

SONG FIGHTS

When male birds go tune to tune

BY SUSAN MILIUS

To make a basic point, let's stroll into an alternative universe where song sparrows sound a little unusual. It's spring, and a young male perched on top of a shrub is belting out, "The hills are alive with the sound of music..." When he finishes, the older male who owns the territory sings the same verse. The youngster switches to "Raindrops on roses and whiskers on kittens..." No, this isn't friendly homage to old musicals. It's war, and the youngster isn't doing well. In the next round, it abandons Broadway, does some quick rap tunes, and flees.

Back in our universe, song sparrows do spar musically, although with chirps and trills rather than words. This competitive singing settles many challenges without birds' resorting to pecking and dive-bombing each other.

The rules of these contests have intrigued observers of birds, especially after recording equipment enabled experimental biologists themselves to pick a song fight with a bird. Advances in digital recording with its glorious possibilities for tweaking, retrieving, and analyzing these encounters have opened even more arenas.

Biologists have discovered some of the aspects of bird song that make a difference in a competition. As in the imaginary sing off, it matters whether a rival sings a song his opponent knows—or can fake.

A particularly provocative move in a song contest is getting attention now. Just as people don't always politely wait for a member of, say, another political party to finish a comment, birds in a fighting mood start singing prematurely to overlap the end of a rival's song.

New findings are also expanding notions of contest structure, with some species effectively playing doubles, as one male-female pair challenges another.

THIS LAND IS MY LAND Perhaps the best-studied aspect of song clashes is song matching, and some of the best-studied matchers are the song sparrows in a Seattle park bordering Puget Sound. For 2 decades, Michael Beecher of the University of Washington in Seattle and his students and collaborators have monitored the fortunes of these birds. In a typical year, about 150 male sparrows defend territories in the park. Unlike the same species on the East Coast, the West Coast birds don't migrate.

"These are small birds, but they have big voices," says Beecher. A male song sparrow holding forth can be heard several territories away. "Song," says Beecher, "is a long-distance signal." When rivals get close enough to see each other, they often stop singing. At very close quarters, they softly twitter before they attack.

When Beecher started the sparrow studies, earlier research on territorial birds held that males don't recognize their neighbors—"which we doubted," Beecher recalls. He and his students devised a playback experiment to see whether the birds reacted to a neighbor's song differently than they did to a stranger's.

The investigators observed that the birds, indeed, were slower to fly over and check out recordings of the familiar bird than of a stranger. The flaw in previous work had been playing the songs inside the tested-male's territory. A male bird "hates anyone in his territory—he doesn't care who it is," Beecher says. To see the distinction between neighbor and stranger, Beecher's team played potential-intruder songs from just outside the boundary.

To learn more about how neighbors communicate, Beecher next turned to song repertoires. A male song sparrow, like males of some three-quarters of bird species, performs more than one song as it patrols its territory and faces off other males. Just why birds have developed this vocal variety has been a considerable puzzle.

Early proposed explanations had considered songs interchangeable, all conveying the same message: "This is my turf." For example, one such idea, which Beecher describes with indulgent affection, was named after *Beau Geste*, a Gary Cooper movie about the French Foreign Legion in North Africa. At a dire moment in the movie, the heroes create the illusion of a bigger force by propping up their dead comrades and rushing around to fire

shots near each corpse. The *Beau Geste* theory envisioned that multiple songs would make a male's territory appear to be held by a forbiddingly large population.

Beecher dismisses the idea for song sparrows, because while a Gary Cooper sparrow would stay out of sight and sing only one song from each spot, the actual bird typically sings from a perch that's easy to see and starts new songs without shifting position.

Another idea, one that's still under consideration, traces multiple songs to female preference. Many males use the same vocal repertoire during courtship and territory defense. This theory likens a large song repertoire to a peacock's tail and other female-enticing visual displays.

This notion may well apply to species with big repertoires,



AVIAN IDOL — A West Coast male song sparrow can closely mimic several of a neighbor's songs, so the two birds match each other trill for trill should a border dispute break out. Spectrogram (inset) shows how closely two neighbors' songs match.

such as Europe's nightingale, Beecher says. In those species, a male reels off dozens of distinct songs, and in both the lab and the field, the more extensive the repertoire, the better he charms the ladies. In other species, though, repertoire size stays modest and field studies haven't found a bonus for having one of the larger song collections in the neighborhood.

