

Book reviews

HANDBOOK OF AVIAN HYBRIDS OF THE WORLD

By Eugene M. McCarthy

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This is a valuable piece of research that attempts to succinctly detail all known, putative, suspected and even additional potential avian hybrid crosses (both captive and natural). Printed on the front endpapers is a complex *Abbreviation Key* and, given that this is constantly required in using the book, it could have been usefully printed also on the back endpapers. Most text figures are maps that show hybrid locations/zones. The bibliography contains c. 5,300 full references. Exhaustive cross-referencing and indexing make the finding of any species/hybrid quick and easy.

The contents comprise: an *Introduction* that includes *Using This Book* (11 pp.), *Identifying Hybrids* (4 pp.), *Hybrid Zones* (9 pp.), *Hybrid Populations and Taxa* (4 pp.), *Causes of Hybridization* (2 pp.), *Underreporting* (4 pp.) and *Future Research* (2 pp.); the *Cross Accounts* (298 pp.); *Appendices 1 Canary Crosses* (6 pp.), *2 Dubious Reports* (4 pp.) and *3 Internet Citations* (4 pp.); *Works Cited* (159 pp.); and an *Index of English and Scientific Names* (68 pp.).

The 36-page *Introduction* explains the format with which the core of the book will later treat what is known of individual cases of hybrids and hybridization. Here we are introduced to the 32 abbreviations, later used within the *Cross Accounts*, that indicate various types and rates of hybridization, reversibility of crosses, which sex was which species in a given cross, fertility/viability of hybrids, the nature of wild breeding contact (e.g. breeding range overlap, altitudinal contact zone, etc.) and miscellaneous subjects (usefully including the identification of publications illustrating any given hybrid). Further, this section usefully reviews avian hybrids and hybridization. The author is to be congratulated for his thorough tackling of a subject that always arouses lively discussions among ornithologists. Here the *Introduction* suffers from disjointed presentation, however, with a tendency to jump from one topic back to another. One major point to which we would alert readers is to remind them that there is a huge, very relevant, literature on hybrids, hybridization and hybrid zones in non-avian organisms. A further point to remember is that the *Introduction* treats two extremely different topics. One is the study of individual hybrids. This covers ways in which they form and their fertility or sterility, and viability or inviability. The other is the discussion of populations interpreted to be of hybrid origin and to get here one makes a major biological leap to very different and diverse territory. One is now considering the evolutionary and genetic origin of individuals in a population perceived to be phenotypically intermediate between their

two supposed parental populations. We found ourselves constantly asking questions about statements and concepts where we felt the author had not really nailed down the issues involved or their complexity. For example, the discussion tends to focus on individual hybrid zones somewhat at the expense of going further to the evolutionary significance of why they cluster. In an Australian context, we note that Julian Ford's work is cited here more for individual cases and not so much for the broader evolutionary questions he was tackling. Some more examples follow.

The author discusses at some length whether he will refer to zones of hybridization or intergradation. True, choice of words can often be difficult and one sometimes just has to make a decision. We felt that his decision to use hybridization instead of intergradation risks missing the point of the science behind study of these zones. Hybridization will be used, we are told, instead of intergradation to avoid the impression that judgments are being made concerning proper taxonomic status. Surely, in the light of his full discussion about hybridization and taxonomic interpretation, the author has made precisely such a judgment here about the origin or cause of a population's phenotypic intermediacy and thus its taxonomic status.

The dogma in ornithology has long been that hybridization between supposed parental populations after their former isolation, i.e. secondary contact, is the cause of these zones. Occasionally, courageous and rather lone voices might have dared to express that that may not be the predominant cause of these zones. Contact zones, they have argued, might more often be 'primary' with the intergradation being due to selection along an environmental gradient, for example. To be sure, ornithologists have tried to discern whether zones of contact are primary or secondary but the dogma of secondary contact has prevailed. Now this notion is in the book's *Introduction* but it is confusingly delivered. It is here that the impact of Short's (1969), nothing if not influential, review on taxonomic aspects of avian hybridization (*Auk* 86, 84–105), though listed in the Bibliography, might have been discussed more. We noticed no reference to how different species concepts can guide one's interpretation of these situations. Nor is there reference to phylogenetic contexts in which one can discuss hybridization. An example is the notion that the genetic capacity to hybridize is itself something that can be shared by taxa and populations that are not each other's closest relatives. Arguably more important is that there is little reference to what we should expect to see in molecular data when these different views are tested at that level. These issues all seriously impact how one interprets these zones.

