Reproductive Sociality

Cooperative Breeding in Birds. Long-Term Studies of Ecology and Behavior. PETER B. STACEY and WALTER D. KOENIG, Eds. Cambridge University Press, New York, 1990. xviii, 615 pp., illus. $90; paper, $34.50.

Few aspects of social behavior have so seized the interest of evolutionary biologists during the last 20 years as has cooperative breeding in birds. For most of the world's roughly 9000 species of birds, nests are attended by one or both parents. Yet in a non-trivial fraction of birds (over 220 species thus far), additional attendants (helpers) have been documented. Such behavior poses a challenge to evolutionary biology because of the difficulty of understanding how it could have been shaped by natural selection: Why do reproductively mature individuals forgo breeding on their own, and why do individuals care for the young of others? Cooperative breeding also provides revealing situations for dealing with general problems for group living, potential matings between relatives, kin recognition, reciprocity, dispersal and life history, and strategies for obtaining limited breeding positions.

Here Stacey and Koenig and 30 additional authors confront these issues. More than half of the 19 chapters integrate 10 or more years of research; none involve less than 3 years. *Cooperative Breeding in Birds* thus emphasizes long-term studies with comprehensive data on demography and reproductive success and documentation of variation in social and life history behavior in temporally heterogeneous environments. Combining previously published work with unpublished data, new analyses, and discussion of controversies in this field, the book is an attempt to curate the enormous literature on cooperative breeding as well as to provide a forum on the subject. Perspective is added in the final chapter by J. N. M. Smith, who summarizes the forms and ecological correlates of cooperative breeding and assesses the hypotheses that have been advanced to explain the phenomenon.

The stereotype of cooperative breeders as extended families that defend territories throughout the year in limited habitat in stable environments, perhaps based on the first species that were studied extensively, does not stand. The 20 species covered in this book include non-territorial colonial species, flocking species, species in which the sexes defend different territories, species whose cooperative behavior varies with environmental conditions, and territorial species for which suitable habitat remains unused. Species vary in the number of active nests within the cooperatively breeding group, the number of females that contribute eggs, and the number of males observed copulating with breeding females. Species also vary in the genetic relatedness of helpers to breeders. Moreover, nine of the studies involved more than one study site and documented geographical variation in the dynamics of cooperative breeding.

As might be expected from the diversity of circumstances in which cooperative breeding occurs, there is no universal explanation of why some mature individuals forgo breeding on their own. In most species, helpers are young birds that delay dispersing and remain with their parents. Well-identified ecological constraints against dispersal and independent reproduction include the risks of dispersal itself (Woolfenden and Fitzpatrick for Florida scrub jays), the unavailability of suitable habitat or adequate resources for settlement (Koenig and Stacey for acorn woodpeckers; Walters for red-cockaded woodpeckers; Curry and Grant for Galapagos mockingbirds), and low reproductive success of pairs due to predators (Rabenold for stripe-backed wrens) or to uncertain or difficult breeding conditions (Emlen for white-fronted bee-eaters; Reyer for pied kingfishers). However, as is recognized by Smith and several others, species without cooperative breeding experience the same types of ecological problems. Noncooperative species in comparable habitats (generally tropical) have not been studied as extensively.

There are also numerous adaptional explanations for helping. In cases where individuals are likely to have contributed or fertilized eggs, "helping" may be a primarily selfish behavior directed toward one's expected offspring (Davies for dunnocks; Koenig and Stacey for acorn woodpeckers; Koford, Bowen, and Vehrenkamp for groove-billed anis). More complex hypotheses have been advanced for the deeper problems posed by the numerous species in which helpers are not breeders. The importance of kin selection, through which helpers may increase their inclusive fitness by caring for relatives, is clearly shown by Rabenold for stripe-backed wrens, Reyer for pied kingfishers, and Emlen for white-fronted bee-eaters. Related helpers may experience longer-term direct benefits such as inheritance of territory, as Woolfenden and Fitzpatrick show for Florida scrub jays. Particularly intriguing are the direct benefits to unrelated helpers. Ligon and Ligon show that green woodhoopoe helpers enlist the aid of unrelated nestlings in future attempts to acquire breeding status on other territories. Reyer demonstrates that unrelated male helpers in pied kingfishers become future breeders with the females they help.

