BACKGROUND AND LEFT: DAN SALISBURY

Male common loon performs a "penguin dance" in defense of his nest. Background: Little Tomahawk Lake lies in the author's Wisconsin study area.

Troubled Waters

Loons' territorial fights are no laughing matter.

By Walter H. Piper

The battle was so intense it set my pulse racing. Just a few yards from my canoe, far from the shore of Wisconsin's Burrows Lake, two male common loons brawled fiercely. The lake's resident male was fighting off a young intruder intent on displacing him from his territory. The two combatants lunged at each other, grasped each other's heads with their bills, rose up out of the water, and pummeled each other viciously with their wings. A loud thwack broke the high-noon stillness as each blow landed.

After several rounds of grappling and pounding, each lasting close to a minute, the fight took an even uglier turn. The resident loon, which reigned over the entire 150-acre lake, seized the intruder's head in his bill and held it beneath the surface. The water seethed as the intruder thrashed desperately to free himself, a flailing leg or wing occasionally breaking the surface. After a minute and a half, he broke away, fled thirty yards underwater, and came up for a badly needed breath of air. His respite did not last, however: the resident dived and stalked him underwater until he managed to escape, somewhere off in the distance.

It was the suddenness and violence of the contest that took me aback. Only moments before, the two combatants and the resident female had converged and paddled slowly about in a tight circle—a common, ritualized social behavior in loons that appears relaxed and nonthreatening. After the clash, as my pulse rate returned to normal, it dawned on me that if the so-called "circle dance" could erupt into a desperate battle for territory ownership, it must not be as amicable a behavior pattern as loon biologists had imagined—more a steely-eyed sizing up of the competition than an afternoon meet and greet. Moreover, it seemed that the stakes of the contests go beyond just territory ownership; the combatants' very lives are at risk.

My understanding of the loon territorial system was based on a strong foundation of prior research. With several collaborators, I have been studying common loons (*Gavia immer*) since 1993 in a swath of a hundred small glacial lakes in north central Wisconsin. The lakes, along with sphagnum bogs and forests of red and white pine, quaking aspen, and paper birch, make up a landscape that stretches north to the southern shore of Lake Superior. The common loon is the most familiar of the world's five loon species, all of which belong to the genus *Gavia* and summer in northern North America and Eurasia. It is easy to recognize by its stark black-and-white plumage and its nocturnal calls, which include haunting wails and tremolos reminiscent of human laughter. In our study area, my colleagues and I have marked many adult loons and their chicks with individualized combinations of colored leg bands. Most loons in the area have grown accustomed to humans, so we can approach them closely in canoes to monitor reproductive and territorial behavior.

Common loon pairs spend each spring and summer living and breeding on territories comprising an entire small lake or part of a large one. During a decade of research prior to the showdown on Burrows Lake, which took place in 2002,

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Male loons fight for territorial possession; the resident bird (at left in first six images) eventually dives underwater to escape.

we had learned that single loons frequently intrude into a mated pair's breeding territory. A typical pair faces between two and six intruders, most of them female, each day from April to August. Usually the visits are quick and inconsequential: an intruder flies into the territory, circle-dances with the resident pair, lingers for ten minutes or so, and then departs. Occasionally, however, a contest for ownership ensues between the intruder and its same-sex counterpart. If the intruder prevails, it evicts its counterpart and pairs with the mate. Successful male usurpers kill any resident chicks; intriguingly, though, we've never had a successful takeover by a female when chicks are present.

DANIEL AND GINGER POLESCHOOK

Male loon takes flight after receiving a deep abdominal wound from a resident male whose territory he attempted to usurp.

Before Burrows Lake, the battles we had seen were short—usually lasting just a few seconds—and if the territory owner turned out to be at a disadvantage he or she invariably beat a hasty retreat. We had documented only one apparent casualty. It was in 1996, following a battle on another lake in our study area. A territorial male fought sporadically with an intruder during the course of several days, became too injured to feed himself, and disappeared. Having witnessed only a single incident so dramatic, we had dismissed it as an isolated event, perhaps the work of an overly aggressive "rogue" intruder. When I witnessed the deadly encounter on Burrows Lake, I began to wonder whether I'd been missing an important pattern.

