THE SOCIAL BEHAVIOR OF BIRDS

Why Birds Gather, Scatter, Dominate, Flock, Fight, Feed and Breed.... the Way They Do.

By Frank B. Gill

THE NEEDS FOR food and for protection are the most pressing requirements of any living creature, determining where and how to live and the degrees to which behavior is social or asocial, and cooperative or competitive. It is sometimes advantageous for an individual to go it alone; at other times there is safety in numbers. Among birds we find many variations in the spacing of individuals. At one extreme, Solitary Eagles live alone on exclusive expanses of tropical mountain forest. At the other extreme, Social Weavers cluster together in gigantic communal nests. Whether a bird lives alone or with others, the fact remains that space, the intelligent use of which is crucial for survival, is limited. Ultimately, of course, birds must share space, and they have evolved various ways of doing so. Whether breeding or not, birds may space themselves at regular intervals over large territories, congregate in large numbers, or cluster in small groups. In this chapter, we examine the spacing behaviors of birds, and outline the specific costs and benefits of territoriality, coloniality, and flocking.

INDIVIDUAL SPACING BEHAVIOR

Most birds maintain a small individual space around them wherever they go. Swallows, for example, space themselves at regular intervals on a telephone wire. Sparrows and sandpipers feeding in large flocks also maintain small distances from one to another, as if each were surrounded by an invisible force field. This space increases their individual foraging efficiencies and reduces the frequency of hostile interactions.

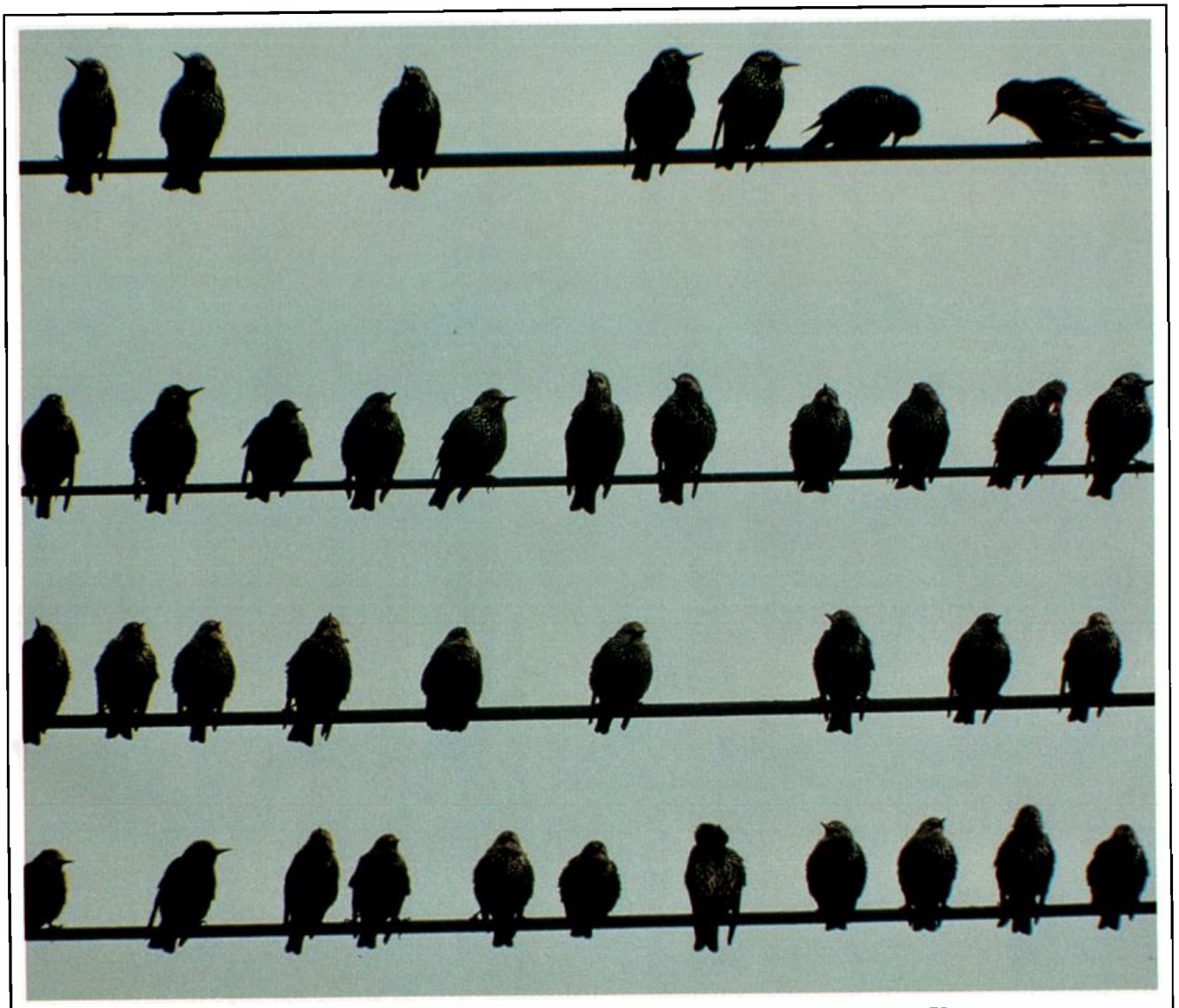
The tendency of individuals to separate promotes uniform patterns of spacing. If birds landed on a field at random, some sites in the field would remain empty, and others would receive several birds in succession, resulting in random patterns of association. In all probability, the birds would not sit quietly after landing. Individuals close to one another would move apart and fill the unoccupied spaces. Such regular, or uniform, dispersion patterns are typical of birds that occupy relatively uniform habitats. Killdeers residing in large fields, American Robins nesting in suburbia, and American Kestrels wintering along roadsides space themselves in a regular manner.

