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Acoustic directionality of red-winged blackbird (*Agelaius phoeniceus*) song relates to amplitude and singing behaviours

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Sound waves typically radiate from a vocalizing animal with unequal amplitude in different directions; this may profoundly affect communication, favouring adaptations that use or compensate for this directionality. Previous studies suggest that variation in directionality among vocalization types is related to function, with vocalizations such as alerts being relatively omnidirectional, thus maximizing the number of surrounding receivers, and vocalizations such as courtship calls being relatively directional, thus reducing eavesdropping by beaming sounds at the targeted receiver. Here we examine variation within a vocalization type, bird songs, to test hypotheses about how variation in song directionality relates to singing behaviour and the social context of singing. We measured the directionality and amplitude of red-winged blackbird songs in the field using calibrated microphones encircling the bird. We found variation in directionality among song types, possibly allowing males to select songs from their repertoires with directionality to suit the social context. We found support for the hypothesis that the amplitude and directionality of songs are related, with more-directional songs delivered at higher amplitudes. In addition, we found support for the hypothesis that directionality is negatively related to the degree of male rotation on the perch between vocalizations, suggesting that males may combine omnidirectional songs and rotation to broadcast their songs, and may face the receiver and produce directional songs during direct interactions. We also observed variation in directionality among note types within songs. These results suggest that directionality plays an important role in shaping song structure and singing behaviour in red-winged blackbirds.

Keywords: active space; *Agelaius phoeniceus*; amplitude; bird song; communication; directionality; red-winged blackbird

Sound waves radiate in all directions from a vocalizing animal; when sounds are not equally loud in every direction, the vocalization is considered to be directional. Directional radiation of signals can occur in all modalities: acoustic, visual, chemical, vibrational and electrical (e.g. Bradbury & Vehrencamp 1998; McNett et al. 2006; Peters & Evans 2007). For example, the radiance received by a female assessing a structural colour patch on a male will vary depending on the orientation of the male relative to the sun and to the female (e.g. Endler 1992; Sweeney et al. 2003; Fleishman et al. 2006). Directionality in radiating signals is likely to have important implications in animal communication and thus the signal-production structures and behaviours that affect directionality may be subject to selection, similar to other features of signals that can affect the efficacy of transmission, such as frequency and temporal patterning in acoustic signals (Marler 1955; Morton 1975; Richards & Wiley 1980; Nowicki 1987; Podos 1997, 2001).

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There are a number of means by which directionality may affect the quality of the signal received, as well as the number and identity of receivers for a signal. Because higher frequency sounds are more directional than lower frequency sounds, receivers may assess the spectral properties of a vocalization to determine whether the sender is facing the receiver (Witkin 1977; Hunter et al. 1986; Larsen & Dabelsteen 1990; Dantzker et al. 1999; Miller 2002; Lammers & Au 2003). Because the sender's orientation relative to the receiver will affect the amplitude received, directionality will affect the receiver's ability to assess information about the sender conveyed by amplitude, such as size (Morton 1982; Arak 1983). Directionality may also affect the shape and size of the 'active space' of the vocalization, the area in which the signal can be detected, because active space is determined in part by the amplitude of the sound waves relative to background noise (Brenowitz 1982a). Furthermore, directionality will affect the number and identity of receivers for a signal. More-omnidirectional vocalizations will maximize the number of surrounding receivers that detect the vocalization, whereas more-directional vocalizations will allow animals to beam the sound to a target receiver and decrease eavesdropping (Witkin 1977; Larsen & Dabelsteen 1990; Dantzker et al. 1999; Brumm & Todt 2003; Dabelsteen 2005). Thus, omnidirectional vocalizations may also be beneficial when the receiver's location is unknown, whereas directional location may be used when receiver location is known. These effects of directionality on acoustic communication may select for adaptations that allow animals to either compensate for directionality or make use of directionality when communicating.

