



## BOOK REVIEWS

EDITED BY BARBARA E. KUS

*The Condor* 105:164–169  
© The Cooper Ornithological Society 2003

**Avian Incubation: Behaviour, Environment, and Evolution.**—D. C. Deeming [editor]. 2002. Oxford University Press, Oxford, UK. xiv + 421 pp., numerous text figures and tables, 2 plates. ISBN 0-19-850810-7. \$85.00 (hard cover).

Avian incubation might conjure in the mind of the layperson an image of a robin sitting motionless on eggs and, in the mind of the poultry technician, an industrial force-draft oven maximizing broiler production for an obese consumer market. As editor D. Charles Deeming reveals in his opening sentence to *Avian Incubation*, the vast majority of the roughly 9000 bird species relies heavily on stereotyped aspects of bird-egg contact incubation to ensure development of offspring. However, the stereotypy of incubation belies not only its underlying complexity but also its myriad adaptive variations among and within species. Thus, to a behavioral or physiological ecologist concerned with the conflicting interests of a female barn owl and her embryo, avian incubation might conjure images of an egg-broodpatch feedback loop wherein broodpatch blood flow and heat transfer are precisely controlled by variations in egg-surface temperature and embryonic nitric oxide emissions, both avenues of communication enabling embryonic manipulation of parental behavior and physiology. Or, if it does not, it will after reading this book, a comprehensive and often engaging account of everything that is part of this intricate yet subtle process.

Pervading *Avian Incubation* is a theme of species diversity, particularly in incubation behavior but also in the characteristics of nest building and eggs. The basis for this diversity might stem from the fact that breeding environments and reproductive strategies are varied while embryonic requirements are not. That is, to meet the rigid requirements of the embryo, inter- and intraspecific variation in adult behavior and egg-laying physiology enable reproduction anywhere from the xeric dunes of the Sahara to the soggy tussocks of a northern bog and over an elevational range of 6500 m. Of course, such diversity can only be captured with the comparative approach, an approach readily adopted by several of the book's authors, many of whom distill data from a vast diversity of species into their proper ecological and evolutionary contexts.

Deeming has organized the book thematically, beginning with one of his own chapters on the evolution of avian reproduction and continuing with a group of chapters that schools the reader in some fundamentals of avian reproduction. This includes two more chapters by Deeming, both of which provide basic information on the functional anatomy and morphology of the egg, the process of embryonic development, and how each

of these might relate to incubation behavior. Perhaps due to my own biases, I was disappointed that he mentioned neither the role nor even the existence of certain yolk components now garnering much attention. These include yolk androgens (Schwabl 1993), carotenoids (Royle et al. 2001), and immune factors (Saino et al. 2002), each potentially involved in dynamic interactions with incubation patterns that may modulate nestling growth and the sibling social hierarchy. This aside, these informative chapters prepare the reader for much of the remaining book.

The next theme centers on factors affecting the behavior of incubating birds and embryos. It is headed by Carol M. Vleck's update on the current state of the field in the neuroendocrine control of incubation. Vleck includes not only a thorough discussion of the endocrine-behavior basics but also a number of intriguing conceptual considerations, underlying the author's appreciation for evolution and diversity. Deeming follows this with his own account of the remarkable diversity of behavioral patterns falling under the incubation rubric, and the section closes with a captivating chapter by Robert B. Brua on interactions between embryo and incubating parent. Those who assumed such interactions were limited to embryonic tapping sounds and chirps during the final hours before hatching will be impressed with the communication modes available to an embryo not only in need of heat, but also, perhaps, signaling its identity (in crowded colonial situations) or its imminent hatching. For example, there is now evidence that the ubiquitous signaling molecule nitric oxide, released by the egg, interacts with brood-patch receptors to modulate brood-patch blood flow and hence heat output! Due to parent-offspring conflict and the fact that communication functions to manipulate receiver behavior or physiology, this exciting area of study raises a number of questions concerning the proximate and ultimate explanations for embryonic communication. For example, how is nitric oxide release controlled? How does certainty of maternity or paternity influence sensitivity to embryonic signaling and thus affect where along the conflict continuum the trade-off resolution for incubation pattern lies?

As a start to answering such questions, an understanding of how the incubation environment is maintained would help, and that is precisely what the next group of chapters provides. Bob W. Lea and Hillar Klandorf begin with their comparative chapter on nature's little hot-water bottle, the brood patch. This edematous, defeathered portion of the breast and abdominal area, under precise control of pituitary hormones and gonadal steroids, enables the efficient trans-

fer of heat from parent to egg and also possesses additional, somewhat surprising characteristics. Afferent input via the brood patch may control clutch size through feedback inhibition of egg production, and the changing sensitivity of the brood patch over the course of incubation may influence nesting behavior as well as parental collection of nest materials. Additionally, this chapter is a helpful segue into J. Scott Turner's quantitative models on the biophysical maintenance of egg temperature, through which he arrives at some unexpected predictions for incubation patterns and how they should change as the embryo develops. Despite the dependence of his models on relatively simple systems, Turner never loses sight of the natural world and reminds the reader throughout of its vagaries, each of which will impact behavior and embryonic development in innumerable ways.

