ECOLOGY

Female Eavesdropping on Male Song Contests in Songbirds

Daniel J. Mennill,* Laurene M. Ratcliffe, Peter T. Boag

Male song reflects the quality of the singer in many animals and plays a role in female choice of social and copulation partners. Eavesdropping on male-male vocal interactions is a means by which females can compare different males' singing behavior directly and make immediate comparisons between potential partners on the basis of their relative vocal performance (*1*, *2*). Using an interactive playback experiment followed by microsatellite paternity analysis, we investigated whether female black-capped chickadees (*Poecile atricapilla*) base their reproductive decisions on information gained through eavesdropping.

Black-capped chickadees are socially monogamous songbirds that follow a mixed reproductive strategy in which one-third of broods include young that are not related to their social father (*3*). From 1999 to 2001, we assessed dominance ranks in a free-living population of chickadees at Queen's University Biological Station, Canada, to predict which males were likely to be sought for extrapair copulations (high-ranking males) and which males were likely to lose paternity within their nests (low-ranking males) (*3*, *4*).

At the start of the breeding season, when male-male song contests are common and females actively solicit copulations, we used interactive song playback to engage territorial male chickadees in countersinging interactions with a simulated intruder (*5*). We performed 6.0-min playback trials to dyads of neighboring high-ranking and low-ranking males from the same winter flock. In control treatments, we mimicked natural territorial encounters; we simulated an intruder that sang submissively (Fig. 1A) with the high-ranking playback subject and sang aggressively (Fig. 1B) with the low-ranking neighbor. In experimental treatments, we attempted to alter eavesdropping females' perceptions of their social mates; we simulated an intruder that sang aggressively with the high-ranking playback subject and sang submissively with the low-ranking neighbor. To test whether interactive playback altered the normal pattern of paternity in the nests of subject males, we conducted paternity analysis on blood samples collected from offspring (*6*).

High-ranking males that lost song contests with a simulated intruder lost paternity in their nests (Fig. 1C); high-ranking males that received playback simulating an aggressive intruder showed a significantly greater level of paternity loss than high-ranking males that received playback simulating a submissive intruder (control I; Fisher's exact test, $P = 0.05$) and a significantly greater level than a control group of high-ranking males that received no playback (control II; $P = 0.05$). As predicted (*3*, *4*), we observed little extrapair paternity in the nests of high-ranking males that received submissive playback and high-ranking males that received no playback. Thus, females paired to high-ranking playback subjects adopted a mixed reproductive strategy after hearing brief song contests in which their mate fared poorly. This change in female reproductive decisions after short playback sessions suggests that information available through eavesdropping plays an important role in female assessment of male quality.

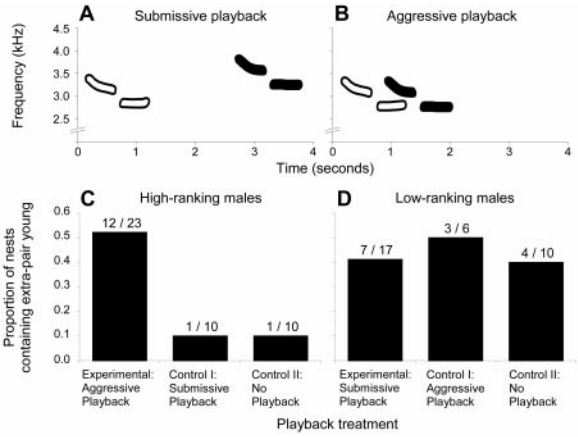

Fig. 1. Sound spectrograms of vocal interactions recorded during (**A**) submissive playback trials in which the simulated submissive intruder (black) avoided matching the pitch and overlapping the songs of the subject (white) and (**B**) aggressive playback trials in which the simulated aggressive intruder (black) matched the pitch and overlapped the songs of the subject (white). (**C**) High-ranking males who received aggressive playback treatment lost paternity significantly more often than high-ranking males who received control treatments. (**D**) Low-ranking males who received submissive playback treatment did not lose paternity significantly less often than low-ranking males who received control treatments.

