

## REVIEWS

EDITED BY WALTER BOCK

**Avian endocrinology.**—August Epple and Milton H. Stetson (Eds.). 1980. New York, Academic Press. xv + 577 pp. \$34.00. **Biological rhythms in birds.**—Yuichi Tanabe, Katuhide Tamaka, and Takanori Ookawa (Eds.). 1980. Tokyo, Japan Scientific Societies Press, and New York, Springer-Verlag. ix + 373 pp. \$49.60.—These two volumes contain 56 (27 in one, 29 in the other) individual contributions presented as the proceedings of symposia held in Spain and Japan. There is considerable overlap in the subject matter covered as well as in the authors. The volumes will be treated separately first, and comments will be added that are appropriate for both.

*Avian endocrinology* includes a wide range of topics in endocrinology from environmental and neural regulation of hormone secretions to reproductive, metabolic and behavioral activities of hormones. Almost all of the contributors are recognized authorities.

Several papers discuss the roles of circadian and circannual rhythms in regulation of seasonal reproductive conditions. It is generally agreed that the daily photoperiod entrains a circadian rhythm of photosensitivity. If light coincides with the photosensitive phase, as it might do if daylength is sufficient, gonadal stimulation occurs. According to one line of reasoning called an external coincidence model, the coincidence of light with a photosensitive phase directly induces gonadal development by way of responsive photoreceptors and neuroendocrine pathways. The simplicity of this model seems to be its principal asset and at the same time its principal shortcoming. Demonstrations of prolonged gonadal stimulation in photoperiodic birds maintained under constant dark conditions are not easily reconciled with such a model.

An internal coincidence model for photoperiodism proposes that there are two circadian neuroendocrine oscillations that interact temporally to produce complexes of neural and hormonal activities. Changes in the phase relations of these oscillations, which occur on a seasonal basis and as consequences of daylength, cause changes in the complex response produced. In the photoperiodic response, one oscillation that includes a circadian rhythm of photosensitivity is entrained by the daily photoperiod; the other oscillation is coupled to the first in various relations as a consequence of light acting at different phases of the photosensitivity rhythm.

Assenmacher and Jallageas argue that the internal coincidence model may account for many of the conditions that relate to photostimulation. They discuss data that show that metabolic and behavioral conditions are produced by a temporal interaction of hormonal rhythms thought to be expressions of two neural oscillations. Farner and Gwinner, on the other hand, dismiss an internal coincidence model. Their stated reasons are that the model is too complex, that it is unproven, and that their unpublished and unspecified experiments rule it out in White-crowned Sparrows. It seems fair to say that neither model is either proven or disproven and that both will probably need modifications to account for additional information.

Given the demonstrations of important roles for circadian rhythms in photoperiodism and the widespread belief that the pineal is a major circadian pacemaker, one might conclude that photoperiodic regulation of reproduction could not occur in pinealectomized birds. Such is not the case, however. Although Binkley does not pose this anomaly specifically, she does seem to recognize the problem and offers an ingenious solution. She cites evidence that the eyes may also secrete metatonin so that pinealectomy removes only one source of this antigonadotropic hormone. Despite a masterful presentation, the reader will recognize that giant gaps still exist in the integration of pineal research with other kinds of circadian and hormonal studies.

Because much recent work has been done with birds that demonstrates important roles for circadian rhythms in photoperiodism, it would be easy to forget that this relation was first demonstrated, almost 50 years ago, in plants as well as animals. Almost 30 years elapsed from the time of the pioneering work by Bünning until Hamner in 1964 provided a clear demonstration of a similar system in birds, which forced avian workers to abandon their more simplistic models.

Having noted that avian endocrinology has benefited greatly from pioneering research performed in other fields, it may be permissible now to point out some important researches on birds reviewed in this volume that advanced knowledge in other areas as well. One such example not generally appreciated by mammalian workers is the research done on the Bursa of Fabricius. Hormonal aspects relating to this organ are reviewed by Glick, who also did much of the pioneering work. Research on the immunological role of the Bursa greatly increased our understanding of immune systems, not only in birds, but in all other vertebrates as well.

Demonstrations of protein receptors for ovarian hormones in the avian reproductive system greatly advanced our understanding of hormone action at the cellular level. Cell receptors for hormones are discussed in papers by Ishii and by Tanaka. Except for a review of prostaglandin effects on oviposition by Hertelendy, however, there is no consideration of second messengers that transduce hormonal interaction with receptors into cellular activities. This deplorable deficiency is an indictment of the deficiency of such research in birds rather than of the organization of this symposium.

Although not inclusive of all the fine contributions in *Avian endocrinology*, special mention seems appropriate for contributions on calcium regulation by Clark and Simkiss, gastro-intestinal hormones by Hazlewood and by Sitbon and co-workers, and the renin-angiotensin system by Kobayashi and co-workers.

