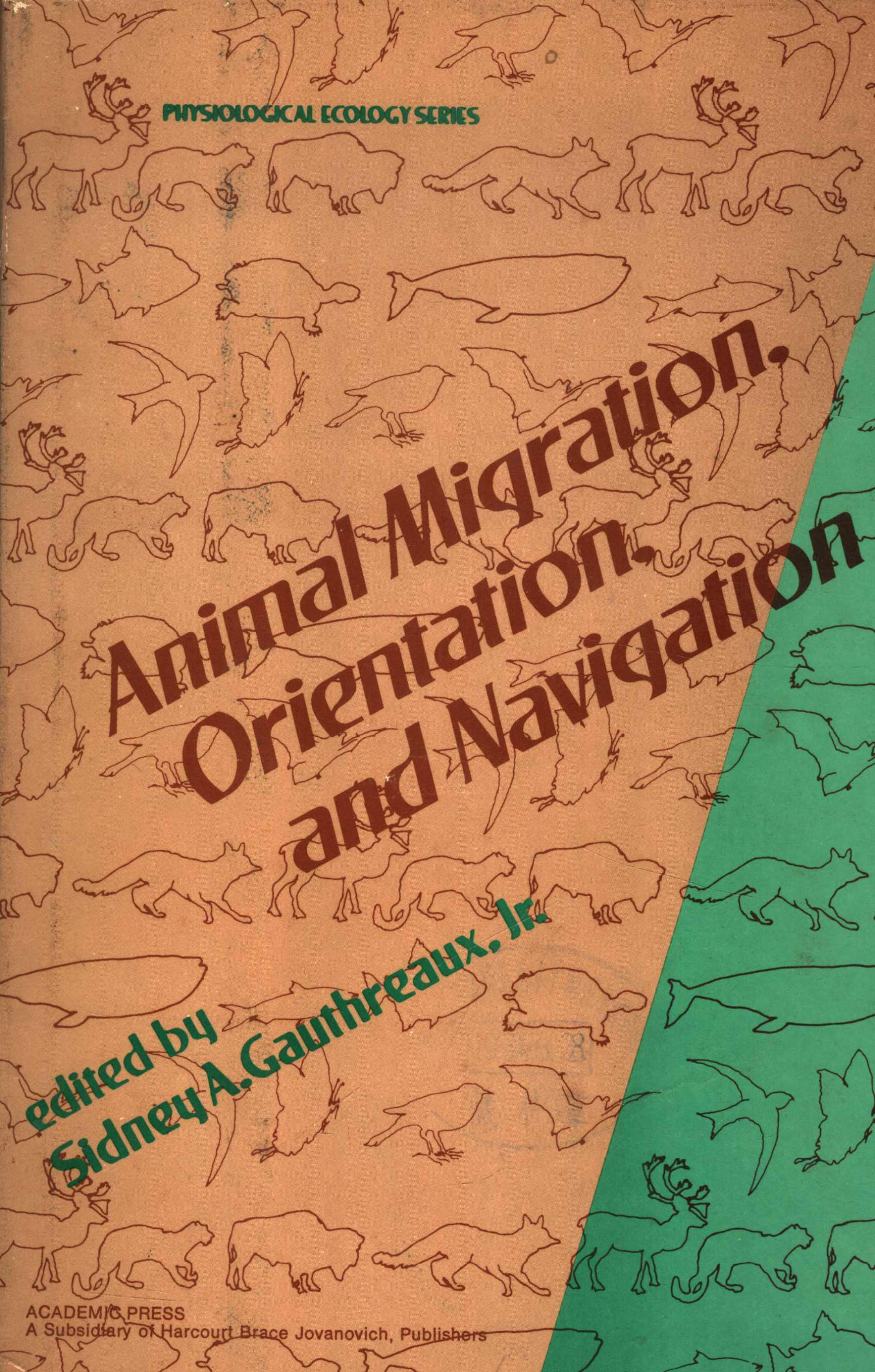

PHYSIOLOGICAL ECOLOGY SERIES

Animal Migration, Orientation, and Navigation

edited by
Sidney A. Gauthreaux, Jr.

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Preface

From the outset, the organizational plan for this volume was to be different from those published previously. Most books on animal migration have chapters devoted to a particular taxonomic group, and within a chapter various aspects of migration are discussed. In this volume the chapters are arranged by major aspects of animal migration, and within a chapter information from diverse taxonomic groups is included. In this way similarities and differences are more apparent.

Seven aspects of animal migration are included: evolution of migration, climatic and meteorological influences, biological clocks and phenology, bioenergetics, physiological control, sensory systems, and orientation and navigation. The biological clocks and phenological aspects are integrated in the chapter on climatic influences and the sensory aspects in the chapter on orientation and navigation.