Playback mimicking a submissive intruder did not reduce the level of extrapair paternity in the nests of low-ranking males (Fig. 1D); paternity loss by low-ranking males that received playback simulating a submissive intruder was not significantly different than for low-ranking males that received playback simulating an aggressive intruder (control I; $P = 1.0$) or low-ranking males that received no playback (control II; $P = 1.0$). The females paired with low-ranking males that received submissive playback may have engaged in extrapair copulations before playback sessions or may have heard natural male-male song contests in which their partner revealed his low-ranking status. Whereas females paired to low-ranking males normally overhear their mate win some song contests and lose others, females paired to high-ranking males are only accustomed to hearing their mates win. As such, two short playback sessions were sufficient to alter high-ranking, but not low-ranking, females' perceptions of their partners' status.

We tested the alternative explanation that unusual patterns of extrapair paternity could have arisen from females reacting to changes in their partners' postplayback behavior, rather than from eavesdropping per se. We detected no significant changes in male behavior after playback (*5*), further suggesting that changes in female reproductive decisions arose through female eavesdropping on male song contests.

Our results support the idea that information may be transferred between individuals in a communication network rather than simply within a dyadic context (*2*) and provide a conceptual link between the attractive and repellent properties of male song where mate attraction and territory defense may be simultaneous functions of a common signal. Finally, our results show that short playback sessions can have long-lasting and far-reaching effects on individual fitness.

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6. Paternity was analyzed by polymerase chain reaction amplification of two highly variable microsatellite loci. Offspring were considered extrapair young if they had one ($n = 44$) or two ($n = 22$) allelic mismatches with their social father. The combined exclusionary power was 0.91 given one known parent.
7. We thank R. DeBruyn, A. MacDougall, D. Aiama, A. Boone, P. Christie, L. Colgan, M. Cunningham, S. Doucet, J. Hodson, B. Meigs, S. Ramsay, N. Vreeswyck, and landowners adjacent to the study site for assistance and the Natural Sciences and Engineering Research Council of Canada, the American Ornithologists' Union, the Animal Behavior Society, the Association of Field Ornithologists, the Frank M. Chapman Memorial Fund, Queen's University, and the Society of Canadian Ornithologists for funding.

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USA TODAY

05/02/2002 - Posted 03:27 PM ET

Health & Science

Female chickadees love the lead singer

WASHINGTON (AP) — The love life of a female chickadee could make a country music classic: "If your song don't pass muster, buster, I'm gone."

The lady chickadee has a cheatin' heart, quick to find another lover if her mate fails to win his daily song contests with rivals. In effect, she decides that if her mate is a loser, he won't be the only papa in her nest, say researchers at Queen's University in Kingston, Ontario.

Daniel Mennill, co-author of a study appearing Friday in the journal *Science*, said mates of high-ranking male black-capped chickadees are more likely to be unfaithful than are the mates of lower-ranked males.

"Females are accustomed to hearing their high-ranking mates dominate a song contest," Mennill said. "It is quite a shocking event to their ears to hear them lose a song contest."

When that happens, he said, the female will sneak out before dawn and meet with a rival male for a coupling. Then she flies back home as if nothing happened and continues to live with her partner.

"These extra matings are just short copulations — about 30 seconds," said Mennill. The long-term partners "do remain mated, in a social sense."

The effect of these extra matings is that some chicks in the nest have been fathered by some other male chickadee, he said. And the betrayed male apparently never knows.

Mennill said he established by DNA analysis of blood from the chicks that one or two birds per clutch had a father than the one that raised them.

Male chickadees are challenged virtually every day to a song contest with rival males. They use the contests to defend territory and nests.

"It is only the males that sing," said Mennill. "Every male chickadee has only one song — two notes that sound like 'fee-bee.'"

One male sings and the other then sings back in a competition that may last for several minutes.

"If a male is very aggressive, he'll go through a set of routines where he will match the pitch and try to overlap the song of his opponent," Mennill said.

While this is going on, the female is listening, gauging who is winning. If her mate loses, she remembers.

