
"In this book, we and most authors agree that unless wildlife has some use to people, then wildlife will not be valued by people. If wildlife has no value, then wildlife and its habitat will be destroyed to make way for other landscapes" (p. 3). These sentences clearly identify the utilitarian or "use-it-or-lose-it" philosophy of conservation advocated in this volume. Arguments over the ethics of human exploitation of other animals are not developed; rather, sustained harvesting of wildlife is presented as the most effective means of conserving biological communities in the Neotropics. The contention that wildlife should be conserved for its own sake has provoked much resistance, even in North America where economic hardship and population pressures are far less severe than those in most Latin American countries.

The purpose of this volume, therefore, is to document how wildlife is exploited and to offer prospects for the sustained use of wildlife as a basic tenet of conservation policy in the Neotropics. The extent to which each of the diverse chapters in this volume succeeds reflects the spotty knowledge of the basic ecology and natural history of many of the most intensively harvested species. Taken as a whole, however, the book succeeds very well in presenting a case for sustainable exploitation rather than just preservation of wildlife.

Many chapters in Robinson and Redford's book include kinds of data that seldom appear in ecological journals. For example, hunter interviews and estimates of income from ecotourism and the export of parrots, teigu (Tupinambis spp.) lizard skins, and rhea feathers are presented. Some of these figures are surprising. For example, between 1976 and 1984, nearly 8,000 k of rhea feathers were exported from Argentina (p. 18). Average annual export of teigu lizard skins (mostly for cowboy boots) numbers 1,250,000 skins (p. 303). At least 1.4 million parrots were exported from Neotropical countries between 1982 and 1986 with a retail value of $1.6 billion. These figures are not viewed as a conservation problem (e.g., evidence of overexploitation) but as an indicator of a conservation opportunity. The basic argument is that preserving the habitats of these economically important species will guarantee the continued availability of these sources of income. Even the parrot trade, which has been blamed for the declines and even extinction of some species, can be used as a tool for habitat preservation if parrots can be harvested from nest boxes in the wild (Chapter 24). Similarly, ecotourism can provide local employment, revenue, and even funding to help maintain the infrastructure of local parks and preserves.

The book covers diverse taxa (i.e., herps, mammals, and birds) and very different systems of exploitation such as sport hunting, market hunting, and game ranching. Given this diversity, we believe that the optimism generated by studies of economically important wildlife must be tempered by a realization of some limitations on wildlife use in the Neotropics. Silva and Strahl's chapter on human impacts on Cracidae is particularly sobering. At first glance, cracids appear to be ideally suited for exploitation by hunting. Cracids contribute by far the most avian biomass taken by hunters in most forested areas and are remarkably abundant in many forests. Some species average more than 50 kg/100 ha, a biomass greater than that of all the breeding species of a typical temperate zone forest bird community. In some Venezuelan forest sites, guans (Penelope spp.) have population densities as high as 37 individuals/100 ha, which would likely make them one of the 5 or 10 most abundant species in the community, a remarkable figure for such large (> 1,100 g) birds. As Silva and Strahl's data show, however, forests subjected to even moderate hunting pressure have much lower cracid population densities. Using a simple population model, they argue that cracid productivity is too low to withstand the kinds of continuous hunting pressure that more productive temperate game animals can withstand. Cracids can probably only withstand local hunting in extensive forest preserves. The loss of such dominant frugivores as guans and curassows may lead to a reduction of seed dispersal and long-term changes in plant communities in fragmented habitats where hunting is intense.

The low productivity of many other tropical animals may also limit their utility. Mittermeier (Chapter 7) argues that primate populations will only survive in areas where human populations remain small relative to the surrounding areas of undisturbed forest. Smythe (Chapter 15) argues that pacas (Agouti pacas) bred in domestication are a potentially productive source of protein. Whereas Smythe has pioneered several interesting techniques for ranching pacas, it appears that their reproductive rate is still too low for producing adequate amounts of affordable meat.