In Chapter 1 on the evolution of migration, Hugh Dingle provides a summary of the migration strategies of animals in the context of a time, space continuum. His efforts demonstrate clearly the importance of migration to the study of population biology and evolutionary ecology. Continuing this approach in Chapter 2, I examine the influence of long- and short-term climatic cycles on the spectrum of migratory patterns found in nature, from biogeographical migrations to the diel migrations of planktonic organisms. Charles Blem covers the bioenergetics of animal migrations in Chapter 3 in terms of the cost of transport, the energetic requirements of various migra-

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tion strategies, and the energy stores of the migrants. His efforts to integrate his topic with those covered in other chapters is very successful. In Chapter 4 Albert Meier and Albert Fivizzani discuss the physiological basis of animal migration, paying particular attention to the recent endocrinological findings on the timing and energetic aspects of various migration strategies. They also cover some of the developments that concern the physiological basis of migratory orientation. In Chapter 5, the last in the volume, Kenn Able does a thorough job of examining the array of mechanisms used in direction finding by migrating animals and the sensory systems that are essential to the orientation mechanisms. Although these authors had little or no collaboration during the preparation of their chapters, the final results of their efforts mesh together surprisingly well.

This volume would not have been completed without the kind, yet forceful encouragement of the series editor, T. T. Kozlowski. During the initial phases of planning his advice was indispensable. Much the same can be said for the staff of Academic Press, whose patience toward the end deserves some form of special recognition. My gratitude to my wife Kay and my children David and Renee is hard to express. They were very understanding of my long hours at work and my frequent distractions from family affairs. My final thanks go to my colleagues who so graciously agreed to contribute a chapter to this volume. Without their efforts, this volume would not have been possible.

Sidney A. Gauthreaux, Jr.

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SIDNEY A. GAUTHREAUX, JR. (Ed.), Animal Migration, Orientation, and Navigation

In preparation

F. JOHN VERNBERG AND WINONA B. VERNBERG (Eds.), Functional Adaptations of Marine Organisms

ANIMAL MIGRATION, ORIENTATION, AND NAVIGATION

Most of the books that have been written on animal migration treat different taxonomic groups in separate chapters, and within a given chapter cover the various aspects of migration. In this volume the reverse is true. Separate chapters are devoted to the various aspects of animal migration, and within a given chapter the pertinent information on various taxonomic groups is included. By organizing the volume in this manner proper emphasis is placed on the different aspects of animal migration and comparisons between taxonomic groups are facilitated.

The aspects of animal migration treated in this volume include: ecology and evolution, climatic influences, energetics, physiology, and mechanisms of orientation, navigation, and homing. The first chapter considers migration in relation to current ecological and evolutionary theory and emphasizes the important role of migration in life history strategies. The second chapter covers the influence of long-term and short-term climatic factors in shaping the temporal and spatial patterns of dispersal and migration, and the energetics of migration, particularly the energy reserves and the energetic costs of migration, are reviewed in the third. The fourth chapter treats the physiological mechanisms that direct preparation for and adjustment to migration. The fifth and final chapter emphasizes the diverse mechanisms that animals use in finding their way during migratory journeys.

The coverage of the various taxonomic groups in each chapter is exhaustive (from the daily vertical migrations of planktonic organisms to the biogeographical migrations of animals in response to glacial cycles), and one can begin to appreciate the diverse migratory responses that organisms show to the spectrum of environmental changes in space and time.

Jacket designed by Al Green

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POPULATION DYNAMICS

Alternative Models

BERTRAM G. MURRAY, JR.

A Volume in the PHYSIOLOGICAL ECOLOGY Series

1979, 224 pp./ISBN: 0-12-511750-7

This volume establishes a foundation for a new paradigm of thought on population dynamics. Although explicit models for describing population phenomena are emphasized, empirical data are also presented. The quality of the models is evaluated with respect to those proposed by others, and areas in need of research are considered.

CONTENTS:

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Contents

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2 The Influences of Long-Term and Short-Term Climatic Changes on the Dispersal and Migration of Organisms

Sidney A. Gauthreaux, Jr.

3 The Energetics of Migration

Charles R. Blem

4 Physiology of Migration

Albert H. Meier and Albert J. Fivizzani

5 Mechanisms of Orientation, Navigation, and Homing
Kenneth P. Able

1 *Ecology and Evolution of Migration*

HUGH DINGLE

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I. The Phenomenon of Migration and Some Problems of Definition

Since antiquity people have been aware of animal migrations. Frequently this was because migrants profoundly influenced livelihood. For example, locust plagues are mentioned in the Bible (Genesis and Proverbs), northern groups have depended on the seasonal appearance of marine (Eskimos) or terrestrial (Amerindians, Lapps) mammals, coastal Amerindians have fished for salmon, and African tribes have followed the wet and dry season movements of large ungulates. Yet knowledge of migrations, especially of birds and butterflies, was not always based on practical considerations. The beauty of these organisms and their spectacular movements have excited both curiosity and artistic responses. Bird migrations were known to both Aristotle and Homer and the flights of birds and butterflies are featured in English poetry from the Elizabethans to the present.

Because of these readily observed and spectacular movements both popular and scientific views of animal migration have incorporated long distance return movements. Thus return movements were established early on by vertebrate biologists as the criterion for "true migration" (Landsborough Thomson, 1926; Heape, 1931). Landsborough Thomson described true migrations as "changes of habitat, periodically recurring and alternating in direction, which tend to secure optimum environmental conditions at all times" (1926, p.3). Because return movements were unknown except in rare instances, insects and most mammals were specifically excluded. Later authors (Heape, 1931; Dorst, 1962; Harden Jones, 1968; Orr, 1970) have adopted similar definitions often emphasizing a distinction between migration and other movements. These latter were referred to as "emigration," "nomadism," "passive dispersal," and the like (Heape, 1931; Williams, 1958).