Mennill proved the chickadee cheating by recording some of the bird songs and then engaging in a singing contest with a male bird.

"The main effect is that the female is more likely to engage in extrapair copulations if the high-ranking partner was bested."

If a male chickadee doesn't win daily song contests with rivals, he may return to an empty nest.

"A few times I have seen a male follow the female and it did turn into a bit of a fight between the two males and the two females," said Mennill. "But usually these things are very quick and the female can sneak away and be back before her mate notices."

The females of high-ranking males are most likely to cheat, he said. Rank among chickadees is established in the fall when the birds gather in flocks that will last through the winter. Somehow the birds establish an Alpha, or primary, male and female, a Beta, or second in rank, male and female, and so on.

"There is an Alpha chickadee for whom the others make way at a food source," Mennill said. "The lowest ranking bird has to wait for everyone else."

Even though chickadee partners may stay together for years, the birds do have a system rather like divorce, said Mennill.

If, for instance, the Alpha female dies or is grabbed by a hawk, then the Alpha male becomes a nestwrecker.

"Within 24 hours, the Beta female will divorce her partner and pair with the Alpha male, leaving the Beta male alone," Mennill said. "The females will do a lot of social changing in order to pair with a higher ranking male."

Sounds like another country song.

By Paul Recer, The Associated Press

NATIONAL POST
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Why do female chickadees cheat? Singing duels at dawn

Margaret Munro
National Post
May 3, 2002

Daniel Mennill has been up before dawn all week to check on his cheating chickadees. And the tale the Queen's University researcher has to tell is about as X-rated as it gets in the avian world.

When a female black-capped chickadee hears her mate lose a singing duel, she is likely to sneak off in the early morning. Once in the rival's territory, she sets her wings a quivering. The male quickly clues in. After a split-second coupling in the bushes, the female heads home. She then proceeds to lay an egg or two fertilized with the rival's sperm. The offspring are reared by her unsuspecting mate.

"It's really quite remarkable," says Mennill, who tracks 200 chickadees in the forest north of Kingston. He and his colleagues have shown -- through tests of blood taken from young birds -- that up to one-third of female chickadees cheat on their mates.


A female chickadee.

Not only has Mennill seen the cheating chickadees in action. He has also figured out that females decide to seek sex elsewhere after eavesdropping on spring-time singing contests between males -- contests that can be heard in most parts of Canada this week.

Mennill uses pre-recorded chickadee songs to have singing duels with the male chickadees. "When I make a female's mate sound like a loser, she changes her reproductive strategy and goes to a neighbouring male for copulation," Mennill says. The findings are detailed in the journal Science today.

Chickadees, which are usually monogamous, have an impressive social hierarchy. Couples in a flock mate on the basis of ranking -- the alpha male with the alpha female, followed by the second- and third-ranking pairs. But "if the alpha male in a flock dies, the beta male will divorce his mate and move up to mate with the alpha female," Mennill says.

In spring, the chickadee couples stake out their territory to build nests. The females lay their eggs -- one every morning until there are seven in the nest.

