Marking Loons, Making Progress

Walter Piper, Jay Mager and Charles Walcott

Common the common loon may be, but it's behavior remained enigmatic until the emergence of bird-marking techniques that have now begun to yield long-term findings. Almost two decades reveal that loons do not mate for life, as so long supposed, that breeding pairs may be intruded upon by both male and female invaders, and that territorial fights between mailes can lead to fatalities 30 percent of the time. In fatal fights, the invader is always the victor. Sonogram studies reveal that the signature of these territorial birds, their yodel, is both characteristic of individuals yet also changes as their physical state and circumtances change.

Loon Territoriality
http://www.cornell.edu/video/?videoid=1166

15-minute video of the authors discussing behavior, study and capture of loons in the wild.

Internet Bird Collection
http://ibc.lynxeds.com/species/great-northern-diver-gavia-immer

Videos, photographs and a recording of loon song.

Marking Loons, Making Progress

Striking discoveries about the social behavior and communication of common loons are revealed by a low-tech approach: individual marking of study animals

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Anyone who has spent time on lakes in the northern United States or Canada is familiar with the common loon. Its haunting calls are emblematic of wild places. They captivate the listener. The ringing tremolo, for example, suggests maniacal laughter; the wail recalls the distant cry of a person in distress. Despite their humanlike qualities, though, the vocalizations of loons are acoustically complex and not easily deciphered by humans.

Even when not vocalizing, loons are charismatic creatures. They are striking in appearance: clad in black with lines of bright white ovals on their wings, intricate white badges on the sides of their long necks and delicate white "chinstraps." Their burning orange eyes seem to miss no detail. They are most often encountered foraging, making dives of a minute or more in duration to pursue fish and invertebrates underwater, propelled by their powerful legs. After watching the speed and agility of a loon passing under one's canoe, one can only pity a sunfish! Naturally enough, loons are loved and admired by humans who share their northern lakes.

The common loon is the most abundant and widespread of five species of loons that are distributed throughout the Northern Hemisphere, breeding across Canada and the northern United States and wintering along the Pacific and Atlantic coasts. Loons are socially monogamous: Pairs defend territories on freshwater lakes and build nests on islands or shorelines, where the female of the pair lays two eggs. Most clutches fall prey to raccoons, skunks and other predators during the four weeks of joint incubation by male and female. The chicks that survive to hatching are semiprecocial—downy, eyes open, and able to leave the nest to swim and dive soon after emerging. Chicks are warm brown in color, which allows them to hide effectively among rocks and logs near shore while parents are engaged in foraging and social interactions with other loons. Parents feed and attend to chicks constantly for 11 weeks, after which the chicks can feed themselves.

Most of our knowledge of common loon biology was expertly summarized in Judith McIntyre's 1989 book, *The Common Loon: Spirit of Northern Lakes.* When it was published, the book was as remarkable for what it could not say as for what it could. Missing or rudimentary were an understanding of the mating system, territory acquisition by young adults, territory defense by established breeders, and, tantalizingly, the functions of loon vocalizations.

The principal reason for our ignorance about loon behavior was simple: Observers could not identify and distinguish the individuals they studied. One might think the intricate plumage patterns of adult loons would make identification easy, and loons do display distinctions in fine plumage details, such as the number of lines and branches in neck badges, but these features can only be reliably distinguished with the bird in hand. Instead of serving as dependable ID badges, loon markings can create the illusion in observers' minds that the males and females they observe each year are the same as those seen the year before, when in fact that is not certain. Complex behaviors such as calls and social interactions may seem to dependably distinguish a familiar bird to attentive observers—but even apparently peculiar behavior may be stereotyped and thus deceptive as an identifying feature.

Band Practice

The assumption of many observers that loon pairs mate for life could be put to the test only after 1992, when David Evers and his team refined the nocturnal spotlighting technique and began to capture and mark hundreds of adults each year with colored leg bands. In this method, animals are located with a spotlight, then researchers creep up on them with an electric motor boat. Adults can be confused and frozen in place by an imitation of the chick distress call (a hoarse, plaintive whistle). Chicks can be immobilized by the "hoot" contact call that adults give each other and chicks. Both can then be scooped up with nets.

