Birds of Prey

Eleonora's Falcon. Adaptations to Prey and Habitat in a Social Raptor. HARTMUT WALTER. University of Chicago Press, Chicago, 1979. xiv, 410 pp., illus., + plates. $35. Wildlife Behavior and Ecology.

Each autumn some 5 billion migratory birds leave their nesting grounds in Europe and cross the Mediterranean Sea and the adjacent area of the Atlantic Ocean to spend the "winter" in Africa. Most of this moving mass is embodied in about 100 species of small passerine birds, which migrate mainly at night and seek a landfall at daybreak. Waiting to exploit this source of food are approximately 10,000 Eleonora's falcons (*Falco eleonorae*), which nest on islands and sea cliffs from Cyprus to the Canary Islands. On the basis of nine field trips between 1965 and 1977 and by careful use of published information, Walter has produced a study that carries us partway toward an understanding of how the morphological, behavioral, and physiological traits of this falcon have been modified by natural selection to fit the species into a unique breeding-season niche.

During its long migrations and on its nonbreeding grounds in Madagascar and the Mascarene Islands, Eleonora's falcon feeds mainly on flying insects; but on the breeding grounds this 300- to 500-gram falcon becomes a hunter of small birds, which it captures when they are at maximum risk over open water. In analyzing more than 5000 remains of prey Walter identified 90 species of birds, but three species of shrikes (*Lanius*) and half a dozen species of warblers (*Sylvia*) and other muscicapids make up most of the prey. From calculations of energy requirements for adults and young during the breeding season and of prey biomass Walter estimates that the total falcon population consumes annually about 1.6 to 2.0 million birds. While the impact of this predation on the total number of migrant birds crossing into Africa is negligible, its influence on the numbers of the highly targeted species is less clear, nor is it known what selective influences the predation may be exerting through the culling of weak or otherwise less fit individuals. These are intriguing subjects for future study.

The basic reproductive adaptations of the falcon to its food relate to timing and spacing. Eleonora's falcon breeds later in the year than any other Palearctic nesting species. It lays its eggs in late July and August, and hatching coincides with the beginning of the large-scale migratory movements of small birds in late August and early September, so that the young falcons are reared during the peak period of fall migration, when small species of birds are most abundant. No other Northern Hemisphere bird of prey has evolved such a late breeding season, although a related African species (*F. concolor*) produces young at the season that coincides with the trans-Saharan migration of Palearctic birds.

Eleonora's falcon nests in colonies, a habit that has become well developed in only three other, small, mainly insectivorous species of *Falco*. Nesting colonies range in size from a few pairs to several hundred birds, and the defended nesting territories are quite small, 1 to 200 square meters. Colonial nesting allows the entire population to take advantage of the limited nesting habitat on cliffs and islets that are optimally located to intercept the fall passage of migrants over open water.

There is just enough time for the young to mature and fly before the passage of migrants has dwindled to an unexploitable level. According to Walter the young leave their nest areas within 15 days after first flight, although his data are meager. Are the young then independent of parental care? If so, they have a remarkably short period of fledgling dependency, for even young kestrels are fed by their parents for three to four weeks after leaving the nest, and for some large falcons the time varies from two to several months. Walter does not make the point, but the heavy fat deposits laid on by the young falcons while they are being fed by their parents may serve to tide them over from the time their parents stop feeding them until they have developed the ability to catch insects and occasional birds. A fledgling falcon with a fat-free weight of 350 grams can accumulate more than 100 grams of fat while being fed birds by its parents. Even with the necessity to fly several hours a day in migration, this is enough energy to last the young falcon for a week or more.

Through a detailed comparison of the nesting colony on Paximada in the Dionysian Islands northeast of Crete with the one on the Isles of Mogador (now Essaouira) in the Atlantic off the coast of Morocco, Walter has demonstrated significant behavioral and ecological adjustments of Eleonora's falcons to local conditions that modify the availability of migrant birds to the falcons. The Mogador falcons begin nesting about a week earlier than those on Paximada; they lay an average clutch of 2.98 eggs (mode = 3) compared to an average of around 2.1 (mode = 2) on Paximada; the number of young surviving to leave the nest on Mogador averages about 2.5 (excluding human depredations), and on Paximada about 1.5. The adult falcons on Mogador hunt throughout the day and even at night, delivering an average of 3.06 birds a day to their nests, whereas those on Paximada hunt only for a few hours in the morning and deliver an average of 1.38 birds a day. These differences are explained by the following facts: The fall migration begins earlier in the region of Mogador than in the eastern Mediterranean; larger numbers of Palearctic migrants pass over into Africa in the western sector than in the eastern; and the location of Mogador in relation to points of departure from Europe is such that many

Adult female Eleonora's falcon "assuming an eaglelike posture." [From *Eleonora's Falcon*] migrants continue to pass over those islets all day long, whereas Paximada is located so that migrants are likely to pass over only in the morning hours.

Using assumed figures for mortality—56 percent in the first year, 22 percent in the second, and 19 percent in subsequent years—Walter claims that the lesser availability of prey and the lower rate of reproduction place the Paximada and other eastern Mediterranean populations in jeopardy in terms of replacement. This is true only if breeding does not begin until the third year; but recent banding studies on Mogador show that breeding begins in the second year, and even the lowest annual rate of production reported by Walter, 1.26 young per pair, will yield 216 potential recruits for each 190 needed to maintain a stable breeding population.