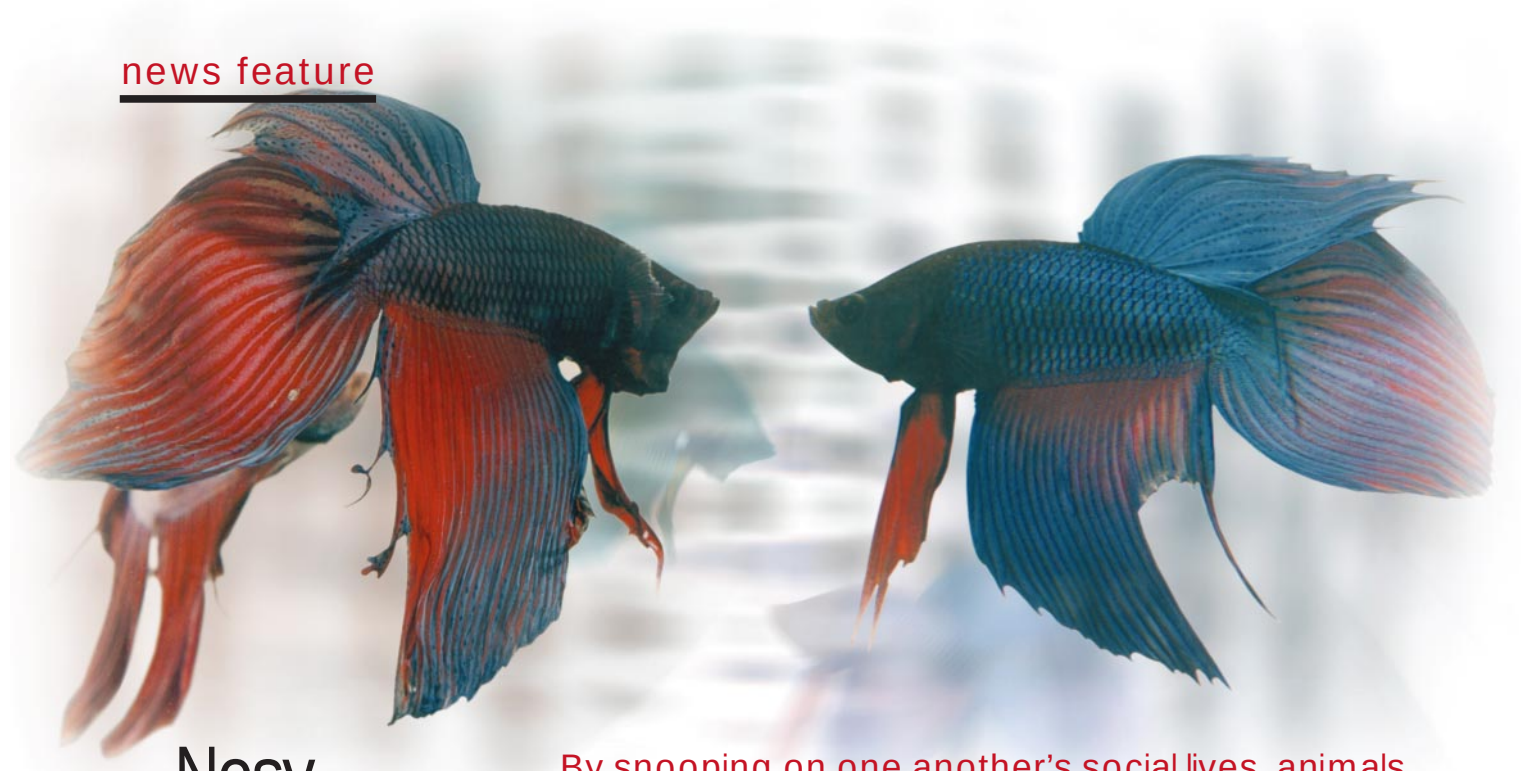
But the shells around the tiny eggs do not harden until just before the egg comes out. "So the sperm can actually fertilize the egg almost at the last possible moment," Mennill says. Which is were the singing duels come in.

The male hangs around his territory, singing his plaintive "Phee Bee" song with all his might, and mating when his female partner is willing.

Curious to see if the singing contests could help explain why a third of females cheat, Mennill decided to compete himself. When high-ranking males lost a song duel to Mennill's aggressive playback "rival," they also suffered a paternity loss. The impact was less dramatic on low-ranking males. Mennill and his co-authors say this may be because mates of low-ranking males are used to hearing their partners win some and lose some.

Males seem to be wise to the cheating behaviour. "They spend a lot of their time following their females around," says Mennill. "Often, the male hears the noises associated with the copulation and rushes over and it turns into a big fight."

Males do not, however, get aggressive with their cheating partners. To lose one egg to a rival is not that serious because he still gets to father the other nestlings, Mennill explains. And the female is key to survival of those offspring.



R. F. OLIVEIRA

Nosy neighbours

By snooping on one another's social lives, animals can work out how to behave when they meet in the future. John Whitfield listens in on the natural world's eavesdroppers.