Because this volume contains many worthwhile contributions by recognized authorities, and certainly ranks among the better symposium proceedings in its field, it seems an opportune moment to reflect on the deficiencies of such proceedings in general terms. It is axiomatic that integration is poor. A specialist can learn much from reviews of neural pathways and nuclei for photostimulation and of circadian and circannual variations in hormone concentrations. How this information relates to larger more integrative questions is left mostly to the imagination of the reader. When specialists do attempt to relate their work to the total animal, their efforts often resemble descriptions of an auk by a coterie of blindfolded martians.

To be sure, a determined search can turn up many nuggets of interesting ideas and information that can be used by a generalist to construct images that denote a larger reality. For example, George believes that a sharp increase in secretion of arginine vasotocin may be the trigger for migration, and Ghosh describes a seasonal change in the ratio of norepinephrine/epinephrine secretion by the adrenal. But the reader will have to use imagination in trying to discern a trigger for the trigger or the meaning of a shift in catecholamine ratios. In searching further, the reader may find that epinephrine stimulates the formation of angiotensin II, which prepares the cardiovascular system for increased activity and stimulates release of arginine vasotocin (from review by Kobayashi and co-workers). In turn, arginine vasotocin may be expected to increase memory (of migratory routes and cues?) and mobilize fat reserves for energy (back to the review by George, who is one of the few who tried, with some success, to relate specifics to the general biology of birds). Unfortunately, one must already have a broad understanding of avian biology before he can enjoy this kind of mental gymnastics.

Although the title, *Biological rhythms in birds*, might lead one to believe otherwise, less than half the contributions actually deal with biological rhythms. About one-third of the volume deals with neural and endocrine control of behavior when loosely defined. The remaining papers cover a wide spectrum of biological topics.

Two of the more interesting papers that relate to rhythms deal with sleep mechanisms. Karmanova, the token Russian among six non-Japanese contributors, describes sleep characteristics in vertebrates from an evolutionary point of view. She believes that slow-wave sleep and paradoxical sleep evolved simultaneously as adaptations to the daily periodicity of illumination. Bour and Corner describe the development of sleep mechanisms in chicks from their beginnings *in ovo* until they assume adult patterns several weeks post-hatch.

A group of five papers dealing with egg-laying is perhaps the most useful segment of this volume. Frequent sampling of blood during egg-laying sequences in chickens, ducks, and Japanese Quail reveals that several hormones reach peak levels about 3–6 h before ovulation. The surges of luteinizing hormone and progesterone are set by the daily photoperiod and are thought to be functionally significant in the timing and induction of ovulation.

Neuroendocrine regulation of egg-laying is another area of pioneering research in birds that had fundamental influences in other areas of biology. More than 30 years ago, Fraps demonstrated the existence of a neurogenic stimulus that causes the release of ovulation-inducing hormone (luteinizing hormone) in chickens. Similar findings in mammals were subsequently reported amid great acclaim. Neither the five papers in *Biological rhythms in birds* nor the review by Sharp in *Avian endocrinology* dwell on the historically significant contributions in this field. However, Sharp does provide an especially astute account of the current status of endocrine regulation in the female reproductive system.

Wada (in *Biological rhythms in birds*) presents convincing evidence that a circadian rhythm of reproductive responsiveness to light (photosensitivity rhythm) bears a specific temporal relation (is closely coupled) with a free-running circadian rhythm of locomotor activity. Based on their roles in regulating locomotor activity, Wada concludes that the suprachiasmatic nucleus of the hypothalamus and the pineal, to a lesser extent, are pacemakers for circadian rhythms.

Whether such a generalization is justified depends on whether a circadian rhythm of locomotor activity is an adequate index for other circadian rhythms. Because the rhythm of locomotor activity dampens out

when birds are transferred to continuous light (from Wada), whereas rhythms of oviposition do not (from Konishi), a reader might wonder whether there are too many eggs in one or two baskets.

Radioimmunoassay methodology and materials have been developed for several avian hormones and used for intensive investigation during the last decade. Most attempts to produce satisfactory materials for assay of follicle stimulating hormone (FSH), however, have been unsuccessful. Ishii and Sakai provide a summary of their researches, which characterize the amino acid and carbohydrate compositions of this important reproductive hormone. They outline how they purified chicken FSH and produced an antibody that is highly specific and sensitive. A counterpart for this paper in *Biological rhythms of birds* is one by Goldsmith and Follett in *Avian endocrinology*. Goldsmith and Follett discuss assays of LH, thyrotropin, and prolactin as well as of FSH.