Of course, biologists are still looking at evolutionary implications of repertoire size, says Jane Reid of the University of Cambridge in England. In the November *Animal Behaviour*, she and her colleagues present long-term data from Mandarte Island in British Columbia. They report that among young couples, a newly settled female laid eggs earlier—improving chances of success—if paired with a male with a big repertoire rather than with one that sang fewer songs.

ANYTHING YOU CAN DO Although Beecher doesn't rule out sexual selection as a force pushing the evolution of repertoires, he has focused on the songs' uses in disputes among males. In the early 1980s, John Krebs, now of the University of Oxford in England, and his colleagues studied territorial male great tits, European members of the chickadee family. The results suggested that a diverse repertoire enables males during tense moments to mix or match songs with those of a neighbor to express degrees of aggression.

Beecher and his collaborators tested this idea in song sparrows and, over the years, found some new twists. During his first year, a young male learns songs from several older, territory-holding males. That wraps up his song learning for life. When the youngster stakes his own territory, he typically settles near these same older males, for example, claiming a bit of land at the intersection of their territories and then trying to expand its size. Typically, these young males share at least 2 of their 6 to 12 songs with each neighbor.

When researchers at the boundary of a male's territory repeatedly played him a song that resembled one of his own but that came from a sparrow he'd never heard before, the male typically repeated it. Beecher calls this gesture type matching. While singing, the bird approached the loudspeaker, finally hopping around the shrubbery near it, as if searching for an intruder to trounce.

Beecher concluded that song matching is an aggressive move, indicating a willingness to escalate the confrontation.

Yet when the song sparrows in these early tests responded to recordings of their rivals next door, 85 percent of the time they sang a different song, but one that the neighbor also knew. These 1992 experiments took place well into the breeding season, after males had settled their boundary disputes. By picking an alternative but still-shared song, what Beecher calls repertoire matching, the bird signals, "I know who you are."

Song sparrows can also use songs to defuse tension, Beecher now argues in a paper in an upcoming *Animal Behaviour*. His research team waited until a male sang one of the songs shared with a neighbor. The researchers then pretended to be neighbors spoiling for a fight and played back the exact song. Such effrontery provoked each test male to come to the end of its territory. The researchers then played either an unshared song or a different one from the shared repertoire. For 11 of the 13 birds in a test, the unshared song was more calming, as indicated by less of a tendency to charge the loudspeaker. Thus, the songs that birds don't share could save a male's tail feathers when he needs to back down in a hurry.

These graded responses make sense, says Beecher. A male may

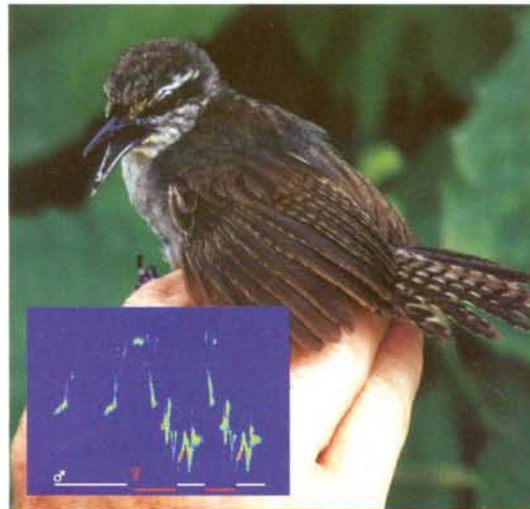
need the all-out threat for strangers but something milder for the sparrow next door.

That neighbor would "take your territory if he could," says Beecher. "He'd take your female if he could; in fact, they're probably already engaging in extrapair copulations. But you sure prefer him to the alternative, some new guy you haven't worked things out with yet."

A test in birds that can't match whole songs comes from song sparrows in Pennsylvania, the subjects of a long-term study by Steve Nowicki of Duke University in Durham, N.C., and William Searcy of the University of Miami. Some of these sparrows migrate south for the winters, and young males don't learn whole songs from tutors but pick up pieces to combine into unique songs of their own.

When it comes to a song contest, males may rely on shared snippets embedded in otherwise different songs, says Rindy Anderson, a member of the Searcy lab. She played for male sparrows hybrid songs created electronically from bits of a male's own vocalizations mixed with unfamiliar bits from a stranger. Males seemed to make the closest match they could to the experimental hybrid song. As they sang, partial matchers approached the speakers more closely than nonmatchers did. Partial matching may signal aggression, Anderson and her colleagues suggest in an upcoming *Animal Behaviour*.

Matching, therefore, may be widespread even in birds that don't share complete songs.