In contrast, Craig and Jamieson argue that helping at the nest may not require explanation in terms of adaptation, because proximity of mature individuals to a nest with dependent eggs and nestlings may stimulate parental behavior. According to them, additional explanations may be ad hoc adaptationism. However, there are numerous examples of variation in helping among individuals that are explained by kinship and would be difficult to explain by exposure to the stimuli of eggs and nestlings. For example, in white-fronted bee-eaters, Emlen provides strong evidence of kin discrimination of helpers over five classes of coefficients of relatedness (0.0 to 0.50) to the breeders within a helper's clan. The hypotheses of kin selection, reciprocity, and demographic constraints have a deeply conceptual adaptional framework that neither requires nor freely admits ad hoc explanations.

There are several chapters that employ geographical comparisons to expose ecological constraints associated with cooperative breeding. Koenig and Stacey, comparing populations of acorn woodpeckers in California and New Mexico that differ in the distribution of breeding group size, suggest that group living can be forced on young either because both optimal and marginal habitat are limiting (California) or because territory quality is so variable that individuals are better off remaining on high-quality territories (New Mexico). Reyer, using doubly labeled water to assess energy expenditure of parental pied kingfishers at two African lakes that differed in fish species and fishing conditions, found that more parents had helpers (and greater numbers of helpers) at Lake Victoria where breeding required more energy. Geographical comparisons such as these will be important for future studies of other species.

In conclusion, *Cooperative Breeding in Birds* is a valuable compendium of data and ideas that will provide the impetus for further research on this exciting topic. The book is timely given the enormous literature in this field and the realization that a new generation of studies will be needed to test long-range predictions of rival hypotheses. For specialists and those developing a research interest in cooperative breeding it is indispensable. While there is much of interest to general ornithologists, sociobiologists, behavioral ecologists, and evolutionary biologists, not all of these may wish to read each data-rich chapter. It is thus unfortunate that there are no summaries for individual chapters. However, each chapter is subsectioned in detail, and the overall introduction by Stacey and Koenig and the summary by Smith point the way to studies that may be of particular interest to non-specialists.

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Caste Systems

Social Insects. An Evolutionary Approach to Castes and Reproduction. WOLF ENGELS, Ed. Springer-Verlag, New York, 1990. vi, 265 pp., illus. $52.40.

The castes of social insects provide a challenge to biologists at two levels of analysis: Why did they evolve, and how is a developing insect channeled into becoming a sterile worker or a reproductive queen? This volume describes advances in our knowledge of caste formation that have occurred in the 19 years since the publication of E. O. Wilson's classic *The Insect Societies*. The 13 authors, only one of whom is a North American, bring a decidedly European view. All groups of social insects are represented in the volume, and the literature reviewed is both extensive and up to date.

The emphasis is functional. The interplay of nutrition, hormones (especially juvenile hormone), and behavioral dominance in determining the fate of a developing social insect is presented in detail. Considerable information is also presented on the diversity of caste systems occurring in termites, ants, wasps, and bees. The resulting picture is more complex and interesting than the rather simple paradigm that has been adopted by most modelers of social evolution.

Especially noteworthy are the chapters by Michener on halictine (sweat) bees and xylocopine (carpenter) bees. Michener presents a new caste terminology for sweat bees, summarizes recent findings in reproduction and caste determination, and convincingly argues for multiple origins of true sociality within the Halictinae and the need to study variation among and within populations. He characterizes carpenter bees by their long adult life and their tendencies for extended parental care, mutual tolerance, and partial reproductive division of labor. This has led to the frequent evolution of facultative castes rather than true sociality in the Xylocopinae.