A number of interesting papers are found in the menagerie in *Biological rhythms in birds* that do not rest easily under the general title of biological rhythms. In one of them, Watonabe describes the inter-hemispheric transfer of learning. An interesting phenomenon is that pigeons, trained with one eye to respond positively to a line tilted 135° and negatively to one tilted 45°, responded in an opposite manner when tested with the other eye. Because children and students often display behavior opposite to their training without so much as batting an eye, many parents and teachers may not consider such activity remarkable. Birds, however, are unusual in that they have completely crossed optic chiasmata, so that both eyes must be used in order to transfer impulses to each of the two hemispheres.

Those interested in exotica may enjoy reading about a plebeian counterpart of falconry. Yamashita describes methods of capturing and training cormorants to catch fish for their human handlers.

This book serves the useful purpose of making available some information that we otherwise might not have. But many of the individual contributions are more like abbreviated research papers than thoughtful reviews of existing knowledge. Symposia volumes are unavoidably deficient in focus; this one compounds that problem by including a wide assortment of subjects that have little relation with one another.

We live in an age of hyperspecialization, sustained in part by invitations to present authoritative papers at symposia. More and more is written about less and less until there are a multitude of answers for questions no one cares to ask. Many hotly defended models or hypotheses would not exist at all if more specialists and readers understood the rudiments of biology apart from their own narrow fields.

Those with special interests in the field will especially appreciate the numerous thoughtful contributions in *Avian endocrinology*. Volunteers are needed to assemble the interesting information and ideas provided into broader frames of reference that might entice biologists away from their narrow perspectives.—ALBERT H. MEIER.

**British tits.**—C. M. Perrins. 1979. London, William Collins Sons Co. Ltd. (The New Naturalist Series No. 62). 304 pp., 16 plates, 93 figures. £6.50.—Titmice of the genus *Parus* are a conspicuous element of woodland bird communities of western Europe, and some species are familiar year-around residents of city parks and suburban gardens. Titmice have been the subjects of long-term studies in Britain and on the Continent, and the means by which four or five species coexist during the nesting season have intrigued ecologists for decades. These birds also provide textbook examples of problem solving ("string pulling," the opening of milk bottles). Thus, they are of particular interest to layman and specialist alike, and a natural history of the British species is a welcome addition to the bird watcher's bookshelf.

This book is an outgrowth of studies of titmice initiated in 1947 by the late David Lack. For over 20 years Christopher Perrins has played a major role in those studies, which have been conducted principally in Wytham Wood, near Oxford. The bulk of the text deals with two species, the Great Tit (*P. major*) and Blue Tit (*P. caeruleus*), which are particularly amenable to study by virtue of their abundance, sedentariness, age differences in plumage, and acceptance of nest boxes. Most of the findings have been reported in the literature, but their collection and integration in one volume is a convenience.

In a brief Introduction the titmice are placed in their systematic, distributional, and ecologic setting. Thereafter, a chapter is devoted to each of the species that occurs in Great Britain: the Coal Tit (*P. ater*), Great Tit, Blue Tit, Crested Tit (*P. cristatus*), Marsh Tit (*P. palustris*), and Willow Tit (*P. montanus*). Each account (5–8 pages in length) deals with recognition traits, voice, and molts, and includes maps of British and Eurasian distributions, diagrams of seasonal changes in foraging sites, and a synopsis of breeding habits. The Long-tailed Tit (*Aegithalos caudatus*) is afforded a chapter despite its inability to grasp food with its feet, its closer social ties (group territories, communal winter roosting, nest helpers), and construction of massive domed nests.

There follow in sequence chapters entitled: Ecological differences between species, Home ranges, territories and communication, Food requirements, feeding rates and weights, Feeding habits and irruptions, Breeding biology, Breeding season and moult, Clutch-size and reproductive rates, Growing up and growing old, Population studies, and Of prey and predators. A bibliography of 430 titles (cited in text by number) and an 8-page index conclude the book.

The specializations by which the species of titmice that occur in Europe avoid ecologic overlap are discussed in greater detail than in Lack's survey (1971, *Ecological isolation in birds*, Cambridge, Massachusetts, Harvard Univ. Press). The major focus is on food relations, but nest-site segregation also is considered. Interspecific interactions are accorded considerable significance in the evolutionary shaping of the differences, both morphological and behavioral, among the species.

In the next several chapters the problems that the titmice face in living their daily lives at different seasons are explored. Food shortage is viewed as a recurring hardship. Only when the birds shift to feeding on caterpillars on oak leaves in the late spring (annually) or when beechmast is plentiful in autumn (irregularly) is food considered superabundant. In midwinter an individual may lose 10% of its body weight overnight despite the insulation of its roost cavity, and spend 75–90% of the daylight hours in foraging. Yet the most difficult time may be in late February when food supplies are depleted, a conclusion supported by progressive weight loss even though daylength for foraging is increasing. The emphasis on food is pursued further in a review of Gibb's studies of the Coal Tit, in which bird populations declined through the winter, paralleling the decrease in available invertebrate prey items. Storage of food facilitates overwintering, especially among the conifer-dwelling species of northern Europe. The Great and Blue tits, however, are not known to store food; the numbers surviving the winter in Britain vary with the availability of beechmast. Influx of these two species into southern Europe in some winters is closely linked to failure of beechmast production in more northerly regions.