Other species, especially those with comparatively high reproductive rates, offer better prospects. For example, Werner (chapter 14) reports on successful techniques for ranching green iguanas (Iguana iguana) whereby iguanas are hatched and reared in captivity and then released into forests where they attain sufficient mass for harvesting. The effectiveness of this "put and take" strategy in conserving forest habitat remains to be determined, but the approach appears promising.

White-winged Doves (Zenaida asiatica) [chapter 18] and whistling ducks (Dendrocygna spp. [chapter 19])

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are proven and promising candidates for sustained harvest, respectively. White-winged Doves are an established gamebird in the southwestern U.S. where populations are threatened by conversion of breeding habitat to agriculture. In one of the more traditional wildlife management chapters, Purdy and Tomlinson discuss the harvest and management of doves in the U.S. and Mexico. Interestingly, hunting by Mexican citizens is minimal (p. 262); thus, this chapter is a good example of problems arising from competing interests.

One of the most promising approaches to preserving Neotropical wildlife is to surround major parks and preserves with buffer zones. By allowing hunting, limited timber extraction, ecotourism, and low-impact agriculture (e.g., slash and burn) in buffer zones, local communities can benefit from the existence of parks and preserves. The preserve can act as a population source for cracids, primates, and other animals that can only withstand local hunting pressure because of low reproductive rates. Local communities therefore have an economic stake in preserving the parks and, importantly, discouraging poaching within the parks.

In a thoughtful discussion of future prospects, Freese and Saavedra (Chapter 28) advocate management plans for one to three focal species, thus avoiding the dilution of limited financial and technical resources. Research for wildlife in the Neotropics (and, we believe, elsewhere) must include biological and nonbiological factors such as market forces. Freese and Saavedra also advocate more intensive research on wildlife management in simplified production systems such as timber production areas and agricultural systems. Improved management of these systems will be particularly beneficial because such areas are often near densely populated areas.

The editors of this volume should be commended for putting together a diverse array of chapters and for including many Latin American authors. We also commend the editors’ sensitivity in acknowledging that the North American model for wildlife management is infeasible in most Neotropical countries. Most chapters are cautious and careful to point out the limitations of the available data. The need is urgent for data and models to start generating socioeconomic benefits and exploitation strategies from complex neotropical systems.—SCOTT K. ROBINSON AND JEFFREY D. BRAWN, Illinois Natural History Survey, 607 E. Peabody Drive, Champaign, IL 61820.

VARIATION IN CONFLICT AND COOPERATION


Ever since I realized that Nick Davies found the perfect species for the study of ecological and evolutionary correlates of mating systems variation, I have had profound regard for his insight (and not a little envy), for I have long thought that studying intraspecific variation in mating behavior was a sure-fired way of plumbing the intricacies of natural selection and evolutionary process. All the better that he found Dunnocks, 

Prunella modularis, in his own backyard. Dunnocks aren’t particularly attractive being instead the quintessential little brown bird. Apparently, they don’t even have interesting songs to recommend them to bird watchers. Never mind. The Inquirer-like luridness of their intimate daily lives is splendid and makes up for their dullness of plumage and voice. Davies book is also splendid, being an explanation of his 10 years of watching and recording Dunnock lives and times.

Davies makes three main points in the book: (1) Conflicts of interest among and between females and males, in which each individual behaves to maximize their own reproduction, results in the variable mating system. (2) Conflicts of interest underlie apparently cooperative behavior. (3) Dunnocks use simple rules to organize and guide their behavior.