Use of the more conservative term 'intergradation' often can imply that the data to discriminate between the two alternative hypotheses of primary and secondary contact are not in hand. More importantly then, we would not yet be in a

position to interpret a given zone's evolutionary history and significance. Once ascribed to hybridization, one is invoking all sorts of interpretations that may or may not be defensible. This is an old issue, we admit, but the advent of molecular data has reinvigorated it. Molecular studies that could have been cited here came to mind to highlight this point. In particular, there is the body of work on Australian magpies by Jane Hughes and her students (e.g. *Emu* **103**, 337–343) and R. Ogden and R. Thorpe's (2002) work on Caribbean lizards (*Proceedings of the National Academy of Science*, USA **99**, 13612–13615). In Australia, the surface is just being scraped to use molecular data to build on the work of J. Ford, L. Short, R. Schodde and others on zones of intergradation. Aside from the landmark studies on magpies from the Hughes lab, work on the Australian Ringneck (*Barnardius zonarius*) (Joseph, L. and Wilke, T. (2006) *Emu* **106**, 49–62), though published too late to appear in this book, has shown how some zones interpreted to be secondary in a species complex may well be secondary and others primary. Other recent work has shown that in the Singing Honeyeater (*Lichenostomus virescens*) (Joseph, L. and Wilke, T. (in press) *Journal of Biogeography*) the weight of evidence currently favours primary intergradation for all of its putative zones of intergradation. Notably, the author has not cited earlier morphological work in support of this alternative hypothesis (Wooller R. *et al.* (1985) *Biological Journal of the Linnean Society* **25**, 355–363).

Almost inevitably in a book of this sort, authors run a further risk that is similar to the kind just illustrated of getting into deep water when they tackle geography and taxonomy beyond their home turf. Some do it better than others, who come adrift, and in this book we see hints of the latter. We are told with no hint of the example's true complexity that the 'Adelaide Rosella, *Platyercus adelaidae*, is the natural hybrid of [the Crimson and Yellow Rosellas] *P. elegans* and *P. flaveolus*' respectively, and that its distribution can be viewed as a hybrid zone. This relegates the complexity introduced by clinal variation within the Adelaide Rosella, not to mention the occurrence of Adelaide Rosella-like birds hundreds of kilometers away along parts of the western foothills of the Great Dividing Range, to insignificance. Conversely, the author's description of how the subspecies of the Galah (*Eolophus roseicapillus*) geographically contact each other does not reconcile with the most recent primary discussion (Schodde, R. and Mason, I. (1997) *Zoological Catalogue of Australia*, Volume **37.2**, CSIRO Publishing) of the subject. This reflects not just the traps we are discussing here for authors of books like this but also the almost unforgivable situation that we in the Australian ornithological community still do not clearly understand the population-level diversity of this most familiar Australian bird. At least molecular work on the Adelaide–Crimson–Yellow Rosellas is in the pipeline (L. Joseph in prep.) to try and help rectify these sorts of

cases. And on it goes. The zone of contact in the Spotted Pardalote (*Pardalotus punctatus*) complex is cited with reference to Julian Ford's work as fitting an environmental mosaic model such that where sclerophyll and mallee meet these birds form a hybrid zone. That's fine but we should like to see acknowledgement that molecular data probably offer the only way to discern what different models predict in testable ways.

At the end of the day, these are reviewers' quibbles. We would not want readers to lose sight of the courageous and helpful synthesis that the author has assembled. We learned much from it and that is more important.

The bulk of the book consists of the *Cross Accounts*, presented in systematic order (of Sibley and Monroe (1990) *Distribution and Taxonomy of Birds of the World*, Yale University Press) with hybrids listed alphabetically within each family or group. It is thus frustrating to find 'Cross Accounts' printed at the head of each right hand page (and the book title, pointlessly in our view, atop each left one) when the family or families dealt with on each page would have been infinitely more useful there. The *Cross Accounts* summarise whether a hybrid occurs naturally or in captivity, the geography of wild crosses, fertility of hybrids, and rates of occurrence. When known the sexes of the crossing species are indicated and a symbol indicates if a cross is known to be reversible (i.e. in the parent sexes).

