BOOK REVIEWS

Ménages à Plusieurs

Dunnock Behaviour and Social Evolution. N. B. DAVIES. Oxford University Press, New York, 1992. xiv, 272 pp., illus. $70; paper, $28. Oxford Series in Ecology and Evolution.

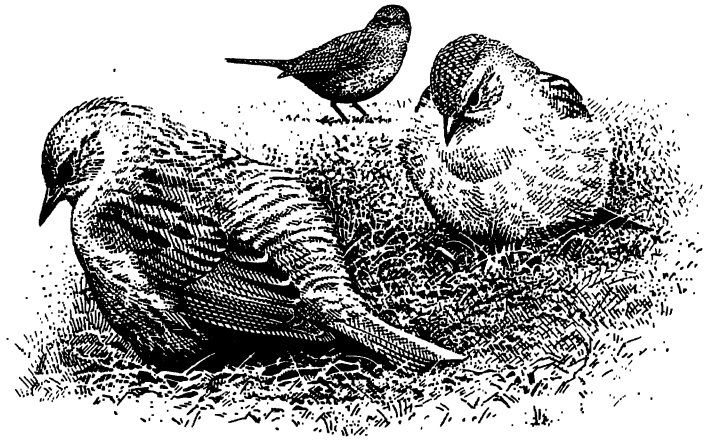
Like humans, but unlike most other vertebrates, approximately 90 percent of bird species form socially (though not always genetically) monogamous pairs whose members frequently divide parental care duties. Is social monogamy prevalent in birds because two parents are necessary to breed successfully, or because ecological conditions restrict opportunities to acquire additional mates? A decade ago, several researchers discovered that a common European bird, the dunnock (*Prunella modularis*), exhibits an extraordinarily variable mating system that has the potential to provide answers to these questions. While almost half of dunnock breeding groups are monogamous, the remainder are divided between polyandrous trios of a female with two males, more complex polygynandrous groups of two or more females with two or more males, and occasional polygynous trios of a male with two females. In this monograph Davies summarizes a decade of work analyzing how the different mating systems of dunnocks arise and their social and reproductive consequences.

Although Davies touches on topics ranging from precopulatory displays to the reasons why dunnocks succumb to nest parasitism by cuckoos, the book's core is a series of chapters that extensively document three main conclusions. First, different mating systems arise through the interaction of independent settlement on territories by each sex. Females settle in relation to the spatial distribution of food, occupying larger areas where feeding habitat (low shrubbery) is more dispersed. Various mating combinations then result from competition among males for space. For example, where female territories are small, a single male may monopolize one or sometimes two females. Where female territories are large enough to overlap two males, the male territory borders break down as they attempt to follow her around, producing a polyandrous group in which one male dominates the other. The effect of the food distribution on a female's territory size and subsequently her mating system is nicely confirmed by provisioning experiments.

The second theme is that reproductive conflicts of interest underlie breeding cooperation within all mating systems. Careful measurements of the breeding success of individuals in different mating combinations reveal that females do best when they can acquire two males to assist with feeding chicks and worst in polygyny, when they may receive no male assistance at all. Males, on the other hand, do best under polygyny, where a second mate more than compensates for lowered breeding success per female, and worst in polyandry, where shared paternity dilutes the benefits of increased brood size. Davies shows how these reproductive conflicts make sense both of preferences shown by individuals for alternative mating systems and of behavioral conflicts among group members. The latter are particularly apparent in polyandrous trios where the female attempts to copulate with both males, thus ensuring help from each later, while the alpha male attempts to prevent the beta from mating. The outcome is chaotic activity during the female's fertile period, with some of the highest rates of copulation known among birds.

Finally, Davies examines how allocation of parental care by males is modulated in relation to prospective payoffs. Where males have a choice of two females to assist, they appear to choose the option in which help will have the largest effect on offspring survival, which means the larger brood. Where more than two males are involved, individuals adjust either the degree of chick feeding (polyandry) or which female they assist (polygynandry) in relation to their prospective share of paternity in the brood. These studies provide the most detailed and convincing analysis to date of the factors that modulate parental effort in birds. With aid of some simple field experiments, Davies also shows how male dunnocks, without access to a modern molecular genetics lab, can estimate their paternity: they watch for the appearance of eggs within a day or two of having mated with the female.

Can dunnocks tell us why most other



Dunnock territorial behavior. "Two neighbouring males meet on the boundary between their territories and display, with their body feathers fluffed out. The female paired with the male on the right watches in the background. Males defend territories against males and females defend territories against females. Various mating systems arise depending on how the male territories overlap the female territories." [From *Dunnock Behaviour and Social Evolution*]

Dunnock and nest parasite. "Soon after hatching the cuckoo chick, still naked and blind, ejects the dunnock's eggs out of the nest, one by one. The dunnock never interferes, even as its reproductive success is destroyed in front of its own eyes." [From *Dunnock Behaviour and Social Evolution*]

birds are socially monogamous? Here we move onto thinner ice. In the final chapter Davies argues that the necessity for biparental care has been oversold and that limitations on opportunities to acquire additional mates are more important determinants of monogamy in birds, a distinctly mammalian point of view. If this is so, why have alternative mating systems, and particularly polyandry, not evolved more often in birds? Davies suggests that dunnocks may be exceptional both because their dependence on small insect prey makes additional male help highly beneficial to females, who consequently attempt to acquire additional mates, and because the habit of foraging in dense cover makes it difficult for an alpha male to evict a persistent sexual competitor. The answer then may lie in the economics of competition between males, and especially in the female's role in adjusting the payoffs.

