without fully considering whether there is an alternative, more prudent strategy" (p. 2).

Stares describes in detail the military uses of space systems, the potential ways to attack or otherwise interfere with such systems, and the possible countermeasures to protect them. His description and analysis are fully documented and up-to-date. He demonstrates that the United States and the Soviet Union use space systems extensively and for similar purposes but accomplish their purposes in different ways: the United States uses a small number of highly sophisticated, multifunction, long-lived satellites, whereas the Soviets use a larger number of simpler, single-mission satellites that require much more frequent replacement.

Stares goes on to trace out a number of scenarios in which ASAT weapons might be used. In most such cases he finds that attack by ASATs would have only limited utility and would pose a strong possibility of escalation. "Even in the conflict scenarios in which ASAT attacks seem to offer some tangible benefits, the presence of alternative, nonsatellite systems and the adversary's ability to reconstitute space assets rapidly could significantly reduce the desired effect" (p. 141). Moreover, any benefits of U.S. use of ASAT weapons against Soviet satellites would have to be balanced against the potential loss of U.S. satellites in an ensuing ASAT duel. Since nondestructive methods exist for neutralizing the most worrisome Soviet space systems, Stares finds that the advantages of an arms control agreement limiting ASAT development, testing, deployment, or all three outweigh the drawbacks.

Even under such an agreement, the risk of covertly developed ASATs will remain, as will the possibility that non-ASAT systems (such as ballistic missiles) could be used to destroy satellites. However, the existence of such "residual" ASAT systems "is not a valid case against arms control. Rather, it is an argument against placing too much reliance on a small number of satellites, since they will become even more vulnerable in the absence of arms control" (p. 179). Stares argues that under an arms control regime, the threat from residual Soviet ASAT attack can be reduced to acceptable levels through increased system redundancy and enhanced satellite survival measures.

Stares suggests that U.S. policy makers "steer a middle course between outright prohibition and no constraint whatsoever" (p. 183). Since the balance of costs and benefits of ASAT development may change in the future, he calls for the United States to retain the option to deploy an ASAT at a later date. He sets out a number of unilateral measures that he believes the United States should conduct, such as improving the survival capability of U.S. space systems, maintaining a minimum ASAT research and development effort, and refraining from ASAT weapons tests as long as the Soviets hold to their previously announced ASAT test moratorium. He also argues that the United States and the Soviet Union should consider negotiating agreements such as a formal, limited-term, renewable ASAT test moratorium, a ban on space weapons, and guidelines for permissible antimissile research that would not result in the development of de facto ASATs.

In the final chapter, Stares brings the discussion back to ballistic missile defense, recognizing that ASAT limitations will inherently constrain SDI testing because the technologies are so similar. Indeed, "SDI promises to become a breeding ground for new generations of ASAT weapons if nothing else" (p. 181). However, in attempting to formulate an ASAT limitation that would still leave room for long-term research on strategic defense, Stares relegates SDI to a role that most of its critics would be comfortable with—a laboratory program that remains years away from developing deployable hardware and that refrains from running afoul of any conceivable Antiballistic Missile Treaty interpretation.

Resolving the ASAT issue requires that implicit or explicit decisions be made concerning SDI. Although it is likely that SDI policy will determine ASAT policy, rather than the other way around, this book makes a strong case for the urgency of addressing space arms control before it is too late.

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Avian Sociobiology

Population Ecology of the Cooperatively Breeding Acorn Woodpecker. WALTER D. KOENIG and RONALD L. MUMME. Princeton University Press, Princeton, NJ, 1987. xvi, 435 pp., illus. $55; paper, $16.95. Monographs in Population Biology, 24.