These topics are developed in a thorough manner, enabling the reader to evaluate the conclusions drawn. In this respect the book is much more than an updating of the chapters on titmice in Lack's "Population studies of birds" (1966, Oxford, Oxford Univ. Press), and the style makes for more leisurely reading. Nothing is glossed over; if data are lacking or a phenomenon is poorly understood, the author so states. His caution in the interpretation of sparse data (e.g. p. 249) is laudable in a book for the general reader. There is a moderate amount of repetition, which gives each chapter a degree of independence.

The timing of the breeding season receives considerable attention. If hatching is to coincide with the peak in abundance of leaf caterpillars, the female must "predict" some 24 days in advance when to lay the first egg. (Some clues are provided in the relationships of the onset of breeding to patterns of spring weather.) The female requires 40% additional energy to produce a clutch, the weight of which, in the Blue Tit, exceeds the female's own weight. The contribution of the male in "courtship" feeding augments his mate's food intake to a significant degree, as food is scarce during egg-laying. That inference is supported by the lower weights of those eggs laid at the beginning of the nesting season. Even with the apparent food limitation at that time, Perrins suggests that the ideal time for first clutches might be still earlier, for leaf caterpillars have diminished in abundance by the time the first broods fledge. Accordingly, survival of fledglings to 3 months of age in British oak woods is higher in early broods than in later ones, and clutch size declines in the small proportion of Great Tits (less than 5%) that attempt second broods. Further, hatching in second broods is asynchronous, but is not so in first broods. Thus, the timing of the breeding season of the Great Tit in Wytham Wood appears to represent a compromise between two alternatives, both food-influenced.

The studies at Oxford have produced a wealth of information on the breeding biology of the Great Tit. For example, prospects for survival of fledglings are brighter if they were hatched early in the season from a clutch of average size, and if their female parent were 2–4 yr of age. Data are available to demonstrate that clutch size in females varies in the same direction as that of their mothers with reference to the mean for the population in a given year. From a hypothetical complement of 8.6 eggs (the long-term mean at Wytham), only 4.8 nestlings will fledge, on the average, because one nesting in every three will be destroyed. Only one of those fledglings will survive to participate in nesting the following spring. The vacancy it will fill results from an annual adult mortality of 44% for males and 52% for females. An interesting finding is that survival improves slightly with age through the fourth year in *P. major*.

The sparseness of the data base for the post-nesting stages stands in sharp contrast to that summarized above, for juvenile Great Tits are difficult to capture before mid-autumn. Much of the 78% mortality of first-year birds occurs within their first post-fledging month. Proportionately more of the juveniles that survived were those that were heavier as nestlings (either from smaller broods or earlier ones). Perrins infers that food must be difficult for them to obtain at this time, for those juveniles that could be recaptured had lost weight progressively. Further, he suggests (p. 171) that learning to locate food may

be critical at this stage, but that explanation could hardly account for the differential losses of lighter birds.

The availability of food for foliage-gleaning birds is exceedingly difficult to quantify in structurally complex, broad-leaved woodlands. Nevertheless, shortage of food alone is unconvincing as a major source of mortality, especially at a time when adults are undergoing an energy-demanding annual molt. (In the last chapter the author implicates *Accipiter nisus* as a very serious predator on newly-fledged tits.)

An alternative explanation for the disappearance of the lighter fledglings might be found in the aggressive behavior that is evident among juveniles. Yet it is discounted as occurring before autumn territorial behavior (largely by adults) commences. Although emigration is acknowledged as a response to encounters with other juveniles, a direct effect of aggressive behavior on the mortality is not conceded. Certainly as those emigrating juveniles move into unfamiliar terrain, their susceptibility to predation must increase. Further, a parallel to Glase's findings (1973, *Living Bird* 12: 235) of sex and age differences in the foraging sites of members of winter flocks of Black-capped Chickadees (*P. atricapillus*) that provide a mechanism for socially-mediated starvation seems applicable to the juvenile Great Tits at an earlier time of the year. [However, Krebs and Perrins (1978, pp. 23–47 in *Population control by social behaviour*, F. J. Ebling and D. M. Stoddart, Eds., London, Institute of Biology) suggest social factors rather than food shortage as the probable explanation for the disappearance of the lighter birds.]