Individuals may space themselves uniformly in small areas, but in larger areas they may tend to separate by greater distances or to clump together. When birds fly from a field in a flock, the distances between individuals within the flock are small and uniform. The distances between different flocks are substantial. Flocking Snow Geese in winter fields clump together, but on a larger scale, the distributions of the flocks themselves may be random, uniform, or clumped.

TERRITORIALITY

Birds aggressively establish, maintain, and protect their spatial relationships; aggressive individual assertions of status or rights to resources are normal parts of avian social life. Assertion of spatial rights is very apparent in territorial birds, which must win and continually maintain exclusive rights to particular areas, food supplies, or mates. Territorial behavior is a primary form of aggressive spacing behavior that has intrigued naturalists since Aristotle. H.E. Howard's *Territory in Bird Life* (1920) formally introduced scientific inquiry into the subject. Research on avian territoriality has now established three major aspects of territorial behavior:

1. Acts of display or defense discourage rival birds that would otherwise enter or approach the territorial space.
2. Primary if not exclusive use of a territory is thereby limited



A flock of European Starlings spacing themselves at regular intervals. Photograph/Johann Schumacher/VIREO.

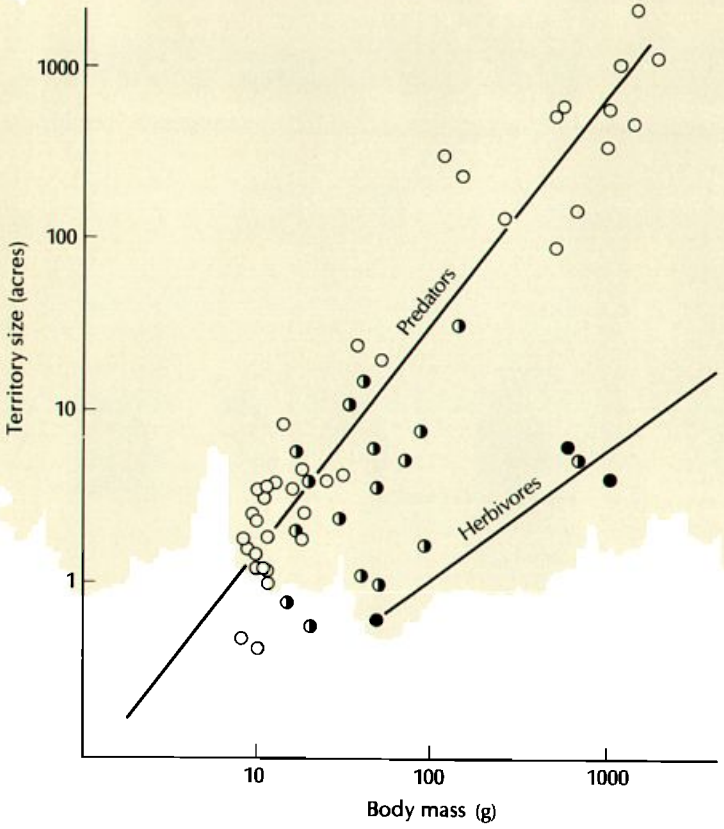
to the defending individual and, perhaps, its mate and progeny.