Cooperative breeding, in which an individual forgoes reproducing and instead helps another individual to reproduce, poses a potential problem to the theory of natural selection. The concept of inclusive fitness has provided the key to understanding the apparently altruistic nature of cooperative breeding in animals, at least on a theoretical level. At the empirical level attempts to understand cooperative breeding have often centered on birds. A number of long-term studies of the ecological and behavioral patterns associated with cooperative breeding are now coming to fruition, most notably those of Glen Woolfenden and John Fitzpatrick on Florida scrub jays, Jerram Brown on Mexican jays, and Koenig and Mumme on acorn woodpeckers.

The acorn woodpecker (*Melanerpes formicivorus*) exhibits perhaps the most complex social organization of any cooperative breeder so far studied. Acorn woodpeckers often live in family groups of up to 15 individuals. In California where Koenig and Mumme studied them, groups consist of one to four breeding males, usually one or two breeding females, and zero to ten nonbreeding offspring from prior nests. Each group defends an all-purpose territory including one or more granaries—trees riddled with holes for storing acorns—and produces only one nest at a time. Up to three females may lay in a single nest, and all breeding males presumably contribute to paternity of offspring. Breeders of a given sex are almost invariably closely related to each other, but breeding males are generally unrelated to breeding females. Offspring born into a group remain there into adulthood as nonbreeders until they either disperse and become breeders elsewhere or inherit and breed in their natal territory. Territorial inheritance occurs following the death of all breeders of the *opposite* sex in a group, an event that creates a reproductive vacancy.

There are two basic questions that must be answered before cooperative breeding can be understood: Why do offspring remain as nonbreeders in their natal groups for up to several years? and, once groups are formed, why do group members cooperatively care for young that are not their own? In this book Koenig and Mumme focus almost exclusively on the former. What results is perhaps the best single study of cooperative breeding in a vertebrate yet published. This book illustrates repeatedly how good information on demography can lead to an understanding of the evolution of social organization.

Koenig and Mumme's study of acorn woodpeckers began in 1971 (when the project was initiated by Michael and Barbara MacRoberts) and has continued to the present, often in collaboration with other people. This book uses mainly data gathered through 1982. It is not simply a compilation of the authors' earlier papers but contains extensive new information. The authors' primary approach was to band birds, census the population, and record nesting success. The results and analyses will be of wide interest to population biologists, and this book is a

gold mine even for readers without sociobiological inclinations.

Koenig and Mumme begin with an overview of the characteristics of their population and emphasize the strong dependence of the acorn woodpecker on acorn crops and granaries. Granaries provide a focus for group activities and define territories that may last for 12 or more years. Both clutch size and reproductive success are most strongly correlated with the number and energy content of acorns stored. Nests fail and territories are abandoned when acorn stores run out. The authors next analyze the effect of nonbreeders on the reproductive success of the group and conclude that their presence has little overall effect in this species and probably in most other cooperative breeders. Males tend to profit directly from living in cooperative groups, male survivorship being positively correlated with group size. Virtually all nonbreeders that survive to their first spring eventually obtain breeding positions somewhere. Koenig and Mumme conclude that space competition per se is not the critical feature of cooperative breeding systems because many other territorial species also face space competition. Whether they are correct remains to be seen; I found discussion of space competition one of the few poorly argued sections of the book.

The authors thoroughly analyze territorial inheritance in acorn woodpeckers and find that, although either sex may inherit the territory, inheritance by males is more common because of demographic patterns. The probability of handing down high-quality territories (ones with large storage facilities) to descendants is high. To understand thoroughly how natural selection affects fitness of long-lived individuals such as acorn woodpeckers, one must measure lifetime reproductive success. Koenig and Mumme are among the first to have long-term data on individual reproductive histories, although most of their study animals are presumably still alive. They calculate effective population size and conclude that acorn woodpeckers are not prone to an unusually high degree of inbreeding, despite their social organization. The opportunity for selection is relatively high.