Evers and his colleagues showed not only that one could capture loons, despite their large size (4–5 kilograms) and tendency to dive when threatened, but that one could do so with sufficient frequency and predictability to maintain a marked study population. The time for systematic investigation of loon behavior had come.

By cobbling together breeding pairs banded by Evers's team with some that we banded ourselves using his technique, we began to examine loon territorial behavior in 1993 in Oneida County, Wisconsin. As an investment in the future, we banded not only adult loons but also chicks of five weeks of age or older, whose legs had grown large enough to hold the plastic bands safely. Our banding and observation occurred within a cluster of about 100 glacial lakes ranging from 4 to over 500 hectares in size comprising a roughly circular area 50 kilometers in diameter.

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Figure 1. Some study organisms are more charismatic than others. The common loon, *Gavia immer*, is talkative, athletic, handsome and until recently somewhat mysterious. The development of an efficient capture and banding technique has allowed long-term study over the loon's life span, which can pass two decades. After 18 years of study on banded populations, there are still questions remaining about the progression from chick to battler to homesteader to ancient, but there has also been a harvest of answers. The authors review current knowledge of the domestic arrangements, real estate transactions and conversations of these captivating animals. Photograph courtesy of Carol Henderson.

Most lakes in this area are surrounded by summer cottages and have high boating activity. Thus, although scenic beauty is diminished on human-impacted lakes, loon pairs that live and breed on them are tame enough that we can approach within 5 meters to identify individuals by their leg bands and record their social behavior.

Observation of marked loons on their territory allowed us to put to the test the popular conception that loons mate for life. Indeed, we soon learned that male or female pair members—always one or the other, not both—routinely vanished from their territories, leaving, for example, a marked male and unmarked female where there had previously been a marked pair. A few such disappearances would not have been surprising. After all, loons are subject to disease, injury and predation, just as other animals are, and we might expect that a breeder that died would be replaced by a new breeder. In most cases, however, we located the missing pair member on a vacant lake immediately adjacent to its original territory. The behavior of these birds was sometimes more subdued than it had been—more resting, less foraging and social activity—and in some cases obvious lacerations or defeathered patches were visible on their heads or necks. In time, we accumulated enough such observations that we began to understand that both males and females were in a constant struggle to protect their territories from intruders, which sometimes were able to evict a resident and seize the territory for themselves.

Unwelcome Mat

The regular eviction of owners from their territories caused us to turn our attention to a segment of the loon population that is obvious even in the absence of marked birds: floaters. Floaters—male and female adults that lack territories but otherwise resemble territory owners—are abundant within the population. Though initially we had no idea about the age or origin of these floaters, since they were unbanded, their visits to the lakes defended by territorial pairs are routine, averaging 2–5 visits per day throughout the breeding season (April to August). The intrusions we observe most often are highly stereotyped. They begin when a floater lands in the lake. The original pair becomes highly alert, their heads held almost comically high above the water as they scour the surface for the foreigner. The pair then proceed in tandem toward the intruder. Almost invariably, the three loons converge, engaging in a series of social behaviors—head bows, circle dances and splash dives. The intruder leaves within 30 minutes. Although the lack of marked floaters made our conclusions speculative, it seemed that a typical floater spent much of its time systematically intruding into established territories, staying from 5 to 30 minutes and then departing.

Figure 2. Loons build their nests close to the water. If threatened they can simply slide off the nest and disappear below the surface of the water. The incubating loon above is lowering its head because of the presence of the photographer, a common loon behavior when a human approaches its nest. This behavior reduces the visibility of the loon to a potential predator on the lake. Photograph courtesy of Dan Salisbury.

