Book reviews

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Book reviews

Price T. 2008. Speciation in birds. Roberts and Co, Colorado. ISBN 9780974707785. Soft cover, 470 pp. Euro 58

Despite its title, Ian Newton's otherwise excellent book "The speciation and biogeography of birds" turned out rather brief on the subject of bird speciation (reviewed in Ardea 92/1). This meant that we were still without a satisfactory modern update on the writings of Mayer and Lack, by now more than fifty years old. Now, there is a book that fills this gap, written by one of the most influential investigators in the field. In "Speciation in birds" Trevor Price guides us through the main issues in speciation. In accessible prose, he assesses the importance of factors like geographical isolation, ecological selection and sexual selection in the divergence of bird populations. The last few chapters address processes involved in the later stages of speciation, namely reinforcement, hybridization and genetic incompatibilities. These chapters are especially strong. The book is presented in an attractive lay-out and illustrated with many colour figures. The arguments are illustrated by a rich variety of examples, ranging from broad-scale patterns in island birds to detailed experiments with zebra finches. Further insights are obtained from domestic breeding (although this analogy in my view doesn't always work; e.g. page 239). Overall, the book presents a comprehensive state-of-the-art of avian speciation research.

Price's main thesis is that Mayer was right: bird species form mainly under allopatric (geographically isolated) conditions. Speciation in sympatry occurs in birds, but only under very unusual circumstances. Here, it is important to bear in mind that we are talking about birds only. Although still controversial, there is mounting evidence in insects and fish that speciation can sometimes occur in the face of substantial gene flow. Price is of course aware of this and doesn't make Mayer's mistake of trying to generalise the patterns seen in birds to other groups. But in birds, the case is strong. Thus, Price builds this into a general framework, illustrated in figure 2.3. Bird populations can become reproductively isolated by independently accumulating mutations, which takes a long time in isolation. Or, they can diverge because they are subject to different ecological selection pressures, which potentially proceeds much quicker. I was not very convinced by Price's placement of sexual selection and sexual conflict in this scheme. On page 29 he explains that these selection pressures rely on independent mutations in allopatric populations. These need time to arise and thus divergence through this mechanism is assumed to be slow. But how is this different from ecological selection? Ecological selection also needs mutations to work on. The point of invoking sexual selection is that in principle it can sweep new mutations to fixation very quickly and because they affect mating patterns they can almost instantly lead to assortative mating. Therefore, if anything, sexual selection should lead to reproductive isolation quicker, not slower, than ecological selection.

The focus on birds has other consequences too. Birds are very easy to observe and knowledge on their biogeography is unrivalled. However, they are much less congenial to experimental manipulation than for example fruit flies. Thus, birds are the group of choice when interested in broad-scale patterns of diversity. Not surprisingly, this book relies heavily on such patterns. Because of the correlative nature of such data, firm conclusions are often difficult and Price does an admirable job of considering the various alternative explanations. That does not mean that the book is unbiased. For example, Price's dislike of purely Fisherian models of sexual selection has been a recurring feature in his writings. The flipside of this personal tinge is that the reader is treated to a number of less-conventional points of view, many of which I found very interesting. For example, it is refreshing to see signalling traits released from the straightjacket of sexual selection and instead interpreted in a wider framework of social selection. I wholeheartedly agree with Price's assertion that ".... the emphasis placed upon this mode of [sexual] selection has come at the neglect of other forms of social selection." (p. 158). Having said that, how the non-sexual component of social selection could lead to species divergence remains somewhat vague. Price makes a strong case for population divergence in socially selected traits. But population divergence is not speciation. For that, the populations need to mate assortatively when in secondary contact, which means we are back in the sexual realm.

Discussions on avian species diversity often seem to get bogged down in endless arguments over species concepts and taxonomic rearrangements, not least in The Netherlands. Often more time is spent on arguing over whether phenotype X should be labelled a species or not, rather than enquiring into why we are having these decision difficulties in the first place. These problems are not new. In fact, they were very prominent in Darwin's time, yet some circles seem not to have moved on. For all those who are genuinely interested in where all the wonderful diversity in birds comes from and why some species are so ill-defined, this book is a must-read.