The latter part of the book addresses why offspring are retained in groups. As in other cooperative breeders, offspring are constrained from dispersing and breeding on their own by limitation of resources, in this case granaries. The authors' analyses indicate that dispersal when possible is a superior alternative to nondispersal and helping, and thus ecological constraints have been paramount in the evolution of nondispersal and delayed breeding. The role of indirect selection in the evolution of helping behavior is explored, and it appears that important gain in inclusive fitness results from delayed dispersal. The major way nonbreeders enhance their indirect fitness is by increasing the survivorship of male breeders. Koenig and Mumme suggest that there is no selective advantage to helping per se and that this long-debated phenomenon may be selectively neutral. I find this suggestion plausible, but it is not likely to be embraced by all sociobiologists interested in cooperative breeding. Finally, the sharing of mates and nests is explored, and the analyses reveal that males in mate-sharing duos and trios enjoy enhanced fitness over males nesting singly but that females who nest jointly have lower fitness than do females breeding singly. Why a substantial proportion of males still breed solitarily and some females still nest jointly is not clear.

One of the most perplexing results in the book is the calculation that stored acorns represent only 4.6 percent of an individual's total energetic needs between December and June. The authors conclude that stored acorns cannot be the only or even the major source of food, yet throughout the book the importance of acorn stores is made obvious. My guess is that the 4.6 percent figure is based on faulty energetic analyses of acorns (possibly because very few individual acorns were analyzed) and that acorn stores actually represent a much larger fraction of each individual's total energetic needs.

I found little to quarrel with in this magnificent monograph and was continually impressed with the depth and thoroughness of the analyses. The book is well written and, in keeping with Princeton's tradition, well edited and produced. At times there is an over-reliance on tables, and figures would have illustrated data more effectively. The tone of the book is a refreshing change from that of other recent literature on cooperative breeding that is marred by egocentric and vitriolic exchanges. This book has none of that and reviews other work fairly and adequately. It would have benefitted from a broader perspective in places; discussion of work on other social but non-cooperatively breeding birds and mammals would have provided interesting parallels. As their study continues, the authors should consider simple experimental manipulations. The study so far has been strictly observational and correlational, and the one experimental manipulation described (adding granaries) is inconclusive because of small sample sizes. Manipulating the number of breeders and nonbreeders in a territory, territory quality, and sex ratios of broods, to name just a few possibilities, could provide very interesting information.

Above all, Koenig and Mumme's book underscores the value of long-term field studies, not only for the study of cooperative breeding but for an understanding of animal demography and social organization in general. Many critical questions in population biology can be answered only by such studies. This book is a landmark achievement and will have a major impact on population ecology and sociobiology. With Woolfenden and Fitzpatrick's equally impressive *Florida Scrub Jay*, also published by Princeton, cooperative breeding is now one of the better understood forms of vertebrate social behavior.

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A Social Insect

The Biology of the Honey Bee. MARK L. WINSTON. Harvard University Press, Cambridge, MA, 1987. xii, 281 pp., illus. $29.95.

In 1954 the Bee Research Association published *The Behaviour and Social Life of Honeybees* by C. R. Ribbands. Partly because Ribbands's book itself stimulated research it soon became out of date, past the stage when it could readily or usefully be revised. For many years there has been no single volume in English that deals solely and comprehensively with the biology and behavior of the honey bee. Mark Winston's book is an admirable and worthy successor to Ribbands's. If anything it has a somewhat wider scope, especially in dealing with the origin and evolution of honey bees and with honey bee anatomy.

I greatly enjoyed reading each chapter. But of particular interest to me were the sections on the division of labor among worker bees, swarming and reproduction, and the behavior and biology of tropical honey bees, which contain much that is recently discovered and reflect the special research interests of the author.

Winston provides one of the most masterly reviews I have read of the age-related activities of worker honey bees and how they can be adjusted to a range of interacting colony and environmental conditions, including amount and type of brood to be fed, adult population, amount of comb available, nest characteristics, amount of stored food, available forage, temperature and weather, and the colony's racial origin. It illustrates the complexity of the information we already have but strongly indicates that we still know remarkably little about how the individual bee actually perceives the task