What might floaters gain from such territorial visits? The energetic investment required to fly between many lakes, find territorial pairs and interact with them seemed too great for birds to engage in without reward, yet most intrusions were seemingly peaceful affairs, not knock-down-drag-out contests for territorial ownership. Although we seldom observed social interaction between male intruders and female pair members, it seemed plausible that male intruders were not usually bent on usurping the territory, but instead were interested in mating with the resident female and thus siring young without rearing them. The avian literature abounds with such examples of "extrapair parentage," especially in songbirds, and many scientists have found it despite little or no behavioral evidence of "extrapair matings." Actually, one might expect that a female pair member who mated outside of her pair bond—perhaps as a means to ensure fertile eggs or to improve the genes of her offspring—would do so furtively, so as not to cause her mate to suspend parental care. To explore the possibility of extrapair parentage, we took blood samples from males, females and their one or two chicks and used DNA fingerprinting to analyze parentage. The results were clear: not a single case of extrapair parentage in 58 young from 47 families.

While we might have hoped for more colorful findings, we had all but eliminated the possibility that floaters were males systematically intruding into territories to attempt to copulate with the breeding females.

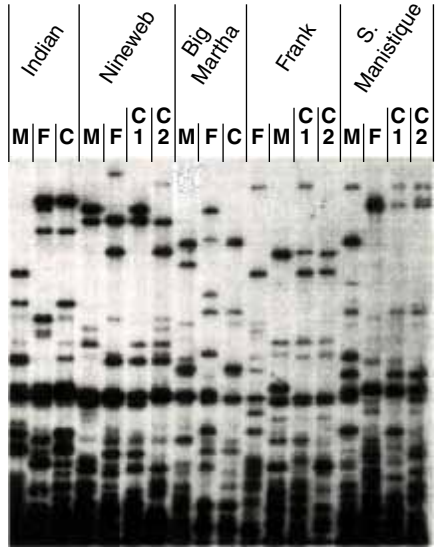

Figure 3. Multilocus DNA fingerprints of five loon families, including males ("M"), females ("F") and chicks ("C", "C1", "C2"). Fragments are passed from parents to offspring in Mendelian fashion. Thus the overall similarity of parents' fingerprints to their offspring's reveals the statistically confirmed conclusion of genetic monogamy.

Hostile Takeover

If intruders were not males looking to mate secretly with the territorial females, what were they doing? The answer was not obvious. Still, by analyzing rates of intrusion into each territory and tracking the tendency of each territory to produce chicks, we discovered a link. In years following chick production by a territorial pair, the rate of intrusions increases by 60 percent. Moreover, territorial takeovers—by males and females both—are also significantly more common in years following chick production. In short, intruders appear to target recently successful territories for takeover and often succeed in taking over those territories. Why are recently successful territories favored? Because reproductive success is highly autocorrelated in loon territories. That is, a territory that produces chicks in year 1 is very likely to produce chicks in year 2, either because chick production indicates a high-quality territory or because conditions favorable for producing chicks (such as a low density of raccoons) tend to last for several years. So

an intruder that succeeds in usurping a successful territory one year is likely to be rewarded with a favorable environment for breeding the subsequent year.

Although simple observation of loon pairs and temporal patterns of territorial intrusion gave us great insights into territory acquisition, we have only now started to achieve a fuller picture of the process. Birds that we marked as chicks have returned to the study area as adults (having acquired their adult plumage after a year or two residing as juveniles in salt-water areas) and begun to usurp territories. Male floaters that are 3 to 4 years old, we have learned, almost always acquire a territory by "founding"—settling in a vacant lake or part of a large lake and pairing with an available female. At age 5 or 6, males suddenly begin to battle for established territories. Finally, old males—those of at least 15 years—behave like very young males: They found territories, eschewing open combat. Females, on the other hand, show no relationship between age and mode of territory acquisition, being just as likely at all ages to acquire territories by settling without conflict in a vacant territory or by wresting ownership of a territory by force.

Capture and recapture of marked individuals has allowed us to document a change in the loons' body condition as they age that parallels changes in territory acquisition. Males have relatively low body mass when 4 and 5 years old, which increases steadily from 6 to 10 and then declines late in life. Female body mass fluctuates very little with age. The correlation between mode of gaining a territory and male body mass suggests that males avoid territorial confrontations when their body condition is marginal and take advantage of good body condition during young adulthood to seize territories by force. Males have good reason to avoid contests for territory ownership when not in prime condition: About a third of male takeovers (but not female ones) result in the death of a combatant, nearly always the original resident.

