

REVIEW

The Florida Scrub Jay. Demography of a cooperative breeding bird.—Monographs in Population Biology, No. 20. Glen E. Woolfenden and John W. Fitzpatrick. 1984. Princeton, New Jersey: Princeton University Press, 406 pp., 56 tables, 88 figures. \$45.00 hardcover, \$14.50 softcover.—In 1935, Alexander Skutch first described the phenomenon of “helpers at the nest,” birds in addition to parents attending to the needs of nestlings. In the ensuing 50 years, perhaps as many as several hundred species have been reported to be cooperative breeders. Although many of these remain almost unstudied, the best known is the Florida subspecies of the Scrub Jay, *Aphelocoma c. coerulescens* (a form geographically confined to Florida). This distinction is a result of the commitment by Glen Woolfenden of the University of South Florida, later joined by John Fitzpatrick, to a long-term demographic investigation of a population of the jay. This impressive book is a progress report on the jay investigation and includes thorough analysis of the first ten years of data (1970-1979) on the population biology of individually color-banded Florida Scrub Jays.

This monograph contains ten chapters and 13 appendices. The first two chapters introduce the investigation and the methods used. It is impressive that in these days of much ballyhooed field manipulations and perturbation experiments, the Scrub Jay data have been and continue to be collected via non-intervening acute observation on a rigorous sampling regime. In fact, Woolfenden has been quite outspoken about his desire *not* to manipulate the Scrub Jay system, in order to maintain the pristine condition of this study population. Chapters three through ten discuss aspects of the population biology of the Florida Scrub Jay and are titled: The Scrub Jay in Florida; The pair bond; Helpers; Territory; Dispersal; Reproduction; Survivorship and the life table; and Evolution of Florida Scrub Jay sociality. Each of these chapters begins with a synopsis and ends with conclusions based upon the data presented in the chapter. Considering the amount of data found in most chapters, both the synopses and conclusions are quite welcome. Also included are 33 “case histories”; succinctly written, these describe details of the social history of particular family groups of jays. The case histories are included to elaborate aspects of discussion or to note exceptions to statements about social patterns. They are interspersed throughout the first half of the book and do much to emphasize further the individuality of the jays.

Woolfenden and Fitzpatrick draw numerous important conclusions from their wealth of data and are careful to distinguish conclusions from speculations and “best guesses.” I have space here to discuss several findings and interpretations. First, who are helpers and whom do they help? Florida Scrub Jays are monogamous. The majority of helpers are one year old jays that remain in their natal territory and help their parents raise more young (siblings of the helpers). Approximately half of the breeding pairs of jays have helpers in any breeding season, and the average group size is three jays, the breeding pair and one helper. The sex ratio of yearling helpers is 1:1, but older helpers are predominantly males. Many female helpers (but relatively few males) disperse in the fall of their second year (at 14 to 17 months of age), and they move an average of three and a half territories (slightly more than one km); as is true for most birds, females disperse farther than males. In family groups with more than one helper, there is a rigid dominance hierarchy among helpers of the same sex, and the oldest male helper is in the best position to gain a breeding territory in this population, which exists at carrying capacity. Securing a territory may be accomplished in several ways: (1) taking over a territory made available by the death of or injury to the owner; (2) “budding” off a separate territory from the group territory; (3) inheriting the group’s territory should the breeding male or breeding pair disappear; or (4)

establishing a new territory between existing territories. The first two account for more than 80% of the known instances of males obtaining breeding space. Helping benefits male helpers because it provides opportunities for obtaining territorial (=breeding) space. Although this is primarily a waiting strategy, I was intrigued with the possibility that helpers intent upon obtaining breeding space might actively remove a neighbor. Woolfenden and Fitzpatrick (pp. 272-73) note cases where a breeding adult's territory was seen to be invaded by a neighboring helper of the same sex shortly before the breeder's disappearance. Insofar as the disappearance of a Scrub Jay probably means death (see below), one is left wondering to what extent a young jay will go in order to secure a spot in the breeding population.

Woolfenden and Fitzpatrick argue that color-banded jays that disappear have died rather than dispersed beyond the study area. They support this claim with several types of evidence: (1) the well-known restriction of the Scrub Jay to the extremely patchy scrub habitat; (2) known dispersal distances for large numbers of jays in the study population [mean for males: 0.90 territories or 304 m; mean for females: 3.44 territories or 1,163 m]; and (3) surveys conducted in scrub habitat beyond the study area. Since dispersal is a major component of the social system of the Florida Scrub Jay, such information on dispersal distances and fate of dispersers is critical. Most investigators of avian social systems work with open populations in which it is not known whether individuals that disappear have died or simply dispersed beyond the study area. Woolfenden and Fitzpatrick can say much more about the "costs" of dispersing if, as they claim, the fates of dispersers are known.

