our progress in understanding the diversification of life histories, and how science works in general. Real movement in science depends on two key ingredients: the excitement and anticipation generated by new approaches and compelling new ideas, and the direction offered by reflective consideration of alternatives. During the 1940s, at the beginning of the scientific consideration of life histories, these ingredients were embodied by David Lack, on one hand, and by Reginald Moreau and Alexander Skutch, on the other. Lack carried the day. This was at the same time a glorious victory for certain powerful concepts and a sad loss for untested alternatives. The best science achieves a balance between conviction and reflection. In contemplating the diversity of life histories, we are studying an immensely complex phenomenon. All facets of our efforts to understand this phenomenon, including our basic foundations of natural history and theory, must be constantly re-examined and re-evaluated to balance our tendency to adopt seductive paradigms and approaches. These are engines that power science; reflection is needed to provide direction.

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