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Bird territories: A key to understanding bird behavior

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The role of amateur ornithologists in developing a major scientific theory.

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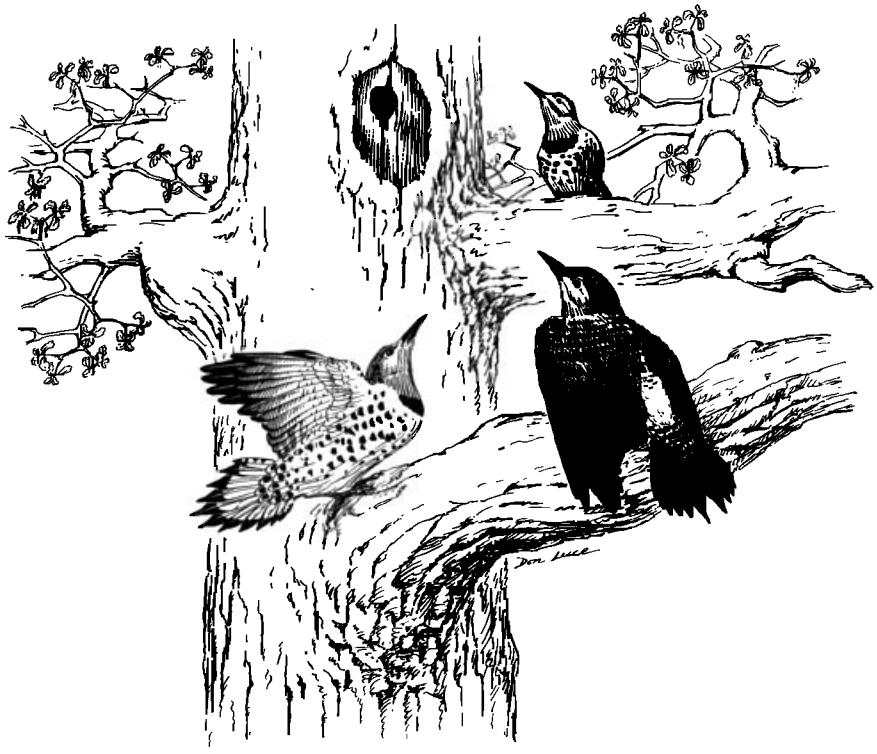
FOR THE CAREFUL FIELD OBSERVER, perplexing questions arise with the arrival of birds in spring. Why do male Red-winged Blackbirds migrate two or three weeks before the brown, striped females? Why do orioles sing incessantly during the first week of their arrival from the south? What could possibly motivate two flickers in a garden to flick their wings and bob their heads at each other, and then tumble together with flashing yellow wings? Scientific theories are most intriguing when they offer a single, simple explanation for such disparate phenomena, and the theory of territoriality has this advantage. The concept of territory provides insights from which any amateur naturalist can benefit, since it explains much about the daily behavior of animals. Not surprisingly, the concept was originally developed by amateur naturalists, bird watchers whose patience and skill for careful observation allowed them to detect a pattern in the frenetic spring activity of birds.

One of these bird watchers was Eliot Howard, an English businessman who lived in a house among pastures and woodlands overlooking the River Severn. Before leaving for work in Worcester, where he was director of a steel-manufacturing firm, Howard arose before daylight and spent the early morning hours observing the birds near his house. In 1920, after decades of watching the behavior of birds, he wrote *Territory in Bird Life*, a book that greatly changed the study of birds and other animals. Before this time, ornithologists had studied birds primarily by shooting them for their skins and collecting their eggs and nests, organizing these into collections and naming the different forms. This was a necessary stage because it was essential to impose some order and apply some labels to the bewildering variety of thousands of different kinds of birds. Howard, how-

Yellow-headed Blackbird males arrive in a breeding marsh area before females. They evaluate the habitat for food availability and safe nest and roost sites, commit to a specific patch for an entire season, and thereafter invest heavily in defense of that territory. Because these decisions have been made independent of the presence of females, when they arrive, they are in a position to assess the quality or fitness of a male and his patch of real estate and to then choose a mate. Males make habitat decisions while for females, selecting a mate is equivalent to making a territory decision. Photo/S.R. Drennan.