3. A territory is a fixed area defended continuously for some period of time, even if only hours, in either or both the breeding and nonbreeding seasons.

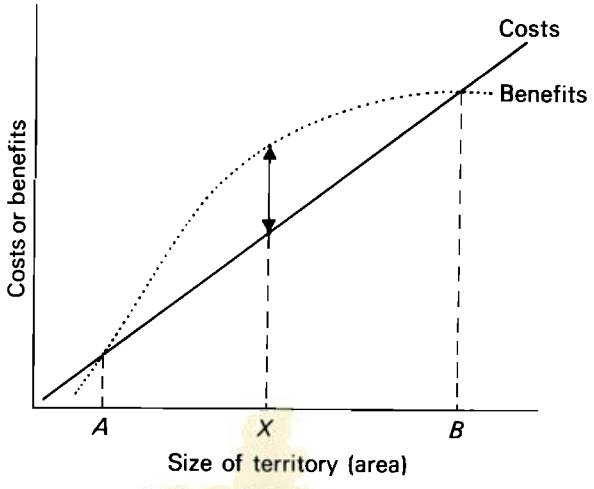
Ornithologists once thought that the territorial behavior of birds was genetically programmed and static. In fact, territorial behavior is flexible and dynamic. Great Tits, for example, forego defense of their winter territories on the coldest days to save essential energy. The territorial behavior of Sanderlings is manifest only at low tide; at high tide this sandpiper feeds or roosts in flocks. However, in years when Merlins take up residence in their area, Sanderlings are often not territorial because isolated individuals would be too vulnerable to the predatory falcons.

The simplest territories are those with only one type of resource, such as the feeding territories of hummingbirds in fields of flowers or those of sandpipers on a beach at low tide. At the other extreme are the one- to two-acre all-purpose nesting territories of landbirds, which are used for male display, courtship, nest seclusion, and feeding. These territories enable individuals to space themselves rather uniformly to reserve essential resources, reduce predation, and control sexual interference by neighbors and vagrants. In suitable habitats, territories are usually contiguous areas separated by boundaries that, though invisible to us, are well defined.

The average sizes of territories increase directly in relation to body size, energy requirements, and food habits of the various species of birds. This suggests a general importance of food resources to the territorial individual. Variations within species are even more revealing. Pomarine Jaegers, for example, defend small breeding territories of 19 hectares when lemmings, their principal food, are abundant, and territories of 45 hectares when lemmings are scarce. The feeding territories of Ru-



Territories or home ranges of birds increase directly in relation to body size, energy requirements, and selection of food types. The correlation suggests that territory size is geared to the food and energy requirements of the bird. Predators have higher daily energy requirements than do herbivores, which have correspondingly smaller territories. (After Schoener 1968)



Territories of intermediate sizes (A to B) are economically defendable because the benefits exceed the costs. The costs of defense increase as territory size increases. The benefits relative to need (dotted line) increase rapidly at first but then reach a maximum value when needs are filled, as would be the case when food is in excess. Optimum territory size is at X, where the net benefit is greatest. (From Davies 1978a)

fous Hummingbirds and Golden-winged Sunbirds decrease in size as flower density, and thus the quantity of nectar, increases.