In Chapter 11, Deeming constructs an attractive hypothesis for the evolution of the altricial developmental mode. High rates of egg-turning in albumen-rich eggs hastened embryonic development and the potentially costly incubation period, opening a window for a new developmental mode among birds. Here, Deeming takes the comparative approach, an approach in keeping with the theme of this book but which also demands from its practitioners a certain level of responsibility. Because individual species (or any taxonomic unit, for that matter) are not statistically independent units, making comparisons among them requires correcting the data for phylogenetic relationships (Garland et al. 1999). Deeming does not do this, weakening the support for his hypothesis. Indeed, I found it disappointing that a book so dependent on species diversity and the comparative approach almost completely fails to acknowledge the existence of this technique (but see Underwood and Sealy's chapter on egg coloration).

Glenn K. Baggott and Kate Gaeme-Cooke then lead the reader into the nest's microbial world, an area proving to be a fertile field of study, in part the result of a burgeoning interest in immunocompetence and sexual selection in birds. Still, some of the information in this chapter is sure to surprise even the specialist. For example, who would have guessed that a bacterium dependent on the nutritional resources of the eggshell cuticle participates in a symbiotic relationship with the bird through slow alteration of the cuticle structure and the steady enhancement of shell vapor conductance?

The next group of chapters highlights the diversity of incubation strategies found among birds. It begins with David T. Booth and Darryl N. Jones's chapter on incubation in megapodes, a group that uses natural heat sources such as composting litter heaps or geothermal activity for egg incubation, and continues with a look by the late Bill A. Calder, III, at another end of the incubation spectrum where hummingbird behavior resides. But some of the most compelling examples of the diversity of incubation come from birds that breed in extreme environments. As Cynthia Carey reveals, the thermal and gaseous requirements of eggs do not differ among breeding environments; thus, certain components of incubation, eggs, or the nesting microenvironment must vary between benign and extreme

environments to compensate for their radically different ambient conditions. Carey describes a range of behavioral and physiological specializations, including the more than five-month fast of the incubating King Penguin (*Aptenodytes patagonicus*) and the grebe's eggshell vapor conductance, which is 2.7 times that of comparable species laying in surroundings less mesic than the grebe's floating island of soggy vegetation.

No compendium on avian incubation would be complete without a chapter on brood parasitism. Like their nonparasitic hosts, obligate brood parasites face a diversity of nesting environments and ambient temperatures and therefore draw from an extraordinary behavioral and physiological repertoire to ensure the successful development of their offspring. Still, as authors Spencer G. Sealy, D. Glen McMaster, and Brian D. Peer point out, we are in need of more research on just how it is that a parasite's egg can thrive in such a diversity of incubation environments.

Of particular interest is the next set of chapters on ecological and evolutionary aspects of avian incubation. This begins with Percy N. Hébert's chapter on factors affecting the onset of incubation behavior. Early incubation onset (relative to clutch completion) may induce hatching asynchrony and thus influence the energetic costs of rearing the brood and the probability of brood reduction. Interestingly, timing of incubation onset may vary with environmental factors, suggesting that a conditional strategy for hatching asynchrony may enable the modulation of energy outlay to maximize prospects of current as well as future reproduction. The trade-off between the relative prospects of current and future reproduction is a cornerstone of life-history theory, which for birds has rested on the assumption that the major cost of reproduction is incurred during the egg-laying and nestling phases. But the extent to which the incubation phase levies a cost has been a contentious issue since S. Charles Kendeigh's seminal work in the 1960s. In Chapter 20 of *Avian Incubation*, Joost M. Tinbergen and Joe B. Williams review the evidence and conclude that incubation, indeed, can be energetically costly, particularly when it is cold and when clutches are large. Jane M. Reid, Pat Monaghan, and Rudi G. Nager then discuss the extent to which incubation costs (energetic and otherwise) may impinge on reproductive success and therefore to what extent incubation plays a role in the life-history trade-off between current and future reproduction. Of particular interest here is the notion that incubation costs may vary among individuals. For example, if incubation limits extra-pair mating opportunities, low quality individuals unlikely to obtain extra-pair matings would pay less for incubation in terms of its costs to fitness. It is refreshing to see in this penultimate chapter (and elsewhere in *Avian Incubation*) such an emphasis placed on individual variation. The multiple levels at which variation in both the causes and consequences of incubation can occur are an underlying theme throughout *Avian Incubation* and illustrate the extraordinary range of a behavior so ubiquitous among bird species.

In his closing chapter, Deeming summarizes areas of avian incubation needing additional study. In particular, he calls for more research on the control mech-

anisms underlying incubation onset, on the gaseous communication between embryo and parent, and on the proximate basis of hatching asynchrony. He also suggests that efforts at protecting endangered species and habitats may improve with knowledge of incubation behavior. It is interesting that he ends on this note, because one obvious omission from this book is a chapter focused on conservation.