Territorial encounter between Northern (Yellow-shafted) Flickers (Colaptes auratus). *Two female flickers (foreground) display aggressively near a nest cavity while a male watches passively. During high-intensity territorial displays, flickers face one another and bob their heads. At the same time they reveal the bright yellow on the underside of the wings and tail by raising the wings and spreading and twisting the tail (Lawrence 1967). Illustration/Don Luce.*

ever, inspired many ornithologists to study the biology of birds in a different way, in the field watching the activity of individual birds. His conception of the territory, an area defended by a male during the breeding season, demonstrated how a useful and general theory could be derived from careful bird watching.

Howard watched the Reed Buntings (*Emberiza schoeniclus*) that nested in a marshy meadow near his house. The Reed Bunting, an inhabitant of marshy edges in Europe, is a small brown finch with black head and throat. Howard noticed that in winter these buntings left the wet meadows and reed-beds, where they had spent the summer, to forage in open cultivated areas, often in the company of other species of finches. They normally returned to the marsh only at night, when groups of buntings roosted together low in the rushes. Curious about how these winter habits changed as spring approached, Howard watched the birds through the cold mornings of February. In mid-February he noticed a change: instead of joining flocks of finches in the usual feeding areas, male buntings scattered across the marshes. Each male selected a prominent position, the top of an alder or tall reed, where it sang and preened. Early in the season it often left this spot, flying a long distance to the feeding grounds. But as spring approached, these absences became shorter and less frequent, and soon the male Reed Bunting spent all of its time at its selected spot in the marsh.

While female Reed Buntings were still foraging together in winter flocks, the males spent more and more time singing their tinkling song from their special perches. If another male approached the perch, he was driven away. Fighting often occurred in such situations. The male was usually not joined by a female until late March. The pair then drove other, neighboring pairs away from the area around the singing perch. Later, nests were built and eggs laid, and the frequency of both singing and fighting declined.

Howard (1920) explained these events in terms of the need for a plot of marsh, a territory, in which a pair of Reed Buntings could find a nest site and search out enough food to raise their young. The competition for territories is such that males leave their winter feeding grounds for a few hours each day in late winter to claim an area and protect its boundaries. Defense of the territory becomes increasingly imperative as the season advances, and when a female joins the male, the pair cooperate in defending their plot against other Reed Buntings. Song is used mainly to proclaim territory-ownership to other Reed Bunting males. Often males enter a fight in full song.

In Howard's view, territoriality consists of two components: (1) the occupancy of a particular plot of ground and (2) defense of this area against intrusion by members of the same species (other than the mate). Territories vary greatly in size, from the square miles patrolled by a falcon to the half acre of willow thicket claimed by a warbler. Howard even considered the tiny areas around the nests of cliff-nesting seabirds to be territories, since they are defended against other individuals of the same species. A pair of Common Murres (*Uria aalge*) or Razorbills (*Alca torda*) defends the few square feet of cliff ledge where their nest will be built. They defend only the nest site, not a food source, since they forage over broad areas of ocean. Similarly, male Ruffs (*Philomachus pugnax*) defend tiny areas on a display arena where males congregate solely to mate with females. Howard also considered these to be territories, and he probably would have agreed with the simple, broad definition suggested by Noble (1939): "territory is any defended area."

Howard's book awakened many ornithologists to the phenomenon of territoriality. How could such an apparently obvious and predominant aspect of bird behavior have been overlooked for so long? Actually many earlier authors had described territorial defense in birds (Lack 1944). Aristotle described the defense of large areas by ravens and eagles in *Historia Animalium*. The "walks" (apparently territories) of semidomestic Mute Swans (*Cygnus olor*) are described in 17th century English game laws, and many early ornithologists described territorial behavior. In 1868, a German biologist, Bernard Altum, wrote *Der Vogel und sein Leben (The Bird and His Life)*, a book that describes territoriality in birds in much the same detail and manner as Howard's *Territory in Bird Life* (Mayr 1935). Howard's discovery of territoriality more than 50

years later was apparently independent, since he had not read Altum's book. More important, it was Howard who convinced others of the general applicability of territory theory and the usefulness of studying the behavior of individual birds.