Simple relationships between food abundance and territory size, however, do not necessarily demonstrate that food and energy requirements alone control territory size. Territory size also depends on the density of competitors for the available space. When population density is low, territorial American Tree Sparrows regularly use only 15 to 18 percent of their large territories. They concentrate their activities in the core section but also defend a less frequently used buffer zone. In years of high population density and increased competition for breeding space, denser packing of smaller territories eliminates the buffer zones. The nest territories of Royal Terns actually pack into a hexagonal configuration resembling the cells in a bee's honeycomb.

Territorial defense incurs costs as well as benefits. Conspicuous display can attract predators. The time and energy required to display, patrol territorial boundaries, and chase intruders can be a major investment. Territoriality is favored when the resulting benefits outweigh the incurred costs. The central requirement is that adequate resources be economically defensible. Two features of resource distribution, temporal variability and spatial variability, determine whether territories are economically defensible. Resources that change rapidly in time invite opportunistic use, not site-specific investment or long-term commitment. Aerial insects whose locations and densities shift frequently, for example, are usually not defensible food resources. Territorial sunbirds, which do not tolerate each other near chosen flowers, will sit side by side in a bush while they catch passing insects.

Sites that are extraordinarily rich

in resources attract hordes of competitors and may be indefensible as a result. No gull would attempt to maintain a feeding territory on a garbage dump where thousands of other gulls vie for the same scraps. Similarly, Sanderlings do not always defend their feeding territories on California beaches. Beach space with few prey is not worth defending, and beach space with dense concentrations of prey (isopods) is not defensible because no single Sanderling can keep the hordes of other Sanderlings away. Thus, Sanderlings defend only territories on beach sections with intermediate densities of prey. The size of the territories they defend on the controllable beach sections also reflects the necessary defense effort: Where there is more competition, smaller territories are formed.

The costs and benefits of the feeding territories of nectar-feeding birds are unusually straightforward and easily defined. Hummingbirds and sunbirds defend particular clumps of flowers for several days to several weeks or longer. Golden-winged Sunbirds in Kenya, for example, defend about 1600 flowers of a mint, which produce enough nectar each day to satisfy an individual's energy requirements. Golden-winged Sunbirds defend these territories when the benefits exceed the costs. The primary cost is the energy required to chase intruders, approximately 12.5 kilojoules per hour. The territorial sunbird benefits by having an assured, adequate food supply. The sunbird also saves energy by feeding at nectar-rich flowers on its territory rather than at nectar-poor, undefended flowers visited frequently by other sunbirds. The territorial sunbird can satisfy its feeding requirements in less time each day than a nonterritorial sunbird and thus can spend more time sitting, which costs less energy (1.7 kilojoules per hour versus 4.0 kilojoules per hour). When a defense investment of 3 kilojoules per day causes the average nectar volume to increase from 1 to 2 microliters per flower, a 6-kilojoule net savings of energy is realized. When the projected savings are less than the investment, the territory is not defended.

Although birds usually defend territories against others of the same species, interspecific territorial defense is not uncommon. Golden-winged Sunbirds defend their territories against a variety of nectar-feeding birds, as do territorial hummingbirds. In the winter, Northern Mockingbirds defend berry-rich feeding territories against other species, especially those that would eat some of the berries. The intensity of a mockingbird's defense increases with the potential threat to its food supplies. Some other species defend nesting territories against other closely related species.

Birds assert themselves more effectively on familiar ground or home territories than when they are strangers in a new place.

Territories may be occupied and defended by a single bird, a mated or cooperating pair of birds, an extended family, or even a group of unrelated individuals. Small groups of wintering tits and chickadees, for example, defend woodlot territories containing both food and roosting holes. Groups of four unrelated Willow Tits establish common winter territories by late summer. Group membership, which includes male and female pairs of both resident adults and newly settled first-year birds, is stable throughout the winter. In addition to protection of food stores for the winter, spring territorial breeding opportunities emerge from the winter communal effort.

DOMINANCE

Birds assert themselves more effectively on familiar ground or home territories than when they are strangers in a new place. Territorial owners usually win encounters with intruders. For one thing, during high-speed attacks and chases, the owner can use familiar details of the territory to its own advantage. Because territorial owners have an investment to protect, they do not usually give up a fight as easily as a newcomer. Acorn Woodpeckers, for example, vigorously defend their tree granaries against squirrels, jays, and other Acorn Woodpeckers. These granaries hold valuable stores of winter food; in addition, each of the many holes (up to 11,000) represents an investment of 30 to 60 minutes of drilling time. These woodpeckers defend trees that are riddled with empty holes as well as those with holes that contain acorns.

