

contexts in which they are commonly used. Further study is necessary to determine how the results of an investigation like this one are affected by season, to what extent complex information can be conveyed through call vocalizations in birds, and how reliance on calls may vary with song repertoire size.

We owe special thanks to Bruce Falls for the use of his recording and broadcasting equipment and his tapes of White-throated Sparrow song, and to David Airey for help with statistical analyses. We also thank the Cornell University Laboratory of Ornithology for the Benning Fund Scholarship to CEC.

LITERATURE CITED

- BORROR, D. J., AND W. W. H. GUNN. 1965. Variation in White-throated Sparrow Songs. *Auk* 82:26–47.
- DARLINGTON, R. B. 1990. Regression and linear models. McGraw-Hill, New York.
- FALLS, J. B. 1969. Functions of territorial song in the White-throated Sparrow, p. 207–232. In R. A. Hinde [ED.], *Bird vocalizations*. Cambridge Univ. Press, Cambridge.
- FALLS, J. B. 1988. Does song deter territorial intrusion in White-throated Sparrows (*Zonotrichia albicollis*)? *Can. J. Zool.* 66:206–211.
- FALLS, J. B., AND J. G. KOPACHENA. 1994. White-throated Sparrow, p. 1–30. In A. Poole and F. Gill [EDS.], *The birds of North America*, No. 128. The Academy of Natural Sciences, Philadelphia, and the American Ornithologists' Union, Washington, DC.
- FICKEN, R. W., M. S. FICKEN, AND J. P. HAILMAN. 1978. Differential aggression in genetically different morphs of the White-throated Sparrow (*Zonotrichia albicollis*). *Z. Tierpsychol.* 46:43–57.
- HOUTMAN, A. M., AND J. B. FALLS. 1994. Negative assortative mating in the White-throated Sparrow, *Zonotrichia albicollis*: the role of mate choice and intra-sexual competition. *Anim. Behav.* 48:377–383.
- KNAPTON, R. W., AND J. B. FALLS. 1984. Differences in parental contribution among pair types in the polymorphic White-throated Sparrow. *Can. J. Zool.* 61:1288–1292.
- KOPACHENA, J. G., AND J. B. FALLS. 1993. Aggressive performance as a behavioral correlate of plumage polymorphism in the White-throated Sparrow (*Zonotrichia albicollis*). *Behaviour* 124:249–266.
- KREBS, J. R. 1977. Bird song and territorial defense. *New Scientist* 70:534–536.
- KREBS, J. R., R. ASHCROFT, AND M. WEBBER. 1978. Song repertoires and territory defence in the Great Tit. *Nature* 271:539–542.
- LOWTHER, J. K. 1961. Polymorphism in the White-throated Sparrow, *Zonotrichia albicollis*. *Can. J. Zool.* 39:281–292.
- LOWTHER, J. K. 1962. Colour and behavioural polymorphism in the White-throated Sparrow, *Zonotrichia albicollis*. Ph.D. diss., Univ. Toronto, Toronto, Ontario, Canada.
- LOWTHER, J. K., AND J. B. FALLS. 1968. White-throated Sparrow. In O. L. Austin Jr. [ED.], *Life histories of North American cardinals, grosbeaks, towhees, finches, sparrows and allies*. Part 3. U.S. Natl. Mus. Bull. 337:1364–1392.
- MARLER, P., AND C. EVANS. 1996. Bird calls: just emotional displays or something more? *Ibis* 138:26–33.
- NELSON, D. A., AND L. J. CRONER. 1991. Song categories and their functions in the Field Sparrow (*Spi-zella pusilla*). *Auk* 108:42–52.
- SEYFARTH, R., AND D. CHENEY. 1990. The assessment by vervet monkeys of their own and another species' alarm calls. *Anim. Behav.* 40:754–764.
- THORNEYCROFT, H. B. 1976. A cytogenetic study of the White-throated Sparrow, *Zonotrichia albicollis*. *Evolution* 29:611–621.
- WEARY, D. M., AND D. L. KRAMER. 1995. Response of Eastern chipmunks to conspecific alarm calls. *Anim. Behav.* 49:81–93.