After the first month, survival of fledglings is considerably improved; the reduction in numbers appears constant month-by-month as in adults. The ratio of first-year birds to adults in autumn gives a fair prediction of the level of the next year's breeding population in the Great and Blue tits, especially if beechmast is plentiful. But the survival of adults over winter is rather constant; thus, a decline in the breeding population level in the following spring is largely at the expense of the first-year birds. A high breeding density usually is reflected in a decrease in reproductive output, contributing to long-term fluctuations in numbers. It is the elucidation of the mechanisms by which these fluctuating populations are regulated (i.e. brought back toward the stable state) that has been the focus of the investigations of titmice at Oxford for several decades. The topics in breeding biology and sources of mortality discussed above have been brought to bear on the question of regulation, a quest that sustains the interest of the reader in the later chapters.

Year-to-year changes in territory size have led some investigators to conclude that this activity could limit the number of pairs breeding in an area. Territorial behavior in the Great Tit in autumn may enable older males to re-establish their holdings, but Perrins contends that spring territoriality has not been demonstrated conclusively to have prevented any individuals from breeding. The principal reduction in numbers occurs long before it is manifest. Some pairs are crowded into suboptimal habitats, however, where their prospects of successful breeding are lowered. Nonetheless, Perrins concludes that "... territorial activity results in the spacing out of the birds and this may be its sole function in spring."

Concerning density-dependent factors, Perrins concludes that (p. 252) "... in addition to any effects of territorial behaviour, during at least five stages ... the numbers may be affected by their density; the clutch-size, the proportion of second broods, the number of eggs taken by weasels, the post fledging survival and the winter survival ... ." The third and fourth of these represent a departure from Lack's views (1966, *op. cit.*).

Comparisons to studies of titmice conducted elsewhere in England and on the Continent proved instructive in tempering the conclusions from the Wytham population. The oak woodlands in Britain are atypical in that the interval of abundance of caterpillars is brief. In pine woodlands in Britain and in both woodland types on the Continent the availability of insects is extended, and second broods are more common. On the Continent the titmice tend to be less sedentary, and the bearing of social interactions upon emigration of first-year birds is more evident.

The British counterparts of the North American chickadees are the least investigated of the species reported in this book. Their populations are rather sparse and they seldom accept nestboxes. These traits have influenced ornithologists who have investigated the chickadees in North America to focus upon the same kinds of studies pursued with the Marsh and Willow tits, i.e. social organization (including territoriality), communication, and foraging behavior, usually with color-marked birds. In many instances, late summer has provided the same obstacles that have hindered the investigation of fledged young of the Great Tit at Wytham. In a sense, then, studies of parids on opposite sides of the Atlantic have been complementary.

I found the book remarkably free of errors. The citation for "Smith, S. M. (1972b)" should have read "Smith, S. T. (1972)." Many of the figures will be familiar to students of bird populations. In a few cases graphs might have been extended beyond the date of publication where data surely were available (e.g.

Fig. 75, dealing with the survival of nesting birds to the following year). The bibliography (with citations into 1978) is particularly useful in that it includes references to unpublished dissertations and regional publications.

Christopher Perrins has written a substantial and readable "ecological natural history" of a cluster of species that rank among the better known of the world's birds. As such, the book is a fitting addition to the New Naturalist Series. In addition to serving as a well-indexed reference work, "British Tits" will enhance the reader's appreciation of the rash of studies currently being reported by the Oxford group. Beyond the book, the author is to be commended for his leadership in directing students to investigate topics that extend our understanding of population processes in these well-studied birds.—KEITH L. DIXON.

**Wild geese of the World.**—Myrfin Owen. 1980. London, B. T. Batsford Ltd. 236 pp. Foreword by Sir Peter Scott; eight color plates and illustrations by Joe Blossom, graphs, and maps. £ 15.00.—The true geese consist of 15 species now consolidated into either *Branta* or *Anser*. Gone, for now at least, are "*Philacte*," "*Chen*," or other genera, but the geese, fortunately oblivious to the ways of taxonomy, fly on in their spectacular skeins across northern skies. Bar-headed Geese cruise through oxygen-thin Himalayan passes, Snows flock the Arctic tundra, and Barnacles brave passage across the North Atlantic to Spitsbergen. The diversity of the group is at once both awesome and challenging, but in *Wild geese* Owen presents a thorough treatment that will, I'm sure, become a standard of scholarship for anyone interested in anatids. The evolution of clutch sizes, thoughts on migration mechanics, body condition, and much more of interest are addressed in the pages of this eight-chapter volume.

Chapter 1 is a primer on classification devoted, of course, to the family Anatidae and the true geese. Many North American readers will take issue with Owen's version of Canada Goose classification wherein eight races are recognized. The giant, *Branta canadensis maxima* is merged with *B. c. moffiti*, *B. c. taverneri* is amalgamated with *B. c. parvipes*, and *B. c. asiatica*, ". . . which is either extinct or has always been indistinguishable from *B. c. leucopareia*," is combined under the latter's rubric. But no matter, as I expect that the Canada Goose will keep those on the taxonomic hustings busy for years to come. Owen nonetheless is forthright and his views are clearly stated for lumper or splitter to examine.

