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Songs of male humpback whales, *Megaptera novaeangliae*, are involved in intersexual interactions

JOSHUA N. SMITH*, ANNE W. GOLDIZEN*, REBECCA A. DUNLOP† & MICHAEL J. NOAD†
*School of Integrative Biology, University of Queensland
†School of Veterinary Science, University of Queensland

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Male humpback whales produce complex songs during the breeding season, yet the singing behaviour of males and whether songs function in male contests and/or through female choice are still poorly understood. We investigated song function by obtaining simultaneous observations of the positions and movements of singing and nonsinging whales in real time during their migration off the east coast of Australia. We collected movement data by acoustic tracking using a hydrophone array, land-based visual tracking and observations from a small boat. Of the 114 singers analysed, 66 (58%) associated with conspecifics. Singers were significantly more likely to join groups containing a mother–calf pair than other groups. Males started to sing after joining groups only if they consisted of a mother–calf pair not escorted by another male. Singers also associated longer and sang for a significantly greater proportion of time with mother–calf pairs than any other group type. Associating with mother–calf pairs has been shown to be a reproductively successful strategy for males. In contrast, whales that joined singers were usually lone males; these associations were brief and singers typically stopped singing in the presence of other males. This is the highest reported incidence in humpback whales of males singing when escorting females and supports an intersexual function of song in humpback whales. We suggest that males joining singers are prospecting for females rather than engaging in male social ordering and that singing may incur the cost of attracting competing males.

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Social interactions among animals occur over a broad range of contexts, including during intrasexual competition and mate choice, and the performance of individuals in these interactions can be important in resolving conflicts over access to mates or space (Bradbury & Vehrencamp 1998). Songs are patterned acoustic signals that are used in social interactions among many taxa and are important for communication (Smith 1996). Singing typically functions at a distance to mediate social relations between conspecifics by providing information on the singer such as identity, sex and location (Smith 1991). Information on a singer's behaviour may also be conveyed through the organization and timing of the song. In the singing interactions of songbirds, for example, the degree to which a male overlaps his song with that of another singer can indicate the male's level of aggression and readiness for conflict (Naguib 2005; Naguib & Kipper 2006).

Male songs are usually sexually selected traits that function to repel rival males (intrasexual selection) and/or attract mates (intersexual selection) and occur in many species of birds, frogs, insects and, to a lesser extent, mammals (Searcy & Andersson 1986; Kroodsma & Byers 1991; Andersson 1994). Evidence for sexual selection of song has historically come from patterns in the contextual use of song, its effects on an audience and correlations with the mating system (Catchpole 1982; Andersson 1994; Catchpole & Slater 1995). Whereas song may have

Correspondence: J. Smith, School of Integrative Biology, University of Queensland, St. Lucia, Brisbane, Queensland 4072, Australia (email: j.smith@sib.uq.edu.au).

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several functions, the degree to which it functions for the repulsion of rivals versus for mate attraction, and the aspects of singing behaviour that are important to each function, are likely to vary with species (Slater 2003; Marler & Slabbekoorn 2004).

Humpback whales migrate annually from high-latitude summer feeding grounds to low-latitude winter coastal breeding and calving grounds (Dawbin 1966). Males exhibit no parental care and the mating system best resembles polygyny (Cerchio et al. 2005). Males commonly take part in direct male–male competition for single females, associate with mothers with calves (referred to as escorting) and sing long, complex, highly structured songs during migration and on the breeding grounds (Payne & McVay 1971; Winn & Winn 1978; Baker & Herman 1984; Cato 1991; Clapham et al. 1992; Charif et al. 2001). These behaviours may represent alternative mating tactics (Baker & Herman 1984; Cerchio et al. 2005).

