

'Dear Enemy' Notes

A neighbor's song means more than music to a hooded warbler's ears

by Renée Godard and Haven Wiley

On a balmy April morning, the bottomland hardwood forests near Chapel Hill in central North Carolina are deceptively peaceful. As we stand in the dense understory of arrowwood, with its pale new foliage, two black-and-yellow sprites fly furiously back and forth across an invisible boundary. They are so oblivious to our presence that they almost brush our legs in passing. After about ten minutes of this twisting through the arrowwood, the tiny birds separate by some fifty yards. Each takes a station just below the crowns of the oaks and hickories and begins to belt out its own version of a ringing song. The black cowls over yellow faces reveal that these rivals are male hooded warblers. They have come to the forest to begin the breeding season.

One of the birds wears two lightweight, red plastic bands on each leg. He was one of the first males we banded for identification here at our study site, the Mason Farm Biological Reserve, and he has returned to exactly the same location in this 370-acre woodland for the fourth consecutive year, an exceptional record. His rival, as yet unbanded, is probably less than one year old and is staking a territorial claim for the first time.

Like many migrating songbirds, hooded warblers spend the winter in warmer climes. They winter from Mexico to Panama and begin to make their way north in March. By April, they have reached their summer quarters, which extend from the Gulf coast north to southern Michigan and east to Connecticut. The birds we have been observing have each just returned from their Mexican and Central American retreats and are now in serious competition for real estate. Their female counterparts will arrive in about five to ten days. To attract a mate and eventually raise healthy young, each male needs a territory of some twelve to twenty-five acres of forest with a luxurious understory of shrubs like arrowwood. The old-growth bottomland forests in the Reserve are an ideal habitat; each year five to ten hooded warbler pairs nest here. Only about half of these birds, however, survive the winter

and round-trip migration from one year to the next. The color-banded old-timers are among the first to return, and each quickly reclaims his former territory. In contrast, newcomers ready to breed for the first time must find an opening vacated by a male that failed to return. This precise "site-faithfulness" of returning males is one of the remarkable features of migration for many songbirds. Why should males not move from one year to the next? After all, they might have settled for an inferior territory the first year they bred; surely some of them could upgrade their location in a subsequent year.

Part of the answer lies in the relationships of neighbors. Male hooded warblers, like many other male songbirds, have a number of ways of dealing with rivals in adjoining territories. The simplest interaction of neighboring males is simply singing within earshot of one another. Our systematic observations have shown that the average male hooded warbler spends 55 percent of each early spring morning just singing. When, on occasion, a male meets a neighbor at a disputed boundary, singing ceases and chasing begins, sometimes escalating to fighting. When the females arrive, aggression intensifies. Intermittent chasing can last for two days before both parties tentatively accept a boundary. But once boundaries are established, neighbors quickly develop a respect for them. Males can then sing close to the edge of their territory without provoking an attack from a neighbor. Such apparent amicability does not, we have noticed, prevent them from occasionally venturing surreptitiously into one another's territories.

The birds have become what evolutionary biologists have termed *dear enemies*. Instead of constantly battling, two individuals appear to call a truce; while not becoming allies, they can at least avoid continual contests. Our studies suggest that an important factor of this détente is the hooded warbler's ability to recognize a neighbor's songs. Each male's repertoire consists of five to ten stereotypical patterns of notes. Each song is recognizable



A male hooded warbler refreshes himself in a Texas stream.
Barth Schorre; Bruce Coleman, Inc.





A female hooded warbler, left, arrives at the species' breeding grounds about a week later than the first males. For an early spring male migrant, below, a still-bare branch in New York City's Central Park provides a perch from which to dart out and catch insects. If males return too early, cold and scarcity of insects can be deadly. But if they arrive too late, all the best territories will be taken.

Arthur Morris



as a hooded warbler's—although some do not come very close to the descriptions in standard field guides—yet each has at least a few details that make it characteristic also of the individual.

The ability of male songbirds to discriminate the fine, individual differences in the songs of rivals, both known and new, was established through experiments several decades ago. Our experiments with hooded warblers in the Mason Reserve since 1987 have demonstrated that these birds are even more discerning. A male hooded warbler can recognize the songs of each one of his neighbors and can also learn their usual locations in relation to his territory. To demonstrate this ability, we chose twelve hooded warblers from the Mason Reserve and adjoining woodlands as study subjects. First, we played a tape recording of a neighboring warbler's songs just inside a subject's territory near the boundary shared with that neighbor. Then we broadcast the same tape, also just inside but now on the opposite side of the subject's territory, near a boundary shared with a different neighbor. (Because in an experiment of this sort, the order of presenting the two playbacks might influence

the results, we played neighbors' songs to half of the subjects in reverse order.) Subjects often quickly approached the speaker and searched frantically for the apparent invader. However, our subjects responded much less vigorously to neighbors' songs coming from the expected direction than to the same songs emanating from the opposite direction. Hooded warblers, then, know each neighbor's songs, and know just where they should come from. To our subjects, a playback of a neighbor singing on the wrong boundary signaled a serious territorial invasion.