Following Howard's lead, many ornithologists were inspired to study territoriality in birds during the 1930s and 1940s. One of the most informative studies was done by another amateur, Margaret Nice, who spent eight years studying the Song Sparrows (*Melospiza melodia*) around her house in Columbus, Ohio. Nice was a well-educated woman with a passion for research (Nice 1979). She began watching birds at the age of nine, and later studied the development of her own children (particularly their acquisition of language). Still later she intensively studied garden birds such as Mourning Doves (*Zenaida macroura*), Brown-headed Cowbirds (*Molothrus ater*), and, most important, Song Sparrows.

Nice's greatest contribution was developing a method for studying individual birds over a long period of time. Howard had indicated the importance of studying individual birds, but he had to depend on individual peculiarities (a broken leg, a white area on the feathers) to identify them with certainty. More commonly he was forced to identify individuals by their location on a particular territory, but this meant that many of his conclusions were based on circular reasoning. How could he know that the same individual defended a territory throughout the breeding season if he identified the individual only by its presence on that territory? Nice was one of the first workers to overcome this problem by using color-coded leg bands. Each Song Sparrow was trapped and four plastic bands with a unique color combination were placed on its legs, in addition to a more permanent numbered aluminum band. Each bird could then be identified and its behavior observed from one year to the next. In 1932 Nice had marked 136 Song Sparrows, including nearly every adult on her floodplain study area. Ironically Nice came to know her birds so well that she could identify many individual males by their songs. Each male has a unique repertoire of six to nine distinctive songs.

The two-volume work, *Studies in the Life History of the Song Sparrow* (Nice 1937, 1943), was based on many hours of careful observation of individually recognizable birds. Nice found that males usually returned to the same territory year after year, regardless of whether they over-wintered in the local area or migrated. One male, the famous 4M, lived to be at least 9 years old and retained virtually the same territory thoughout this period. The position of his territory shifted progressively westward by a total of 50 meters between 1930 and 1934, but later returned to its original location. However, females seldom remained with the same male from one year to the next; if they survived the winter, they normally appeared on another territory with a new male at the beginning of the next breeding season. Occasionally they even switched mates during the middle of the summer, and raised their second brood of young on another territory. Both males and females defended the territory, usually against individuals of the same sex. Interestingly, many individuals banded as nestlings showed up in succeeding years on territories in the immediate vicinity of their parents' territory.

An early photo of Margaret Morse Nice taken in Chicago, circa 1920. With no formal ornithological training, she made significant contributions to the field. Photo courtesy of Marjorie N. Boyer.

Nice's work had confirmed most of Howard's conclusions about the nature of territories, but the banding technique allowed her to discover much more. She had followed the life histories of individual birds and their offspring for so many years that she could delineate the boundaries of territories not only in space, but also through time. The maps of territory boundaries, and the particular males and females that occupied each territory, can be compared through several succeeding years, providing a detailed chronicle of the history of one population of Song Sparrows.

A male Song Sparrow proclaims its territory by singing in early spring. Illustration/Julie Zickefoose.

Nice with two of her daughters, Constance and Janet, in the late 1940s. Nice served as a mentor and role model for many. The Margaret Nice Ornithological Club in Toronto was named in her honor. The club began after women were denied membership to the then all male birding clubs. Photo/Smithsonian Institution.

Many studies of the territorial systems of particular species of birds followed the field work of Howard and Nice. The new evidence was presented within the framework of a continuous debate about the definition and function of territories (Lack and Lack 1933, Nice 1941, Hinde 1956). Later Brown (1964) published an essay that presented the concept of territoriality in a new way. He emphasized that aggressive defense of space (territoriality) will evolve only if two conditions are met. First, there must be competition for some scarce resource and enough competition to make the time, energy, and risk required for aggressive defense worthwhile. Second, the resource in short supply must be defendable. If the resource is mobile, transient, or widely scattered, it may be impossible (or prohibitively expensive in terms of time and energy) to defend. As Brown points out, this may be the case with many seabirds, which forage over broad stretches of the ocean that cannot be defended against other individuals. Defending a small patch of ocean would not be useful, since the prey are transient and require constant searching. However, as Howard (1920) pointed out, cliffs favorable for nesting (with wide enough ledges and proper protection from the surf) are in short supply, so many seabirds defend small territories in the immediate vicinity of their nests. In this case, territoriality evolved because there was competition for a resource (nest sites), and the resource (a compact area) could be defended by a pair of birds.