The Condor 101:845–848
© The Cooper Ornithological Society 1999

MICROGEOGRAPHIC SONG DISCRIMINATION IN A NONTERRITORIAL PASSERINE, THE BOAT-TAILED GRACKLE¹

DAVID S. MELMAN AND WILLIAM A. SEARCY²

Department of Biology, University of Miami, Coral Gables, FL 33124

Abstract. We used playback in the field to test Boat-tailed Grackles (*Quiscalus major*) for the ability to discriminate local songs from foreign songs. Male grackles responded more strongly to songs recorded at

their own colony than to songs recorded at colonies 4–13 km distant. Female grackles showed little response to either local or foreign song.

Key words: bird song, Boat-tailed Grackle, *Quiscalus major*, song discrimination.

¹ Received 21 January 1999. Accepted 16 June 1999.

² Corresponding author.

Female Boat-tailed Grackles (*Quiscalus major*) nest colonially in reeds or trees. A male Boat-tailed Grackle

may defend a small colony as a territory, but individuals do not defend larger colonies (McIlhenny 1937, Selander and Giller 1961). Instead, groups of males form linear dominance hierarchies in the vicinity of large colonies with position in the hierarchy greatly influencing a male's opportunity for mating (Post 1992, Poston 1997). The hierarchy is a queue, in that males start near the bottom and advance to higher rank as they age and as higher ranking males die or disappear (Post 1992, Poston 1997). The stability of such a queue would seem to require that males in a given colony be able to discriminate between own-colony males and other males. Accordingly, we tested Boat-tailed Grackles for their ability to discriminate own-colony males from foreign-colony males via song.

We tested for colony discrimination using field playback of song. Field playback on a territory typically produces a strong aggressive response from the territory owner, presumably because the owner seeks to expel the intruder he assumes is producing the playback songs. It is not clear that we should in general expect any response to field playback in a nonterritorial species, but pilot experiments showed that both male and female Boat-tailed Grackles may approach speakers playing song near colonies (C. A. Searcy, unpubl. data). Our *a priori* prediction was that if Boat-tailed Grackles can discriminate own-colony from foreign-colony song, then males would show stronger response to playback of foreign song, as this might represent a new male trying to insert himself into the queue.

METHODS

Songs were recorded during the fall of 1997 in Dade County, Florida, at four sites where Boat-tailed Grackles breed: Baptist Hospital, Coral Reef Park, Tamiami Park, and Tropical Park. These sites are separated by distances of 4–13 km. Recordings were made using a Sony TCM-5000EV cassette recorder, a Sony ECM-170 microphone, and a Sony PBR-330 parabolic reflector. Recordings were made at several locations at each site and from multiple males at each location, to minimize the possibility that any single individual would be recorded more than once.

For playback we used primary song, which consists of three phrases: an introductory series of harsh "treet" notes, a low-pitched rattle, and a terminal series of "treet" or "cheat" notes (Selander and Giller 1961, Post et al. 1996). This is the song that typically accompanies the ruff-out display posture. We chose by ear the best recordings from each site and digitized them using the Canary 2.1 program (Charif et al. 1995). We then used spectrograms produced by Canary to make our final choices of four playback songs from each site. We chose songs that were at least 8 sec long, contained little background noise, and consisted only of treet notes and rattles. If the songs we chose were over 10 sec, we shortened them by removing treet notes in the final phrase using the sound editing functions of Canary. Thus, the final playback songs were all 8–10 sec long. The Canary editing functions also were used to filter out low frequency background noise. We then added enough seconds of silence to produce a file 15 sec long and copied the file 40 times

onto a cassette tape to produce a playback tape 10 min long.

We performed four paired playback trials at each of the four selected colony sites. Each paired trial consisted of one own-colony song presentation and one foreign-colony song presentation, in random order, and spaced 1 hr apart. Each of the 16 tapes was used once in an own-colony playback and once in a foreign-colony playback.