At All Costs

The observation of lethal combat was, in fact, a great surprise. It seems to be quite rare in animals—although this conclusion is tentative, as most field studies have limited capacity to observe lethal contests and recover corpses of slain individuals. Most fatal fighting has been detected in short-lived species, like fig wasps and spiders—groups wherein an individual might get only one opportunity to reproduce and should be expected to battle mightily for that opportunity. Loons do not fit this model, as they often live upwards of twenty years. Why would an animal with a long life expectancy ever get caught in a battle that might cost his life? Can a territory be worth so much that a male should risk death to hold onto it?

Figure 4. Loons are sturdy, dense birds, which facilitates plunging dives for fish but makes taking flight a challenge. They need a substantial water runway to do so. The loon's legs are set far to the rear, which is a fine configuration for swimming but nearly useless for walking on land. A loon that mistakes a wet road for a lake is doomed unless it can convey itself to a large enough body of water. Photograph courtesy of Dan Salisbury.

One hypothesis that might help explain fatal fighting in male loons holds that the value of a territory to its owner might increase greatly over time, justifying vigorous territorial defense. The key to understanding a male's stake in his territory lies in nesting behavior. When a pair nests and succeeds, they tend to reuse the successful site, which makes sense, as its success likely indicates a location safe from nest predators. When a pair fails, they usually move the nest. This intuitive "win–stay, lose–switch"

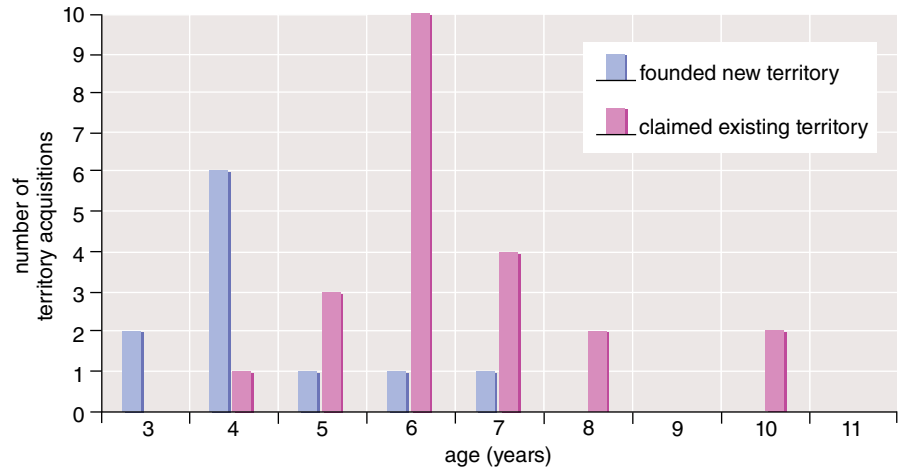

Figure 5. Males show stark changes in their mode of territory acquisition with increasing age. Males 3 to 4 years old found new territories in vacant lakes or parts of lakes; males of 5 to 8 years almost always claim an occupied territory, which requires them to evict the current resident.

Figure 6. This fight between two male loons ended with a 16-minute chase across the surface of the water. About 30 percent of male battles end with a fatality, always the resident male. Analysis of this intriguing finding suggests that loons make sophisticated, high-stakes investments in defense of nesting sites and acquired familiarity with local territories. At right, a 3-year-old banded intruder flees after a brief visit to a defended territory. Photographs by Dan Salisbury.

rule is widespread in vertebrates and has been shown to improve nesting success in loons and many other species. Since we had marked breeding pairs, we could ask, "Which pair member is using the rule?" We answered this question by looking at use of the nesting rule under different scenarios.

When the male from the previous year returned but the female had been replaced by a new bird, the pair continued to use the rule—as did pairs in which both male and female from the previous season had returned. On the other hand, new male/old female pairs ceased reusing successful locations, and, indeed, selected nest sites with no more success than new male/new female pairs. Moreover, pairs containing a male with past breeding success on the territory were 41 percent more likely to produce chicks than were pairs with an inexperienced male.