Brown's theory allows for greater flexibility in discussing territories, since any resource—food, a nest site, a place to roost, a mating site, or a space containing all of these—can be both in short supply and defendable. His theory also indicates what must be measured—the level of competition for resources and the concentration and permanence of resources—to explain the presence or absence of territoriality in a particular species.

One implication of Brown's theory is that habitat determines the type of territory a bird will defend. Individuals will defend a resource that is in short supply and that can be protected, and different resources will meet these conditions in different habitats. If nest or display sites are defended, the territories will be small, but defense of the food supply often requires a large territory. Consequently, although closely related species of birds tend to have similar territorial behavior, they may have very different sorts of territories if they live in dissimilar habitats and protect different types of resources.

The relationship between habitat and territory is well illustrated by Crook's (1964) comprehensive study of the behavior of 70 species of weavers. These attractive birds are a conspicuous feature of the landscape in Africa and parts of Asia. The males of most species have brilliant yellow-and-black or red-and-black color patterns, and they weave elaborate, spherical nests with small entrance holes. Crook studied many species of weavers, garnering additional information from the writings of British colonial administrators who had been amateur bird watchers. Nearly every human settlement in Africa has a tree filled with woven nests and chattering, fluttering weavers, so these conspicuous and intricate weaver societies were irresistible subjects for many naturalists.

Some species of weavers have large territories, while others defend a tiny space around their nests. Crook found that this difference depended upon the habitat. The weavers of the tall, lush rain forests of West Africa are insect-eaters, and both the male and female gather food for the young. Insects are a relatively abundant and dependable source of food, so a pair of weavers can defend a plot of forest large enough to provide food for themselves and their young. Hence, the forest weavers are generally territorial, with individual pairs spaced regularly throughout the forest. Also, because the best protection against predators in the thick rain forest is to be quiet and unobtrusive, these weavers are very secretive, hiding their nests in dense vegetation.

In contrast the weavers of the African savannah are gregarious, foraging in large flocks in open country and nesting in large colonies, with dozens or even hundreds of nests in a single tree. The seeds these savannah weavers feed upon are concentrated in local areas. Because these concentrations are sporadic and temporary, they cannot be protected and monopolized by a territorial pair. The weaver flocks must move across large expanses of the savannah to find these concentrations of seeds, much as seabirds must move to find schools of fish on the ocean surface. Foraging in

flocks may help these birds detect predators, since there are more eyes to watch for activity in the surrounding grasslands. Although they cannot defend their food supply, these savannah weavers can defend their small nest sites from other weavers, and it is important that they do so, since nest sites are in short supply. Savannah weavers prefer to nest in special and relatively unusual places that offer protection from snakes and other predators. They concentrate their nests in trees surrounded by water or a human village, or next to a hive of bees or the nest of a hawk. Each male weaver builds a domed grass nest and hangs upside down from it, displaying with fluttering wings and singing until he attracts a female. The female then takes over the nest, lays eggs, and raises the young alone. Seeds are an abundant and concentrated source of food, so the female can feed the young without the male's help. Meanwhile the male builds a new nest and attempts to attract another female. The males constantly defend the tiny territories around their nests from other males. Like the forest weavers, they defend an area, but it consists of a few branches around a group of nests in a tree rather than a large tract of forest. In both cases, however, the territory protects an essential resource (food supply or nest site) that is in short supply and defendable against other weavers.

