

## **Antipredator Defenses in Birds and Mammals.**

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## Reviews



EDITED BY R. TODD ENGSTROM

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*Editor's Note.*—We published a solicited review by Daniel M. Brooks of *Curassows and Related Birds* (2004; J. Delacour and D. Amadon with updates by J. del Hoyo and A. Motis) in the July 2005 issue of *The Auk* (122:1018–1019). We did not know that Dr. Brooks had submitted essentially the same review to at least four other journals: *The Ibis*, *Conservation Biology*, *Oryx*, and *The Wilson Bulletin*. Further, Dr. Brooks was involved with early stages of publication of the book and did not inform us of his association. Multiple publication of the same review in different journals defeats the purpose of having more than one viewpoint considered: it is unfair to the authors, publishers, and the scientific journals. To partially correct this unfortunate situation, we here publish an independent review of *Curassows and Related Birds* by Nigel Collar.

**Curassows and Related Birds.**—Jean Delacour and Dean Amadon, with an updated chapter by Josep del Hoyo and Anna Motis. 2004. Lynx Edicions, Barcelona, Spain. 476 pp., black-and-white maps and figures, 56 color plates, 6 dichotomous keys. ISBN 84-87334-64-4. Cloth, \$75.00.—*Curassows and Related Birds* (1973) blazed a trail for new research into the Cracidae. The challenge was particularly met by Stuart D. Strahl in the second half of the 1980s, when he encouraged (with major support and small grants—totaling more than \$500,000 over 10 years—from what is now the Wildlife Conservation Society) research on cracids throughout the Neotropics. With coalescing interest in the family via the (later World Conservation Union–World Pheasant Association [IUCN–WPA]) Cracid

Specialist Group, which Strahl founded, a whole body of new data was generated; and when, in 1992, the International Council for Bird Preservation (ICBP; now BirdLife International) listed more than a quarter of all cracid species as "at risk of global extinction," a further surge of conservation-oriented fieldwork followed. Moreover, the opening up of the Americas to birdwatchers and scientific ornithology alike has meant the rich proliferation of new information on cracids from nonspecialist sources as well.

A second edition of any book on birds 30 years after the original must always present real difficulties. In this case, over and above the exceptional quantity of new material to be incorporated, there was the problem of authorship: Jean Delacour was long dead, and Dean Amadon unable to participate actively in the new work. Perhaps it was this unusual circumstance that caused the normal procedure—to integrate new data and insights into the original text—to be discarded in favor of reproducing the first edition's text, maps, and illustrations unaltered (except in format and but for a couple of very minor adjustments) and gathering all the new material—Al Gilbert's illustrations of downy young, and Josep del Hoyo and Anna Motis's "update chapter"—into the last third of the book, a solution initially as odd and disorienting as wiring high-tech speakers to a wind-up gramophone. There is an appropriate recommendation for the separate citation of the update chapter; but another one, inviting the whole book to be considered simply a second edition—"Delacour and Amadon (2004)"—is misleading because, in reality, there is Delacour

and Amadon (1973) and del Hoyo and Motis (2004), plus the new Gilbert plates. Readers of *The Auk* have already had an enthusiastic review of the first two-thirds or so of this book (Auk 91:445–448). What primarily concerns us here is the new material.

But first, let me say that this new edition is even more handsome than its illustrious forebear. It is printed on glossier paper, on smaller pages, and in smaller font, but of course comes out substantially longer, so that the whole has a satisfyingly chunky feel. The color plates are now bunched together in the middle of the book—doubtless sacrificing a certain immediacy and intimacy, but in fact also making visual comparisons more practicable.

The "update chapter" is a hefty 154 pages of detailed synthesis, the evidence being worked together in clear English with considerable skill and thought. It only updates the species accounts, not the original chapters on systematics, characters, morphology, plumages, habitats, reproduction, aviculture, or conservation, though relevant information on these matters is worked into the species accounts, each of which is allowed at least a couple of columns, and often four or five pages. The key subject areas of such a review (taxonomy, distribution, habitat, etc.) are picked out in bold in the appropriate paragraph for ease of reference, and each country in the conservation status review is signaled with small capitals. Possibly the greatest disappointment is that no new maps have been produced to refine the now very antiquated ones of the first edition, but the update authors are meticulous in reviewing the new distributional evidence and placing the old maps in context. All their material is scrupulously attributed to origin, and it is a testimony to their diligence (and to the ornithological endeavors of the past three decades) that the new reference list, with 645 citations, is more than 50% longer than the original one, and includes, as a gauge of the exhaustiveness of the bibliographical trawl, 22 doctoral theses. In the species accounts in the first edition, great chunks were quoted verbatim from their sources. In the update chapter, everything is much more digested and compact, but the authors generously find space for personal communications from a host of field workers with direct experience of the species in question, greatly adding to their section's authority and value.