From a male's perspective, then, nesting on a familiar territory is a good deal better than nesting on an unfamiliar one, because he knows where to nest and is far more likely to produce young there. Hence, one can see why a male who knows where to nest on his territory might fight furiously to keep it. A territorial male that accepts defeat by an intruder vying for his territory accepts a sharp decrease in reproductive success.

The "familiarity" hypothesis for fatal fighting among males generates one clear prediction that we can examine immediately: The males that perish during territorial contests should usually be resident males—those with a large stake in staying put. Intruders that challenge them should be less likely to be truly dogged in a territorial contest, as they do not know the territory and will have to learn by trial and error how to use it in the event that their eviction attempt succeeds. We quickly confirmed this prediction, as nearly all males found dead after territorial battles were territorial owners. Combat is a mutual endeavor, like a dance, and yet the owners were the only combatants that fought unto death. The record of numerous combats shows no such commitment from invaders. Combining this finding with our recent findings with respect to male territory acquisition, we can infer that fatal battles are those that pit an experienced owner, who might have declined a bit in body condition from his prime, against a young, fit, 5- to 8-year-old floater.

As satisfying as the familiarity hypothesis seems, it has a glitch. A 41 percent bonus in reproductive success for the resident male is not trivial, but it seems an insufficient payoff to make a male risk his life. After all, even a male that accepted eviction from his territory and was forced to move to a new one would likely recover his lost reproductive success within 3 to 5 years. Why risk death?

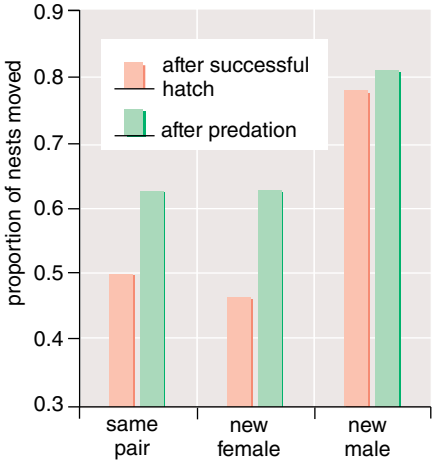

Figure 7. The graph compares movement of nest location between consecutive nesting attempts by loon pairs of different compositions. If both male and female returned from the previous year ("same pair"), pairs tended to position the nest according to the success of their last attempt, reusing successful sites and abandoning ones where eggs had been predated. Turnover of the female pair member ("new female") did not alter the use of this nesting strategy. But turnover of the territorial male from the previous year resulted in nests being relocated, regardless of success.

The "desperado" hypothesis might help explain fatal fighting. Perhaps the decline we have detected in older males is rapid enough that there might be some greybeards out there with just a year or two left to live. If so, and if old males can *detect* their loss of condition, they might well become "desperados"—individuals with so little time left that it becomes worthwhile risking their lives for another year or two on a familiar territory, instead of accepting displacement to an unknown territory for a year or two of marginal reproduction. While the hypothesis seems sound, we are still collecting enough data on very old males of known age to test the desperado hypothesis robustly. In this case, 18 years of data is not enough!

Caller ID

The dramatic changes that occur during the lifetime of a territorial male raise the possibility that the male-only territorial call, the yodel, might also change as a male ages. A ringing advertisement of territorial behavior, the yodel consists of an introductory phrase that rises in pitch followed by one or more "repeat syllables," which comprise two brief, frequency-modulated notes. Investigation within and between breeding seasons has shown that each male's yodels are unique in terms of timing, frequency and frequency modulation. In effect, the yodel of a male is his "voice," recognizable to humans who know it and probably also to other loons. The variability and acoustic complexity of the yodel suggests that it might contain information about the signaler in addition to his identity.

At first glance, it seems quite likely that the yodel conveys information about a male's ability to defend a territory. Almost all yodels occur when a male is in a tense interaction with an intruder that has landed on its territory or when an intruder is flying overhead. So yodels appear to be "aimed" at specific territorial opponents. If so, we should expect that a yodeler wishes to communicate something about himself or his motivation to defend his territory—perhaps in an effort to save himself the trouble and energetic cost of a lengthy confrontation or battle. One crucial bit of information that a male might want to communicate is his body size or condition. We might hypothesize that a large or fit male, who would be a formidable opponent, would want to communicate that, if possible, through his yodel.

