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THE EVOLUTION OF AVIAN BREEDING SYSTEMS

By J. David Ligon

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Animal mating systems — the social and sexual relationships that males and females form in order to reproduce — once seemed quite straight-forward, especially in birds. It was simply a matter of enumerating how many partners of the opposite sex an individual of the species had during a breeding season or occasionally a lifetime. Scientists were typically males, so in most cases it boiled down to how many mates most males had. Most species were easily packaged into: one female to each male = *monogamy*; more than one female per male: *polygamy* (or to be more technically precise, *polygyny*). In the rare cases where females mated with more than one male it was *polyandry*; with *promiscuity* covering everything else or just those that are too complicated. Until fairly recently, much of the literature used this convenient terminology, often confidently assigning entire taxonomic groups to one or other of these categories. For example, David Lack, in his enormously influential 1968 book, *Ecological Adaptations for Breeding in Birds*, pronounced that almost all passerine families were monogamous, a statement repeated in print countless times since. If only it had been so simple! Lack's seemingly obvious observation — most birds clearly do breed in pairs (at least in the temperate northern hemisphere) — has provided the null hypothesis for a vast effort within contemporary ornithology. Initially, researchers studied the obvious exceptions to monogamy, but later focussed more closely on the behind-the-scenes behaviour of apparently monogamous species. The outcome has been a truly revolutionary re-assessment of avian mating systems.

As we all know now, the combination of far-ranging theoretical models, detailed observations, neat experiments and, especially, the advent of powerful molecular techniques, have changed our simplistic views of mating systems forever. Today, it is the norm for studies of those previously 'monogamous' species to show high rates of matings outside the sanctity of the pair bond. And the range of mating systems, even within the same species, may span the full range of the traditional categories. Mating systems research these days is a vast enterprise, encompassing increasingly complex combinations of ecology, genetics, behavioural observations and other highly specialised approaches. Hundreds of new studies and models, as well as revisions and techniques, are published in dozens of journals and books each year. Keeping abreast is a major undertaking. A critical and comprehensive review of the field, something that synthesised, analysed and summarised the field has been sorely

needed. This book provides a valuable, but inevitably incomplete, contribution toward this need.

David Ligon was one of the young pioneering biologists of the 1970s, whose field work (on African Green Woodhoopoes) helped to provide the findings that galvanised world-wide interest in cooperative breeding in birds. Since then he has worked on numerous other aspects of avian mating systems, most notably those of Red Jungle Fowl, at the University of New Mexico. And Australia and Australian ornithology played a key role in the birth of this book. It was during a sabbatical at the University of New England in 1990, that the first sections of the book were prepared. A decade later (the delay blamed primarily on a stint as Departmental Chair!), this big and ambitious book is the result.

From the first sentence, the reader is made fully aware that this treatment of mating systems is going to be thoroughly evolutionary in flavour. In particular, the importance of sexual selection is promoted as fundamental to our understanding of mating patterns and behaviours from a contemporary perspective. With this conceptual slant, considerable attention is given early in the book to explaining how sexual selection influences the evolution of morphology and behaviour in birds. The importance of this concept to the book's approach can be gauged from the fact that six of the main chapters are primarily related to sexual selection or the closely related field of mate choice.

Following the broad-ranging 'primer' on sexual selection and contemporary evolutionary approaches given in the Introduction, we move into two similarly conceptual chapters, 'Sexual selection: theories of female mate choice' and 'Ethological concepts and sexual selection'. The latter offers a very useful critique and comparison of the terms and concepts of the foundational period of the development of animal behaviour. This is useful because the concepts are often misused and poorly understood by more recent students of animal behaviour, whose orientation is primarily evolutionary and 'ultimate' as compared to the more 'proximate' approaches of ethologists. Currently, there is considerable antagonism between these two camps of animal behaviour. Ligon provides a welcome reminder (something of which Tinbergen himself was entirely cognisant) that a full understanding of animal behaviour requires both ultimate and proximate approaches.

The seven chapters that follow each deal in some detail with a major area of research activity over recent years (almost all conducted during the last two decades, an indication of the vigorous nature of this remarkably young field). These include: signals, both morphological (ornaments) and auditory (bird song); the role of parasites and fluctuating asymmetry; empirical approaches to the main hypotheses (such as 'good genes'); the role of phylogenetic studies; speciation; mate choice; and the role of parental care. (It is good to see that Australian groups such as the bowerbirds

and fairy-wrens are well covered.) Each of these fields is huge and the book attempts to review them all thoroughly yet concisely. This is not always successful; many a time one wishes for more detail or a little more background to a particularly complex issue or the full rounding-out of an example. But just how much bigger would this already large book then become?

The remaining six chapters of the main text concern recent ideas and field studies on those original classifications of mating systems, monogamy, polygyny and polyandry. They also cover issues that have received considerable attention within or around these systems: extra-pair copulations (the reality for most apparently monogamous species); cooperative breeding; and lekking.

The concluding chapter is an attempt at providing some guide to the research priorities that emerge from this vast arena of avian evolution. As is obvious to the reader that gets this far, despite the prodigious efforts expended on a bewildering array of species from every remote corner of the globe, almost every subfield requires more study. Nonetheless, Ligon suggests that there are some areas that may be especially theoretically fruitful, as well as challenging, for future work. These include more detailed phylogenetic studies of male ornaments and display traits, the multiple role of hormones (especially testosterone) in sexual selection, the role of 'sensory bias' in mate choice (are females predisposed to select certain types of stimuli) and the role of sexual selection in speciation. Particularly fascinating topics include the question of multiple ornaments, especially those other than plumage — wattles, caruncles,

snoods, knobs, etc., and the significance of carotenoids as indicators of male quality. Why are so many of the former apparently irrelevant to mate choice?

This is, quite clearly, not one of those books that one settles down with at the end of the day. Rather, it has been written as a comprehensive guide to some of the influential debates and concepts of contemporary evolutionary biology (much of which just happens to have been based on studies of birds). As such, however, it is not always as satisfying as it could be. One problem facing the author was undoubtedly the sheer volume of material being covered and the overwhelming deluge of information and contrary views presented in the literature. What many readers need is not only the essence of these debates, but also some assessment of the relative strengths and weaknesses of the arguments. Ligon seems to have been at pains to be fair to everyone's views and opinions, but has been reluctant to state where his beliefs lie and perhaps also which ideas he feels are unsustainable. This may be inevitable when attempting such a vast and rich field but it does significantly diminish the value of this major and very important review to readers that are looking for a straightforward statement of which hypotheses are supported, and which are not. Nevertheless, this book will be the first port of call for those seeking material on the topic for teaching, for postgraduates getting into the subject, as well as for active researchers in the field.

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