Perhaps the entries which most immediately demonstrate the care and thoroughness del Hoyo and Motis have brought to their endeavour are those for the White-winged Guan (*Penelope albipennis*) and Alagoas Curassow (*Mitu mitu*). In 1973, the White-winged Guan was believed extinct and given just over a page of text, whereas the Alagoas Curassow was treated glancingly as a nominate subspecies, possibly extinct, and allowed perhaps 20 lines within the account of Razor-billed Curassow (*M. [m.] tuberosum*). The updated accounts offer four and three succinct pages, respectively. The stories they tell, clearly and in detail, of the rediscoveries and ensuing study and conservation are remarkable in themselves. Both species are supported by captive breeding programs; indeed, the Alagoas Curassow survives only because of aviculture, virtually its last population having been captured by a bird-fancier in the late 1970s. Ironically, this illegal and unconscionable act probably secured the species from the rampant hunting and forest-clearing that are now, following surveys in 2002, judged to have rendered it extinct in the wild. Nevertheless, the precious captive stock was allowed to miscegenate with Razor-billed Curassows, and only chance allowed the birds to pass into more dedicated hands. So there is still hope; and the update chapter is the place to read all about it.

The illustrations in the first edition were of particularly high caliber, and Gilbert's new material, which shows for the first time in color the downy plumages of all genera of the Cracidae, maintains his own standards from 30 years before. Plate 43, depicting five stages in the growth of a White-winged Guan, is as attractive as it is instructive, and all these downy young are beautifully done. Gilbert's treatment of his material bespeaks an irrepressible devotion.

Quirky and irksome as the structure of the book is, this new edition of *Curassows and Related Birds* is an outstanding feat of repackaging and upgrading and has converted what was in some ways a high-class coffee-table book into a solid reference manual that will serve the family and its students long into the future. It will surely come to be regarded as a very fitting tribute to Dean Amadon, who so regrettably died before he could see the final, first-rate product.—NIGEL J. COLLAR, *BirdLife International, Wellbrook Court, Girton Road, Cambridge CB3 0NA, United Kingdom. E-mail: nigel.collar@birdlife.org*

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**Antipredator Defenses in Birds and Mammals.**—Tim Caro. 2005. University of Chicago Press, Chicago, Illinois. xv + 591 pp. ISBN 0-226-09435-9 (cloth) and ISBN 0-226-09436-7 (paper). Cloth, \$95.00; paper, \$38.00.—The author, who has focused his career on empirical and comparative study of antipredator defenses in mammals, has expanded his purview to include birds in this comprehensive, gracefully written book. Although Caro writes mainly on two homeotherm groups, he includes material on other vertebrates and insects where they are particularly illustrative of evolutionary principles. In line with the author's intention "to integrate all functional and evolutionary perspectives on antipredator defenses," the book's components are arranged sequentially to mimic the series of events in a predator–prey encounter. Thus, after an introductory section, chapters are arranged in the following order: morphological and behavioral adaptations to avoid detection, vigilance, conspecific warning signals, signals of unprofitability, antipredator benefits of grouping, morphological and physiological defenses, nest defense, mobbing and group defense, flight and other behavioral patterns of last resort. A terminal chapter considers questions for future work and is largely devoted to conceptual issues linking material covered in various preceding chapters. The work is technically clean and is graced with lovely and topical sketches at the head of each chapter. The treatment is quite nonmathematical and, where equations are presented, they are explained quite clearly. The level of analysis is largely noninstructive with regard to deficiencies of experimental design and analysis, a weakness perhaps inevitable in a work of such scope.

We are told that the book took five years to complete, a claim readily believable given the 87 pages of references. In considering the book in detail, I have emphasized conceptual issues as applied to birds, particularly issues where opportunities for future research are apparent. The introductory chapter's focus on olfactory predator recognition is confined to mammals. The lack of material on birds suggests research opportunities on taxa with known olfactory

competence (e.g. vultures, procellariiforms, kiwis, oilbirds).

Chapter 2, "Morphological Traits to Avoid Detection," begins with discussion of crypsis—put forward as probably the most widespread predator defense in homeotherms—then follows with sections on countershading and contrasting colors. Discussion of bitterns seems misplaced in the mammal section, rather than with the rest of Aves. In considering the adaptiveness of hornbill females plastering themselves and their young into cavity nests, the author misses the advantage of the female conducting the prebasic molt simultaneously with incubation and nestling feeding (with food passed from the male). The chapter contains brief mention of "masquerading," whereby an animal closely resembles an inanimate object, and notes that such adaptations are relatively common in insects, amphibians, and fish. We are told that no systematic study currently exists on the distribution and ecological correlates of masquerading in birds. Likewise, the whole subject of disruptive coloration in birds needs systematic analysis featuring attention to phylogenetic-independent contrasts.

