

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 (*Parus 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

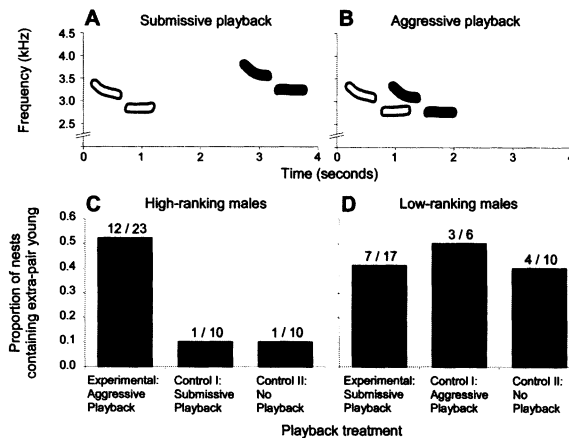


Fig. 1. Sound spectrograms of vocal interactions recorded during (A) submissive playback trials in which the simulated submissive intruder (black) avoided matching the pitch and overlapping the songs of the subject (white) and (B) aggressive playback trials in which the simulated aggressive intruder (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.

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.

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 ag-

gressive 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.

References and Notes

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5. See supplemental information available on Science Online at www.sciencemag.org/cgi/content/full/296/5569/873/DC1.
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.
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Biology Department, Queen's University, Kingston, Ontario K7L3N6, Canada.

*To whom correspondence should be addressed. E-mail: mennilld@biology.queensu.ca