Ethology 80, 218—222 (1989)

ISSN 0179-1613

Department of Psychology and Department of Zoology,
University of Texas, Austin,
and Department of Psychology, University of Washington, Seattle

The Display of the Blue-black Grassquit: The Acoustic Advantage of Getting High

WALTER WILCZYNSKI, MICHAEL J. RYAN & ELIOT A. BRENOWITZ

With 2 figures

Received: January 4, 1988
Accepted: May 6, 1988 (G. Barlow)

Abstract

Male blue-black grassquits (*Volatinia jacarina*) display by leaping vertically above the top of the dense grass in which they perch and emitting a high pitched call. Acoustic-transmission experiments demonstrated that calls broadcast from above the high grass typical of grassquit habitat attenuated less over distance than identical calls broadcast from typical perch heights within the grass. By leaping when they call, grassquits might enhance the distance over which their call can be detected.

Introduction

Blue-black grassquits (*Volatinia jacarina*) are small, black seed-eating birds common in grass-land habitats of the New World tropics. During the rainy season when breeding occurs, males defend contiguous nesting territories within the high grass of overgrown meadows or scrubland (ALDERTON 1963; MURRY 1982). Territories are relatively small, ca. 25 m in diameter (MURRY 1982).

When occupying territories, males produce a combined visual-acoustic display (ALDERTON 1963; WEATHERS 1986). Grassquit males leap 30—45 cm straight up from perches in the grass. The leap takes them well above the tops of the grass, where the wings are extended. The bird then reverses direction to return to its perch. During the leap, the male usually emits a high-pitched, buzzy trill. Grassquits sometimes jump without calling, and occasionally call without jumping, but the visual and vocal displays are usually performed together (ALDERTON 1963; authors' unpubl. obs.).

U.S. Copyright Clearance Center Code Statement: 0179-1613/89/8001-0218$02.50/0

Leaping above the vegetation enhances the display's visual component. Males often perch many cm below the top of the grass, and the nesting sites occupied by both sexes are even lower (ALDERTON 1963). A visual display given from the normal perching position is unlikely to be seen by perching conspecifics. Combining the leap with the vocalization may also enhance the bird's acoustic signal. Acoustic transmission studies of the vocal signals of birds (MORTON 1975; MARTIN & MARLER 1977; MARTIN et al. 1977; BRENOWITZ 1982) and frogs (BRENOWITZ et al. 1984) have shown that increasing the height of an emitter tends to decrease excess attenuation of the signal. Thus by leaping above the grass before calling grassquits could lessen the attenuating effects of the dense vegetation surrounding their normal perches. We investigated this hypothesis by measuring the amplitude of taped grassquit calls broadcast along transects through typical grassquit habitat in the Republic of Panama.

Methods

The transmission of *Volatinia jacarina* calls was assessed at an abandoned airfield (Chagres Field) by the Panama Canal near Gamboa, Republic of Panama. The field was covered with a dense growth of grass and weeds approx. 100—120 cm high interspersed occasionally with small shrubs. Blue-black grassquits were commonly observed displaying in this field. Measurements were made during midmorning in July 1987 under conditions of high humidity, very light winds and temperatures of about 29 °C.

Three 20-m transect lines were placed in different areas of the field, taking care to minimize disturbance of the vegetation along the measurement line. A portable loudspeaker with built-in amplifier was positioned at one end of the transect line. A Nagra IV-D tape recorder was used to play a tape recording of a series of 3 calls from different males through the speaker. The three calls varied slightly in amplitude, but were otherwise almost identical. Calls were broadcast from approx. 25 cm below the top of the grass and again from a height approx. 25 cm above the top of the grass. For the three transects, speaker heights (measured to the center of the speaker) were 95, 92, and 95 cm above the ground when placed in the grass, and 142, 142, and 155 cm above the ground when placed above the grass. At all times, the amplitude settings on the tape recorder were held constant and the speaker faced directly along the transect line.

The amplitudes in dB sound pressure level (SPL, re: 0.002 dynes/cm^2) of each of the three calls in the series were measured with a Bruel & Kjaer 2230 digital precision sound-level meter (fast RMS setting) at distances of 1, 5, 10, 15, and 20 m on each of the transect lines. The A-weighting scale was used to filter out high amplitude, very low frequency noise from wind and ocean liners. The filter frequency band did not overlap the frequency band of the grassquit call. The microphone of the sound level meter was held stationary at the height of the lower speaker position for all presentations (i.e., regardless of whether the speaker was in the low or high position) to mimic the position of a receiving bird perching in the grass. The microphone was directed at the center of the speaker. At the 1-m distance, this necessitated a substantial tilt of the microphone when the speaker was elevated.