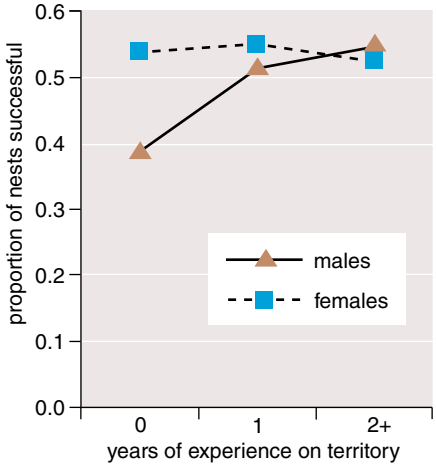

Figure 8. The nesting success of males and females is compared according to their length of experience on a territory. As a consequence of using the "win–stay, lose–switch" rule, males improve their breeding success markedly between their first and later years. Females, which do not control nest placement, show no such improvement.

Figure 9. The soundtrack of the wild in many northern territories, the yodeling of the male loon is an announcement of territoriality consisting of an introductory phrase followed by repeat syllables. Male loons have a consistent yodel year after year, unique to themselves, but if they change territories, they often change their yodel. Photograph courtesy of Nathan Banfield.

In fact yodels do betray information about the fighting ability of the yodeler. The information is encoded in the dominant frequency of the yodel—the frequency of the yodel that is of greatest amplitude, or loudest. However, dominant frequency is closely correlated not with body size but with body mass. Thus, it seems that heavy males are potentially signaling their body condition through their lower frequency yodel. We also found a correlation between change in body mass and dominant frequency from one year to the next. That is, males whose yodels rise in pitch from one year to the next have lost body mass over that period and those whose yodels become deeper have gained mass. A loon listening to a male's yodel, therefore, could instantly get information about its condition, and, if it recognized the same male yodel from the year before, could learn whether the male was gaining or losing condition.

It is one thing for humans to use acoustic analysis software to learn that features of loon calls contain information about the loons themselves and quite another to show that loons listening to the signal actually perceive and act on this information. To see whether receivers might use information about body condition within loon calls, we played three versions of a stranger's yodel to territory holders: 1) the original yodel, 2) the original yodel decreased in frequency by 200 hertz (a change that left the altered call within the normal range of loon yodels), and 3) the original yodel increased by 200 hertz (which also remained within the natural frequency

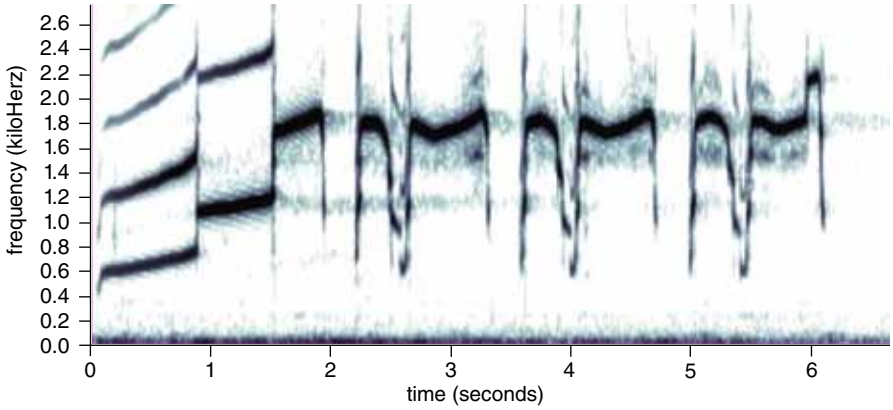

Figure 10. This sonogram of a male loon's yodel shows the introduction followed by three repeat syllables at the end. Measuring the frequencies of two notes and the duration of the introduction and space between the notes allows us to tell different loons apart by their yodel. Analysis of many yodels indicates that the loon is announcing his identity, fitness and willingness to fight.

range). We found that territorial males responded more quickly and aggressively towards yodels that were shifted to lower frequencies. This result suggests that loons view low-frequency yodels as more threatening. They really do pay attention to frequency! It remains to be seen, however, whether loons listening to yodels have the capacity to remember and learn from differences in yodels compared across years. If so, they might use this ability to target territories of declining owners for takeover attempts.