This is a largely impressive compilation of extensive data, widely dispersed in the literature, and while reluctant to point out trifles we did notice the following: within *Bowerbirds* (p. 211) the citations to Frith and Frith (1998) for the *Amblyornis macgregoriae* × *A. subalaris* cross, to Frith and Frith (1995) and to Frith *et al.* (1995) for the *Chlamydera maculata* × *C. nuchalis* cross, to Gould (1969) [which should read 1869] and to Iredale (1950) for the *Ptilonorhynchus violaceus* × *Sericulus chrysocephalus* cross lack the symbol the author states should be applied to publications that include an illustration of the pertinent hybrid (as these all do). The same omission is also true of the *Birds of Paradise* citations Frith and Frith (1996b) for the *Lophorina superba* × *Parotia carolae* cross (p. 230) and Frith and Frith (1996a) for the *Paradisaea rudolphi* × *Parotia lawesii* cross (p. 231). It must therefore be allowed that there may be additional such, trivial, omissions. In describing the *Ptilonorhynchus violaceus* × *Sericulus chrysocephalus* cross it is stated, 'it has the general appearance of a ♂ Regent,' when this hybrid actually has the general appearance of the other putative parent species (i.e. that of a male Satin Bowerbird).

There is, perhaps inevitably in such a massive compilation, some inconsistent treatment of theoretically potentially crossing taxa. For example within *Bowerbirds* the potential for crossing between *Amblyornis macgregoriae* × *Archboldia papuensis* is detailed, because the two species meet at an 'altitudinal contact zone', and yet even more likely potential bowerbird crosses, between species with overlapping breed-

ing ranges, are not (e.g. *Chlamydera cerviniventris* × *C. nuchalis* and *C. cerviniventris* × *C. lauterbachii*). Moreover, to follow the above theoretical *A. macgregoriae* × *A. papuensis* bowerbird hybrid treatment consistently within the birds of paradise (let alone other families) would involve so detailing every sympatric/parapatric polygynous species pair.

In browsing the *Cross Accounts* we were surprised to find under *Kookaburras* (p. 119), the author's conclusion that the Spangled Kookaburra (*Dacelo tyro*) is a putative hybrid between Rufous-bellied (*D. gaudichaud*) and Laughing (*D. novaeguineae*) Kookaburras as representing, in his terms, an inferred 'extensive natural hybridization'. McCarthy states that *D. tyro* 'is intermediate in morphology and range and is thus a PHP [putative hybrid product] of this cross'. While McCarthy does qualify his PHPs as denoting cases of 'probability, not certainty', we cannot see *D. tyro* as being any more morphologically intermediate between *D. gaudichaud* and *D. novaeguineae* than is presented by the geographical intermediate of countless other trios of congeneric species. Moreover while *D. tyro* is restricted to central southern New Guinea and the Aru Islands, *D. novaeguineae* does not occur on New Guinea or the Aru Islands (and, as *D. leachi* is also mentioned in this account, the author is obviously not confusing that species, which does occur on mainland New Guinea [but not on the Aru Islands] with *D. novaeguineae* that does not and is confined to Australia). McCarthy also considers *D. leachii* to be morphologically intermediate between *D. gaudichaud* and *D. novaeguineae* (but closer to the latter) and observes that it is also geographically intermediate, but does not allude to any specific implication of this observation. We find the interpretation of *D. tyro* as representing a putative hybrid inexplicable and would suggest that should there be many similar examples in this work, the results of the author's search for hybrids might be seen as far too inclusive.

Our latter comments should not be seen as significantly detracting from the great value of this work. Indeed it is highly recommend as an invaluable addition to every biological reference library and to all ornithologists with the slightest potential interest in or need for avian hybrid information. The mountain of molecular work to be done on zones of intergradation will benefit from reference to this book, for example. Unfortunately it represents another example (see also *Emu* 105, 95–96) of an, already expensive, OUP title unjustifiably (i.e. taking into account exchange rates and freight costs) priced a good deal higher in Australia than elsewhere. This is doubtless as frustrating to authors, wanting their work widely utilised, as it is to Australasians lacking access to an institutional library or budget.

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BIRD COLORATION

VOLUME 1. MECHANISMS AND MEASUREMENTS

VOLUME 2. FUNCTION AND EVOLUTION

Edited by Geoffrey E. Hill and Kevin J. McGraw

2006. Published by Harvard University Press, Cambridge, Massachusetts. Vol. 1, 589 pp., 32 colour plates, hardback, \$US95, £59, \$A160, ISBN 0-674-01893-1; Vol. 2, 477 pp., 32 colour plates, hardback, \$US95, £61.95, \$A160, ISBN 0-674-02176-2.