In his preface, Deeming expresses hope that this book will be useful not only to those interested in avian reproduction, but to those interested in artificial incubation and to both professional and amateur ornithologists alike. In fact, individual chapters should be of interest to any number of behavioral and physiological ecologists, biophysicists, and evolutionary biologists, regardless of whether or not they study birds. Rooted in solid science, *Avian Incubation* is geared for a scientifically minded audience but is likely to be of some use to people from a variety of disciplines.

On the book's cover is an illustration by Simone End of an egg-tending owl. The notion that owls incubate eggs should not surprise anyone, but what first comes to mind when thinking about them might be either their exquisitely sophisticated neural coordination of auditory and visual sensory input underlying their keen predatory skills, or perhaps their spooky hoot. This picture serves to remind the reader that the single phenomenon of incubation is as diverse as it is fundamental. In *Avian Incubation*, Deeming succeeds in making this known.—KEITH W. SOCKMAN, Department of Psychological and Brain Sciences, Johns Hopkins University, Baltimore, MD 21218. E-mail: sockman@jhu.edu

#### LITERATURE CITED

- GARLAND, T., JR., P. E. MIDFORD, AND A. R. IVES. 1999. An introduction to phylogenetically based statistical methods, with a new method for confidence intervals on ancestral values. *American Zoologist* 39:374–388.
- ROYLE, N. J., P. F. SURAI, AND I. R. HARTLEY. 2001. Maternally derived androgens and antioxidants in bird eggs: complementary but opposing effects? *Behavioral Ecology* 12:381–385.
- SAINO, N., R. P. FERRARI, R. MARTINELLI, M. ROMANO, D. RUBOLINI, AND A. P. MØLLER. 2002. Early maternal effects mediated by immunity depend on sexual ornamentation of the male partner. *Proceedings of the Royal Society of London Series B* 269:1005–1009.
- SCHWABL, H. 1993. Yolk is a source of maternal testosterone for developing birds. *Proceedings of the National Academy of Sciences* 90:11446–11450.

**Extinct Birds, Second Edition.**—Errol Fuller. 2001. First edition 1987. Cornell University Press, Ithaca, New York. 400 pp., 200 color illustrations, 104 black-and-white illustrations. ISBN 0-8014-3954-X. \$49.95 (cloth).

This handsomely illustrated volume is a revision of a 1987 edition that provides historical and biological information about recent, extinct birds. Since 1987, more birds have come to be considered extinct, and,

unexpectedly, a few species have been found and can be taken out of the extinct category (at least for now). Fuller's book provides a tremendous amount of detail about each of 85 bird species worldwide that have (apparently) gone extinct since 1600. Each account provides information about the history of discovery of a species; its distribution, description, measurements, and biology; and usually the grim facts of its demise. Fuller has done an excellent job of summarizing the earlier literature on each species, some via direct research on original sources, and some clearly obtained from excellent early authoritative works such as Rothschild (1907) or Hachisuka (1953). He has not been comprehensive at surveying or interpreting the more recent literature, especially the modern technological and paleontological advances in our understanding of the distributions, biology, and ecological consequences of the extinction of these birds.

The book begins with a short introduction, and is followed by the species accounts organized in taxonomic groupings (with ratites, doves, parrots, and songbirds having the lion's share of extinct species). Each section begins with a brief introduction that describes extinct subspecies, and rare and endangered forms within the group. Fuller quotes extensively from published and unpublished writings of ornithologists and other historical figures that observed, studied or described the taxa. Ratites are dealt with first, including the extinct elephant birds of Madagascar and moas of New Zealand. Fuller tells some wonderful stories about putative encounters between Westerners and moas long after they were presumed extinct. He speculates about the plumage of moas: perhaps they had colored wattles and fleshy combs like cassowaries, or perhaps were feathered more like emus? However, there is no mention in the section about the published DNA analyses of moa remains, or about the ecological consequences of moa extinctions detailed by paleoecologists. The series of DNA studies by Alan Cooper and Alan Baker (e.g., Cooper et al. 1992, Haddrath and Baker 2001) are either unknown to Fuller or ignored. Yet, these studies more clearly place the moas in a phylogenetic context than the works that Fuller cites, and they provide evidence about the evolutionary relationships and divergence among moa species.

This aspect of the book is a bit troubling—that much of the more recent, relevant literature is not included in the synopses. By my rough assessment, with regard to genetic studies alone, Fuller did not refer to recent (and not so recent) papers that contain DNA data and analyses for moas (*Dinornithiformes*), an elephant bird (*Aepyornis*), the Dodo (*Raphus cucullatus*), Solitaire (*Pezophaps solitaria*) and Passenger Pigeon (*Ectopistes migratorius*), the Great Auk (*Alca impennis*), Hawaiian and Laysan Rails (*Porzana sandwichensis* and *P. palmeri*), the Stephen's Island Wren (*Xenicus lyalli*), the PioPio (*Turnagra capensis*), and the Huia (*Heteralocha acutirostris*). These omissions are bothersome, but by no means do they detract from the overall worthiness and usefulness of the book.

Perhaps what makes this book so interesting and different is the ancillary historical information provided about each bird. In particular, I enjoyed reading the biographical accounts and detail about personal char-