The fourteen chapters revolve around these themes of conflict and cooperation guided by simple rules. These chapters deal with: (1) Why Davies chose Dunnocks (hints in the early literature that they did some “odd” things). (2) Descriptions of Dunnocks (little brown birds that skulk around gardens) and the study site (quite small, being an area of the botanical gardens at Cambridge). (3) The structure of the population showing that Dunnock mating patterns vary (monogamy, polygyny, polyandry, and polygynandry—all in the same garden!). (4) Competition for habitat and mates (females settle first influenced by food distributions; males settle later determining the mating system). (5) Factors influencing competitive success (older males were more likely to be polygynous and were better able to dominate other males). (6) Sexual conflict as evidenced by mate guarding and mating (males peck females’ cloacas prior to mating, which stimulates females to eject sperm from previous matings; males have large testes and packed seminal glomera containing massive amounts of sperm suggesting high levels of sperm competition). (7) Social behavior in relation to genetic parentage (there is no conspecific nest parasitism; 99% of offspring are sired by resident males; and males only feed nestlings after they have had copulatory access to females). (8) Comparison of reproductive output as a function of differences in mating patterns (male help matters to females, so that female reproductive success is highest when females are helped by two males in cooperative polyandry and lowest in polygyny). (9) Conflicts of interest between individuals (male reproductive success is highest in polygyny and lowest in cooperative polyandry). (10) Variation in parental effort by females and males in pairs and trios (female provisioning rates change only after all males have been removed; α male provisioning remained constant when the β male was removed, but β males worked harder when the α male was removed). (11) Allocation of paternal efforts between broods (males always chose options likely to increase their reproductive success). (12) The relationship between parental effort and genetic parentage (experimentally removed males only fed chicks if they had gained matings during egg-laying and the amount of effort expended by males was influenced by their share of matings). (13) Parasitism by cuckoos 

Cuculus canorus (Dunnocks accept cuckoo eggs and dutifully feed cuckoo chicks at great cost to their own repro-
ductive success, because cuckoo chicks kill Dunnock chicks). (14) Theories and ideas about sexual conflict, parental care, and mating systems (a review of prominent mating systems ideas and speculation that the conventional view that females base mating choices on pairing status of males may be wrong).

Readers who have followed Davies' published articles about Dunnocks will not find much new data; however, the book is an easy way to learn all about Davies' Dunnocks at once, and I rather enjoyed reading it this way. Davies' writing style is charming and I found the book as engaging as Nick is in person. As might be apparent from the list of topics Davies embraced, he asked all the right questions for our times, yet his book is not thoroughly modern. Vestiges of typology remain in the way Davies sometimes speaks about Dunnocks and this is paradoxical given Davies' focus on variation between and among individuals. Throughout the text there are references to "the Dunnock." This is a pet peeve of mine, but it is this peeve that made me like the title, so simply and refreshingly different from what it might have been (e.g., "The behaviour and social evolution of the Dunnock"). Davies' Dunnocks title reflects the non-typological body of his work, so I was surprised at the lapses in the text.

The scale of this study is worth noting. It took place at The Garden at Cambridge in an area of 16 hectares. In those 16 ha in any given year there were about 80 breeding Dunnocks and many hundreds of individuals of other bird species. The ten years of study from 1981 to 1991 involved 427 adults, 206 females and 221 males. What struck me about these numbers and the size of the study site is how relatively small they are. Despite or perhaps because of, the small physical scale of this study, the intellectual scale was large. Davies and his coworkers had apparently very intimate knowledge of each of their subjects that facilitated detailed analyses of the aspects of behavior on which they focused. Davies' writing and experimental results fit expectations about selection on individuals so very well, (that data didn't fit modern day expectations). It was befuddling not to find any, though I suppose the fact that I—uncharacteristically—had little response to it. In contrast to many of the books I've read and/or reviewed, my copy is not littered with my hastily scrawled remarks; I didn't respond with alternatives to each of Davies' conclusions; and, I had no extended arguments with him in the margins. Obviously, it's a good book, but my, perhaps, idiosyncratic response to it is that as good as it is, it wasn't nearly as much fun to read as those books that have forced me to think hard about preconceived notions and alternative conclusions. And, yet without a doubt, this is one of the best-ever studies in behavioral ecology and social evolution. —PATRICIA ADAIR GOWATY, Institute of Ecology, University of Georgia, Athens, GA 30602-2602.


This volume is based on a NATO Advanced Research Workshop on Demographical, Physiological, Behavioral and Genetical Aspects of Population Biology of Passerine Birds held at Evisa, Corsica, France, October 3–8, 1989. As noted in the volume's preface, the workshop brought together an impressive group of 53 scientists from 15 countries of Europe, North America and North Africa to discuss the population biology of passerine birds. The stated aim of the workshop "was to present and discuss in an integrated way the state of the art in this rapidly developing field of research." The volume is organized in seven major sections.