Among several problems of evolutionary ecology discussed, two are worth special notice: Territoriality and sociability among species of the genus *Falco*, and the "reversed" sexual size dimorphism in raptors. Walter depicts (fig. 57) ten models of territoriality among falcons, grading from the purported mutually exclusive, all-purpose territory of *F. sparverius* to the extremely social condition in *F. naumanni*, in which there is group defense of a colonial nesting area but apparently little defense of specific nesting sites by individual pairs. Eleonora's falcon differs from the latter only in that pairs do defend a small area around their nests. Fieldworkers who have been studying the approximately 200 pairs of prairie falcons (*F. mexicanus*) nesting along just 130 kilometers of canyon in the Snake River Birds of Prey Study Area of Idaho will be surprised to discover that Walter has included this species in his territory model 2, representing species in which the pairs are so dispersed that they are not in "periodic contact" with each other. Walter has tried to relate his models of dispersion to the geography of suitable nesting sites and to temporal and spatial patterns of prey availability, but such an effort is perhaps premature for the genus *Falco*.

Why female falcons and other birds of prey have evolved a larger body size than the males of their species has been much discussed in recent years, but no one has come up with an explanation that satisfactorily accounts for all of the relevant facts, including the fact that some female raptors are actually smaller than their males. Walter usefully calls attention to the likelihood that many variables act in concert to influence the *degree* of sexual size dimorphism in raptors. Students of this subject will be particularly interested in table 24 and figures 58 and 59, in which five degrees of size dimorphism are compared against ten variables: prey dispersion, prey size, prey character, resident status of raptor, home-range defense, size of nesting territory, social status, nesting sites, division of labor between the sexes, and nest type. Walter shows that for 14 species of falcons R. W. Storer's dimorphism index based on wing length ranges from 0.6 for *F. naumanni* (least dimorphic) to 14.4 for *F. peregrinus* (most dimorphic). Eleonora's falcon, with an index of 3.4, ranks only third from *F. naumanni* and is less dimorphic than the species of kestrels. There does seem to be some association between an increase in the dimorphism index and increasing prey size, time and energy invested in capture, division of labor between the sexes, and size of nesting territory or home range for these 14 species, but other species, such as the small, highly size-dimorphic *F. rufigularis*, introduce exceptions. Walter's own hypothesis about why the female is the larger sex in raptors—that her large size has evolved as a mechanism to protect her developed follicles when she strikes against prey in her hunting attacks—would seem to be negated by the fact that the females are entirely sedentary during gonadal maturation and ovulation and are fed by the males.

As far as the extreme reversed size dimorphism of the bird-eating falcons and accipiters is concerned, the hypothesis first set forth in detail by C. M. White and T. J. Cade (*The Living Bird*, 1971) still has merit. Because the smaller males are better adapted to catch small birds and the larger females, which hunt late in the breeding season, are better adapted to catch large birds, the size difference maximizes the hunting capability of a pair during the breeding season, when there is a high demand for food by the adults and young and dispersed, resident prey must be taken from a circumscribed hunting area around the nest. In the case of Eleonora's falcon, the prey is constantly being replenished by the flow of migrants, and there is no advantage in the female's hunting or specializing on species different from those taken by the male; hence there has been little selection for a difference in size between male and female.

Sometimes digressing from its main theme and even abstruse in places, this book is nevertheless an instructive attempt to relate the social organization and individual behavior of a colonial nesting raptor to the spatial and temporal characteristics of its migratory prey and to the geographic and topographic features of its nesting habitat. The study poses more questions than it answers, as it should. It provides an important body of information on which future students of Eleonora's falcon will be able to build a more quantitative and analytical autecology.

TOM J. CADE
A. LUDLOW CLARK
Section of Ecology and Systematics, Division of Biological Sciences, Cornell University, Ithaca, New York 14850

Celestial Mechanics

Instabilities in Dynamical Systems. Applications to Celestial Mechanics. Proceedings of a NATO Advanced Study Institute, Cortina D'Ampezzo, Italy, July 1978. VICTOR G. SZEBEHELY, Ed. Reidel, Boston, 1979 (distributor, Kluwer Boston, Hingham, Mass.). xxiv, 314 pp., illus. $39.50. Nato Advanced Study Institutes Series C, vol. 47.

This volume consists of 20 research and survey papers, together with another 19 brief seminar reports. Unfortunately, the title of the book is somewhat misleading: for the most part, the only types of dynamical systems considered are those arising in mechanics (usually celestial mechanics). Nevertheless, the inclusion of the word "instability" in the title is most welcome. It underlines the recent resurgence of interest among dynamical astronomers in nonlinear, unstable behavior. In the past, researchers in celestial mechanics have often concentrated on stable phenomena, aiming to prove, for example, the stability of the solar system. But, as Szebehely remarks in his contribution to the book, the prediction of instabilities may be the first step in research on stability and is often the most important.

Two main themes emerge from the book: the stability or instability of periodic solutions in the n-body problem and the problems of instability in the large, or global instability. Among authors dealing with the former, J. D. Hadjidemetriou details the evolution of stability along families of periodic solutions that bifurcate away from known circular or elliptic Keplerian solutions of a restricted problem. Generally, he finds that such orbits maintain their stability, losing it only at resonances. V. Markellos contributes a numerical study of certain families of symmetric and nonsymmetric periodic orbits of the full three-body problem that bifurcate away from planar solutions. Building on the basic work of Zare and Szebehely and McKenzie, A. E. Roy ex-