Chapter 3 concerns behavioral mechanisms for avoiding detection, the material divided into changing the timing and extent of activities, selecting different habitats from predators, and altering patterns of feeding and reproduction. A major portion of this chapter concerns a comprehensive review of work on nest-site placement and nesting behavior: habitat type, distance from habitat edges, habitat patch size, vegetation around the nest, nest height, proximity to other nests, distribution of nests, proximity to predator-detering social insects, and other categories of refuge. The section concerning edge effects on nest mortality points out that much is to be learned from intensively following nest predators as they "process" habitat edges. Studies employing artificial nests come in for criticism; one matter that stands out as being particularly difficult concerns olfaction and mammalian predators. The scent cues of both bird nests and researchers are not well understood and, therefore, not well controlled. The section on behavior reducing the probability of nest detection by predators omits Steve Lima's work on optimal food-delivery rates. In the mammal section of the chapter is a passage claiming that kangaroo rats remain in

more open habitat than pocket mice because, among other adaptations, they have inflated auditory bullae that permit them better to hear sounds made by incoming owls. There does not appear to be any experimental support for this idea. Discussion of Lima's theoretical work on where to forage concludes by saying that future models need to incorporate energy gained from foraging and risk of predation into a single currency of fitness. This will be a daunting task; what common currency is valid short of number of grandchildren? Throughout the book, the word "carnivore" is taken to denote, solely, a member of the mammalian order Carnivora, rather than being used in the larger ecological sense of "flesh eater" (the latter sense applicable to creatures from ciliophorans to cetaceans). In the chapter summary, the interesting general point is made that because of flight, birds have evolved fewer adaptations to avoid detection by predators than mammals have.

Chapters 4 and 5 review the recent deluge of empirical and theoretical work on vigilance as an antipredator adaptation. An important conundrum concerns the extent to which living in groups is an adaptation for sharing vigilance or for diluting the probability of being taken by a predator at any given level of group vigilance. Furthermore, despite much effort, we still do not understand why cheating on extent of vigilance by animals in a group setting does not seem to exist, though the need to continually monitor the flock-departure behavior of flock-mates may provide a clue to the absence of cheaters. In considering vigilance in mixed-species foraging groups, the author fails to emphasize adequately that cost:benefit ratios for various component species may be influenced by their relative social dominance status within the mixture.

Further along in chapter 5, we are told that "male vigilance may be determined by both natural and sexual selection." Presumably, notwithstanding this shorthand prose, the author realizes that sexual selection is but one variety of natural selection. This ornithologist is curious to know how the ears of mule deer (*Odocoileus hemionus*) "have interesting parallels with heterophyid rodent ear structure." The chapter concludes by acknowledging that there seem to be so many factors affecting vigilance that, for now, we cannot get past the checklist stage to theory except to notice that vigilance

before and after a predator has been detected may have different causes and functions.

Chapters 6 and 7, respectively, are devoted to warning signals directed to conspecifics and heterospecifics. Birds, ground squirrels, ungulates, and primates provide the bulk of examples, with the behavior of ground squirrels having undergone the deepest analysis. (Except for one mention, behavior of another group of social mammals, the cetaceans, is absent from the book.) The author notes the rather puzzling lack of high-frequency alarm calls in Australian passerines. How the structure and frequency of normal contact calls might be responses to predation risk receives no attention, but the author notes that the energetic cost of alarm-calling has not been studied. Ultrasonic alarm calls apparently occur in ground squirrels; do they occur in birds? Richard Dawkins's suggestion that one function of alarm-calling may be to cause other members of a group to behave cryptically, reducing the likelihood of a predator spotting the group, has apparently never been tested. Also needing work is the notion that alarm-calling is mutually beneficial to all members of a group because any predator thwarted by an alarm call is less likely to hunt again in the same area. (This is another example of potential payoffs to study of predator behavior.) The author claims that such reciprocal altruism is more likely to apply to mammals than to birds, but he forgets that many permanent-resident birds live in flocks with stable long-term membership. False-alarm warning calls are known to occur in several avian species, particularly subordinate species in permanent-resident mixed-species flocks. We await application of signal-detection theory to this phenomenon. Could it be that deceptive alarm calls are most common in visually occult environments where independent detection of predators by each individual in a group is less certain? We are told that "the excitement of research on alarm calls" stems from the possibility of evaluating broad questions at both comparative and experimental levels.