Regardless of the primary appeal of birds, be it the quest for diversity of the twitcher, the search for aesthetics by the artist, or the groping for understanding of the scientist, colouration looms large. From the electric brilliance of a hummingbird or fairy-wren, the exquisite patterns on the plumage of an owl-nightjar, or the Eskimo-like vocabulary my colleague Rob Magrath has used to describe the more humble plumage variation in white-browed scrubwrens, colours define our ability to recognise and appreciate birds to an extent rivalled only by song. Despite this, scientific progress in understanding the evolution of colour patterns has lagged behind the comparable investigation of song. Experimental manipulation of song is comparatively easy: record a song, play it back through a speaker, and watch what happens. Audiophiles interested in high fidelity reproduction of music and spies interested in eavesdropping have provided all the technology needed to measure and manipulate sound. There are a few tricks to be taken into account. For example, we need to be careful in assuming that listeners (e.g. a predator) can hear all the frequencies in a song, and we need to recognise that wavelengths attenuate differently depending on the environment in which they are transmitted.

Colour, by contrast, is trickier. First, birds see colours in a different and superior way to humans. Unlike humans, which have three colour receptors in the retina, birds have four, and the spectral sensitivities of these four are spaced in such a way that birds can see wavelengths we cannot, particularly in the ultraviolet, and discriminate in a more refined way among the colours that we can see. Second, given this difference, what appears conspicuous or cryptic may be quite different for birds and humans. Over the last decade there has been an explosion of interest in the consequences of these differences, leading to the development of new methods, new concepts and new theory. Australian birds have played no small part in these developments, particularly through John Endler's sophisticated investigation of the evolution of colour in bowerbirds and the ornaments with which they decorate their bowers, and the recognition of special mechanisms of colour production in parrots. Now Geoff Hill and Kevin McGraw have edited these two initially intimidating volumes in the first attempt to synthesise this rapidly growing field, and to allow novices to acquaint themselves

rapidly with the growing array of techniques that have been developed to deal with the superior visual capacity of birds.

Volume 1 deals with two broad topics. The first provides an overview of the measurement of colour and its perception in different environmental contexts. The second looks at the production of colour, starting with the chemistry and physics, and proceeding to the underlying biology, with chapters addressing hormonal, genetic and dietary determinants of colouration. While some of the 12 chapters are reviews of topics already treated reasonably in the primary literature, some topics are thoroughly reviewed here for the first time. The chapter on quantification of colour by Andersson and Prager fills a particularly important gap, and the chapters on physics and chemistry are to be commended for treating all the various mechanisms for producing colour in a common framework. Perhaps because I work on the superb fairy-wren, a bird where colour is produced by the structure of the feathers rather than its pigments, I enjoyed Prum's chapter on structural colours most, but all these chapters are clearly written and very well illustrated. The chapters on regulation of colour reveal considerable progress, but I am sure that the respective authors would agree that they highlight how often we are ignorant of the underlying biological control, and how much work remains to be done.

By contrast, Volume 2 focuses on the evolution of colour patterns in response to their functional role in signalling or in crypsis, and in the environmental context in which signalling takes place. Unsurprisingly, as sexual selection remains the hottest area in behavioural ecology, two of the longest chap-

ters are Geoff Hill's review of the role of female choice of male plumage in the evolution of colour patterns, and Griffith and Pryke's review of the benefits of female choice. However, many other topics are addressed. For example, Kilner reviews the colouration of nestlings and young birds, including the extraordinary mouth markings of nestling finches, and Amundsen and Pärn analyse the oft neglected topic of colouration in females.

Both volumes are augmented by sets of well-chosen colour plates that illustrate key concepts and examples. As might be expected, some illustrations are deeply striking, such as the skin caruncles of a velvet asity or the eccentric head-dress of a royal flycatcher, and they are always informative. Unfortunately, the colours in some of the plates in my review copy of Volume 2 were washed out. Despite the 20 authors, the editors have done a commendable job in maintaining evenness in style and feel. The authors are well chosen. Put simply, these will be the texts that guide the development of this fascinating area for the immediate future, and will have a lasting role as well. They are the most significant texts on avian evolution published for many years. It would be easy to quibble about the price, but in this case the works are of real substance and lasting significance. No student of bird colouration can afford to do without regular access to a copy.

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