Evaluating the success of males exhibiting alternative behavioural tactics is difficult, however, because copulation has never been observed in this species. Whereas direct physical competition among males in competitive groups seems to represent intrasexual competition by males for access to mature females (Tyack & Whitehead 1983; Baker & Herman 1984; Clapham et al. 1992; Weinrich 1995), there is less evidence for a specific function of the song in humpback whales. The 'song' is a patterned, highly repetitive and structured production of song units of variable frequency as opposed to their 'social vocalizations' that are discrete, nonpatterned sounds that occur year round. Songs of humpback whales are transmitted culturally (Guinee et al. 1983; Noad et al. 2000) and within any given population all males usually sing the same song at any given time. Changes in the song occur over a season, with all singers making the same changes at approximately the same time to maintain concurrent song-matching (Winn et al. 1981; Payne et al. 1983; Helweg et al. 1990; Cato 1991; Dawbin & Eyre 1991; Guan et al. 1999; Cerchio et al. 2001). Males incorporating novelty into their songs may drive changes in the song (Noad et al. 2000; Cerchio et al. 2001).

The singing behaviour of humpback whales is still poorly understood, owing largely to the lack of focused studies concentrating on behavioural aspects of individual singers and of broad-scale data detailing the interactions of multiple singing and nonsinging whales over a large area. Determining the function of song and other male mating behaviours is particularly difficult because there is no easy way to identify the gender of whales in the field and the duration and timing of oestrus in females remain unknown (Clapham 2000).

Studies on humpback whale song in the past have largely focused on population differences (e.g. Winn et al. 1981; Helweg et al. 1990, 1998; Dawbin & Eyre 1991) and temporal changes in structure and pattern (e.g. Winn & Winn 1978; Payne et al. 1983; Payne & Payne 1985; Cato 1991; Mednis 1991; Cerchio et al. 2001). The few studies that have concentrated on behavioural aspects of individual singers have shown that, although singing whales are usually lone individuals, song seems to be important in interactions between conspecifics (Tyack 1981; Frankel et al. 1995; Darling & Bérubé 2001; Noad 2002; Darling et al. 2006). Social associations on the breeding grounds tend to be fluid and a prominent feature of male behaviour is the frequent alternation between singing and escorting a female (Darling et al. 1983; Baker & Herman 1984; Clapham et al. 1992). None the less, the functional relevance of the song in the interactions between singing males and conspecifics remains unclear.

Debate surrounds whether the song of humpback whales is used to attract potential mates through an elaborate acoustic display (e.g. Tyack 1981) or operates as a form of male social sorting (Darling & Bérubé 2001; Darling et al. 2006). Whereas the song's complexity in particular suggests the former (Helweg et al. 1992), direct observations of singers interacting with other whales support the latter, as most reports have been of interactions with other males (Tyack & Whitehead 1983; Baker & Herman 1984; Darling & Bérubé 2001; Darling et al. 2006). An exception to this is reported by Medrano-Gonzalez et al. (1994), who recorded two instances of females approaching and joining singers.

The context in which song is used is important for identifying and determining possible functions of song (Catchpole & Slater 1995); therefore to understand better the context of song use by humpback whales, we examined interactions between individual singing whales and nearby conspecifics. The purpose of the study was to document first-order interactions involving singers and to investigate how these interactions affected the subsequent singing behaviour of the whales. The specific aims of the study were to: (1) determine whether the frequency of interactions involving singers relates to the sex of individuals and/or group compositions of whales that singers could associate with; (2) determine whether group composition affects the singing behaviour of males; (3) test for differences in the duration of time singers associate with whales in different group compositions.

METHODS

Study Area and Population

We conducted this study at Peregian Beach on the east coast of Australia (26°30′S, 153°07′E) during the southward migration of the east Australian population of humpback whales in September and October of 2002, 2003 and 2004. We tracked interactions between singing and nonsinging whales acoustically and visually and monitored them over a 15-km radius at the study site (Fig. 1). This has been the site of previous combined broad-scale visual and acoustic tracking of individual whales (Noad & Cato 2001, 2007; Noad 2002; Noad et al. 2004; Thode et al. 2006; Dunlop et al. 2007). This study was part of a larger collaborative project known as the Humpback Whale Acoustic Research Collaboration (HARC).

Passive Acoustic Localization of Singers

We tracked singers acoustically in real time using a static array of five hydrophones deployed off the coast (Fig. 1).

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