



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).

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).

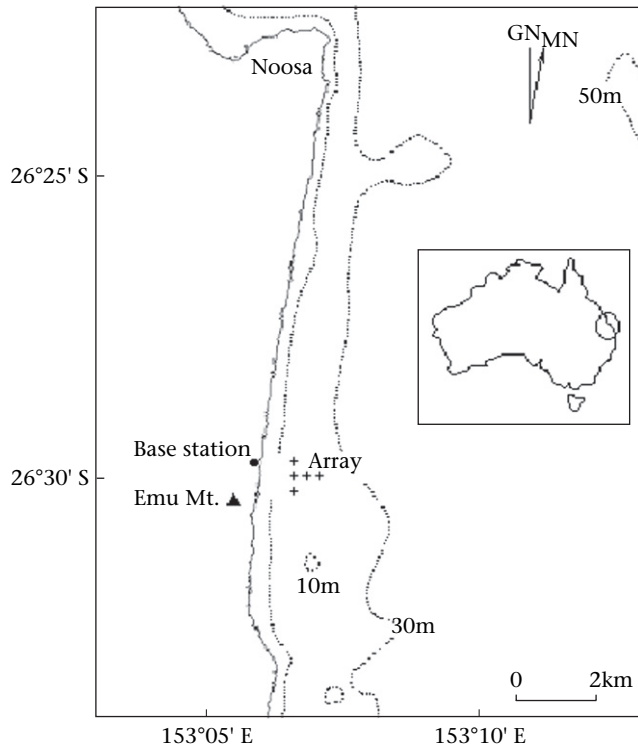


Figure 1. Peregian Beach study area and inset map of Australia showing the approximate location of Peregian Beach. Map shows the arrangement of the five-hydrophone buoy acoustic tracking array (+) and the locations of the base station (●) and the visual tracking platform, Emu Mountain (▲).

Hydrophone buoys were arranged in a T configuration, spaced approximately 700 m apart and anchored in 18–28 m of water, with the base of the array (buoys 1, 2 and 3) placed in a line approximately 1.5 km offshore running parallel to the beach and buoys 4 and 5 placed in a line seaward of buoy 2 and spaced 500 m apart. Radio signals from the hydrophone buoys were received at a base station located directly behind the beach (Fig. 1) and passed through two computers, one for recording and the other for tracking singers. Further detailed explanation of the construction and arrangement of the hydrophone array can be found in Noad et al. (2004). We determined the positions of singers using the acoustic, multichannel, tracking software Ishmael (Mellinger 2001) using the differences in the arrival times of the selected sounds at the five hydrophones. We obtained accurate positions of the five hydrophones each season by surveying their positions from the shore using theodolites as well as by repeated GPS measurements from a boat. Although the calculated bearings from the array to singing whales were generally very accurate, calibration measurements showed there were small errors with the estimates of range. At 2 km from the array, the error in range for a single sound was less than 50 m, whereas at 10 km there was an error of up to 1000 m. The accuracy of sound location was significantly improved, however, by taking the mean position of several estimates over a brief period (1–3 min) and using four or five hydrophones rather than three. This reduced the error in range to around 50 m at 10 km.

Land-Based Visual Observations

We conducted real-time visual tracking of all whales moving through the study area from the peak of a nearby 73-m-high hill (Emu Mountain) set 700 m back from the beach. The view was unobstructed in all directions, with coastal features allowing a 145° view of the ocean to the horizon (~30 km). We conducted observations daily from 0700 to 1700 hours in two teams of four or five volunteers under conditions up to and including early Beaufort sea state 5 (a wind speed of approximately 20 knots). Despite this, we used data obtained only in Beaufort sea state 4 or less. To measure the horizontal and vertical angles to the whales we used a theodolite (Leica TM1100) connected to a notebook computer running the visual tracking program Cyclopes (E. Kniest, University of Newcastle), which calculated positions of the whales in real time, accounting for tide height and refraction. We made calibration measurements to determine the accuracy of the theodolite measurements by comparing positions of the boat that were determined simultaneously by theodolite and GPS. This showed the system to be accurate to within 100 m at a range of 10 km. Every observation included time of surfacing, group size and behaviour, travel direction and group composition, and we collected environmental data such as sea state, wind speed, wind direction, glare, cloud cover, precipitation and effective limit of visibility hourly.