In chapter 2 we find well-organized species accounts. These are divided into description (of plumage, etc.), geographical variation, numbers and distribution (accompanied by clear maps), breeding biology, winter biology, and conclusions about exploitation and conservation. For the latter, Owen states, "In some cases there is conflicting information from various sources and in these cases I have selected that which seems most likely to be correct." One might have wished for something less eclectic in a treatment such as this, but I find the conservation notes quite appropriate and, overall, the species accounts of merit.

Chapter 3 initiates the heart of this book. In this and subsequent chapters, Owen integrates the wealth of data available for the World's true geese into comprehensive statements—with a due amount of speculation in some cases. Social behavior marks his beginning point, with units devoted to pair formation, flocking, breeding, and family relationships. This is followed by a chapter on movements and migration and discussions of the factors affecting these and navigation. Molt migration, in particular, receives a thorough examination, but Owen is forced to conclude the obvious, namely that explanations for this phenomenon ". . . are theoretical and have little supporting evidence other than circumstantial."

Summer biology is the next subject. This, of course, is largely devoted to the breeding season, and Owen makes a sincere and successful attempt to bring together the vast literature of the World's journals into his treatment of reproductive biology and ecology. We find one of the best summaries available of the influences of latitude and energetics on such phenomena as egg weights, clutch sizes, and gosling development. Well-documented generalities lumping the biology of several species are presented (e.g. gosling weights and fledging times) but species-specific relationships also are described (e.g. the interesting nesting association between the Red-breasted Goose and birds of prey). Here, and in later chapters, instructive graphics portray numerous relationships, from the literature, from original data collected at the Wildfowl Trust, and from the author's own extensive fieldwork.

Chapter 6 treats winter biology. Sections describe the evolutionary background of winter nutrition and the birds' adaptations for this period and the influences of latter-day agriculture on winter distributions and feeding behavior. Owen's working hypothesis is that geese have been limited historically by the carrying capacity of the wintering grounds, in ways not unlike Errington's "bottleneck" theory. Recently, however, the advent of refuges, coupled with land cleared for cereal crops, has largely offset this limitation. (Now, adequate breeding habitat and the conditions experienced there seem to control goose

numbers for the most part.) This subject leads Owen into reviewing crop depredations in Europe and North America, a problem that still is unresolved satisfactorily in many cases.

The dynamics of goose populations are next in line. Subjects treated include census and productivity estimates, ways geese are captured for marking, age and sex determination, factors affecting recruitment (minimum breeding age, egg losses, body reserves and nesting success, etc.), and mortality. The chapter concludes with a discussion of how these and other factors (e.g. man's exploitation) interact to regulate goose populations.

In the final chapter, the conservation of the World's geese is described. Methods of hunting and the legislation controlling exploitation are compared among regions of the World, particularly between Britain and the United States. The impacts—not always favorable—of refuge management receive considerable attention, largely in response to the ambitious program in North America. These include the increases of geese on refuge lands and their effects on distributions elsewhere, changing survival rates, and the much-heralded restoration efforts for Nenes and Giant Canada geese. Owen's concluding remarks will not fall on deaf ears (of biologists, at least); he calls for the maintenance of species diversity and the preservation of traditional goose habitats. Changing patterns are, of course, the way of nature, but these often are far different than those man thrusts upon wildlife. How much diversity and habitat still enduring in a rapidly changing world are not without their consequences—for geese and man alike.

Three appendices summarizing the details of breeding data (egg size, breeding latitude, incubation period, etc.), body weights (by sex and age classes), and body measurements (wing, culmen, and tarsus) are useful inclusions. A bibliography of more than 400 citations and a brief index conclude the text.

My brief outline of *Wild geese* does not present a fair resume of Owen's excellent treatment—a more comprehensive review would be lengthy indeed. The book presents marvelous coverage of the birds and the volume of literature they have stimulated. Owen's own extensive work with Barnacle Geese highlights many of the sections, but the treatment is by no means parochial. Barnacles represent one of the World's more discrete goose populations, and the sponsorship of the Wildfowl Trust fortunately has permitted Owen's studies of the species in far-off Spitsbergen as well as nearer home in Great Britain.