The volume begins with a Presidential Address by von Haartman entitled "Breeding Time of the Pied Flycatcher Ficedula hypoleuca." In this paper, von Haartman used data from nearly 50 years of breeding ground studies to describe the key events in the flycatcher breeding cycle and to relate these events to external variables. For example, he noted the existence of a positive relationship between May temperatures and the appearance of the first egg in the studied flycatcher population. Habitat also appeared to be a relevant factor, as birds in pine forests began laying earlier than those in more productive birch forests. The paper concludes with a figure showing a 48-year time series of three different variables reflecting breeding time of the Pied Flycatcher, and with the interesting observation that year-to-year variation in breeding time seems to have increased since the mid-1960s.

The second section of the volume is entitled "Reproductive Biology and Population Regulation" and
contains 12 chapters. A primary component of all but three of these chapters was a comparison of survival rates and/or components of reproductive rate among different populations. In some cases, the studied birds represented neighboring local populations (chapters by Perrins; Dervieux, Isenmann, Clamens and Cramm; Moali and Isenmann). In other chapters, the studied populations were within the same country or region (chapters by van Balen and Potting; Blondel and Pradel; Zandt, Strijkstra, Blondel and van Balen). In still other cases, estimates of reproductive and survival parameters were compared to similar estimates for populations in other regions and countries (chapters by Hildén; Fidalgo; Martin and Bellot).

In some of these chapters involving geographic comparisons, the approach was to test for differences between demographic parameters and then develop a posteriori explanations for these differences. Other chapters used the preferable (in my opinion) approach of specifying a priori hypotheses and associated predictions that were then tested using the geographic comparisons. For example, Blondel and Pradel were motivated by predictions from life-history theory that animals in stable and predictable environments (such as islands) should exhibit a particular set of life history characteristics, including low reproductive rate and high adult survival rate. They studied Blue Tit (Parus caeruleus) populations on Corsica and in a mainland forest in southern France. They noted that some components of reproductive rate were indeed lower on Corsica than on the mainland and that they thus expected higher survival for the Corsican birds. However, capture-recapture estimates of adult survival did not differ between the populations, leading the authors to suggest that less-studied components of reproductive rate (proportion of birds breeding, age at first breeding, post-fledging survival) might differ between the two populations.

The three chapters in the second section of the book that did not use geographic comparisons involved efforts to identify factors associated with year-to-year variation in population size using estimates of population size and related quantities over time. McCullum's descriptive population studies of Mountain Chickadees (Parus gambelli) in New Mexico were accompanied by experimental additions of food and led to the suggestion that changes in population size were influenced by food availability and by differences among individuals in behavioral responses to food availability.

Dhondt, Matthysen, Adriaensen, and Lambrechts studied Blue Tits in a Belgian woodland. They presented results of a "key-factor analysis" that reportedly provided evidence of density-dependence of certain factors, but because of sampling correlations, I did not find the analysis convincing. However, they also used capture-recapture models in conjunction with data on marked birds to study factors influencing survival. This work was nicely done and provided good evidence that both winter temperatures and breeding density influenced survival of female tits.

Lebreton developed a model for the Great Tit (Parus major) population at Wytham Wood, England. Lebreton modeled population count data with Poisson branching process models that incorporated density-dependence, various environmental variables, and demographic stochasticity. Various models were fit to the tit data using maximum likelihood methods. The analyses led to the identification of winter and early spring temperatures, beech production the previous year and population density the previous year as important influences on the rate of population change. This chapter contains the most innovative methodology in the book and presents the most reasonable approach to modeling population count data that I have encountered.

Researchers in the United States are already following Lebreton's suggestions for extending his modeling approach to handle measurement error.

The third major section of the book is entitled "Between-Individual Variation Within Populations." The included six chapters form an interesting "mixed bag" in terms of both questions addressed and methodological approaches. Gosler discussed Van Valen's "Variable-Niche" hypothesis, specified predictions and then concluded that comparative data on bill size variation within and among four Parus species from Wytham Wood supported the hypothesis. Henrich-Gebhardt used both descriptive and experimental (brood manipulations) approaches to investigate factors influencing fledging size and weight of Great Tits in Switzerland and found evidence that importance of factors varied from year to year. Power's chapter presented an excellent review of the North American studies by him and his students on genetic parasitism in the European Starling (Sturnus vulgaris).