When the speaker is elevated, but the microphone is not moved, the distance between them increases. At 1 m, a 10—17 % difference in distance to the microphone from the two speaker heights results. At farther measurement points, elevation causes relatively less change for the two speaker heights. At 5 m, only a 0.4—0.6 % difference is introduced, and beyond this distance the difference is negligible.

Polynomial equations were fitted to the mean call amplitudes at each distance for each speaker height and used to estimate the maximum distance at which the test calls remained detectable. For each of the three calls, the amplitude difference between heights at each distance along each transect was calculated. These data were used to test the null hypothesis that broadcast height did not influence the amplitude of the call at various distances from the source. The statistical test used was a two-way repeated-measures analysis of variance in which each of the three broadcast calls was replicated across distance and sites. Post hoc comparisons were conducted with a Tukey test.

Results

Reliable amplitude measurements were obtained up to the 15-m distance. Transmission curves for the high and low speaker positions fitted to these measurements are shown in Fig. 1. At 1 m, calls from the elevated position averaged 4.7 dB lower than those from the low position. At 5 m, there was little difference between calls from the two speaker heights. At both 10 and 15 m, however, calls from the elevated speaker averaged 2.7 and 2.6 dB higher respectively. At 20 m, the amplitudes of calls broadcast from the low speaker position were below the ambient noise level (41—45 dB SPL, A-weighting), although calls from the elevated speaker could usually be detected. Therefore, statistical analysis of the data was limited to the first four measurement distances.

The amplitude measurements showed that as distance from the speaker increased, the elevated source moved from being lower in amplitude to being higher in amplitude at the receiver (Fig. 2). The analysis of variance confirms this: the amplitude differences between heights differed significantly among distances

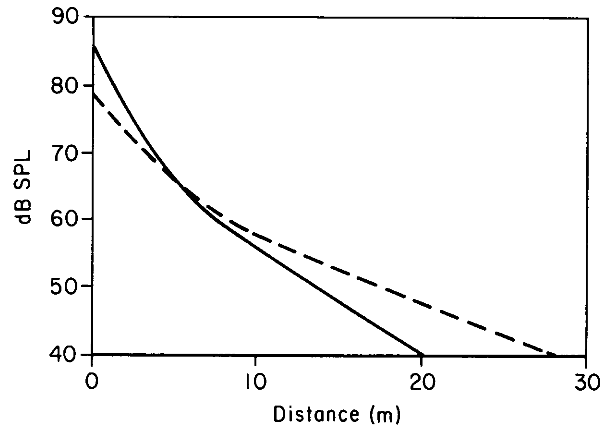

Fig. 1: Changes in call amplitude as a function of distance for calls broadcast above (dashed line) and within (solid line) the grass

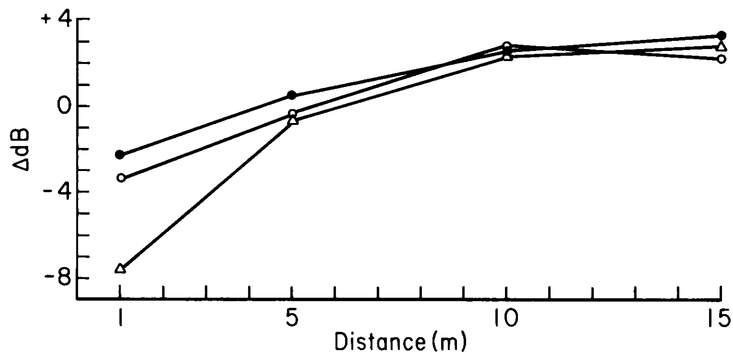

Fig. 2: Difference in call amplitude (upper speaker position amplitude minus lower speaker position amplitude) at the measured distances for each of the three measurement transects

($F = 41.6$, $p < 0.001$). There was a marginally significant difference among sites ($F = 8.04$, $p = 0.04$), but no significant site-by-distance interaction ($F = 0.3$, $p > 0.10$). Post hoc comparisons of the mean amplitude differences among distances using the Tukey test showed that they differed significantly from one another ($p < 0.05$) with the exception of those at the 10- and 15-m distances.

Discussion

Our results suggest that by coupling the acoustic portion of their display with the leap characterizing the visual portion, blue-black grassquits decrease the attenuation of their call. Calls broadcast from above the vegetation typical of grassquit habitats remained higher in amplitude at 10 and 15 m from the source than identical calls broadcast from within the vegetation at a height typical of perching males. This advantage was apparent at each test site, although the analysis of variance showed the sites to be marginally different in their characteristics.

The site differences could be due to a variety of factors such as vegetation structure or microclimatic conditions. We did not explore this, because the purpose of our study was not to investigate site differences but rather to show that on different sites where grassquits reside calls produced above the grass transmit with less attenuation than calls produced from perches within the grass.