Many ornithologists have noticed that former neighbors returning from winter quarters act like dear enemies right from the start. As with our red-banded male that early spring morning, returning males are more likely to dispute boundaries with new birds. Do returning neighbors just remember old boundaries, or are they capable of remembering one another's songs? The latter feat would be remarkable: the birds have had no chance to hear the songs for more than six months. They do not sing for most of the winter. We also know that hooded warblers from the Mason Reserve do not migrate together

because they do not arrive at the breeding grounds together. Nor, presumably, do they winter together in Mexico and Central America.

To test song memory, we duplicated the experiments just described, with an added element. We started our tests on the very day a male appeared in April on his previously occupied territory. Familiar songs of neighbors from the year before, played near the old boundary, elicited little response; to our subjects they must have sounded like an old friend back in his usual place. In contrast, the same songs played near the "wrong" boundary evoked a strong response—a quick approach and frenetic searching. Male hooded warblers do, in fact, remember each neighbor's songs from one year to the next. These birds provide one of the few demonstrated cases of long-term memory in a nonhuman vertebrate. This ability has important practical consequences for a hooded warbler. By returning to precisely the same territory year after year, a male can expect to avoid "bargaining" for boundaries with about half of its neighbors. The time and energy thus saved can be used to deal with other neighbors and to attract and court a female.

A male reacts strongly to a trespass into its territory, a transgression that amounts to an abrogation of a mutually accepted treaty. Does such a trespass have consequences beyond a chase by the subject male? Evolutionary theory predicts that it should. A dear enemy relationship involves reciprocal respect for an arbitrary boundary. Such reciprocity in a potentially exploitative relationship can persist when rivals play tit-for-tat. Rivals must recognize each other individually, so they can keep track of each other. They also must interact repeatedly over an indefinite period of time, so neither can take advantage of the other on their last interaction. Finally, each must retaliate whenever the pact is broken. Our warblers met the first two conditions, and we devised another test to determine if trespass provoked retaliation by the offended male.

We first presented a neighbor's songs

Hooded warblers frequent the understory of woodlands. A male in Point Pelee, Ontario, near the extreme northern edge of the hooded warbler's range, peers at sprigs of poison ivy, right. Below: A pair share in the care and feeding of their young, which are within two days of fledging.

George K. Peck



near the “correct” boundary of a subject’s territory. As expected from our previous experiments, the subject’s response was weak, the normal result for a dear enemy. Then this same neighbor’s songs were broadcast from two locations deep inside the subject’s territory (we stopped the playbacks as soon as the subject arrived nearby, so it would not learn that the neighbor was not actually present). Following this simulated trespass, we once again presented the same neighbor’s songs near the correct boundary. The result was clear: a subject responded much more strongly to a neighbor’s songs following an apparent trespass. When we staged trespasses with a stranger’s songs, retaliation toward a neighbor did not occur. Retaliation was therefore restricted to the trespassing individual, just as predicted for rivals playing tit-for-tat.

Over the years, we have come to appreciate the intricate lives led by hooded warblers. They know their neighbors and work out mutually advantageous relationships with them. The trust required for these relationships, however, is not “naïve.” While not demanding “an eye for an eye” following trespass, they do become antagonistic toward wayward neighbors. We have also noticed that in the days following a simulated trespass, our sub-

jects’ behavior returned to normal. Given a little time, warblers appear to “forgive” their trespassers.

What we have found could well apply to other migratory songbirds that defend territories during the breeding season. If so, our studies suggest another way in which habitat destruction can have devastating effects on populations of migrating birds. For a surviving male hooded warbler headed north for the summer, not all habitat, not even habitat suitable in general for the species, is optimal. Each individual seeks out the one specific place where it has an advantage—its territory from the previous year, where it will meet some of its old neighbors. If a particular stretch of forest has disappeared, our individual migrant must start over.

April is a time of blossoming opportunities. For the hooded warblers arriving on each southerly wind, it is also a time of establishing and renewing relationships, including those with their neighbors. By mid-May, most males in the Mason Farm Biological Reserve will have mates incubating three or four eggs in nests cradled on stems of arrowwood. Those nests that escape predators and cowbirds (about half of the total built) will produce a new generation of hooded warblers to carry on the tradition of dear enemies. □