In most birds, models of sound production predict that radiation patterns will be bilaterally symmetrical, with their maximum radiation point in front of the beak (Hunter et al. 1986; Fletcher & Tarnopolsky 1999). These models predict that the shape and directionality of the radiated sound field will mainly be determined by the acoustic frequency, the position of the head and body, the size and morphology of the beak and the amount of beak movement during vocalization (Hunter et al. 1986; Larsen & Dabelsteen 1990; Fletcher & Tarnopolsky 1999; Nelson et al. 2005). Therefore variation in frequency and posture among call types may affect directionality, as will variation in morphology among species. Previous measurements of directionality in vertebrates range from highly directional signals in echolocating bats and cetaceans and in displaying greater sage grouse (approximately 20–30 dB difference in amplitude between the loudest and the quietest angle measured; Hartley & Suthers 1987; Dantzker et al. 1999; Madsen 2005) to moderately directional signals in songbirds and dogs (approximately 3–10 dB difference; Witkin 1977; Hunter et al. 1986; Larsen & Dabelsteen 1990; Brumm 2002; Frommolt & Gebler 2004; Nelson et al. 2005; Patricelli et al. 2007) to nearly omnidirectional signals in anurans (Gerhardt 1975). Measures of acoustic signals in insects similarly range from omnidirectional to highly directional (e.g. Forrest 1991; Michelsen & Elsner 1999; Michelsen & Fonseca 2000; Jerome et al. 2005).

An additional mechanism by which animals may alter the directionality of their vocalizations is by turning on their perch when they vocalize. Brumm & Todt (2003) found that male nightingales, *Luscinia megarhynchos*; have a moderately directional song and that they rotate on their perch when there is no known receiver, possibly to radiate their song omnidirectionally, and they face their rival when location is known, possibly to beam their sounds towards their rival. These rotation behaviours probably also facilitate visual surveying and visual signalling. Similar behaviours have been described in male northern mockingbirds, *Mimus polyglottos* (Breitwisch & Whitesides 1987). Therefore males may have behavioural strategies to complement the directionality of their vocalizations, and directionality may play an important role in shaping male singing behaviours.

Previous studies have found evidence that the directionality of different classes of vocalizations may be adapted to the function of that vocalization in communication (Larsen & Dabelsteen 1990; Patricelli et al. 2007). For example, Patricelli et al. (2007) found that red-winged blackbird calls used to communicate with multiple receivers (alarm 'cheers' and 'checks' used as conspecific alert and contact calls; Beletsky et al. 1986; Burton & Yasukawa 2001) are more directional than sexually selected vocalizations (precopulatory calls and 'oak-a-lee' songs, Peek 1972; Searcy & Brenowitz 1988; Searcy 1989). Directionality may vary not only among classes of vocalizations, but also within classes. Therefore birds may use song or call variants with appropriate directionality in different situations. Birds with song repertoires may use this tactic. Many species use songs both for advertisements (long-distance attraction of females and defining territory boundaries) and for direct interactions (courtship of females or confrontations with neighbouring conspecifics) (Catchpole & Slater 1995). If songs within a repertoire vary in directionality, males may use song variants or song types that match the social context. Consistent with this possibility, Patricelli et al. (2007) found that red-winged blackbird songs have moderate directionality relative to the birds' other vocalizations, but have the highest standard deviation in directionality among vocalization types. Birds may also alter their rotation behaviours and/or singing amplitudes to complement or counteract the directionality of the song type they are singing and thereby influence how far and to whom the signal is radiated. These possibilities have not yet been explored in any species.

We measured the directionality of oak-a-lee songs used by territorial male red-winged blackbirds. Red-winged blackbirds are polygynous, with harems of up to 15 females nesting on their territories (mean harem size ranges from 1.6 to 6.2 among populations; Searcy & Yasukawa 1995). The oak-a-lee song of the red-winged blackbird is used during direct interactions with rival males and is important in maintaining territory boundaries (Peek 1972); songs are also important in acquiring mates (Peek 1972) and elicit copulation-solicitation behaviours in females (Searcy & Brenowitz 1988). Males have repertoires of five to seven songs (Smith & Reid 1979), and during the breeding season, male song is often accompanied by the song-spread visual display (Peek 1972). Red-winged blackbirds are ideal for the study of directionality in the field because their marsh-grass habitat