Nager conducted descriptive studies to investigate the relationship between temperature and laying date in Swiss Great Tits. The chapter by van Noordwijk reviewed the interrelationships among tree condition, caterpillar density and Great Tit reproductive biology. The discussions of both Nager and van Noordwijk nicely introduced the concept of "reaction norm," the set of phenotypes displayed by a single genotype under different environmental conditions.

The chapter by Clobert, Lebreton and Marzolin was interesting from both methodological and biological perspectives. They first developed a general approach to estimating immature survival rate and age-specific breeding proportions using capture-recapture data. They then showed how to implement this approach using their computer program SURGE and conducted an example analysis using data on the European Dipper (Cinclus cinclus). They found evidence that proportion of breeders among one-year-old birds was higher during flood years, when more breeding sites were vacant. This methodology is likely to be very important to animal ecologists, as the proportion of animals that breeds in a given year has received very little study, yet is an important determinant of population growth.

The fourth section of the book, "Costs and Benefits of Reproduction," contains results of some interesting experimental work by European ornithologists. Chapters by Gustafsson, Källander and Smith, Török and Toth, and Nur discuss some of the advantages of experimental (as opposed to correlational) approaches to investigating possible costs of reproduction (i.e., decreases in future survival or fecundity associated with present reproduction). These chapters, plus that by Orell and Koivula, presented interesting results of brood-manipulation experiments. In some instances evidence
of the hypothesized costs was found. Even when no evidence of a cost was found, authors tended to conclude that costs probably existed in quantities other than those that were estimated or measured.

Ekman and Johansson-Allende investigated possible trade-offs between number and size of offspring in Coal Tits (Parus ater), Willow Tits (P. montanus) and Crested Tits (P. cristatus) on a study area in Sweden. Although species laying larger clutches laid eggs with smaller mass, the authors concluded that this relationship did not necessarily result from a simple trade-off in expenditures from a fixed resource “capital.” Møller, Allander and Dufva presented an excellent review of fitness effects of parasites on passerines. They proposed the view that parasitism is the price paid by cavity nesters and colonial breeders for increased safety from nest predators.

The fifth section of the book, “Behavioural Aspects of Reproduction,” contains seven chapters dealing with a variety of interesting questions about the behavioral ecology of reproducing birds. The studied behaviors include polygyny (Alatalo, Carlson and Lundberg; Askenmo and Neergaard), incubation patterns (Cowie and Novak), helping at the nest (Lessells), departure of nestlings from the nest (Nilsson), infanticide (Robertson) and brood defense (Windt). Some of the studies reported in these chapters were observational and others were experimental. Some of the observational studies relied strictly on the observations of biologists, whereas others used instrumentation to facilitate the collection of descriptive data (the nest-box activity recorder of Cowie and Novak that recorded female incubation pattern and distinguished nest visits by males in Blue Tits; the video recordings of Nilsson to study nest departure of nestling Marsh Tits (Parus palustris)).

Experimental manipulations were very effective in testing hypotheses of interest in some of the reported studies. Nilsson manipulated broods to increase hatching asynchrony and found that nestlings still departed the nest at about the same time. Robertson studied behavior toward young (infanticide vs. adoption) of replacement males in Tree Swallows (Tachycineta bicolor) in Ontario, Canada by removing resident males at nests. Windt studied nest defense by exposing nesting Great Tits to a caged Pygmy Owl (Glauucidium passerinum) accompanied by a mobbing chorus emitted from a nearby loudspeaker. Windt also “handicapped” birds by tying together primaries eight and nine on one wing as a means of studying influences of past and present “costs” on nest defense behavior.