Chapter 7, "Signals of Unprofitability," considers antipredator adaptations occurring once an animal has been detected by a predator. Topics covered include behavior letting the predator know that it has been detected, informing it that the prey is in good condition, displaying powerful physical defenses, or letting the predator know the prey is noxious or poisonous. The

question of “cheating” in signals of prey quality to predators is a fertile area for research. The author’s mention that aposematism evolves only with kin selection is certainly countered by the example of the striped skunk (*Mephitis mephitis*). Using Great Tits (*Parus major*) as model predators, two experiments designed to discover the evolutionary trajectory of aposematic coloration have produced disparate results. In one case, the conclusion was that unpalatability selected for gregariousness, which, in turn, selected for warning coloration; but a repetition of the experiment in another lab produced contradictory results. This situation sets up the delightful prospect for a third, disinterested, party to evaluate simultaneously the conclusions now in place. Considerable attention is paid to the iterative process by which predators come to associate prey characteristics with unprofitability. An experiment had students learning about “prey” unprofitability by experiencing the consequences of choosing displayed pixels. An interesting hypothesis is that heightened conspicuousness of prey is selected because predators conclude that because a prey item is so conspicuous it must have been detected and rejected by other predators in the past, and so must be unprofitable. Although study of aposematism in birds has been hindered by the prevailing notion that bird flesh is neither noxious nor poisonous, comparative study has found negative relationships between visibility and edibility in 38 species of Palearctic birds and in 200 avian species from Africa. The author indicates that a point for future research concerns whether the distastefulness of some bird species affects the hunting tactics of predators. Apparently, the only example of Müllerian mimicry in birds concerns five species of pitohuis in New Guinea that are both conspicuous and toxic.

Chapter 8 details antipredator benefits of grouping, other than shared vigilance. Covered are the dilution effect, transmission of information about danger from predators, erratic escape that may confuse a predator, and several other miscellaneous factors. The dilution effect is a function of the risk per capita of detection times the risk per capita of capture once detected. If this product is lower for animals in groups than for solitaries, grouping should be selected, but presently, data on encounter rates between predators and grouped or solitary prey are quite rare. The Trafalgar Effect is defined as transmission among group members about the presence

of a predator, and is named after the intership communication about the presence of an enemy in Nelson’s fleet. (The British seem very fond of such metaphorical remnants of the Empire; e.g. red queen hypothesis, Beau Geste hypothesis.) The chapter concludes with the generalization that some combination of food type, predator pressure, and body size determines the grouping pattern of homeotherms, and that the grouping pattern coupled with habitat type selects for antipredator alternatives, such as crypticity in solitary species or corporate vigilance in group-dwelling species.

Chapter 9 is devoted to morphological and physiological antipredator defenses. The morphological attributes focus on body size and escape speed, whereas the physiological characteristics concern examples of unpleasant odor or taste. After noting that some prey are physically too large or powerful for a given predator to subdue, the discussion of body size as a defense focuses on energy-input and handling-time spent by the predator on prey of various sizes. The discussion of gape-size limits on prey size considers birds only as prey (e.g. of snakes); but as predators, birds can be gape-size-limited. How large a fish can a heron or cormorant swallow whole? It is claimed that individuals of larger prey species could be subject to fewer predation attempts than individuals of smaller prey species because larger predator species live at lower densities than smaller prey species. But the generalization is also true that larger prey species live at lower densities than smaller prey species, so that capture attempts per prey individual is not necessarily lower for large prey individuals. Picked from the plethora of hypotheses about reversed size-dimorphism in raptors is the notion that the female is larger so she will be better able to defend the nest. Caro notes the different escape tactics found within Aves and points out the opportunity to relate escape tactic to wing morphology. Although birds are far less endowed with morphological means of defense than mammals, many taxa do have spurs. In most spurred species, such structures seem the product of sexual selection, because only males are so endowed; but in 16 species, females also are spurred. We lack evidence as to how spurs might be used against predators and whether individuals experimentally despered might have higher predation rates. In the matter of avian chemical defenses against predation,

fully 80 genera of 17 orders have been reported as being malodorous to humans. Eider ducks (*Somateria mollissima*) defecate on their eggs before withdrawing from a predator, and such deposits have been shown to deter food-seeking ferrets and Norway rats (*Rattus norvegicus*). Brought into the discussion is the complex of nesting adaptations in response to predation risk (e.g. clutch size, nesting attempts per year, nestling developmental rates).