More recent study of a number of organisms, especially insects and zooplankton, has revealed movement patterns which, although they do not involve round trips, have the same function as so called true migrations. That is, they allow exploitation of different habitats as life history requirements alter or as environments change seasonally or successionally. Often these movements are "on the whole a rather quiet, humdrum process . . . taking place all the time as a result of the normal life of the animals" (Elton, 1927), but some are spectacularly dramatic like the movements of migratory locusts. Movements of awkward, fragile organisms like aphids or plankton were considered even by entomologists or marine biologists to involve passive transport by winds or currents (Williams, 1958; Hardy, 1958).

Even apparently weak and fragile organisms, however, are active participants in the migration process. An excellent example is the black bean aphid (*Aphis fabae*) (Kennedy, 1958 et seq.). Like others of its kind, this species has a complex life history involving alternation of winter sexual and summer asexual generations on different host plants (Dixon, 1973). Kennedy focused on the asexual summer generation which arises from the wingless offspring of spring migrants to young bean plants (*Vicia faba*). These parthenogenic females produce wingless young viviparously until crowding occurs or the host plant senesces; in these cases winged offspring are produced which migrate to a new host, settle, lose the wings, histolyze the wing muscles, and produce wingless young parthenogenically.

The entire sequence of flight and settling involves a discrete series of events. The aphid climbs to the top of the plant and takes off, being attracted at this time to blue light (Kennedy *et al.*, 1961). After a period of flight, the individual becomes sensitive to yellow wavelengths reflected from leaf surfaces and descends to search for a suitable host plant. If one is found, settling and larvaposition ensue. By experimentally manipulating host plants encountered by free-flying aphids in a laboratory flight chamber, Kennedy demonstrated that stimuli evoking flight inhibit settling and vice versa. The two behaviors also have complex effects on each other. Depending on the respective excitatory states, one can get antagonistic induction or rebound where inhibiting say flight by settling stimuli results in even greater amplitude when flight stimuli are again presented, or antagonistic depression with the opposite effect. Once airborne, direction of flight is determined by the wind, but duration is under control of the aphid. In many insects, e.g., locusts (Rainey, 1976, 1978), there is behavioral orientation specifically so that migrants are carried downwind. In sum, rather than being haphazard vagabonds at the mercy of the vicissitudes of weather, aphids and other insects have evolved highly specialized behavior to become airborne and to settle and colonize when migration is complete.

So too, have responses to specific stimuli evolved in the larvae of benthic marine organisms to ensure entry into the plankton. An example occurs in the larvae of the stomatopod crustacean *Gonodactylus bredini* (Dingle, 1969). These animals live in rock cavities in the marine littoral. The eggs are laid in the cavities, and the females show considerable maternal behavior (Dingle and Caldwell, 1972). The larvae when hatched remain with the female for three stadia; at this time they are negatively phototactic and strongly thigmotactic, clinging to the sides of the chamber. Virtually at the instant of molt to the fourth stadium, they cease to be thigmotactic and become positively phototactic, responses that take them out of the cavity and into the plankton. At the time of the molt to the postlarva, they again become thigmotactic and settle out to seek shelter in the interstices of the substrate. A similar sequence of behavior is common to other marine invertebrates with planktonic larvae. In a survey of 141 species Thorson (1964) found that the larvae of 82% respond photopositively and migrate to the surface early in life and that most become photonegative when they metamorphose to bottom-dwelling adults.

Some seasonal movements of birds also do not fit classical concepts of true migration. Perhaps the best known example is the red-billed Quelea (*Quelea quelea*) in East Africa (Ward, 1971). These birds migrate at the beginning of the wet season to areas where the rains began some weeks earlier; distance, timing, and direction of movement are dependent on the timing of the rains and the movement of the rain front. During the return from this "early-rains migration" aggregations of individuals stop to breed at suitable locations. Breeding is often repeated, and a given female may produce successive broods in the same breeding season at sites far apart. This "breeding migration" with "itinerant breeding" is apparently an adaptation to an extreme wet–dry seasonal cycle and may occur in other bird species as well (Serventy, 1971).

What is apparent from all these organisms is that, no matter how undramatic or dramatic migrations may be, they involve specialized behavior. This behavior differs from locomotory behavior occurring during the course of other life history events. Thus many birds exhibit *Zugunruhe* or migratory restlessness during the night at a time when they would usually sleep, aphids produce wings and respond to blue wavelengths of light, spiders balloon on long threads, and benthic marine organisms become photopositive in contrast to later photonegativity. Even those species which drift on air or water currents have some means of getting into those currents and staying there. Our working definition of migration is then as follows: *Migration is specialized behavior especially evolved for the displacement of the individual in space.* This is somewhat broader than the definition I have used before for insects (Dingle, 1972, 1974) which fol-

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