The sixth section of the book “Recruitment, Floaters, Immigrants, “ includes chapters involving social organization and movements of birds. Three of these chapters concerned winter flocks, and three dealt with breeding populations. Extensive observations and vocalization recordings of marked Willow Tits in Norway led Haftorn to conclude that juvenile birds shift from one winter flock to another in order to obtain information in flock quality, and then “decide” which flock to join. However, Hogstad, also studying Willow Tits in Norway, used removal experiments to conclude that winter flocks were often saturated and that floaters checked flocks looking for vacancies. Smith observed that the density of floaters influenced replacement of Black-capped Chickadees (Parus atricapillus) in winter flocks in Massachusetts, United States.

McClory and Clobert analyzed the Great Tit data of Wytham Wood and concluded that the somewhat higher survival rate of immigrant (relative to resident) tits found in earlier work was counterbalanced by a slightly lower production of recruits by immigrant birds. Slagsvold and Lifjeld experimentally reduced breeding success of male Pied Flycatchers on a Norway study area by removing females and increased success on another area via the release of these females. Males showed higher return rates to the study site with the increased density of females. Winkel and Winkel transported Pied Flycatchers a distance of 40 km from one study site at the beginning of the breeding season. One-year-old birds tended to breed in the area of release, whereas older birds tended to return to the original area to breed, emphasizing the importance of previous breeding experience as a determinant of site fidelity.

The final section of the book includes concluding remarks by both Perrins and van Noordwijk. The chapter by Perrins contains an interesting discussion of adaptation to local conditions. He noted that the substantial movements of birds among different habitats exposes birds to different selective pressures and reduces the likelihood of evolution of habitat-specific traits. Perrins also noted the potential importance of differential productivity of habitats in the fragmented English landscape and developed a scenario that fits neatly into current discussions of “source” and “sink” populations.

In the book’s final chapter, van Noordwijk described seven basic approaches that have been used in an effort to understand population dynamics. Two of these approaches, the “micro-environment approach” and the “individual variation approach” emphasize variation among individual organisms. Indeed, van Noordwijk stated that the “main question” addressed in the proceedings “seems to have become why individuals are and do as they are and do, in other words to describe and explain the various aspects of our species.” van Noordwijk concluded with the suggestion that an understanding of individuals can lead to mechanistic models permitting conditional predictions of population change.

The emphasis on individual variation in some of the book’s chapters, especially the concluding one, leads to what I view as a potential problem in the study of animal population dynamics. If we adhere to the view that the action of an individual at some point in space and time is a unique event that cannot necessarily be generalized to other individuals or other times and places, then it is not clear to me what it is that a population ecologist should spend his time doing. Under that view, the best we can do is describe what we see and perhaps build an a posteriori story to explain our observations. However, such an approach does not lend itself readily to prediction and does not constitute what most people would call science. This is not to say that nature does not represent such a collection of unique events, only that if it does, then I do not know how a scientist should proceed.

It is my view that we must hope that nature permits some degree of generalization. We then proceed by
identifying potentially important sources of variation (among individuals, times, locations) in whatever quantities we choose to study (e.g., survival probability) and aggregating observations in ways that permit tests of these potential sources of variation. If we overlook important sources of variation and aggregate over them, then our analyses may be misleading. However, I see no way around this potential problem, other than making full use of whatever biological "knowledge" and intuition we may have in the identification of potential sources of variation.

Overall, I liked this volume very much. The contributions varied in many respects, but were of consistently high quality. Two aspects of the volume that especially impressed me were the relatively large number of manipulative experiments that were reported (e.g., the section on costs of reproduction) and the quality of the statistical and analytical methodologies used in the investigations (e.g., the branching-process models of Lebreton and the use of SURGE by Clobert and others to investigate sources of variation in survival rate). This volume should be of great interest not only to ornithologists but to anyone interested in animal population ecology.—JAMES D. NICHOLS, U.S. Fish and Wildlife Service, Patuxent Wildlife Research Center, Laurel, MD, 20708.
Wildlife conservation is the practice of protecting wild species and their habitats in order to prevent species from going extinct. Major threats to wildlife include habitat destruction/degradation/fragmentation, overexploitation, poaching, pollution and climate change. The IUCN estimates that 27,000 species of the ones assessed are at risk for extinction. Expanding to all existing species, a 2019 UN report on biodiversity put this estimate even higher at a million species. It's also being