HALF NOTES — The tropical canebrake wren sings tightly coordinated duets with its mate, switching off parts for fractions of a second. Such couples sometimes face off in singing-doubles competitions. Inset is a spectrogram of his-and-her contributions.

EVERYBODY'S TALKIN' AT ME

Matching isn't the only song characteristic with macho overtones. Much as a person might begin shouting back before an opponent finishes talking, birds on occasion start singing before their rivals stop. It's not a friendly gesture

for people or birds, according to Daniel Mennill of the University of Windsor in Ontario.

Past research in Europe raised the possibility that the bird being overlapped loses more than the overlapper does. Both birds have parts of their signals jammed, but losing the end of a bird song may matter more than losing the beginning. In thrushes, for example, individual birds' songs differ from each other mostly in their middle and end sections, so the later notes might carry more information.

Black-capped chickadees vigorously overlap their one-song repertoire of "fee-bee." To find out whether males eavesdrop on other males' contests, Mennill and Laurene Ratcliffe of Queen's University in Kingston, Ontario, mimicked both sides of a song duel by setting up pairs of loudspeakers outdoors that fee-beed furiously at each other.

In 15 out of 16 trials with a real high-ranking male chickadee as a bystander, the listener approached the speaker broadcasting the song that was overlapping the other, the researchers report in the January *Behaviour*. Mennill argues that those eavesdropper males pick the overlapper as the bird to worry about, so they must consider it more aggressive than the overlapper.

Chickadees can also add that macho edge to their fee-bees by transposing the song to the same musical frequency as a rival's. Ironically, the nightingale, master of a huge repertoire, also matches frequencies, transposing the whistley parts in its myriad songs to copy its rival's.

To see how overlapping and frequency matching work together, Mennill and Ratcliffe used computer playbacks to duel with male chickadees (www.sciencenews.org/articles/20041218/contest.mp3). The two forms of aggression aren't interchangeable to a bird, the researchers reported in the March *Animal Behaviour*. For exam-

ple, overlapping made a bigger change in how closely the birds approached the loudspeaker, but frequency matching more dramatically affected the birds' degree of agitation.

In both these experiments on overlapping, high-ranking males and underclass birds didn't necessarily react in the same way. Mennill suspects that the female audience could explain the difference. For example, high-ranking males seem less eager than lowly ones to approach an overlapping intruder. Earlier work from Mennill and Ratcliffe show that females of high-ranking males are more likely to flit off to away-from-home trysts after hearing their partner challenged in a tough overlapping-song duel. Low-ranking males get cuckolded so often that the outcomes of song contests didn't make much difference. Thus, a high-ranking male has more to lose.

"I think female eavesdropping may have been very important in the evolution of overlapping," says Mennill.

FOUR CALLING BIRDS Experiments until recently focused on male birds, because in most species, singing is a guy's job. Among the species in which females sing, too, perhaps the most dramatic are the duetting species. A male and female take turns performing in such rapid succession that they almost make a single song (www.st-andres.ac.uk/~bmseg/thryothorus.htm).

For the first time, researchers have tested a duetting species, the canebrake wren (*Thryothorus modestus zeledoni*) in Costa Rica, to see whether its elaborate vocal performances include some ver-

sion of song matching. Lorraine Marshall-Ball and Peter Slater of the University of St. Andrews in Scotland describe the work in an upcoming *Biology Letters*.

Pairs of canebrake wrens start a duet with an introductory phrase by the male and then alternate his bits and her bits at high speeds.

The repertoire of each member includes 15 to 20 phrases, and a pair combines these to create a repertoire of 20 to 25 distinct duets.

The researchers set up speakers to simulate an intruding pair. In only one of their tests did a resident pair actually match the whole song of the fake intruders. One member of the pair often sang the same element as its counterpart in the intruder duet did. Within a duet duel, the matching was he versus he and she versus she.

Until recently, studying naturally occurring song contests outside a lab had been too difficult because researchers would have had to sit around with tape recorders and hope to catch the action. But new sound equipment and computer programs will finally break that barrier, says Sandra

Vehrencamp of Cornell University.

She and her colleagues are deploying microphone arrays in a wide range of habitats to record songs. The unattended equipment can run continuously for days at a time. Computer analysis compares the minuscule differences in the time when a sound reaches each microphone and works out where each recorded bird is singing.

After decades of dueling with songbirds, researchers at last are going to be able to sit back and enjoy an orchestra seat. ■



STEP OUTSIDE — Rindy Anderson of the University of Miami relies on a laptop computer to pick an interactive song fight. East Coast song sparrows don't share full songs with neighbors but can match elements (spectrogram is inset).

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