The 44 pages of Chapter 10 are devoted almost entirely to nest defense in birds. A survey of waders found that nest defense was more likely to occur in larger species, in colonial nesters, and in species with biparental care of young. During distraction displays before nest predators, birds appear to use interactive techniques similar to those recently developed for playback experiments; the birds monitor a predator's response, adjusting strength and orientation of distraction display appropriately. Surprisingly, time and energy costs of nest defense have apparently never been measured. Also discussed are the methodological limitations of quantifying nest defense using approaching humans as surrogate predators or employing artificial, or artificially placed, nests. A major theme of the book, well exemplified in this chapter, is that little is known about the long-term effects of such anti-predator behavior on the responses of potential predators. Aside from being deterred in the instant, how does a predator respond over succeeding, hours, days, and beyond? We are told that in both altricial and precocial species, parents give a specific warning call that has the effect of silencing the offspring, an advantage Caro considers to apply only after the young hatch. Is this true? Might eggs stop "peeping" in response to warning calls? A related question asks: because of presumably lower predation risk, do eggs and young of hole-nesting birds vocalize more than those of open-cup nesters? Regarding nest defense and re-nesting potential, it is not clear why the author concludes (on page 354) that nest defense of later clutches in a season should be greater because such clutches tend to be smaller than earlier clutches. Four pages later, we are told the contrary, that Tawny Owls (*Strix aluco*) may defend late clutches less because they are smaller. Opportunities exist for experimental evaluation of the several explanations concerning differences between the sexes in nest defense. On page 364, the author

discusses "predatory strigiformes." Are there any nonpredatory strigiformes? Stemming from the theoretical notion that parental investment (as exemplified by nest defense) should be influenced by reproductive value of the current brood, some studies have shown that broods of heavier young are more vigorously defended than broods of lighter young. These results, however, do not appear to control for parental condition. One might expect the parents of better-nourished (i.e. heavier) young to be better nourished themselves and, therefore, better equipped to spend time and energy on nest defense. The author concludes that study of nest defense in birds is "the most theoretically grounded aspect of antipredator defense in homeotherms, because it takes its predictions directly from parental investment theory using parental defense as a testing ground."

Chapter 11 concerns mobbing and other forms of group defense. Virtually all empirical data concerning mobbing stem from study of birds. Work on swallows has led to the distinction between "active mobbers," which approach closely and may even strike a predator, and "passive mobbers," an oxymoronic label for animals that approach less closely and are silent. While mobbing apparently only rarely results in the mobber being killed by the mobbee, there are certain to be time and energy costs of mobbing, neither of which has been quantified for any species. A central theme of the book—the lack of information on predator behavior—is repeated in this context; we know very little about how a predator's subsequent behavior is affected by an episode of mobbing. Is an Eastern Screech-Owl (*Otus asio*) likely to reduce or desist its hunting in an area where it has been mobbed? Experimental playbacks to radiotagged owls would likely produce an answer. Conversely, does an individual of a prey species learn by cultural transmission, through mobbing, not only the identity but the location of a predator? The author recounts the notion that mobbing may be adaptive in demonstrating fitness to conspecifics, an idea calling to mind Amotz Zahavi's thoughts on "prestige." An arresting fact is brought out in the discussion of mixed-species assemblages as group defense against predators. In Japan, Azure-winged Magpies (*Cyanopica cyana*) breed most successfully near nests of Lesser Sparrowhawks (*Accipiter gularis*), apparently because the hawks drive away

the Large-billed Crows (*Corvus macrorhynchos*) that otherwise would depredate the Azure-winged Magpies' nests. Remarkably, Azure-winged Magpies breeding within 100 m of a Lesser Sparrowhawk pair tended to synchronize nesting with the Lesser Sparrowhawks, but Azure-winged Magpies more than 1 km from a breeding pair of Lesser Sparrowhawks were much more variable in breeding phenology. The disparity suggests that Azure-winged Magpies near Lesser Sparrowhawks time their laying after observing something that indicates the Lesser Sparrowhawks' breeding state—perhaps the intensity of the latter's nest defense.

Chapter 12 is devoted to flight and other "behaviors of last resort." Covered are behavioral freezing in place, startle responses, fighting back, and fleeing. Apparently, freezing of young in response to parental warning is accompanied by bradycardia "in which the heart rate plummets." Why the bradycardia? Does it occur in birds? Although these questions are not addressed, we are told that the whole subject of immobility and the factors controlling it have been understudied. "Regurgitating" stomach oil seems a vast understatement of the projectile vomiting that procellariiforms use as a "last resort" against predators. The section on flight contains nothing of the considerable modeling of avian body-mass trade-offs between starvation risk (smaller body mass) and predation risk (heavier body mass). On days when a female is yolking up an egg, her body mass increases steadily until the egg is laid. Might acceleration and speed of flight from predators have been a constraint on egg size? In the section concerning autotomy of body parts, a last-resort response notable in herptiles, the "fright molt" of birds is mentioned in passing. Development of a standard methodology could provide comparative data on what appears to be a legitimate form of autotomy in some avian species.