Playbacks were performed using a Sony TCM-5000EV cassette recorder and an SME acoustic-amplifier. Amplitude level of the playback was matched by ear to that of a singing Boat-tailed Grackle and then held constant throughout the trials. For each pair of trials, the speaker was placed at the base of a different small tree (5–8 m tall) lacking Boat-tailed Grackle nests. Trees were selected within each colony-site to maximize the intertree distance while remaining within the area used by colony members. The playback trees within a site were 40–300 m apart. There were large numbers of grackles at each site, and although they were unbanded, we think it likely that, for the most part, different individuals responded to the successive pairs of trials at a given site.

Each paired trial started with a 10 min silent control period, followed by the first 10 min playback. After a pause of 50 min, we started a second 10 min silent control period, followed by the second 10 min playback. An observer recorded the number of grackles of each sex that perched in the playback tree, entering these numbers on a flow sheet broken into 10-sec intervals. We decided *a priori* that the response measure would be the cumulative number of seconds that grackles (of a given sex) spent in the playback tree; this measure (bird-seconds) sums the response times of all responding individuals of one sex. The playbacks were all performed during March, 1998, with no more than one pair of trials per site per day.

Statistical comparisons are made using the Wilcoxon matched-pairs signed-ranks test. Sample sizes are the number of pairs of playback trials for the own-colony vs. foreign colony comparisons. For own-colony vs. silent control and foreign-colony vs. silent control comparisons, sample sizes are the numbers of trials.

RESULTS

Response by male Boat-tailed Grackles was significantly greater during both own-colony ($z = 3.2, n = 16, P < 0.01$) and foreign-colony ($z = 2.5, n = 16, P < 0.02$) playbacks than during the matched silent control periods (Fig. 1). At least one male Boat-tailed Grackle landed in the speaker tree during 13 of 16 own-colony playbacks and during 9 of 16 foreign-colony playbacks. Male response was significantly greater to own-colony than to foreign-colony playback ($z = 2.5, n = 16, P < 0.02$). Latency to first response showed a similar pattern: significantly stronger response (lower latency) during playbacks than controls ($P < 0.01$ for both comparisons) and significantly stronger response to own than to foreign playback ($P < 0.05$).

Female Boat-tailed Grackles showed much lower levels of response. Response was not significantly

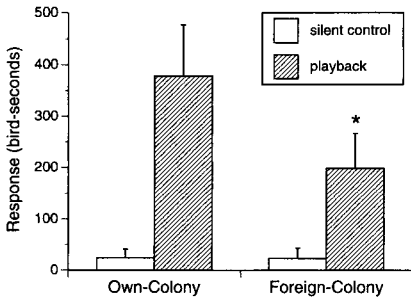


FIGURE 1. Response of male Boat-tailed Grackles to playback of songs recorded from males in their own colony or another (foreign) colony. Response is measured as the number of bird-seconds spent by male grackles in the tree from which songs were played. Silent control periods immediately preceded playback and were of the same duration (10 min). * indicates a significant difference in response to own-colony vs. foreign-colony playback ($P < 0.05$).

greater during playback than during the matched silent control for either own-colony or foreign-colony playback ($z = 1.3$, $P > 0.10$ for both comparisons). One or more females landed in the speaker tree during only 2 of 16 own-colony and 2 of 16 foreign-colony playbacks. Given the low overall response of females, comparing their response to own-colony songs vs. foreign-colony songs is probably meaningless.

DISCUSSION

Male Boat-tailed Grackles responded to playback of songs of conspecific males by approaching the source of the song. When males in territorial songbirds approach playback in this way, the usual interpretation is that the territory owner is seeking to find and evict an apparent intruder singing on his territory. Male Boat-tailed Grackles, however, often have widely overlapping home ranges (Poston 1997) and are usually considered nonterritorial (Post et al. 1996). The response of male Boat-tailed Grackles to song must be interpreted in light of this spacing system and also in light of what we know about the function of their song.

