reviews

Territoriality and adaptation

Jared M. Diamond

Evolutionary Ecology. Edited by Bernard Stonehouse and Christopher Perrins. Pp. vi+310. (Macmillan: London, 1977.) £12.95.

THE late David Lack was a distinguished ornithologist noted for his pioneering evolutionary studies of ecological problems, such as ecological segregation among species, population regulation, territoriality, and reproductive rates. The present volume (not to be confused with the textbook of the same title, by Eric Pianka) consists of a collection of 21 chapters on topics related to Lack's interests, by former students, colleagues, scientific adversaries, and workers whom he influenced at a distance.

The chapters are grouped into four sections. The first five chapters discuss population regulation and territoriality, as illuminated by red grouse (A. Watson), wild rabbits (J. A. Gibb), and great tit (J. R. Krebs), or by controversies that pitted two of the authors (V. C. Wynne-Edwards and D. Chitty) against Lack. Next come four chapters that explore feeding adaptations and ecological segregation in Galapagos seabirds (M. P. Harris), marine Pelicaniformes (J. B. Nelson), seed-eating rodents (M. L. Rosenzweig), and common terns (I. C. T. Nisbet).

The longest section, on breeding adaptations and reproductive rates, consists of eight chapters discussing: arctic geese (I. Newton); great tit (H. N. Kluyver, J. H. van Balen, and A. J. Cavé); cooperative breeding among birds in general (C. H. Fry) and Argentine blackbirds in particular (G. H., C. E., and K. J. Orans); and clutch size in birds (D. F. Owen, C. M. Perrins and R. E. Ricklefs) and in the plant family Compositae (D. A. Levin and B. L. Turner).

The book concludes with four miscellaneous chapters, grouped under the heading of evolutionary adaptations, on systematics of echolocating swiftlets (Lord Medway and J. D. Pye), male group displays in *Chiroxiphia* manakins (D. W. Snow), animal communication systems (A. Zahavi), and big-bang reproduction in yuccas and agaves (W. M. and M. V. Schaffer).

To produce a memorial volume written by 21 different authors or sets

of authors, spanning a wide area of population biology, short enough to sell at a reasonable price, and of high scientific interest is at best a difficult task. The conflicting requirements of these goals weaken the book. Chapters average a frustratingly brief 12 pages in length. This prevents each chapter from giving a major overview of a field or exploring one problem in satisfying detail. The diversity of the content, and the paucity of cross-references between chapters, prevent the volume from developing a 'critical mass' on any single subject except nesting biology. Chapters vary considerably in level of insight. Some good chapters, such as those by Krebs and by Medway and Pye, seem to be so unrelated to the rest of the book that they would have been more effective if they had been published separately as journal articles.

The brevity of chapters is especially unfortunate because population regulation and reproductive rates are complexly determined by multiple factors, the relative importance of which varies with circumstances and with species. In the past, these subjects have often been approached in single-factor, single-species treatments, leading to running controversies that retarded progress. The sections on these two subjects would each have profited from a lengthy chapter synthesising the major factors into an overall scheme, reviewing each factor in detail, and giving examples of species or circumstances where each is important, to place the following chapters in perspective. Overall, I feel that this volume would have been more effective if it had focussed on a narrower span of population biology and consisted of fewer, longer chapters.

These remarks about the book as a whole do not detract from the interest of some chapters taken individually. Three examples must suffice. Watson reviews experiments and observations on the role of territoriality in Scottish red grouse. Between August and November of each year, males establish territories, and females pair with territorial males. The territory provides its owners with exclusive access to food in winter and spring, when food is scarcest and females are forming eggs. Most non-territorial males and unmated

females die of predation or of food scarcity by May. If territorial birds are shot, non-territorial individuals take over the territory, survive well, and breed. Brood size is determined in part by food supply mediated by egg quality formed by females: artificially fertilising the heather results in large broods. Implanting androgen hormone pellets in males makes them more aggressive, and results in their acquiring territories if initially non-territorial or enlarging territories if already territorial.

Newton discusses the extreme set of breeding adaptations that Arctic geese have evolved in response to the short summer. The geese arrive from their southern wintering grounds mated, the females fertilised and ready to lay within a week. Until eggs hatch, the adults survive mainly on fat and protein reserves laid down at wintering and migration areas, and they lose 17–50% of their initial weight. Number of eggs per clutch is greater for early-season clutches or in years with early snow melt. Breeding success varies enormously among years, so that the contribution of young birds to the autumn population may be as low as 1% or over 50%.

Zahavi illustrates the costs incurred by animal communication systems to achieve reliability and minimise cheating. Baby birds beg food from parents by displays that attract the parents' attention but could also attract predators. This risk 'blackmails' the parent into bringing food but inhibits fed nestlings from begging without cause and thereby diverting parents from unfed siblings. Arabian babblers live in groups which jointly defend a territory but of which only one, dominant pair breeds. The dominance hierarchy is maintained not by constant fighting but by a superficially altruistic display: dominant birds offer food to subordinates. That this display represents a dominance manoeuvre rather than altruism becomes clear when a subordinate individual offers food to a dominant one: this constitutes an act of rebellion and immediately provokes a fight. □

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