Chapter 13, the last chapter, describes relationships between the forms of antipredator response treated separately in earlier chapters. Following a section on the synergism between morphological and behavioral responses, material is structured as answers to three questions: why does a given species respond differently to different predators, why do different species use different responses to the same predator, and why does a given prey species show a number of different antipredator responses to

the same predators. The section on coevolution contains an interesting example of the complexity of cetacean behavior. Off the northwest coast of North America, pods of killer whales (*Orcinus orca*) in permanent residence hunt salmon and use pulsed sound to communicate. Pods that are transient hunt marine mammals and do so without using pulsed sound except just after making a kill. The difference in behavior between the two whale types is attributed to the fact that marine mammals can detect killer whale calls, responding with antipredator behavior, but fish cannot detect such sounds. It also seems possible, however, that if resident pods socially dominate transitory pods, the latter may remain silent so as not to reveal their location. The complexity of sorting out coevolutionary relationships among predator and prey is well illustrated by the striped skunk, which uses its aposematic coloration to warn mammalian predators of its noxious odor, but thereby becomes more vulnerable to Great Horned Owls (*Bubo virginianus*) that are undeterred by the odor.

This is an important book. It treats a limited topic encyclopedically, including older references of the sort often overlooked by reviewers in this day of limited electronic databases. It is heuristic throughout in pointing to opportunities for further work, and concludes the last chapter by explicitly detailing "Ten pressing questions." Excellent material for graduate-level seminars, the paperback is not unreasonable in price, and the cloth edition will be a worthwhile addition to institutional libraries.—THOMAS C. GRUBB, JR., *Department of Evolution, Ecology, and Organismal Biology, 300 Aronoff Laboratory, 318 West 12th Street, The Ohio State University, Columbus, Ohio 43210, USA. E-mail: grubb.1@osu.edu*

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**The Geographic Mosaic of Coevolution.**—John N. Thompson. 2005. University of Chicago Press, Chicago. x + 400 pp., 11 halftones, 94 line drawings, 7 tables. ISBN 0-226-79761-9 (cloth) and ISBN 0-226-79762-7 (paper). Cloth, \$75.00;



paper, \$28.00.—I have occasionally received comments from reviewers of my work on hummingbirds and their food plants to the effect that specialization and coevolution are the exception rather than the rule in pollination systems or, alternatively, that coevolution is such a diffuse process that it cannot be analyzed. These comments reflected the reviewers' frustrations from their studies of coevolution at the scale of local populations, which often failed to turn up evidence for reciprocal selection. During the past decade, however, the view of coevolution as either a rare or diffuse process has changed, largely through the influence of John N. Thompson and his theory that coevolutionary processes are best understood by studying them on a geographic scale. In his latest book, *The Geographic Mosaic of Coevolution*, Thompson reviews his theory and the recent evidence in support of it, and discusses its implications for coevolutionary interactions.

Part 1 addresses the framework of the geographic mosaic theory of coevolution (GMTC), beginning with an outline of Thompson's thesis. The next four chapters examine evidence for the major assumptions of his theory, especially differences between populations in genetic structure and outcomes of ecological interactions. In the next two chapters, Thompson presents the theory's assumptions, hypotheses, and predictions, and applies them to understand diversifying coevolution and speciation. Part 1 concludes with a chapter on how the GMTC can be analyzed, in which Thompson discusses 11 forms of evidence for coevolution. Students will want to have a copy of this list taped to their computer monitors as a guide.

Part 2 examines specific hypotheses on coevolution. Three chapters discuss antagonistic interactions and how the geographic mosaic maintains genetic polymorphisms, produces multispecies networks of antagonistic trophic interactions, molds levels of virulence and resistance, and contributes to the dynamics of sexual reproduction. The next three chapters consider how the geographic mosaic may lead to convergence of traits in mutualistic interactions and networks. One chapter is devoted to coevolutionary character displacement. Thompson concludes with a discussion of applied coevolutionary biology. (The book also includes an appendix summarizing all the major hypotheses and predictions.)

Thompson's GMTC makes three hypotheses about coevolution. First, natural selection differs among populations because of differences in how the fitness of one species depends on the other. Second, reciprocal selection occurs only within some local communities ("coevolutionary hotspots") embedded within a matrix of coldspots where local selection is nonreciprocal, creating selection mosaics. Third, because of trait-remixing, species-level coevolved traits will be few in number.

At the simplest level, the GMTC is an argument about the scale of coevolutionary processes. Can the evolution of mutualisms and antagonisms be explained entirely from studies of single populations, or are studies at a larger scale necessary? But the GMTC also emphasizes the complex nature of the dynamics of coevolutionary interactions. Because populations differ in genetic structure and the outcome of ecological interactions, studies of single populations of interacting species may fail to capture the scope of the coevolutionary interaction and the intermixing of traits that results from population structure. Thompson's GMTC thus provides a template for how researchers should design their studies. Rather than begin studies of the coevolutionary process through detailed microevolutionary analyses of interactions in a single population, researchers should first conduct a geographic survey of the interaction and then focus subsequent efforts on areas with and without reciprocal interactions (coevolutionary hotspots and coldspots) and on the trait-remixing that may occur between them. A geographic approach reveals how a third party mediates diversifying coevolution between Red Crossbills (*Loxia curvirostra*) and lodgepole pine (*Pinus contorta*; Benkman 1999), and how specialization by sexes of hummingbirds changes with the relative frequency of their food plants (Temeles and Kress 2003).