The apparent rarity of high-stakes battles was not the only reason I had minimized their importance. Dangerous battles simply don't seem to make sense for loons. In theory, conflicts ferocious enough to cause serious injury or death should only occur among short-lived species that have limited opportunities to breed and cannot reproduce at all unless they fight to do so. Hence, it seems logical that some spiders, fig wasps, and ants suffer fatal injuries in desperate combat for breeding supremacy. But examples of long-lived animals that fight to the death are rare. A common loon's reproductive window isn't as narrow as a spider's. Loons can begin breeding at age four or five and may live more than twenty years. Even adults displaced from their territories usually have opportunities to choose among many vacant territories nearby and settle there to breed with a new mate. If animals have evolved to maximize their reproductive success, as biologists believe, then a loon should never risk its life for a single territory.

Theory notwithstanding, evidence of other serious battles began to mount during the five or so years after the incident on Burrows Lake. During that time, increased funding enabled us to cover our study area more thoroughly than in years past and to improve our communication with lakeside homeowners—who, like us, watch loons with great interest. In June of 2003, a local landowner phoned to tell us about a territorial contest, and we recovered the body of the resident male. Two more nasty brawls occurred in May 2005 and another in June 2006. In each case, thanks to the vigilance of our local contacts, we obtained a rough account of what had happened and were able to find the resident male's body on the shore. A pattern was beginning to emerge.

Studying the outcome of fights is problematic for field biologists, however. Reports of lethal contests are scanty, and locating dead animals is tough if not impossible. What does it mean when a biologist observes a battle, then verifies that a new individual has taken over the disputed territory, but fails to find the displaced resident? Can he or she safely conclude that the exile died? Fortunately for my colleagues and me, evicted loons do not move far. They often take refuge, alone, on a lake adjacent to their old territory. Since our study area is large and includes most of the lakes that displaced residents might move onto, we can be confident that if we cannot find a displaced loon, it most likely died.

Out of sixty-nine males evicted by an intruder since 1993, seventeen—25 percent—we later either found dead or injured, or never found at all. In contrast, the same was true for only two out of fifty-four evicted females—4 percent. To put it another way, females nearly always survive being booted off their territories; males often do not.

When we spotted that trend late in 2006, we were puzzled. True, males are about 20 percent larger than females, and we already had reasons to believe that they are more vigorous than females in their territory defense. They alone produce the species' familiar yodel—actually a territorial display. Yet in all other aspects of breeding biology, the sexes appear similar. Common loon pairs build nests, incubate eggs, and rear chicks together. Both males and females acquire territories by one of several means: eviction; meeting a new real-estate-rich mate whose former mate has died; or establishing a new territory on a vacant lake with an available mate. Critically, the stakes for both in territorial contests seem identical. When a member of either sex loses a breeding position on a territory, it pays a reproductive price, since it must find a new position elsewhere. So why do males fight so much harder than females to maintain their territories?

One possibility is that fighting to the death for a territory represents a "terminal investment." Theoreticians have long predicted that animals nearing the end of their lives should become desperadoes during battles for resources because they have little to lose. There is some evidence to support that hypothesis in loons. Perhaps because of a small but steady extra level of stress from territorial defense, males, but not females, tend to lose weight over the course of their tenure on a territory, which often lasts five years or more. Perhaps males deteriorate physically to a point where they have little hope of being able to claim a new territory and reproduce if they are evicted. If so, they should fight very hard—even to the death—to keep the territory they possess. We do not yet have comprehensive information on the ages of resident males in our study population, however, so we will have to wait several more years to fully test that hypothesis.

Another possible explanation is that territory ownership confers some special benefit upon males. But what such benefit could have passed beneath our radar? I had a hunch that the answer might have to do with nesting.

In April and May of each year, soon after reuniting following a winter apart on the coast of Florida, pairs spend a considerable amount of time poking about near islands and shorelines. Every so often, one bird, usually the male, pauses and bows its head near a potential nest site, emitting soft moaning sounds. Sometimes it reaches underwater, tears submerged vegetation from the lake bottom, and deposits the material next to its body as the foundation for a nest. The pair may work together to accumulate a mound of vegetation that ultimately rises several inches above lake level and provides a platform for the eggs [*see photograph on the following page*]. I had watched the nesting ritual scores of times but

WOODY HAGGE

Loon chases its opponent in a territorial contest.