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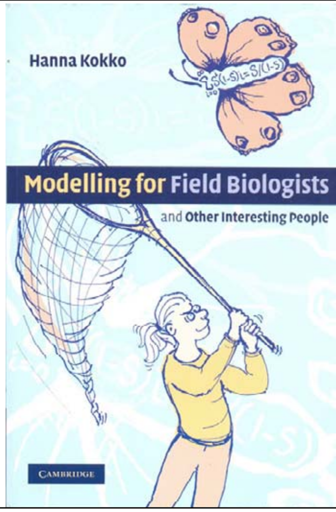
Kokko H. 2007. Modelling for field biologists and other interesting people. Cambridge University Press, Cambridge. ISBN 9780521538565. Paperback, 230 pp. Euro 47



My usual way of reading a theoretical paper goes something like this. I read the introduction and then start at the next section full of determination, but recoil at the sight of the first equation and fast forward to the discussion. I can't make heads or tails of what is in between, which irritates me. After all, I am sure I was able to do integrals in high school. What frustrates me even more is that I have to accept that the conclusions drawn in the discussion follow from what is said in the middle bit and that what is done in there is justified.

If you are like me (or if you don't even pick up a theoretical paper in the first place) you may like to know that we are in good company. Apparently, Theodosius Dobzhansky once admitted to treating the publications of Sewall Wright much in the same way as I have just described. Of course it shouldn't be this way. We should all be able to judge for ourselves if a theoretical model makes sense or not, just like we are able to judge whether any particular experiment or field observation justifies the conclusions drawn from it. Furthermore, if a model leads to an interesting insight, we would like to be able to understand the argument.

So, where to start our quest to demystify the gobbledegook? Here, we have a small book written by one of the more prolific model builders in evolutionary ecology with a title that sounds like she is talking to us (and not to her modelling friends). It turns out to be just the thing we need. Written in an accessible style ("chatty" as she calls it), Kokko takes us on a tour through all the main branches of theoretical biology: population genetics (1- and 2-locus models), quantitative genetics, optimization models, game theory, adaptive dynamics and the enigmatic 'individual-based simulations'. Each technique is explained using a simple worked example, mostly taken from behavioural ecology. This way, the basic workings of the model are illustrated and pros and cons pointed out. Code for Matlab is provided for each of the examples. We learn what makes a quantitative genetics model, how to find an ESS and even how to interpret those dreaded 'PIP-plots'.

Experienced theoreticians will snub this book, but for us mortals it is a very useful publication indeed. Of course, do not expect to be able to build complicated models after reading this book or to understand everything written by the likes of Russ Lande or John Maynard Smith (or Sewall Wright). But it should help making it all a bit less mysterious. That is how Kokko intended this book: as an inroad into modelling and a primer for further reading. Somewhere in the book she says "If reading this book helps at least one empiricist in interpreting at least one important theoretical paper more thoroughly than he or she would otherwise have achieved, I will consider my effort worthwhile." She can rest assured that this goal has been achieved.

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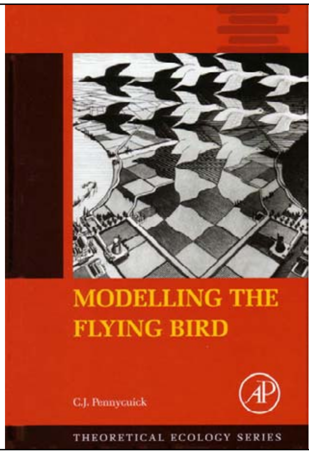
Pennycuick C.J. 2008. Modelling the Flying Bird. Academic Press, Oxford. ISBN 978-0-12-374299-5. Hardback, 480 pp. Euro 60.



Last September I encountered an example of what Carl-Gustav Jung might have called 'synchronicity'. Colin Pennycuick's massive new book and Thomas Alerstam's recent paper on *Flight Speeds among Bird Species: Allometric and Phylogenetic Effects* arrived on my desk nearly at the same time. This caused no small amount of confusion, since I am currently in the process of revising my *Simple Science of Flight*, and have to make up my mind on how to deal with the rapid evolution of our understanding of animal flight since 1990. I reviewed John Videler's *Avian Flight* for Ardea a few years ago. David Alexander's *Nature's Flyers*, Steven Vogel's *Comparative Biomechanics*, and recent books on insect flight are on my shelves. I do attempt to keep up with the literature.

Let me start with the paper by Alerstam *et al.* (PLoS Biology, 2007, volume 5, pp. 1656–1662). It deals with the explanatory power of aerodynamic scaling rules, in particular those that relate cruising speed to mass and wing loading. The authors state that mass and wing loading account for only a limited proportion of the variation in flight speed. In their opinion, the compression of the observed speed range is the result of evolutionary restrictions, which counteract the low flight speeds calculated for species with low wing loading and the high speeds calculated for species with high wing loading. The final conclusion, in their own words, is that "…functional flight adaptations and constraints associated with different evolutionary lineages have an important influence on cruising flapping flight that goes beyond the general aerodynamic scaling effects of mass and wing loading."