There is one puzzling aspect to the finding of "honest signaling" of body size, as animal behaviorists call it. Why would a small male ever yodel, if in so doing he was revealing his small size to all listeners? This practice would seem masochistic—equivalent to asking another male to try to evict you from your territory. Yet small males yodel about as often as do large males. There must be some compensating benefit to yodeling that offsets the disadvantage of telling competitors that you are small.

Indeed, there is more information contained in the yodel than just identity and condition. The mere fact that a male is yodeling reveals that he is territorial, of course, but we wanted to determine whether the number of repeat syllables in a male's yodels communicated something about his aggressiveness. Repeat syllables vary greatly in number from yodel to yodel within and between males, so it seemed plausible that this flexible aspect of the call was being used for this purpose. Indeed, we have learned that males produce more repeat syllables in their yodels when in close encounters with intruders than when intruders were flying over or far away on the water. We followed up this promising piece of field data with an experiment that simulated the intrusion of a male floater into the territory defended by a breeding pair. As expected, territorial males responded more quickly and with more tremolos and yodels of their own to foreign yodels manipulated to have four or seven repeat syllables than to those altered to have only one repeat syllable. Thus, the number of repeat syllables in the yodel is taken by other loons as a signal of high aggressive motivation on the part of the yodeler. So a small male must yodel in order to signal his territorial status and aggressiveness, even though his yodel betrays his small size in the process.

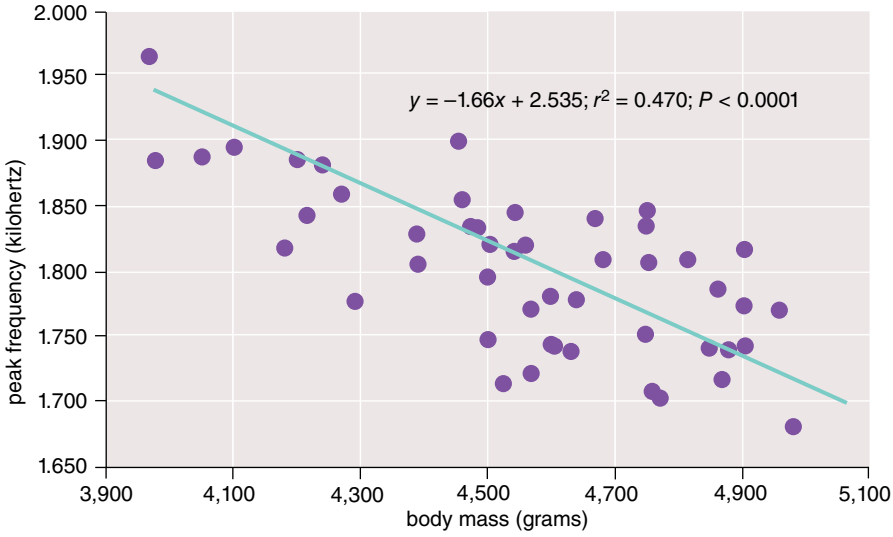

Figure 11. The peak frequencies for yodels of males with low body mass are much higher than those of heavy males, raising the question of why a smaller male would engage in "honest signaling" that would seem to advertise small size—no small matter between competing territorial animals. Possibly the smaller animal is also signaling his aggressiveness in the duel for territory, also no small matter.

We performed a second experiment on aggressive motivation in which we actually altered the quality of a male's territory. Although this might sound daunting, one can improve territory quality simply by constructing a 1 × 1 meter floating platform from cedar logs, adding buoyant material to improve flotation and anchoring this "nesting raft" 20 meters or more from shore. We have shown that nesting platforms increase hatching success by 69 percent by deterring raccoons and other egg predators. Males in territories with added platforms emitted longer yodels compared to their own calls in the years before and after platform deployment and compared to those of control males whose territories had no platforms. These results suggest that males crank up their territory defense when their territory becomes valuable, providing further evidence of how males use yodels to communicate aggressive motivation.