What little is known about song function in Boat-tailed Grackles comes from observing the context of singing. Boat-tailed Grackles produce song together with a postural display, the ruff-out (Selander and Giller 1961). Song and posture are given predominantly by males, but also occasionally by females (Post et al. 1996). Males often sing in small groups (2–7 individuals) (Post et al. 1996), and in this context the song and the accompanying ruff-out posture are clearly directed at the other males in the group. Males in such singing groups may exchange bill-ups, a postural display believed to be aggressive in this and other icterids (Orians and Christman 1968, Post et al. 1996). Male Boat-tailed Grackles also sing when courting females. Other males may approach a courting male and, if he is lower ranking, attempt to disrupt the courtship (Post et al. 1996). Female song and ruff-out are associated with female-female aggressive encounters (Selander and Giller 1961). Song in Boat-tailed Grackles would

thus seem to have both within-sex and between-sex functions, as does song in territorial species. Given this and given the nature of the mating and spacing systems of Boat-tailed Grackles, two interpretations of approach to playback seem plausible: that the responding males are seeking to find the singer in order to assert dominance over him, or that the responding males are attempting to prevent the singer from attracting and courting females. Both motivations may act simultaneously.

Male Boat-tailed Grackles proved able to discriminate own-colony from foreign-colony song. Three distinct mechanisms might account for this ability. First, songs might differ between colonies due to geographic variation. Songs in some territorial songbirds are known to vary over distances as small or smaller than the distances between our colonies (Marler and Tamura 1962, McGregor 1980), and where geographic variation occurs male songbirds are typically able to discriminate local from foreign songs (Tomback et al. 1983, Searcy et al. 1997). Second, the songs of males from a given colony may converge to produce colony-specific songs, as is known to occur in another colonial icterid, the Yellow-rumped Cacique (*Cacicus cela*) (Feeles 1982). Other songbirds showing convergence within groups are able to discriminate own-group from other-group vocalizations (Nowicki 1983). Third, colony recognition could be accomplished by grackles recognizing each male in the colony as an individual. Individual recognition via song has been demonstrated in a number of territorial songbirds (Falls and Brooks 1975, Godard 1991, Stoddard 1996). Analysis of how song structure varies between populations, colonies, and individuals could be used to test these mechanisms.

The ability to discriminate colony members from foreign individuals would seem to be necessary to maintain the kind of social system shown by Boat-tailed Grackles, in which colony males queue up to achieve high dominance rank and mating success (Post 1992, Poston 1997). It is difficult to see how this type of system would be stable unless males could discriminate colony members from non-members and exclude the latter. Discrimination could be by visual signals alone, but the use of vocal signals does provide certain advantages, for example in allowing discrimination of individuals that are out of sight behind bushes or trees, or simply out of the direct line of sight.

Contrary to what we initially expected, response was higher to own-colony songs than to foreign-colony songs. Assuming that approach to playback is an aggressive response, we expected that colony males would respond more strongly to foreign songs, in order to prevent the presumed foreign males from jumping the queue represented by the local dominance hierarchy. One possible explanation for our results is that more than one dominance hierarchy existed at single colony sites in our study. Poston (1997) found that two groups of males were present at one breeding aggregation that he studied, each at opposite ends of the site, and each organized in a separate hierarchy. As males in our study were not banded, we have no check on the number of hierarchies. If more than one hierarchy existed per site, then males from the other near-

by hierarchy may be regarded as the greatest threat, in terms of either jumping the queue or courting females. A second explanation for the pattern of stronger response to own-colony song is that foreign males in general are so strongly discriminated against in mate choice by local females that they represent little threat to an established male's mating success. A third explanation is that males use the songs they hear locally to learn what the species song ought to sound like, and respond less to foreign songs to the extent that they differ from this standard; lower response to foreign song under this hypothesis is simply a non-adaptive consequence of song learning. Further research would be needed to test these alternatives.

We thank Mindy Nelson, Robert Kelley, and Dan DiResta for advice and two anonymous reviewers for comments.

