Variation in singing behaviour reveals possible functions of song in male golden whistlers

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Summary

Male song has been shown to have two major functions, repelling rivals and attracting mates. Yet much debate still exists as to what extent male singing strategies have been influenced by selection pressures imposed by each sex. I use a combination of song recordings and playbacks to investigate how male competition and female choice may have shaped song structure and behaviour in migratory golden whistlers (Pachycephala pectoralis). Song output was low during territory establishment but increased dramatically when breeding commenced. Singing during the female fertile period may be an effective paternity guard against potential cuckolders. During this period, males decreased their song output when more neighbouring females were fertile, possibly reflecting an inability to concurrently guard a mate and pursue extra-pair fertilisations. However, high singing rates were maintained after the fertile period, suggesting that males may also sing to attract extra-pair copulations. Song repertoire size increased with male age and may signal male quality. Repertoires included two broad song-types: simple ‘whistle’ songs and more complex ‘melodic’ songs. Whistle songs were often sung by breeding males and may be more effective at broadcasting information at long-distances. In contrast, melodic songs were commonly sung in close-range male encounters and may contain more information about signaler quality. During vocal contests, males exhibited a range of countersinging behaviours, including song-type switching, song-type and frequency-matching, and song overlapping, which may reflect a hierarchical mode of signalling aggression. Each sex may have imposed different selection pressures on the vocal output of male golden whistlers.

Introduction

Male bird song is an important signal used to efficiently convey information to mates or rival males (Catchpole & Slater, 1995). Many components

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of song structure and singing behaviour are highly conserved between individuals of a species, providing a reliable cue for discrimination by conspecific and heterospecific individuals (e.g., Soha & Marler, 2001; Hauber et al., 2002). However, there is also considerable within-species variation, both among individuals and across time scales. Variation in song parameters among different individuals may reflect differences in signaler quality (Catchpole & Slater, 1995), while temporal variation in song may occur if males synchronise their singing output with the fertile period of females, or adjust output relative to perceived intruder threat during male-male song contests (Møller, 1991; Todt & Naguib, 2000).

Male acoustic signals are generally directed at two classes of receivers: females and rival males, and these may exert different selection pressures on song characteristics. Individual variation in singing behaviour or song complexity may reflect aspects of male quality such as age, genetic fitness or past developmental stress, and these cues are therefore often used by females in mate choice decisions (Searcy, 1992; Hasselquist et al., 1996; Spencer et al., 2004). Males which use song for mate attraction often maximise their singing output during periods in which females are unpaired or, in species in which extra-pair fertilisations are common, during the entire period in which females are receptive (Møller, 1991). Males with the highest song output typically gain more paternity, via increased extra-pair fertilisations with neighbouring females and decreased risk of within-pair cuckoldry (Hasselquist et al., 1996; Møller et al., 1998; Forstmeier et al., 2002).

In contrast, variation in traits used in male-male contests is typically low across the breeding season but increases relative to the threat posed by conspecifics during male-male song contests (Todt & Naguib, 2000; Naguib, 2005). During an interaction, the timing and patterning of singing behaviour relative to the opponent reveals the individual’s social status or willingness to escalate the contest. Male signalling output may vary based on a hierarchy of behaviours. High rates of switching between song-types are often used as a low-level form of aggression in the early stages of an encounter (Kramer et al., 1985; Nielsen & Vehrencamp, 1995; Horn & Falls, 1996). Once aggression levels increase, song-type matching and song overlapping of rival songs become more common (Vehrencamp, 2001; Otter et al., 2002; Mennill & Ratcliffe, 2004). Males may also vary the structure of songs used during these contests (Mennill & Ratcliffe, 2004) or use specific song-types in different contexts. For example, male nightingales use particular song-types for