Our use of marked birds allowed us to track males that moved from one territory to another, and it exposed an unexpected and baffling aspect of their yodels: The yodel changes when a male moves from one territory to another. Specifically, yodels change in the timing and peak frequency of the introductory note and the length of the

delay between the introductory note and first repeat syllable. What does a male gain from shifting his yodel in this way when he claims a new territory? Is he hiding his identity? If so, this might help him evade young males that had been targeting his previous territory for takeover attempts. We would predict, in this case, that the new yodels would be unrelated to their original form, not just modulated in some systematic way that could be decoded. But the changes in males yodels *are* systematic. Shifts in acoustic parameters of the yodels almost always make the male's yodel differ as much as possible from that of the male that resided on his new territory before him. This odd finding supports the hypothesis that males shift their yodels to proclaim that they are new to the territory and should not be confused with the previous male. Such a strategy might make sense. The old male, after all, was humbled and possibly killed, suggesting that he might have been in poor condition and subject to many eviction attempts by floaters. Complete testing of these hypotheses will occur when we detect two or three times as many territory and yodel shifts, at which point we will be able to link the cause of the territorial turnover with the change in the yodel and search also for an impact of the change in ownership on the rate of territorial intrusion.

We have made great strides in understanding how loons gain and defend breeding territories, following systematic capture and marking of our study animals. Marking of individuals has revealed that territorial takeover is common; that among males, only those in prime condition achieve takeovers; and that male loons control where the nest is placed in a breeding attempt, thus acquiring unique familiarity with their territory and increasing the value of the territory to the male. Our vocal analysis has been similarly dependent on recording the calls of marked males. Field observations and playback experiments have shown that yodels betray the yodeler's size and aggressive motivation, and have revealed the curious alteration of yodels by males that have just taken possession of a new territory. Much about loon behavior remains unknown, but systematic marking and study of the species has given us the power to unravel many of the mysteries of this most engaging animal.

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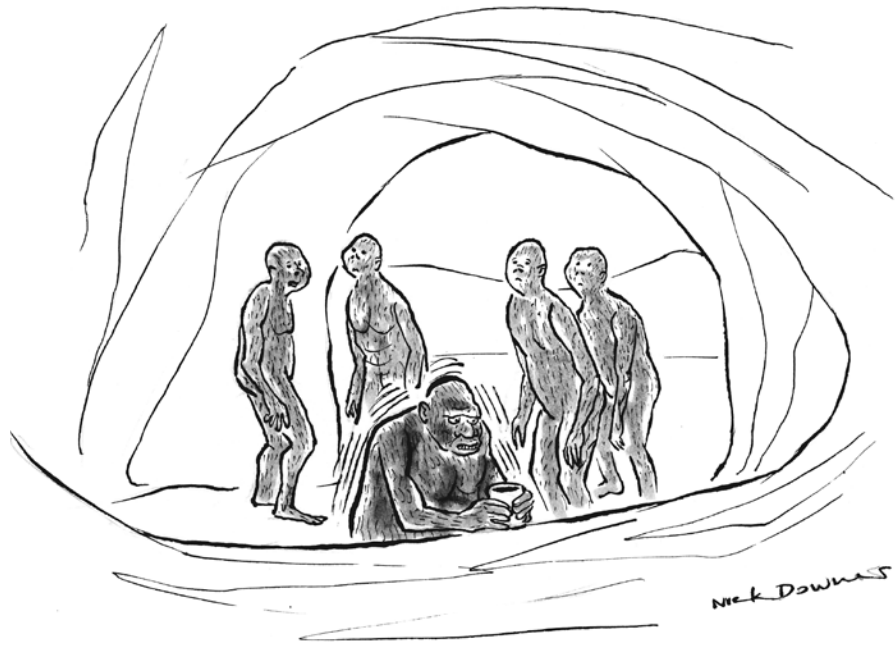

"Him we call 'Java-Man.'"