Looking at *Modelling the Flying Bird* from this perspective, I cannot help but wonder how to reconcile the views of Alerstam and Pennycuick. Both approaches have their strong points, both have drawbacks. In his new book, a much expanded version of his *Bird Flight Performance: A Practical Calculation Manual* (Oxford, 1989), Pennycuick reiterates the position that understandably and rightfully made him famous: calculations based on aerodynamic principles are unavoidable if one wishes to understand the physical basis of animal flight. Biology is one of the natural sciences; if one ignores physics one is bound to cause problems that reduce explanatory power. In my humble opinion, Pennycuick overstated his case when he wrote *Newton Rules Biology* (Oxford, 1992), but Newton certainly rules the physical constraints that the animal kingdom has to cope with. I consider it more appropriate to assert that Darwin and Newton Rule Biology, and that they do so together, not as opponents. In Steven Vogel's words (private communication): "Newton and Darwin are life's co-conspirators." A book that advocates this point of view, however, has not been written yet, at least not for avian flight. Alerstam steps in Darwin's shoes, Pennycuick is Newton's faithful disciple. Apparently, reconciliation is not yet possible. Nevertheless, I keep hoping it will occur before I die.

Modelling the Flying Bird, at 480 pages and a corresponding price, is indeed a massive book. Its core is a richly annotated, densely filled manual for the current version of the computer program that Pennycuick first presented in *Bird Flight Performance*. Most of the shortcomings of the earlier program have been taken care of; in the course of 16 chapters a lot of useful ancillary information is now provided. Chapter 1 deals with the computer model called *Flight*, chapter 2 with the atmosphere, chapter 3 with level flight. Curiously, Pennycuick does not present an explicit discussion of the wing-beat cycle in flapping flight. Simply put, flapping wings act like a two-stroke engine, the downstroke being the power stroke, most effective when the flight speed is substantially higher than in a glide. Chapter 4 deals with vortices, chapter 5 with feathers, chapter 6 with bats, and so on. I particularly like Pennycuick's summary description of the differences between the lungs of bats and of birds. I knew that the lungs of birds are better ventilated than those of mammals, but his Figure 7.9 on page 201 was new to me. There are numerous other little gems as well.

However, I have yet another perspective to cope with. I was trained as an aeronautical engineer, so I feel qualified to present my concerns about Pennycuick's approach to engineering in some detail. As part of meeting the requirements for acquiring a MS-degree I participated in a four-person group assigned to developing a preliminary design for a future competitor of the Fokker Friendship (it was 1959). We had to argue and agree on the propeller diameter, the cockpit window streamlining, the choice of undercarriage, and countless other details. All four of us had taken the required undergraduate courses in aircraft performance, based on textbooks similar to the one by Pennycuick. Though these were useful, they did not deal with the nitty-gritty of such matters as the effects of flight speed and power loading on propeller efficiency and the need for fairings between wings and fuselage.

It is appropriate to present the story of the fairings of the Douglas DC1 here, because it bears directly on Pennycuick's treatment of the 'body drag coefficient', a cornerstone parameter in his computer program. Early wind-tunnel investigations with models of the DC1, the precursor of the famous DC3 Dakota, suggested that the plane would have abominable handling characteristics and excessive drag at low flight speeds. The Douglas design team could not resolve the problem, and went to Theodore von Kármán, one of the pioneers of modern aerodynamics. Professor von Kármán, though a famous theoretician, did not bother with calculations, but crawled into the wind tunnel with a wad of painter's putty, and proceeded to liberally fill the corners between the fuselage and the wings. After the necessary smoothing of these fillets, he crawled out and asked the crew to restart the tunnel. To their surprise, the nasty low-speed behaviour had disappeared completely (*The Wind and Beyond*, by von Kármán & Edson, 1967, Little/Brown, Boston, p. 171). The anticipated top speed increased as well. In Pennycuick's terms, the body drag coefficient had decreased. A little at high speeds, a lot at speeds approaching stall. Fairings can do wonders, if only you know where to put the putty.

Since the appearance of *Bird Flight Performance*, Pennycuick had to revise his estimate of the body drag coefficient more than once. His original choice was 0.4, based on wind-tunnel tests with frozen bird bodies without wings. Swedish wind-tunnel studies with *Anas crecca* and *Luscinia luscinia* in flapping flight forced him to revise his estimate. The 'default value' he now advocates is 0.1, fully four times as small. In *Modelling the Flying Bird*, Pennycuick claims that the early estimate was not representative because the feathers of a frozen bird cause much turbulence in the wake behind a flying bird (Figure 3.4, p. 56). I venture another explanation, one familiar to aeronautical engineers: the "interference drag" between wing and body is *negative* for wings attached to the body at shoulder height. When fuselage and wings are joined, the drag becomes *less* than the combined drag of the two of them separately. This benefit arises because the downwash behind the wing helps to maintain an undisturbed flow over the dorsal feathers. I am exaggerating a little, but I do venture the generalization that birds should consider themselves lucky to have their wings attached at shoulder height. Fairings are not needed; they would also interfere with the necessity to fold the wings when not flying.