Given his efforts to explain coevolution resulting from all forms of ecological interactions at all scales of organization, there are bound to be some weak spots in the book, and Thompson is at his weakest when he lacks sufficient data to support or interpret his hypotheses. For example, in Chapter 11, he presents his hypothesis of coevolutionary alternation, which maintains that predators preferentially attack prey species with low levels of defense, leading to selection for increased levels of defense in

such prey. Because defense costs impose fitness costs in the absence of predation, selection will favor reduced defenses in prey species that are not currently attacked. As the relative levels of defense among prey species change over time, predators attack prey that are currently undefended. Some support for this hypothesis is provided by Davies and Brooke's (1989 a, b) studies of host alternation by Common Cuckoos (*Cuculus canorus*). Still, I wondered how this hypothesis might apply more generally to interactions between predators and prey, as well as how it might be reconciled with decisions at the behavioral level (e.g. optimal foraging theory). To his credit, Thompson notes that he may be wrong, and states that his main purpose is to push discussion of these interactions beyond that of "diffuse" coevolution, which provides no hypothesis for how these multispecies coevolutionary interactions actually evolve. I applaud him for trying, though in these discussions he strays from his geographic message.

The book is at its strongest where Thompson has evidence to support his theory. Thompson notes that he favored the inclusion of studies that have appeared in the 11 years since he published his second book, *The Coevolutionary Process* (Thompson 1994). Even readers familiar with Thompson's work will value his interpretation of recent coevolutionary studies by Benkman, Lively, Brodie, Burdon, Thrall, and others, and what is especially impressive is how masterfully Thompson moves from discussions of gene-for-gene matching and the evolution of sex in parasite-host systems to community analyses of plants and their pollinators. These discussions make good meat for graduate student seminars and provide a ton of material for faculty lectures.

All writers know how difficult it is to begin and end an article, and Thompson succeeds with both. In Chapter 1, he discusses the pervasiveness of coevolutionary interactions on Earth, from coevolved symbiotic interactions that led to mitochondria and chloroplasts, to primary succession that relies on nitrogen-fixation symbioses between rhizobial bacteria and legumes, to feeding on plant tissue made possible for many vertebrates and invertebrates by obligate coevolved symbionts in their digestive tracts, and about six or seven others. These examples of coevolutionary processes in the world around us are how Thompson introduces the subject in public lectures, and they make a

powerful statement for why everyone should appreciate evolution. Readers looking for a way to introduce evolutionary biology to naïve students in an introductory biology course have much to gain from this chapter.

The last chapter, on applied coevolutionary biology, is similarly inspirational. As humans continuously move genes and species around the world, we disrupt existing coevolutionary dynamics and create new ones, especially at the geographic level. Similarly, by fragmenting habitats, we may shift coevolutionary dynamics from a geographic to a local scale in the absence of gene flow. Thus, humans are creating new systems for tests of the GMTC.

To a great extent, current evidence in support of Thompson's theory comes from studies of two-species interactions, with occasionally a third party. Looking at how such simple interactions form multispecies networks will be the next critical step in understanding the coevolutionary process.

In sum, given its attempt to understand coevolution at all levels, from viruses and hosts to lions and their prey, *The Geographic Mosaic of Coevolution* belongs on everyone's bookshelf. Readers will not be disappointed.—ETHAN J. TEMELES, *Department of Biology, Amherst College, Amherst, Massachusetts 01002, USA. E-mail: ejtemeles@amherst.edu*

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**Peregrine Falcon: Stories of the Blue Meanie.**

Jim Enderson. 2005. University of Texas Press, Austin. 253 pp., 15 black-and-white photographs, one map, and 24 pencil sketches. ISBN 0-292-70624-3. Cloth, \$65.00; paper, \$22.95.—A beautiful book rescues a slice of history from oblivion. Jim Enderson has accomplished that for us in this slim, 7-inch by 10-inch volume. It is partly a history of falconry and the Peregrine Falcon recovery program, part personal account of his own participation in these activities, and part reflection on the human adventure this foremost 20th-century conservation accomplishment represents.

Though the imprint was delayed a decade or more, Enderson, like many others, was attracted to raptorial birds by artist Louis Agassiz Fuertes's article in *National Geographic*, published in 1920, titled "Falconry: The Sport of Kings."