Generally birds defend territories only against other individuals of the same species. There are exceptional cases, however, in which the territory is defended against other species. This is often the case with those colonial birds, like weavers and many oceanic birds, in which two or more kinds of birds live in the same colony. In these cases, nest site territories are protected from any intruder, regardless of species. Also, individuals of some species with larger territories defend them against other species that have similar food and nest site requirements. This is the case for the Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*) and Red-winged Blackbirds (*Agelaius phoeniceus*), two closely related birds that occupy the same marshes in north-central and western North America. Orians and Willson (1964) studied the interactions between these two blackbirds at Turnbull National Wildlife Refuge in Washington. Nearly all of the marshes on the wildlife refuge support both species, and

The primary preoccupation of male Red-winged Blackbirds during spring is the defense of a breeding territory. This species is a colonial breeder and is regularly polygynous. Vigorous aggressive displays are costly parental investments, but when successful competitive behavior allows access to multiple females, instead of just one, the potential reproductive payoff is obvious. Photo/S.R. Drennan.

Caspian Terns are highly gregarious, assembling to breed, feed and boldly mob predators. They are unusually vocal with harsh, clipped cries serving aggression, advertisement of territory, and maintenance of contact between parent and young. Nest sites are small and closely spaced. When adults in dense colonies actively defend these sites, pairs with small territories may suffer minimal predation because closely packed adults together form an extremely effective means of defense. Photo/S.R. Drennan.

Black-legged Kittiwakes nest in colonies sometimes so large as to defy credibility. This species is very site tenacious with territorial behavior probably limited to the nest site. Displays are still imperfectly understood, but defense of the nest site and the small area surrounding it often becomes extremely aggressive. Photo/S.R. Drennan.

in every case they have mutually exclusive territories. Red-wingeds establish their territories in March, before the Yellow-headeds have returned from the south, and Red-winged territories initially cover the entire marsh. In April the larger Yellow-headeds arrive and drive the Red-wingeds from the parts of the marsh with deep water and sparse vegetation (usually the center). The Red-wingeds typically retain territories only on the periphery of the marsh. In Washington State, Yellow-headeds are dependent on emerging damselflies to feed their young, and these are most abundant in the more open areas of the marsh (Orians 1980). Red-wingeds, however, can feed their young a great variety of insects, and they nest successfully on the edge of the marsh or even in upland areas. The two species use the same threat displays and songs against one another that they would to defend their territories against members of their own species.

Despite other examples of this sort, birds do not generally exclude other species from their territories. Walk into a woods in eastern North America and you may see a tanager and an oriole singing from the same tree. If you caught these resident birds and marked each one with a combination of leg bands, you could follow them and map their territories, much as Nice did with Song Sparrows. The pattern that emerges from such studies is a series of non-overlapping territories for members of the same species, and broadly overlapping territories for members of different species. For example, the territories of Black-capped Chickadees (*Parus atricapillus*) can be superimposed on those of the White-breasted Nuthatch (*Sitta carolinensis*) which, in turn, overlay those of the Wood Thrush (*Hylocichla mustelina*). Although all three species feed on insects, they forage in different places (foliage, bark, and leaf litter, respectively).

The territories of woodland birds can be envisioned as three-dimensional volumes, rather than two-dimensional areas. For instance, Williamson (1971) described the territories of Red-eyed Vireos (*Vireo olivaceus*) in a mature Maryland forest as 85 foot high cylinders, one to two acres across, extending from near the forest floor to the top of the canopy. Yellow-throated Vireos (*Vireo flavifrons*) nest in the same forest, but they largely limit their activity to the highest stratum. Their pancake-shaped territories cover about ten acres in the upper canopy of the forest. Thus, one Yellow-throated Vireo territory might cap the top of ten Red-eyed Vireo cylinders.

It is only after long and careful observation that the pieces of the puzzle of bird behavior begin to fit together like the interlocking boundaries on a territorial map. The dramatic changes in the habits of birds during spring—the break-up of winter flocks, the sudden morning chorus of bird song, the elaborate and aggressive displays between neighboring males and pairs—are all signs of territorial defense. These insights into bird behavior are the result of the skill, patience and curiosity of amateur naturalists such as Eliot Howard and Margaret Nice. Their contributions formed the basis of the theory of territoriality and changed the methodology of field ornithology.

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