Although an acoustic advantage for elevated emission is apparent at long distances, at 1 m the broadcast from the lower speaker position yielded higher amplitude readings. This is likely the result of the experimental procedure, which kept the microphone at the level of the low speaker position at all times. At short distances this significantly increases the distance from the elevated speaker to the microphone.

The decrease in attenuation rate when the source is elevated allows the call to remain above the ambient noise level, and therefore remain detectable, at a greater distance than when the source is within the vegetation. This increases the active space of the call (MARTIN & MARLER 1977; BRENOWITZ 1982, 1986; BRENOWITZ et al. 1984) that is, the distance over which the call can be detected. This effect is noticeable at 20 m from the speaker, at which point calls from the low speaker position are below ambient noise while identical calls from the elevated position remain approximately 3—5 dB above it.

Although we did not measure call-amplitude levels beyond 20 m, we can use the transmission curves to estimate the distance at which the signal broadcast from the elevated position would fall below the background noise at our study site. Assuming ambient noise levels of 40 dB SPL, which approximates the lowest noise measured at our study site, calls from the elevated speaker at source amplitudes used in this experiment would fall below the noise at a distance of 28 m. Calls from the lower speaker position would attenuate to this level by 20 m. Under these conditions, calling above the grass increases the effective distance of the call by 40 %, and therefore nearly doubles the area over which the call may be detected.

Neither the amplitude of a natural grassquit call nor this species' auditory thresholds have ever been measured, and therefore the true active space of the call cannot be calculated. However, regardless of the amplitude, an increase in active space similar to that calculated here would be apparent when calls are emitted from above the grass.

The attenuation difference could be important in the territorial defense of this species. Grassquit territories are only about 25 m in diameter (MURRY 1982). Gaining an additional 5 or 10 m of active space could significantly increase the penetration of the male's call into the neighboring territories of conspecifics and could also increase the effectiveness of the call as a mate attractant.

Previous studies have noted that increases in height tend to decrease the attenuation suffered by an acoustic signal (MORTON 1975; MARTIN & MARLER 1977; MARTIN et al. 1977; BRENOWITZ et al. 1984; BRENOWITZ 1986) or that vegetation affects signal transmission (WELLS & SCHWARTZ 1982; WILCZYNSKI & BRENOWITZ 1988). Blue-black grassquits are a special case of this phenomenon. By combining the vocal portion of his territorial display with a vertical leap above the grass, a male grassquit can simultaneously enhance the detectability of both the visual and acoustic aspects of his display.

Acknowledgements

We wish to thank N. SMITH and A. S. RAND for providing tapes and equipment for this study, B. CAUSEY, R. ROCHE, and R. STANFORD for field assistance, and S. SILVERMAN for statistical help. We also thank the staff of the Smithsonian Tropical Research Institute for their help in supporting this research. Supported by Smithsonian Short Term Visitor Grants to W. WILCZYNSKI and M. J. RYAN, and a Reeder Fellowship in Ecology to M. J. RYAN.

Literature Cited

ALDERTON, C. C., 1963: The breeding behavior of the blue-black grassquit. Condor **65**, 154—162.

BRENOWITZ, E. A., 1982: The active space of red-wing blackbird song. J. Comp. Physiol. **147**, 511—522.

— —, 1986: Environmental influences on acoustic and electric communication. Brain Behav. Evol. **28**, 32—42.

— —, W. WILCZYNSKI, & H. H. ZAKON, 1984: Acoustic communication in spring peepers. Environmental and behavioral aspects. J. Comp. Physiol. **155**, 585—592.

MARTIN, K., & P. MARLER, 1977: Sound transmission and its significance for animal vocalization. I. Temperate habitats. Behav. Ecol. Sociobiol. **2**, 271—290.

— —, D. QUINE, & P. MARLER, 1977: Sound transmission and its significance for animal vocalization. II. Tropical forest habitats. Behav. Ecol. Sociobiol. **2**, 291—302.

MORTON, E. S., 1975: Ecological sources of selection on avian sounds. Am. Nat. **108**, 17—34.

MURRY, B. G., 1982: Territorial behavior of the blue-black grassquit. Condor **84**, 119.

WEATHERS, W. W., 1986: Thermal significance of courtship display in the blue-black grassquit (*Volatinia jacarina*). Nat. Geo. Res. **2**, 291—301.

WELLS, K. D., & J. J. SCHWARTZ, 1982: The effect of vegetation on the propagation of calls in the neotropical frog *Centrolenella fleischmanni*. Herpetologica **38**, 449—455.

WILCZYNSKI, W., & E. A. BRENOWITZ, 1988: Acoustic cues mediate intermale spacing in a neotropical frog. Anim. Behav. **36**, 1054—1063.

Authors' address: Walter WILCZYNSKI, Department of Psychology, 330 Mezes Hall, University of Texas, Austin, TX, 78712, USA.