Pairs of jays with at least one helper fledge 1.5 times more young than do pairs without helpers (having more than one helper does not increase fledging success). How do helpers help? It is perhaps surprising that, despite helpers feeding nestlings, this activity does not directly lead to more fledged young or young fledged at greater weights than young produced by pairs unassisted by helpers. Parents assisted by helpers simply feed their young less themselves than do unaided parents. Rather, helpers appear to decrease the probability of nest loss through predation. Predation (the evidence implicates snakes in particular) is the primary cause of nesting failure, far exceeding all other losses. Woolfenden and Fitzpatrick speculate that, because helpers feed nestlings and thereby relieve parents of some of the feeding burden, the breeding female can spend more time at the nest and by her presence deter at least some predators. Those of us working with the breeding ecology of birds that build open cup nests are well aware of the high percentage of nest losses to predators. I therefore find the relationship between helpers and reduced nest loss intuitively satisfying; what better way for helpers to help?

On to kin selection. In 1975, E. O. Wilson included discussion of the Florida Scrub Jay social system in "Sociobiology": "Thus the closest kin are strongly preferred - and a basis for the evolution of the altruistic trait [helping] by kin selection exists" (p. 454). In contrast to Wilson's interpretation, Woolfenden has always maintained that the major benefits to helpers are tallied in individual, Darwinian fitness units - that helpers remain on the natal territory and help because they gain in future individual fitness as a result. The data presented here offer some support for that claim. First-time breeders do not produce as many fledglings as experienced breeders, and first-time breeders that have helped more than one year previously fledge more young than those that have helped only one year (although, curiously, their survival rates once they become breeders are lower). While it is true that pairs helped by at least one helper raise more young to independence than do unassisted pairs (mean annual production: 1.45 vs 0.90 independent young), the authors view these Hamiltonian gains as minor and supplemental to the helpers' own Darwinian future gains that apparently result from delaying dispersal until an opening arises in the

population. Helpers would do better in terms of their inclusive fitness to themselves breed rather than help. In this population at carrying capacity, however, the option of breeding is nearly closed for a young jay. Offspring must wait for an opening, and while waiting, they remain on their natal territory and help their parents raise their siblings.

The final chapter of this monograph is a discussion of the evolution of Florida Scrub Jay sociality. Woolfenden and Fitzpatrick argue the demography of the jay population—a population at carrying capacity in a distinct, patchy habitat saturated with long-lived breeders, and characterized by high juvenile and prebreeder survivorship—favors the evolution of delayed dispersal, delayed breeding, and helping, even in the absence of kin selection. Most intriguing, they suggest that even slight changes in the demography typifying the Scrub Jay population could lead to more complex social systems, as are seen in other cooperative-breeding corvids. In particular, a change in the probability of young dispersers becoming established as breeders can have dramatic influence on the social system as modelled by the authors.

I found remarkably few typographical errors for a book of this size. Several of the coefficients of relatedness in Table 5.3 are miscalculated. On p. 65, the authors base an argument for the cost of female dispersal on a comparison of proportions producing a “difference” that does not, however, even approach statistical significance. But, these are relatively minor faults.

There is a final point worth mentioning. The Scrub Jay investigators have been fortunate to have had access to the many hectares of protected scrub habitat on the Archbold Biological Station in Highlands County. It should be of particular interest to Florida readers that non-protected oak scrub habitat occupied by Scrub Jays decreases in area yearly. In addition to the jays, there are many vertebrates, invertebrates, and plants restricted to or most common in scrub habitat, and this entire community is under siege by land-hungry Floridians. Hundreds of hectares of scrub habitat per year are developed or degraded, and only a small fraction remains of the original extent of scrub habitat. The protection afforded by the Archbold Biological Station has made possible the jay project and one hopes will insure the future of the study. It is therefore fitting that this monograph is dedicated to the memory of Richard Archbold, one of the last of the great explorers and renowned patron of the biological sciences. It is sobering to reflect that the extraordinary social behavior of the jays—this best-studied example of a cooperative-breeding bird—might never have been known if an investigation had been started in a non-protected patch of scrub habitat destined for the bulldozer or if a “Woolfenden” type of biologist had attempted to begin such a project in the year 2000 rather than 1970.

Potential readers should be aware that this is a book primarily for biologists. Students of animal social behavior and population biology will surely benefit from reading it. Non-biologists interested in bird behavior and ecology will without doubt find much for them here also, although they may encounter some esoteric patches in the theoretical and mathematical discussion in the final chapter on the evolution of jay sociality.

In summary, Woolfenden and Fitzpatrick's monograph is an extremely important, well-written treatment of the social behavior and population biology of a cooperative-breeding bird. I doubt that there is a current investigator of any other such system who could hope to match this effort with present knowledge—the data for no other species are as extensive as those presented for the Florida Scrub Jay. I am already anticipating a subsequent edition . . . which I presume will appear after the second decade of data collection. I thank Oscar Owre for comments on this review.—**Randall Breitwisch**, Department of Biology, University of Miami, Coral Gables, Florida 33124.