MICHELE P. WOODFORD

Loon couple tend their nest, above, which they made by piling up vegetation; another built-up nest is shown above, right. Sometimes loons simply scrape out a shallow depression in sand or deposit eggs directly on rocks.

had never addressed an important question about it: which mate decides where the nest goes?

Nest placement is crucial in loons. A nest must remain unknown to predators for the four weeks or so it takes for the eggs to hatch and the chicks to leave. Like many other species, loons use trial and error to help them find good nest locations. If their eggs hatch successfully, they reuse the nest site the next year; but if a predator (usually a raccoon) finds and destroys the eggs, the pair moves to a new location for the next attempt. Biologists call that the "win-stay, lose-switch" (WSLS) rule. It seems like a simple, commonsense approach to nesting, yet I suspected that this might be one situation in which loon mates are not alike. If members of one sex happened to be in control of applying the WSLS rule, only they would learn precisely where to nest within a territory, only they would benefit from remaining within a familiar territory over time, and only they might be expected to fight hard to retain control of that territory.

By 2006 my team and I had been marking our birds as well as meticulously locating and plotting nest locations for fourteen years, so we had gathered enough data to probe which member of each of our documented pairs was in charge of employing the WSLS rule. To do so, I asked whether turnover of the resident male or female—or both—disrupted the use of the rule in each territory. My findings were unambiguous: pairs composed of a male that had nested on the territory previously and a female new to the territory used the rule just as effectively as pairs consisting of two experienced mates. On the other hand, pairs composed of a new male and an experienced female almost always moved the nest to a new location, even if the previous attempt had been successful. That is, they failed to use the win-stay part of the rule. In fact, new male–old female pairs were no more likely to reuse a successful site than were pairs in which both members were brand new to the territory.

That came as a bit of a surprise because we'd also found that an intruder was about 50 percent more likely to vie for a territory the year after a set of chicks had successfully hatched there. Loons looking to breed apparently snoop around for good, established chick-producing territories in one year, then return the next to attempt a territorial coup d'état. But prospecting intruders—even male ones—don't appear to take note of successful nest locations, just successful territories.

The finding that males control nest placement had the potential to explain fatal battles among males. A resident male that, over the course of several years, has learned where to nest and where not to nest within a territory averages a 41 percent increase in hatching success. He thus has a major stake in holding onto that territory. Furthermore, we predicted, the resident male—rather than an intruder—should be the one to escalate contests. In other words, only residents should put themselves at risk for injury and death in combat. Sure enough, our data showed that resident males were the only ones to turn up dead or severely injured as a result of territorial battles in our study area.

Still, if the contested territory is worth much less to intruders than to resident males, why do intruders ever allow contests to escalate? Perhaps they simply tend to be fitter than resident males, which steadily deteriorate during their occupancy of a territory. If so, their physical superiority might make battles a low-risk venture. Fittingly, our data from the past few years show that most male usurpers are between six and nine years old and that body mass and aggressive behavior increase precisely during that age range.

I feel fortunate to have witnessed the violent contest at Burrows Lake. Like other biologists, I had considered lethal battles to be rare in territorial animals. With my eyes opened, I was forced to investigate what was at stake for the contestants. Otherwise we might never have learned the importance of male loons' familiarity with their territories and exposed the stark contrasts in males' and females' territory acquisition and defense. And I suspect I am not the only field biologist who still has a lot to learn. At a recent professional meeting where I described fatal contests between owners and intruders, a colleague who studies a certain long-lived mammal remarked to me offhandedly, "Oh yeah. We once had that happen in our study area."

Walter Piper's interest in birds began in the first grade and was encouraged by schoolteachers and especially by his devoted mother, who took him on many birding excursions. He developed a fascination with common loons during summers spent with his family on lakes in New Hampshire and central Ontario. Piper first investigated aggression among breeding birds while studying stripe-backed wrens in northern Venezuela during the early 1990s. He is currently a professor at Chapman University in Orange, California.