LITERATURE CITED

- CHARIF, R. A., S. MITCHELL, AND C. W. CLARK. 1995. Canary 1.2 user's manual. Cornell Laboratory of Ornithology, Ithaca, NY.
- FALLS, J. B., AND R. J. BROOKS. 1975. Individual recognition by song in White-throated Sparrows. II. Effects of location. *Can. J. Zool.* 53:1412-1420.
- FEEKES, F. 1982. Song mimesis within colonies of *Cacicus c. cela* (Icteridae, Aves). A colonial password? *Z. Tierpsychol.* 58:119-152.
- GODARD, R. 1991. Long-term memory of individual neighbours in a migratory songbird. *Nature* 350:228-229.
- MARLER, P., AND M. TAMURA. 1962. Song 'dialects' in three populations of White-crowned Sparrows. *Condor* 64:368-377.
- MCGREGOR, P. K. 1980. Song dialects in the Corn Bunting (*Emberiza calandria*). *Z. Tierpsychol.* 54:285-297.
- MCILHENNY, E. A. 1937. Life history of the Boat-tailed Grackle in Louisiana. *Auk* 54:274-294.
- NOWICKI, S. 1983. Flock-specific recognition of chickadee calls. *Behav. Ecol. Sociobiol.* 12:317-320.
- ORIAN, G. H., AND G. M. CHRISTMAN. 1968. A comparative study of the behavior of Red-winged, Tricolored, and Yellow-headed Blackbirds. *Univ. Calif. Publ. Zool.* 84:1-81.
- POST, W. 1992. Dominance and mating success in male Boat-tailed Grackles. *Anim. Behav.* 44:917-929.
- POST, W., J. P. POSTON, AND G. T. BANCROFT. 1996. Boat-tailed Grackle (*Quiscalus major*). In A. Poole and F. Gill [EDS.], *The birds of North America*, No. 207. The Academy of Natural Sciences, Philadelphia, and the American Ornithologists' Union, Washington, DC.
- POSTON, J. P. 1997. Dominance, access to colonies, and queues for mating opportunities by male Boat-tailed Grackles. *Behav. Ecol. Sociobiol.* 41:89-98.
- SEARCY, W. A., S. NOWICKI, AND M. HUGHES. 1997. The response of male and female Song Sparrows to geographic variation in song. *Condor* 99:651-657.
- SELANDER, R. K., AND D. R. GILLER. 1961. Analysis of sympatry of Great-tailed and Boat-tailed Grackles. *Condor* 63:29-86.
- STODDARD, P. K. 1996. Vocal recognition of neighbors by territorial passerines, p. 356-376. In D. H. Kroodsma and E. H. Miller [EDS.], *Ecology and evolution of acoustic communication in birds*. Cornell Univ. Press, Ithaca, NY.
- TOMBACK, D. F., D. B. THOMPSON, AND M. C. BAKER. 1983. Dialect discrimination by White-crowned Sparrows: reactions to near and distant dialects. *Auk* 100:452-460.

The Condor 101:848-854
© The Cooper Ornithological Society 1999

SPERM COMPETITION AND SPERM LENGTH IN SHOREBIRDS¹

DOMINIC D. P. JOHNSON AND JAMES V. BRISKIE²

Edward Grey Institute of Field Ornithology, Department of Zoology, University of Oxford, South Parks Road, Oxford, OX1 3PS, United Kingdom, e-mail: dominic.johnson@zoo.ox.ac.uk

Abstract. We investigated how sperm morphology varies across 16 species of shorebirds in the Scolopacidae, Charadriidae, and Jacanidae. Sperm were significantly longer in nonmonogamous than in socially monogamous species. Nonmonogamous species also

had significantly longer midpieces and tails than monogamous species. As the midpiece houses the mitochondria for powering the tail, this suggests that sperm competition may select for greater investment in mobility. After controlling for phylogeny and male body mass, sperm tail length was correlated positively to relative testis size. There was no evidence that variation in sperm morphology was related to either male body mass (through allometry) or egg size (via linkage disequilibrium). Instead, our results suggest that sperm size in shorebirds increases with the intensity of sperm competition.

¹Received 27 January 1999. Accepted 22 June 1999.

²Current address: Department of Zoology, Private Bag 4800, University of Canterbury, Christchurch, New Zealand.