Incidentally, airplanes would also benefit if they had their wings at shoulder height, but that choice would lead to an extremely heavy or cumbersome undercarriage and to engines that would be hard to service because of their height above the ground. Nevertheless, some aircraft manufacturers tried. The giant Lockheed C5 cargo plane and its Russian nephews, the Antonovs 124 and 225, have shoulder-height wings. I appreciate the efforts of their builders, but these planes are evolutionary misfits. Only a few of them were built. Countless other stories of this type can be told (I will present a few in the new edition of *Simple Science of Flight*).

The enormous factual complexity of engineering design and development is not all that different from the evolutionary constraints and functional adaptations that Thomas Alerstam et al. refer to in their recent paper. Airplanes are designed with crucial inputs from a wide range of disciplines; their flight performance is just one of the many aspects that have to be considered before the design is finalized. Even then, development continues for years after the first flight of the prototype. A single computer program at the level of Pennycuick's *Flight* does not begin to fill the bill. Thousands of engineers are involved. Their interactions proceed much faster than in biological evolution because the collective human neocortex of these people aims explicitly for functional superiority. 'Intelligent Design' at work, literally. Apart from that, evolutionary constraints in aeronautical engineering are quite similar to those in biological evolution. John Anderson's magnificent *History of Aerodynamics* (Cambridge, 1997) supports my point of view. As far as I am concerned, Anderson's images of the evolution of fighters and bombers in the first half of the twentieth century (p. 356–357) deserve a place in the office of everyone studying the evolution of bird flight.

Seen from this perspective, Pennycuick's chapter 16, which deals with evolution in nature and in engineering, did not convince me at all. I smiled at his description of the 'Squirrel Barrier' (p. 451), but his apparent lack of insight in engineering evolution made me cringe. Clearly, he never read any of Henry Petroski's books, such as To Engineer is Human: *The Role of Failure in Successful Design* (Vintage, 1992). In biological evolution, nature stumbles around until it has found a functional solution fitting the circumstances. In engineering evolution, it is the never-ending sequence of mistakes and failures that pave the path toward Convergence. These processes are similar; one day they may lead to the mental convergence I dream of.

I am very disappointed in *Modelling the Flying Bird*. I had anticipated the opportunity of recommending it as a graduate sequel to my own book. I am terribly sorry, but I can't. Pennycuick indoctrinates; he fails to enlighten. His book is not suited for the classroom, because students will be snowed under by details they cannot judge. It is not suited for biologists' bookshelves either, because they might be seduced into using the Flight computer program without first dissecting it with their own professional tools. Pennycuick continues to promote his private version of orthodox Newtonian dogma. I admire his perseverance, but before too long Darwin will catch up with his zealotry.

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Dennis R. 2008. A Life of Ospreys. Whittles Publishing, Dunbeath. ISBN 978-1904445-26-5. Softback, 212 pp. Euro 26.99

In the age of new sagas, personified by birds equipped with satellite transmitters, Ospreys figure prominently. Never before have we been able to track birds almost real life during their peregrinations across the earth. Irrespective of study design, scientific like the work by the Migration Ecology Research Group of Lund University (T. Alerstam c.s.) or narrative like the website of Roy Dennis (www.roydennis.org), the results are equally fascinating. The power of Dennis's book lies in the background information provided for, especially, the Scottish Ospreys. The story has been told before: wiped out in the 20th century, then recovering on its own (but with a tremendous input of volunteers, to safeguard breeding sites from egg collectors), and now spreading into England and Wales. Roy Dennis is a wonderful advocate of Ospreys, and the love for the birds and their landscape permeates the book from cover to cover. The diary notes, of which I am not sure whether they were written at the time (if so, his handwriting has not changed at all), or prepared for the occasion of this book, are telling stuff, showing a perceptive eye for birds, man and environment. I am quite smitten with people whose enthusiasm for their study subject does not diminish over the years and decades. Dennis surely belongs to that group of people, along with a host of others walking the pages of this book, many credited with life-long involvement in protection and study of Ospreys. For those of us who prefer books over websites, *A Life of Ospreys* is an excellent choice, mixing factual information with personal notes, and illustrated with hundreds of photographs showing every aspect of Osprey life from egg through old age, from Scotland to The Gambia and Cape Verdes.

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