Territoriality is related to the more general phenomenon of dominance behavior. Dominance and aggressive reinforcement of status are a normal part of the social lives of birds. Individuals that win aggressive encounters achieve dominance, and consistent losers become subordinate. As social ranks are established in new groups of birds, losers cease challenging dominant individuals. Dominants use threat displays to assert their status and reserve their access to mates, space, and food. They move without hesitation to a feeder or desirable perch, supplanting subordinates and pecking those that do not yield at their approach. Subordinates are tentative in their actions and frequently adopt submissive display postures.

Rank has its advantages. High-ranking Dark-eyed Juncos and Field

The dominance status of individuals changes with location. The ability of territorial male Steller's Jays to win fights, for example, decreases with distance from their nesting areas rather than ceasing abruptly at a territorial boundary. Similarly, the point of parity among Bicolored Antbirds has been observed to be the approximate boundaries of their overlapping territories.

Sparrows survive longer than low-ranking ones. Subordinate Wood Pigeons obtain less food per hour than dominants, which increases their probability of starving. Low-ranking individuals have less access to good feeding sites and are usually the first to emigrate. Weakened physical condition plus the extra costs and dangers of travel through unfamiliar situations all increase the risk of death.

Dominance status is directly related to age and sex. Generally, large birds dominate small ones, males dominate females, and older birds dominate younger ones. Within an age group or gender, physiology and genetics greatly affect dominance. Aggressive tendencies and dominance status are correlated with slight differences in adrenal gland activity and brain chemistry. Aggressive, dominant strains of domestic chickens can be developed by artificial selection.

The dominance status of individuals changes with location. The ability of territorial male Steller's Jays to win fights, for example, decreases with distance from their nesting areas rather than ceasing abruptly at a territorial boundary. Similarly, among Bicolored Antbirds, the point of parity (the place at which each pair wins 50 percent of the encounters) has been observed to be the approximate boundaries of their overlapping territories. Although expression of dominance and territoriality both relate to specific resources such as food and may be initiated over rather large distances, the two behaviors differ with regard to the site defended, which is fixed in the case of territoriality and movable in the case of dominance. Dominance and territoriality, however, become indistinguishable in the site-dependent dominance systems of Steller's Jays and Bicolored Antbirds. Cases of temporary residency also show more vague lines of definition between the two behaviors. Roving male Bronzy Sunbirds, for example, shift from dominance behavior to territoriality through intermediate states of aggressive behavior. They often displace subordinate sunbirds to feed on certain flowers and then leave, but also they may defend flowers for an hour or so of exclusive access and then leave, only to return later for another period of temporary residence. When conditions are poor and flowers scarce, they defend the territory constantly for several days to several weeks.

Sometimes territorial birds defend a nonstationary resource. Constant defense of a female and her immediate area, for example, borders on territorial defense of a well-defined resource. Such behavior is typical of the Cassin's Finch and other carduelline finches, particularly when an excess of males competes for mates. Glaucous Gulls and Glaucous-winged Gulls defend feeding eiders, a kind of sea duck that brings food to the surface, against other gulls. Sanderlings will defend Willets from other Sanderlings when the Willet has a large sand crab, bits of which fall to the defending Sanderling.

COLONIALITY

Whereas territoriality and dominance behavior reflect an emphasis on competition for resources, coloniality reflects an emphasis on tolerance and sometimes, cooperation. The two main disadvantages to colonial living are that large groups require large amounts of food and that they may attract predators, parasites, and diseases. The advantages, however, far outweigh the disadvantages. Individuals can improve their foraging by watching others. Colonies also provide protection, which is of paramount importance when birds are breeding, brooding, and nurturing young. The alternative to high-density breeding colonies and well-spaced territories are loose colonies such as those of

Brewer's Blackbirds. Unlike pairs of other species that feed in exclusive territories where food is uniformly distributed, pairs of Brewer's Blackbirds congregate at good locations central to large, undefended areas in which the exact location of food varies irregularly. In Washington state, Brewer's Blackbirds nest in defended clumps of greasewood or sagebrush near ponds and marshes. In the morning, they feed on aquatic insects emerging from the ponds, and during the rest of the day they commute to adjacent, undefended fields to feed. Such behavior seems to be the evolutionary basis for true coloniality.