Nosiness isn't nice. But in the past few years, behavioural biologists have shown the trait in a more positive and intriguing light. Animals from fish to songbirds, they have found, can achieve success by keeping watch on their neighbours' social lives. Such eavesdropping may also be woven into the fabric of human societies — and might even help to explain why people often behave charitably.

Prying animals reap significant rewards. They know when to pick a fight and when to back down; who to mate with, and who to cuckold. Not surprisingly, perhaps, researchers have also found that animals behave differently depending on who is watching or listening. Animal communication, experts are coming to realize, has evolved to fit into a social network, rather than being a collection of signals intended simply to impress a particular mate or rival[1].

Eavesdropping shows "how incredibly subtle animal strategies are", says evolutionary biologist Lee Dugatkin of the University of Louisville in Kentucky. This subtlety explains why it went unnoticed until recently — it's tricky to design experiments to tease out the effects on one animal of watching other animals interact. Peter McGregor, a behavioural ecologist at the University of Copenhagen in Denmark, suggests that researchers may also have neglected such experiments because they underestimated animals' cunning. "For most people, fish don't rate when it comes to cognitive abilities," he observes.

Yet McGregor's team has shown that Siamese fighting fish (*Betta splendens*), pictured above, possess considerable social nous. Males of this famously aggressive species defend their territories with displays of fin-waving and gill-raising. But if this doesn't settle matters, things turn physical — sometimes fatally so.

Like human boxers, Siamese fighting fish study their opponents' previous bouts. Males pay more attention to their neighbours when they fight than at other times, McGregor and his colleagues found. And after viewing such contests, males approach the winners more warily than they do the losers, relying more on visual displays and less on biting[2].

Verbal abuse

Some researchers have questioned whether such experiments prove that bystanders scrutinize the interaction between opponents — they might be responding to the animals' inherent toughness or weediness. McGregor's team tackled this issue in great tits (*Parus major*) by using recordings of the birds' songs. To a male great tit, victory is a question of timing. A male threatens a rival by singing over his song, and shows deference by singing only in the gaps between the other's choruses. This allowed the researchers to use the same songs, regardless of any intrinsic property they might have, to denote attack or defence, belligerence or tact.

Setting up two loudspeakers outside a male's territory, the researchers played out duets of differing structures and outcomes. They then moved either the winning or losing speaker into the bird's territory, and noted his reaction. Males sang less to losers[3], perhaps because they regard them as less of a threat, or perhaps because they are more ready to escalate contests with losers to visual displays or violence. A winner got the same cautious treatment as a stranger.

Playback experiments with nightingales (*Luscinia megarhynchos*) yield similar results — except that males intensify their singing towards winners, rather than giving losers the silent treatment[4,5]. Again, it is hard to know whether the differences reflect a more, or less, aggressive response. "The interpretation can go into hand-waving," McGregor admits. But in each case, it is clear that eavesdropping influences the animals' subsequent behaviour.

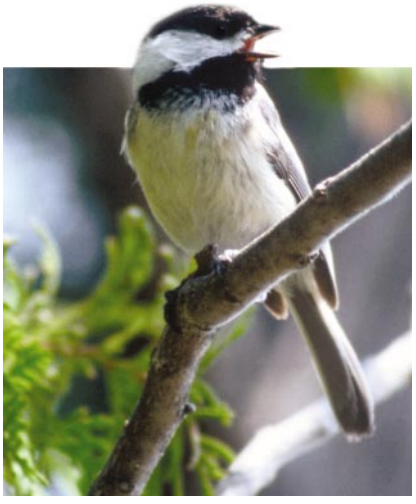
Watching a fight also changes physiology. Cichlid fish (*Oreochromis mossambicus*) that see a contest experience a rush of testosterone, perhaps priming them to fight[6]. Dugatkin believes that the next challenge is to integrate behavioural and physiological data on eavesdropping. "There are very few studies looking at the physiology and behaviour of one system," he says. "I think that synthesis is going to happen soon."