*Wild geese* is not without some minor flaws. Some literature cited in the text did not find its way into the bibliography (e.g. Linduska 1972, Kear 1976), "calca" appeared for caeca in Fig. 31, and references to Figs. 52 and 53 escaped mention in the text. "Further" for farther appeared once (p. 127), as did "Proc." for Trans. in the bibliography (p. 228), and "is . . . data" (p. 116). The volume is rather well produced; a slightly uneven line marred page 159, as did a broken sentence on page 194, and sexes were not distinguished in either the diagram or caption for Fig. 47 (p. 178). Further comments of this nature are not warranted, however, as *Wild geese* is a book worth having despite whatever small errors there may be. The graphics are clearly presented and the many pen-and-ink illustrations by Joe Blossom nicely complement the text. Blossom's water colors of adult, juvenile, and downy geese make an attractive eight-plate centerfold.

What I like about this book is that it tells us a great deal about these magnificent birds, not just a compendia of life histories but a truly incisive look at the inner workings of *Wild geese of the World*. Indeed, Myrfyn Owen has provided us with a book fully worth its price.—ERIC G. BOLEN

**Form and function in birds.**—1979, 1981. A. S. King and J. McLelland (Eds.) London and New York, Academic Press. Volume one, xi + 459 pp., \$74.00; Volume two, xi + 496 pp., \$101.00.—These books are the first two of a three-volume set providing "a definite and extensively illustrated account of avian morphology, surveying the principal features of avian structure and providing an insight into how these structures work in the living bird." Two thoughts arose when starting a review of "Form and function in birds." The first is an assessment of how successfully this goal has been reached. The second is a comparison of this treatise with the two other major series recently published by Academic Press on the biology of birds, namely the three-volume set "Physiology and biochemistry of the domestic fowl," edited by D. J. Bell and B. M. Freeman (1971), and the five-volume "Avian biology," edited by D. S. Farner and J. R. King (1971–1975). Comments on the former question will be deferred to the end of the review, but I would like to examine the latter now without expressing any judgment on which of these three sets is the best. I would state emphatically, however, that these three sets on the biology of birds published by Academic Press are the most important multivolume compendia in ornithology published during the past decade.

Considerable overlap exists between these three sets in the chapter headings, but most similarities end here. Of the authors of individual chapters in "Form and function," only one has also contributed to "Avian biology" and two to "Physiology and biochemistry." Equally little author overlap exists between

the last two sets. Most of the authors in "Form and function" are veterinary or medical anatomists or physiologists, as are most of the contributors to "Physiology and biochemistry." In contrast, most authors in "Avian biology" are ornithologists and zoological anatomists and physiologists. The result is a considerable difference in emphasis of "Avian biology" compared to the other two sets. "Physiology and biochemistry of the domestic fowl" deals with this single species and stresses functional properties of most systems in the avian body; it is the weakest on structural aspects, functional morphology and general biological attributes of these systems. It should be noted that a large amount of physiological and biochemical work in birds has been done on domestic breeds of *Gallus gallus*. "Avian biology" covers all birds (although much of the information comes from a few experimental species) and stresses general biological aspects; it is strongest on functional properties and weakest on morphology. It provides the best comparative analysis of biological attributes in birds. "Form and function" is not restricted to the chicken, but greater emphasis is given to it and to other major experimental birds. The morphology of each system is well covered, but generally much less physiological detail is included. Hence, remarkably little overlap exists between "Form and function" and these other sets published by Academic Press on bird biology. If one requires information on the morphology of avian systems, "Form and function" is the best source by far of these three series.

The opening chapter by A. S. King and D. Z. King on "Avian Morphology: general principles" is designed as a general introduction to the whole treatise. Its title is a bit of a misnomer as it does not deal with principles as such. I believe firmly that general principles in morphology exist (although almost certainly no special principles exist for avian morphology), but will not argue with the view that these principles may be common to all areas of biology. This chapter provides an overview of the structure, function and evolution of birds. It is a good review chapter, giving a very readable and useful coverage of considerable material and a good introduction to the whole series. Its weakness stems from the usual problem of treating a vast subject in a small number of pages; one must always check points in other chapters or in the primary references if they are crucial for any study. Its greatest value is that a coherent picture of the morphology and physiology of the bird as a whole 'individual' is presented, which allows the reader to correlate material in the individual specialized chapters. "Form and function in birds" would be much poorer without this introductory chapter.

The chapter on "Coelomic Cavities" by H.-R. Duncker is an excellent, strictly morphological description of a subject scarcely dealt with in avian anatomy. Basically it is a presentation of the results of original research rather than a review of the literature, as shown by the short list of references; this is a reflection of the previous lack of information on the coelom of birds. The chapter covers coelomic structure in the several major groups of reptiles and of mammals in addition to birds. The illustrations are excellent, and combined with thorough descriptions provide a solid basis for future work on the coelom as well as on the lung-air sac system of birds.

