HUNGRY CHICKS AND MORTAL PARENTS: A STATE-VARIABLE APPROACH TO THE BREEDING SEASONS OF BIRDS

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We here report the results of a dynamic programming model of the breeding season of a bird, patterned after the Black-capped Chickadee (Parus atricapillus) nesting near Ithaca, New York. Optimal breeding seasons fall largely before the peak in food distribution, and this shift appears to be because peak metabolic demands of the brood are coordinated with the peak in food density and because the risk of adult mortality selects for earlier breeding than would otherwise be favored. This latter effect, first proposed by Fisher, may explain the nearly universal observation that early breeding appears to be favored in birds from a wide range of habitats and phylogenies.

Introduction. The time of breeding in birds has long been of general interest to biologists. Charles Darwin (1874, pp. 215–218) collected together data showing that more vigorous females breed earlier. He developed the implications of this observation for his theory of sexual selection, and Fisher (1958, pp. 153–155) provided a numerical elaboration of this idea. Price et al. (1988) recently carried this line of theoretical research forward by exploring how directional selection can appear to act on breeding date without actually causing a shift in the trait’s distribution and by showing how the “Darwin–Fisher” hypothesis could be expressed in quantitative genetic terms (Kirkpatrick et al., 1990). This interest in breeding time has largely concentrated on the consequences of individual breeding times relative to a population-level distribution, rather than the ecological factors affecting the population’s mean.

This latter topic has been pursued by ornithologists asking questions about how and why a breeding season occurs when it does. Baker (1938) cast this

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question in general terms, introducing along the way the now-venerable distinction between proximate and ultimate causes of organisms' features. Since then, studies of the proximate mechanisms of breeding-season determination have contributed an enormous amount to our understanding of the endocrine and reproductive systems of birds (e.g. Murton and Westwood, 1977), and we have learned a great deal more about the ultimate factors that appear to have shaped the timing of breeding seasons (e.g. Perrins, 1970, 1985). The environmental factors to which breeding seasons are most often thought to have evolved are food supply and safety from predators (Perrins, 1985), but several other features of the environment, i.e. daylength and temperature, seem likely to be important.

To weigh the potential importance of daylength, temperature, food supply and predation, we developed a dynamic optimization model for the timing of breeding of birds in temperate environments. We here describe the model and its results and discuss their relevance to our understanding of breeding seasons.

The Model. The optimal time of breeding is determined by comparing the fitnesses of parents that fledge their offspring on different days relative to environmentally dictated cycles in daylength, temperature and food supply.

The breeding-date optimization is a two-step process. Within the annual cycles of parents of each breeding-date phenotype, optimal parental allocations to parental care and self-maintenance are determined by a dynamic program, which also keeps track of the expected fitness of each of these parental phenotypes on any given calendar day. The fitnesses of the various phenotypes differ because they are at different stages of their annual cycles on any given calendar day, and the environmental favorability for these various biological activities varies accordingly (Fig. 1).

The second step in the optimization of breeding dates merely involves comparing the prospective fitness of each of the breeding-date phenotypes on a given calendar date in advance of the breeding season and choosing the breeding-date corresponding to the phenotype with the highest prospective fitness. We compare fitnesses on a date in advance of breeding by any of the competing phenotypes because expected fitnesses change dramatically once breeding has begun. Comparing all phenotypes in the pre-breeding season thus yields a more stable indication of their expected fitness and best mimics the reproductive decision that breeding birds are likely to face in spring.

Each breeding-date phenotype has an annual cycle (assumed, for convenience, to be 360 days in length) of activities in which an adult bird is engaged, and we have arbitrarily defined the final day of each of these cycles as the date on which a parent's offspring fledge. Fledging can occur on any day in the Julian calendar (also assumed to be 360 days long), depending upon the bird's timing of breeding (Fig. 1). Breeding is assumed to require 5 days for nest-