Engels and Imperatriz-Fonseca present a stimulating contrast between the reproductive strategies of meliponine (stingless) bees and honey bees, both based on advanced social colonies founded by swarms. Stingless bee workers are unmated but fertile, and they are responsible for a large proportion of the male offspring in a colony. Moreover, stingless bees are rarely completely monogynous, in contrast to honey bees.

The book does have its drawbacks. Bees are heavily emphasized (six of nine chapters), and termites and ants with their diverse caste systems are allocated only one short chapter each. Despite the book's subtitle, an evolutionary approach is nearly lacking in most chapters. Hypotheses concerning the evolution of castes from the viewpoints of inclusive fitness and the ecological costs and benefits of reproductive altruism are given brief mention at best. The authors generally do not recognize that patterns of evolution of social behavior can be best hypothesized by phylogenetic analysis of non-behavioral characters. The book is poorly edited for grammar, especially the contributions from authors whose native language is not English. A summary chapter should have been included to synthesize the diverse caste systems of the different taxonomic groups.

Nevertheless, this book presents a wealth of information on caste formation and reproduction in social insects that would otherwise be overlooked. It is a valuable building block for future research from a more evolutionary viewpoint.

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Physiological Darwinism

Nature as the Laboratory. Darwinian Plant Ecology in the German Empire, 1880–1900. EUGENE CITTADINO. Cambridge University Press, New York, 1990. xii, 199 pp., illus. $44.50.

In 20th-century America, we do not usually think of physiology as a field with much potential for Darwinian theorizing. Darwinism belongs to systematics, population genetics, ethology, and other related branches of outdoor biology, not to the laboratory-bound study of organic functioning; and it is hard to imagine that anyone might have ever thought otherwise. However, as Eugene Cittadino reveals in *Nature as the Laboratory*, some people have indeed thought otherwise: in the late 19th century, a whole school of German botanists once set out to interpret plant structures as physiological adaptations to the external environment, established and maintained through the action of natural selection.

Simon Schwendener, who initiated this movement with his book *Das mechanische Princip im anatomischen Bau der Monocotylen* (1874) and who trained or supervised many of its practitioners, was not himself a Darwinist. He was simply interested in applying mechanical principles to anatomical structures. However, his more radical follower, Gottlieb Haberlandt, who had a special interest in tissues engaged in photosynthesis, argued that the forms he studied were adaptations to the external environment. Haberlandt initially encountered strong criticism from scientists steeped in the morphological traditions of German botany, who considered structure and function as essentially unrelated phenomena and who insisted that trying to *explain* morphological forms was to speculate beyond the bounds of empirical science. Haberlandt countered that Darwinian theory justified his seemingly teleological assertions: natural selection had divised increasingly complex mechanisms for effecting photosynthesis and other processes as evolution proceeded.

Despite the criticism, Haberlandt soon convinced other botanists to investigate the adaptive significance of anatomical features, and many of them set out to test their assumptions in a variety of environmental settings. Georg Volkens studied transpiration in the deserts of Egypt and Arabia. An enthusiastic imperialist, he later conducted botanical expeditions to the new German colonies of East Africa, the Caroline, Mariana, and Marshall islands of the Pacific, and North East New Guinea. Haberlandt and Ernst Stahl separately worked at the Dutch experimental station established by Melchior Treub in Java. Heinrich Schenck and A. F. W. Schimper spent time working with the Darwinian naturalist Fritz Müller at his home in southern Brazil. The tropics held a special interest for all these investigators, since they assumed that most plants had originally evolved there. Temperate and arctic forms were simply specialized survivors that managed to adapt to the less favorable conditions further north.

According to Cittadino, these late-19th-century Darwinists had their greatest influence on the nascent science of ecology. He acknowledges that 20th-century ecology has been primarily concerned with the study of plant associations, not individual adaptation