The chapter on the "Digestive System" by J. McLelland probably has the greatest overlap with the corresponding chapter in "Avian biology". The present chapter is a complete morphological coverage with little physiology, while that in "Avian biology" is much stronger on functional aspects without sacrificing morphological coverage. Unfortunately, this chapter has several serious weaknesses. The coverage of the bill and tongue is superficial, partly because the jaw apparatus is treated in another chapter. The tongue morphology is not dealt with in any detail, and nothing is presented on its skeleto-muscular system. Basically, the feeding apparatus is not covered, with little said about the mechanisms of feeding, drinking, and swallowing, which contrasts with the active research in these fields (e.g. by Zweers in Leiden). The description of the salivary glands, a difficult subject at best, is weak. The interaction between the digestive system and the respiratory system in the head is not covered. Unless plans exist to treat the feeding apparatus in the last volume, the functional morphology of this important system will receive inadequate coverage except for P. Bühler's chapter in volume 2.

The remaining chapters in volume one on "Urinary Organs," "Female Genital Organs," "Blood Cells," and "Autonomic Nervous System" are all excellent, thorough descriptions of the morphology of each system with detailed descriptions and clear figures. The same is true for the chapters in volume two, which are "Male Genital Organs," "Cloaca," "Phallus," "Endocrine Glands," "Cardiovascular System," "Lymphatic System," "The Cranial Nerves," and "The Functional Anatomy of the Avian Jaw Apparatus." Several of these chapters provide excellent reviews of material that is otherwise difficult to obtain. The sections on the cardiovascular and lymphatic systems are clear and complete descriptions of the whole circulatory system of birds. The chapter on cranial nerves provides what all avian anatomists working on head morphology require—a good description of the cranial nervous system. This description, like many in these two volumes, is based on *Gallus*, with little detail on comparative aspects. While they are excellent accounts, one must be aware of gaps in the information that might stem from the noncompar-



ative treatment. I searched without success for a statement on the small connection between the bases of the trigeminal (V) and facial (VII) nerves seen in *Columba* and in *Corvus*. Possibly variation exists in this feature among birds. The importance of several of these chapters (coelom, cranial nerves, lymphatic system) is that one would be very hard pressed to find another even adequate treatment of this material in the recent literature.

Some shortcomings exist that detract from these volumes. One is a standard problem of multi-authored books, namely a lack of cross-reference between chapters. The cloacal bursa is discussed in chapters 2 (cloaca) and 6 (lymphatic system) of volume two, but without any mention of the other chapter. A lack of correlation exists between the digestive system and the jaw apparatus. Some chapters (e.g. chapter 4, volume 2 on endocrine glands) have no introduction or general summary. Others have extensive introductions on nonavian material that can be easily found in any good comparative anatomy text. But the most serious weakness is an imbalance in the space allotted to the various systems. The chapters on the cloaca and on the phallus are each 40 pages long, which seems excessive for these relatively simple structures that have attracted relatively little attention from avian anatomists. Chapters on the digestive system, circulatory system, and endocrine glands are about 100 pages long, and others are 60–80 pages long. The jaw apparatus was allotted only 30 pages in which the whole bone-muscle-ligament complex and its function had to be described. Although the space was really too restricted to permit justice to this complex mechanical apparatus, Bühler did an outstanding job. Indeed, his chapter is the only real comparative review of the variation of the morphology and function of a particular system in birds. It would have been nice if sufficient space had been available to expand this treatment to the whole feeding system.

It is difficult to see how the remaining anatomical systems, which include the brain and spinal cord, the peripheral spinal nerves, integument, sensory organs, and the entire postcranial skeletal-muscular-ligamentary system, can be covered in a final volume of comparable size to the first two. Clearly, treatment of some of these systems will be quite uneven, which is a consequence of the initial plans of the editors. This unevenness does not subtract from the value of the excellent detailed chapters, but it may well detract from the entire work; we must wait until volume 3 is published before a final assessment can be made on coverage in the entire set.

After a careful evaluation of the pros and cons, my judgment of "Form and function in birds" is that it is a most valuable compendium in avian anatomy. Any serious ornithologist whose work touches in any way on morphology or who needs a good reference to avian anatomy must have these volumes available. "Form and function" balances very nicely the treatment in "Avian biology," so that possession of this earlier work does not preclude the need to obtain this new series. It was necessary, for example, to read the pertinent materials in both sets to understand fully the structure and blood flow in the fetal heart and pulmonary vessels and the changeover from fetal to adult circulation. The same can be said about the urinary system, about the vascular system, and so on. Drs. King and McLelland are to be congratulated for carefully avoiding duplication with the earlier series on bird biology and for organizing an excellent set of volumes on avian anatomy. The individual authors must be congratulated for writing a series of chapters of quite uniform high quality. I have already made considerable use of the chapters on the cranial nerves and on the jaw apparatus and expect that my volumes will become even more thumbed in the years to come.—WALTER J. BOCK.