My one criticism of Davies's book is that it contains little that has not appeared already in the primary literature. For those who have not followed the dunnock story over the past decade, however, it provides an engaging introduction to current questions about the evolution of mating systems, a model of what can be achieved by a judicious blend of field observation and experimentation, and a salutary reminder that solutions to important problems in behavioral ecology may reside in one's own back yard.

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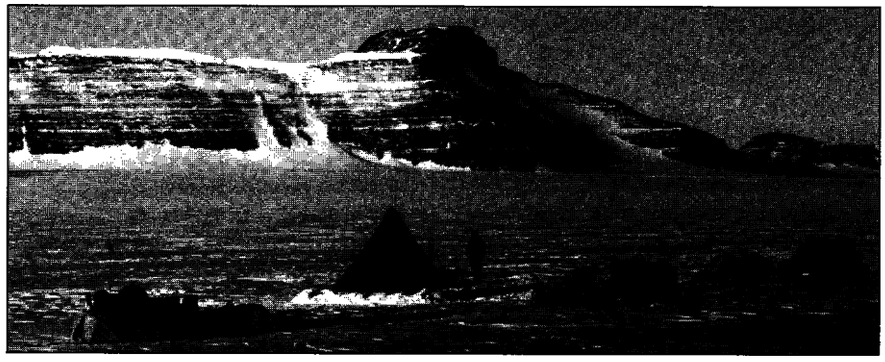
The Seventh Continent

The Geology of Antarctica. ROBERT J. TINGEY, Ed. Clarendon (Oxford University Press), New York, 1991. xxiv, 680 pp., illus., + map. $195. Oxford Monographs on Geology and Geophysics.

Antarctica, the seventh continent, is more than one and a half times the size of Australia and makes up about 9 percent of the earth's continental crust. It is largely covered by ice, only about 2 percent of its area being ice-free. Rock outcrops along the coast, in the Transantarctic Mountains, and in the Antarctic Peninsula make up the only surface expression of the continent beneath the ice. Although it occupies a sizable portion of the earth's surface, Antarctica was the last continent to be explored, owing to its isolation and harsh environment. Though first sighted in the early 19th century, it was not until the beginning of the 20th century that geological investigations were first undertaken in Antarctica as part of Robert Scott's *Discovery* expedition, and not until the late 1950s, beginning with the International Geophysical Year, that geological investigations became a regular occurrence each Austral summer. Since that time, the number and diversity of geological research projects have increased along with the number of nations sponsoring Antarctic research programs. Compared to that in other parts of the world in the early 1980s, however, the pace of geological research in Antarctica was still slow, and in many respects the visibility of Antarctic research and its integration with geological work elsewhere had been less than optimal. In a way, Antarctic geological research had been suffering from a kind of intellectual isolation that perhaps was related to its geographical isolation.



"Jurassic Kirkpatrick Basalt lavas at Scarab Peak, Tobin Mesa, Mesa Range northern Victoria Land. The basalt sequence in the Mesa Range has a stratigraphic thickness of at least 780 m. The black bluff forming the summit mesa is in the high-Ti unit which is about 100 m thick. The underlying Exposure Hill Formation crops out at the base of the long, low ridge trending away to the right (northeast) from Scarab Peak." [From *The Geology of Antarctica*; photograph by D. H. Elliot]

In this compendium of papers Robert Tingey has attempted to produce, for the first time, a comprehensive review of the geology and geophysics of Antarctica in order "to open up Antarctic earth science to a wider geological audience." In the context of Antarctic geological research in the early 1980s, when this book was conceived, there was a glaring need for such a review. A new generation of Antarctic earth scientists was emerging as existing national Antarctic research programs expanded and new programs, particularly the German and Italian ones, were begun. With this book I think Tingey will achieve his goal of stimulating wider interest in Antarctic geology.

The book's 19 chapters describe major aspects of Antarctic geology, from records of Archean and Proterozoic events in East Antarctica through the Cenozoic glacial and volcanic history of the continent. The last chapter discusses the special value of Antarctica as a meteorite bonanza. The authors of all the chapters except that on the Ferrar tholeiitic province are recognized experts on their topics. In keeping with the spirit of the Heroic Age of Antarctic exploration, in which certain things had to be done even if one wasn't fully qualified to do them, Tingey, a self-proclaimed nonexpert on the Ferrar, wrote this chapter as a literature review because, as he says, "an account of the Mesozoic tholeiites is needed in a book of this type." All things considered, I think he has done a commendable job.

I have two criticisms of the book. The first is that some parts of it are more out of date than would be suggested by the 1991 publication date and do not take into account some key discoveries that have both built on and changed the interpretations presented. The second relates to the undiscriminating treatment of isotopic ages. The discussion of isotopic ages of the Proterozoic and Paleozoic is somewhat rambling and confusing, and, perhaps because of the relative paucity of isotopic dates from Antarctica, there seems to be a tendency for all previously published dates to be perpetuated without caveat or reevaluation. Many of the rubidium-strontium isochron dates are rather tenuous, being based on only two- or three-point isochrons, and the dates discussed have not been recalculated with a common decay constant. The lack of a common decay constant translates to a difference of only about 7 million years, which is not large in terms of the general state of geochronology in Antarctica, and knowledgeable geochronologists will identify this problem easily. Nevertheless, it does indicate the need for Antarctic earth scientists to stop citing dates that are not defensible, as well as the need for close scrutiny of all dates that are to be used for interpretations of geological history.

Several chapters are particularly timely because they provide background to important unresolved controversies and ongoing research relating to the history and dynamics of the ice sheets. For example, the chapters "Cainozoic history of the Antarctic ice sheet" by Denton, Prentice, and Burckle and "The Cainozoic glacial record