Preface

An important thrust of ecological theory concerns itself with models whose predictions are derived from Darwin's theory of natural selection, the most general of all models of adaptation. The theory of natural selection in its general form is of limited usefulness, however, in explaining most specific cases. What is required is a series of models of intermediate generality which provides sharper foci into the mode of operation of natural selection upon specific traits. The way in which these models differ from those concerned with dynamics of populations has been clearly stated by Lack (1954a, pp. 4-6). In Lack's terminology models of adaptation concentrate upon the *ultimate factors* which have led to the evolution of attributes presently exhibited by organisms. In contrast, models of population dynamics take the attributes of individuals (or populations) as given and analyze their consequences for short-term fluctuations in response to environmental perturbations. Lack has termed this approach a *proximate factor* approach. Elsewhere (Orians, 1962) I have presented an argument for the importance of this distinction for understanding many of the controversies which have been so characteristic of the history of ecology.

It is clear that both approaches have contributed much to our understanding of ecological systems, and both continue to be employed for appropriate purposes. For the most part, adaptive models are of recent origin, and though theoreticians have dealt with these kinds of problems only a short time, testing of the models already lags behind. It is important that empirical verification or falsification of theories about adaptations be carried out in conjunction with their formulation if theoretical developments are not to deviate excessively from reality. In addition, since these ideas provide powerful bases for the development of predictive ecological theory, they are of immense practical as well as theoretical importance.

Models of natural selection are of two general sorts. One type predicts the behavior and/or morphology of individuals. These are essentially individual optimization models, and they make no assumptions other than the operation of classical Darwinian selection. Their concern is with which phenotypes should be most fit in certain kinds of environments. The second type may be termed population models in which statistical properties of populations are predicted. Some of these models follow directly from models of individual fitness or kin selection, but others require the operation of interdeme or group selection (Williams, 1966). The properties and problems of these models of selection have been reviewed by Hamilton (1964), Maynard Smith (1964) and Brown (1966). The real problem is to find methods by which the action of interdeme and group selection can be identified in the field. The easiest method would presumably be to deduce demonstrable consequences of interdeme or group selection. In practice, however, this is extremely difficult because unambiguous predictions from these theories are not easily made. Moreover, there are many traits which can be explained by group or interdeme selection but which are also open to explanations from Darwinian selection (Williams, 1966). In these cases the predilection of the observer normally dictates which explanation is favored.

In the present study I attempt to test models that predict four types of characteristics of individuals: habitat selection (Levins, 1968; Fretwell and Lucas, 1969), foraging behavior (Charnov, 1973, 1976a, b; Charnov, Orians, and Hyatt, 1976; Emlen, 1966; Krebs, Ryan, and Charnov, 1974; MacArthur and Pianka, 1966; Schoener, 1971); territoriality (Brown and Orians, 1970; Fretwell and Lucas, 1969;

Orians and Willson, 1964), and mate selection (Orians, 1969, 1972). The varied social systems of blackbirds and the structural simplicity of their foraging environment make some aspects of all of these models testable in the marshes of western North America.

The book is organized into an introductory chapter describing my study systems, a chapter describing the resource base supporting breeding blackbirds in western North America, two chapters dealing with adaptations of blackbirds to these resources (Habitat Selection, Foraging Behavior), two chapters on patterns resulting from these adaptations (Variability in Use of Resources; Competition, Overlap and Community Structure), a chapter presenting comparative data on Argentine marshes and blackbirds, and a final chapter examining the structure of marsh bird communities in a more general perspective.

Throughout I use theory in two distinct but complementary ways. One is the familiar practice of designing tests of theoretical constructs that allow rejection or provisional acceptance of their validity. The other is to use theory as a means of gaining insights about what should be examined in nature. It will become evident that this second use of theory has been more important in my studies because available theories concerning the ecological traits I examined are highly simplified and are not readily tested in the complex, uncontrolled field conditions in which I worked. Even if blackbirds are behaving in accordance with theory, the observable patterns will be modified by factors not included in the theory; results, therefore, are open to several interpretations. Nonetheless, during the project, theories repeatedly suggested measurements I would not otherwise have thought of, so that my overall understanding of adaptations of blackbirds has been substantially improved.

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