The first chapter, "The Nature of the Falcon," is a lover's paean to that great bird, called "Blue Meanie" by another distinguished fancier, Grainger Hunt. While at Cornell in 1950, I came to know the other core members of that coterie of falconers and others who would rescue the Peregrine Falcon from the brink: Tom Cade, who became doyen of the recovery program; Richard Fyfe of Canada, who first proposed a Peregrine Falcon breeding project in 1967; Joe Hager, who alerted us to the fact that his Massachusetts Peregrine Falcons were eating their eggs; Joe Hickey, who brought all of us together at a Madison, Wisconsin, conference in 1965; Heinz Meng, who helped Cade get started in breeding falcons; and later, Derek Ratcliffe of England, who first identified the thin-eggshell syndrome.

Indeed, it was on a detour through Colorado Springs in 1973 to see Enderson's small breeding program that I became convinced that if the Peregrine Falcon was to survive the DDT–DDE poison crisis, only the falconers could help it do so. Despite some internal opposition, I was able to add the National Audubon Society's support to the larger recovery program.

Chapter nine is a concise history of falconry in North America, most of it post-World War II.

Enderson has a light touch, and his 14-plus chapters are all informative and captivating. A friend of his, Robert Katona, provided a score of

lovely pencil portraits of the Peregrine Falcon, on the fist and in the sky. A few photographs round out the record.

With characteristic modesty, he refuses credit for helping "save" the Peregrine Falcon. Of course, the monumental effort of some half-dozen breeding programs involved in releasing and "hacking" some 6,500 captive-bred birds of speeded recovery. In the process, a new behavioral type, the urban Peregrine Falcon, was created. But this too was restoration, given that Peregrine Falcons nested on castles and cathedrals in Europe in Medieval days.

The threat was real, however, and we had to act. Even so, given time, and the Peregrine Falcon's far-flung distribution as a nesting bird, Enderson reminds us that it would probably have recovered and re-established itself when we stopped poisoning the environment with fat-soluble, food-chain-contaminating chemical pesticides like DDT and Dieldrin. We accomplished that in 1973 in the United States, so those who helped bring that about also helped "save" the bird.

On page 3, Paul Mueller is credited with synthesizing the molecule of DDT in 1939. This was apparently done by a German chemist, Othmar Ziedler, in 1874, who, however, saw no practical use for it. What Mueller did, working for Geigy in 1939 and the early 1940s, was to show that DDT killed potato beetles and clothes moths.

Eager for an effective insecticide early in World War II, the U. S. military seized upon this discovery and funded the research-and-development costs of mass-producing a new insecticide, which it then used to great advantage in Europe and Africa and in the Pacific theater of operations. At first used as a powder, DDT prevented typhus outbreaks. Our troubles began when it was used with a solvent for aerial application. But a war was on.

After the war, DDT was released for civilian use in agriculture, forestry, and mosquito control. It became the "magic bullet" for most insect control. It was cheap, because its research-and-development costs had been borne by the government. But, inadvertently at first, it poisoned the world. Ironically, its most important use, in public health programs such as malaria control, was made ineffective because mosquitos developed resistance, thanks to widespread use.

On page 151, I am given undue credit for "greasing the skids" for a small grant by the

New York Zoological Society. William G. Conway, that superlative director of the Bronx Zoo, recognized a promising investment when he saw one.

On page 192, we are given a fascinating glimpse into the information “glitches” that all too often plague even our best efforts. In 1979, an AOU committee, no less, resolved that only those captive falcons bred from native stock should be released to the wild. Otherwise, native ecosystems and gene pools would be compromised, we were told. There were two great ironies to this inept activism (let alone that when captive breeding was initiated, there were no native Peregrine Falcons left in the East).

First, Bud Tordoff, one of the most active midwestern participants in the Peregrine Falcon recovery program, was president of the AOU at the time. He belatedly objected, pointing out that the environment itself would shape the population by selecting those birds fit to survive. The U.S. Fish and Wildlife Service

(USFWS) at last agreed the following year. But many of us thought that this question of breeding stock “purity” had been resolved in 1974 at an Audubon conference designed to help the USFWS overcome its difficulties with this very question. Here, William H. Drury, Jr., one of 35 participants, convinced us that nature would do the selecting if we provided the birds.

We thought we had made our case when the USFWS proceeded to appoint recovery teams. We promptly published the results of that Audubon conference, held in Greenwich, Connecticut, and thought we had made a reasonable distribution of complimentary copies to key people. But enough is often not enough.

This book belongs next to Cade and Burnham's *Return of the Peregrine* in any library intent on chronicling what is probably the greatest conservation story of the 20th century.—ROLAND C. CLEMENT, 1199 Whitney Avenue, Hamden, Connecticut 06517, USA. E-mail: [rclement@snet.net](mailto:rclement@snet.net)