



The Ecology and Conservation of Asian Hornbills: Farmers of the Forest

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The Ecology and Conservation of Asian Hornbills: Farmers of the Forest.—Margaret F. Kinnaird and Timothy G. O'Brien. 2007. University of Chicago Press, Chicago, Illinois. xviii + 315 pp., 15 color plates, 60 figures, 32 tables. ISBN 0-226-43712-4. Cloth, \$45.00.—This book presents a lot of information about Asian hornbills—evolution, functional morphology, nutritional ecology, social biology—but its original contribution is to assess how hornbills and forests affect one another. The authors synthesize and analyze data to evaluate ideas, and they include many hypotheses. We learn about the bizarre behavior of Helmeted Hornbills (*Rhinoplax vigil*), which collide in midair, clashing their unique solid casques, in contests at fruit trees. We learn that figs sustain hornbills, that helpers really do help, and that forests are sensitive to hornbill loss and vice versa. The authors have quantitatively tackled difficult issues, like fruiting phenology, seed dispersal, plant population responses to disperser declines, and hornbill population responses to changes in forest cover and configuration. The color photographs of hornbills capture the essence and diversity of these wonderful creatures. The book concludes by grappling with the thorny issues causing destruction of rainforests—reporting on conservation perils and successes and suggesting directions for future work. The authors are understandably smitten with hornbills, and they have written this ambitious account to inspire research and generate conservation momentum.

Several aspects of the book, however, detract from its presentation and rigor, as illustrated by the following examples. The book could have been significantly streamlined. For instance, scrutinizing three molecular phylogenies, each with a different set of species, seems esoteric rather than synthetic. The thorough history of hornbill taxonomic changes, beginning with Linnaeus, especially in the absence of explanations, is excessive. Two hypotheses about the evolution of *Penelopides* that require its implausible extinction on Borneo could have been eliminated, and the text sometimes diverges into matters that seem irrelevant or inappropriate (e.g., spandrels of San Marco, methodology of DNA hybridization).

A more serious problem is the inclusion of poorly supported statements and ideas, as well as misunderstandings. The authors claim that genetic evidence indicates that hornbills should be placed in a separate order, rather than family, but it is not apparent how they reached this conclusion. The unsupported hypothesis that hornbill eyelashes have a communicative function smacks of anthropomorphism, as do words like “unfaithful” and “trustworthy” in describing hornbill mating systems. I found no support for the argument that hornbill sexual dimorphism results from “a male’s need to advertise his quality as a provider.” Allometry and its adaptive implications are confused. Constant proportionality between bill volume and casque volume is an isometric relationship; a proportional increase in casque volume with increasing bill volume is an allometric relationship, but this does not suggest an adaptive cause. The authors’ argument that a hornbill’s casque functions to strengthen the bill lacks a rigorous physical explanation.

The information on hornbill dietary habits is interesting, but some of the nutritional conclusions seem flawed. The authors downplay the nutritional significance of animal foods after noting that hornbills spend a lot of time hunting but have low capture rates. Wouldn’t this suggest that frugivorous hornbills really care about getting some protein-rich animal food? Structural carbohydrates are reported to be higher in hornbill fruits, but these sugars cannot be utilized, so they are nutritionally irrelevant. And hornbills, no doubt, eat fruits for their energetic rewards, so it is confusing when the authors write of hornbills seeking fruits for protein. The unsubstantiated idea that diversity in the fruit diets of animals results from a nutritional need for diet-mixing occurs repeatedly. Figure 4.10, which shows hornbills using figs far out of proportion to their availability, is intriguing, but it could be an artifact of using the relative abundance of trees as a proxy for fruit abundance; figs can produce huge fruit crops.

The analysis of hypotheses about the adaptive significance of nest-sealing by hornbills is confusing. I was especially puzzled by the repeated promotion of the authors’ hypothesis that nest sealing evolved under selection for females to enhance fidelity by their mates. They reason that if all family provisioning responsibilities were forced on males, males would have little opportunity for “infidelity.” It is not clear why male sexual fidelity would benefit females and, if it were somehow advantageous for females not to provision, why nest sealing would be necessary. Surprisingly, the authors dismiss the predator-defense hypothesis, even though they found a suggestive result that hornbill nesting success is substantially greater than that of other cavity nesters ($P = 0.07$) and note that, among hornbills in the genus *Tockus*, resealing of nests by chicks after female emergence occurs in species that nest in especially vulnerable sites. And in evaluating the hypothesis that nest-sealing functions to ward off competitors for nest cavities, the authors downplay observations of intraspecific contests for nest cavities as “hormonal impatience.” But this is a more limited level of analysis (physiological, or proximate); it does not dismiss the evolutionary level (ultimate) of the nest-competition hypothesis.

Kinnaird and O'Brien quantitatively address important ecological issues, but quantitative approaches are only as good as the information used to build them. For example, the authors calculate the “germination rate” of hornbill-dispersed seeds by dividing the number of seeds delivered to nests by hornbills by the number of seedlings counted under nest trees. Comparing this to the “germination rate” of all seeds, the number of seedlings in the forest plot divided by total estimated seed production, the authors conclude that seed dispersal by hornbills “greatly improves the odds that a seed will germinate.” These estimates, however, are not measures of germination rate, but include seedling mortality from germination until discovery. Furthermore, differences in the approach to each estimate and the chain of rough approximations seriously undermine the credibility of this comparison.

The authors estimate hornbill seed dispersal for some rainforest trees and then model the minimum number of hornbills needed to maintain a healthy forest (stable size distribution of trees), the ecologically functional population (EFP). A concern with using size classes in their demographic estimates is that tropical trees are notoriously difficult to age by size, as reflected in the authors’ need to “smooth data” between size classes to avoid negative mortality rates. They then compare

EFP to MVP, the minimum viable population size estimated from simulations that result in a 95% probability of population persistence for 100 years, in the face of environmental, demographic, and genetic variability. Finding that EFP is much larger than MVP, they amplify the argument that conservationists should consider species interactions in generating minimum-population-size guidelines. But these two approaches are quite different; EFP does not address stochastic variation and probability of population persistence that is arbitrarily set in calculating MVP. A more conservative threshold of 99% chance of survival for 1,000 years to estimate MVP would have resulted in an MVP more comparable to EFP. Arguing that a lower threshold is warranted because of the rapidly deteriorating conservation situation in Asia is not reasonable. Perhaps an overall conclusion would be that the best elements of these two approaches could be melded in future models.

The evaluation of the extent and configuration of forest habitats from satellite data illustrates an excellent conservation tool. The

authors employ descriptive statistics to make the point that hornbill vulnerability is dependent on both range size and habitat fragmentation. Using rough estimates of hornbill dispersal potential, they show the logical result that dispersal unites fragments dramatically. From simulations, and then a field study in Sumba, Indonesia, we learn that hornbills are sensitive to forest extent and fragmentation. A drawback to the analysis is that arbitrarily manipulating available habitat by tweaking the model's sensitivity index to human impact gives no link to reality.

Kinnaird and O'Brien bring us up-to-date on hornbill biology and conservation, synthesizing the flush of recent work. Although the book should be read critically, it offers a wealth of information and new approaches to our understanding of hornbill ecology. Let's hope that this work, and the continuing efforts of all concerned with the biodiversity crisis of the "hornbill realm," will lead to effective measures to conserve these natural treasures.—MARK WITMER, 147 *Weston Road, Berkshire, New York 13736, USA. E-mail: mwitmer@lightlink.com*