Avian breeding colonies range in size from a few to millions of pairs. On the Peruvian coast, black and white Guanay Cormorants pack together at densities of 12,000 nests per acre and may attain a total colony size of 4 to 5 million birds. In Africa, 2 to 3 million pairs of the sparrow like Red-billed Quelea nest in less than 100 hectares of Acacia savanna. Colonial birds choose isolated islands, beaches, rookeries, or cliff faces, safe from predators, in which restricted distribution of inaccessible sites favors a high concentration of individuals. Hence, the burrows of nocturnal auklets and petrels riddle the hillsides of oceanic islets; the nest holes of swallows, swifts, and bee-eaters riddle dirt embankments; and caciques and weaverbirds crowd their nests into tall trees over water or into spiny Acacias.

To support large congregations of birds, suitable nest sites must be near rich, clumped food supplies. The huge colonies of Guanay Cormorants and other seabirds that nest on the coast of Peru, for example, depend on the productive cold waters of the Humboldt current. The combination of the abundance of food and the vastness of oceanic habitat can support enormous populations of seabirds, which concentrate at the few available nesting locations. Inland, colonies of Pinyon Jays and crossbills settle near conifer forests, and weaver colonies settle near rich grain fields. In spite of food abundance, large colonies sometimes exhaust their local food supplies and abandon their nests.

When the precise location of good feeding sites varies from hour to hour, colonial individuals use each other as clues for finding food. Seabirds track the locations of small schools of fish by following the line of individuals returning to the colony with food. Bank Swallows, which feed on aerial insects that concentrate in the eddies of shifting breezes, may derive a similar advantage. Observations that seem to support this "information center hypothesis" have been reported for birds as diverse as Tricolored Blackbirds, Bank Swallows, Phainopeplas, and Great Blue Herons. Such advantages are probably side benefits, rather than the principal reasons for coloniality.

Synchronized nesting further decreases risk... because the sudden abundance of eggs and chicks exceeds the daily needs of predators.

Individuals are safer in colonies. Large numbers of colonial birds detect predators more quickly than small groups or pairs and can drive them from the vicinity of the nesting area. The effectiveness with which Common Black-headed Gulls mob predators increases with the number of participants. Nests at the edges of breeding colonies are more vulnerable to predators than those in the centers, and the preference for advantageous central sites promotes dense centralized packing of nests even in ample areas. Synchronized nesting further decreases risk to a particular nest because the sudden abundance of eggs and chicks exceeds the daily needs of predators.

Studies of the Bank Swallow document the advantages and the disadvantages of coloniality. Bank Swallows nest in colonies ranging from a few to several hundred nests, which are built in dirt embankments throughout North America. The disadvantages include increased competition for nest sites, stealing of nest materials, increased physical interference, and increased competition for mates. Burrows in large colonies are more likely to be infested by fleas than those in small colonies. Young swallows in large colonies are apt to wander into the wrong burrow and perish because they are not fed. Adults of this species of swallow learn to recognize their own young by means of individually distinctive calls and thereby do not accept young other than their own. In contrast, Northern Rough-winged Swallows, a related but solitary nesting species, do not discriminate between their own offspring and those of others placed in their nests. There are two primary advantages of coloniality for the Bank Swallow. First, predators are more quickly detected and mobbed. John Hoogland and Paul Sherman (1976) demonstrated this by placing a stuffed weasel near colonies of various sizes and recording the consequences. Second, colonial nesting seems to enable the swallows to keep track of their aerial insect food supplies. Synchronized breeding is apparently important in this regard because those pairs that nest several days later than the majority have trouble feeding their young, many of which die of starvation or are runts. The apparent reason for this is that late breeders are left to find food on their own after most pairs have departed with their fledged young. ■