R. EARLEY/GEORGIA STATE UNIV.

Nosiness alters physiology, says Lee Dugatkin.

Males are not the only

D. MENNILL



S. M. DOUCET

Daniel Mennill found that female black-capped chickadees will cheat on mates that lose fights.

ones noting the results of their neighbours' squabbles — females use the same information to help them to choose their mates. Again using song playback, McGregor's team escalated contests with some male great tits, while backing down against those on neighbouring territories. Subsequently, the mates of defeated males were more likely to visit the adjacent territory[7]. Seemingly disenchanted with their partner — but impressed by what they heard coming from next door — the females were presumably seeking what behavioural ecologists call 'extra-pair copulations'.

Experiments on a closely related species lend support to this idea. Daniel Mennill of Queen's University in Kingston, Ontario, and his colleagues picked playback fights with male black-capped chickadees (*Poecile atricapillus*), and then analysed the DNA of the chicks born to their mates. The researchers found that the female partners of defeated males were about five times more likely to lay eggs fertilized by other males, compared with females who never heard their partner get beaten[8].

Covert struggle

With such high stakes, it is likely that eavesdroppers have shaped the evolution of animal communication. Some behaviours seem adapted to avoid prying ears. In many songbirds, says Mennill, the longest, most evenly matched song duels are the quietest. Where both males are struggling to dominate, he suggests, "they might not want to broadcast what's going on".

The effect of an audience on animals' social interactions is harder to study than eavesdropping, and this work is at an early stage. Again working with fighting fish, McGregor's team has found that males display to each other differently when a female is watching[9]. They reduce their aggression, and switch to conspicuous displays incorporating some of the elements used in courting, such as tail waving. And in July, Michael Kidd of the University of New Hampshire in Durham told the Animal Behavior Society's annual meeting at Indiana University in Bloomington that defeated male fighting fish prefer to court females that didn't witness their humiliation. "They have a fairly strong preference for females that didn't see them lose," says Kidd.

Eavesdropping is thought to help animals to avoid fights they cannot win. But paradoxically, eavesdroppers might make contests more aggressive, according to evolutionary biologist Rufus Johnstone of the University of Cambridge, UK. He used game theory to analyse the costs and benefits of winning and losing fights, and of backing down quickly versus a prolonged tussle. Eavesdroppers, he found, increase the value of victory: an animal that wins its current contest will get the deterrent benefit of a tough-guy reputation, and so is more likely to escalate a fight[10]. "Eavesdropping can evolve to reduce the risk of fighting, but once it becomes established it promotes aggression," says Johnstone.

Replace acts of violence with ones of charity, and Johnstone's model becomes similar to those used to explain apparently selfless kindness. We often help people we are unlikely to meet again. One reason might be that good deeds get their perpetrator a glowing reputation that helps them in the future. Theoretical models suggest that altruism can survive in populations where individuals trust those they have seen cooperate with others, but give nothing to those they have seen behave selfishly[11].

Research by Manfred Milinski, a behavioural ecologist at the Max Planck Institute for Limnology in Plön, Germany, and his colleagues supports this idea. In one experiment, volunteers were given money and told they could donate some of it to the other participants over a series of rounds. This benefited the recipients more than the donors, because the experimenters supplemented each donation. Even though participants could not donate to someone who had given to them, they were more generous towards those who they had seen give to others[12]. In another game, Milinski found that people were more likely to contribute to a public fund if their enhanced reputation could be used to attract private donations from other players[13].

The behavioural science of eavesdropping might soon be tested in the human social marketplace. Milinski's research has attracted the attention of managers trying to control demands on Germany's health service. He suggests that doctors could publish lists of how many treatments they have prescribed and how much each has cost. Even without naming names, Milinski argues, people might be so concerned about gaining a bad reputation that they will be shamed out of seeking needless medical attention. "If peoples' reputation is at stake they are much more cooperative," he says. ■

Good guys win: Manfred Milinski has shown that we help those with a charitable reputation.

John Whitfield works in *Nature*'s news syndication team.

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