A wireless network linked the Emu Mountain computer with those at the base station, providing an exchange of both visual and acoustic tracking data. The visual and acoustic positions were displayed on a single map in Cyclopes at the base station, enabling monitoring of interactions between singing and nonsinging whales in real time.

Interactions and Associations Involving Singers

We called any whale that was acoustically identified as singing a ‘singer’. We defined a group as two or more whales within 100 m of each other, generally displaying coordinated travel and surfacing behaviour (Corkeron et al. 1994). We considered singers to be singing in the presence of other whales when they sang for a minimum of 15 min as part of a group. This minimum time ensured the whale was engaged in sustained singing while in a group with other whales.

Data on interactions and associations involving singers included the periods immediately before and during singing and the remainder of a singer’s association with a group after he stopped singing. An ‘interaction’ occurred when we determined a singer and one or more whales to have approached and joined each other, whereas an ‘association’ refers only to when a singer was with other whales as part of the same group. Thus interactions led to associations; however, singers were sometimes first sighted as part of a group, i.e. already associating with other whales without any approach or joining of the whales having been observed. In the case of singer–singer

interactions, we included data on the interactions of both singers although there was only one association.

We categorized interactions by whether singers actively joined, or were joined by, other whales (Frankel et al. 1995; Darling & Bérubé 2001). The distinction between these was based on a directed movement by one whale towards the other. This was determined by an altered course direction greater than 45°, leading to the whales surfacing within 100 m of each other, which was taken as the time of joining. On occasion, a whale that had not previously been seen suddenly surfaced close to a slowly moving singer and was classified as joining the singer.

Boat Observations and Genetic Sampling

We obtained individual identification photographs and genetic samples of singers and other whales involved in associations with singers from a 5.35- or 5.65-m aluminium centre-console boat. The boat was directed to singers by the base station and we obtained individual identifications of the whales within a group by photographing the unique markings on the whales' flukes (Katona et al. 1979) and lateral body pigmentation patterns (Kaufman et al. 1987). In addition, we recorded the time of the sighting, group size (number of whales within a group), group composition (e.g. escort, singer, mother, calf) and GPS location.

We obtained genetic samples using biopsy tips (Lambertson 1987; Brown et al. 1994) attached to 52-cm carbon fibre bolts with a foam flotation collar behind the biopsy tip and fired from a Cobra III crossbow (150-lb draw; Cobra, Inc., Taiwan) into the dorsum of the whale from a range of approximately 25 m. Biopsy sampling has been shown to have minimal impact on the whales with no detectable response in the whales' behaviour in the majority of cases (Clapham & Mattila 1993; Brown et al. 1994). We preserved the skin in 90% ethanol and the blubber kept frozen at -20 °C for short term and -80 °C for long-term storage.

Sex Determination of Individuals

We sexed individuals behaviourally or by molecular genetic analysis using nuclear DNA extracted from stored skin samples. We extracted the DNA using an ammonium acetate method (Nicholls et al. 2000) and amplified it using a multiplex PCR method similar to that described in Rosel (2003), using primers P15EZ, P23EZ for the *Zfx/Zfy* gene (Aasen & Medrano 1990) and Y53-3c, Y53-3d for the *SRY* gene (Gilson et al. 1998).

Numerous genetic studies of humpback whales have shown that singing and escorting are male-specific behavioural roles and that a whale closely associated with a calf is its mother and therefore an adult female (Winn et al. 1973; Baker et al. 1991; Medrano-Gonzalez et al. 1994; Brown & Corkeron 1995; Bérubé & Palsbøll 1996; Darling & Bérubé 2001). An 'escort' is defined as a whale that is associating with another adult whale known to be female or with a mother-calf pair. When two males are engaged in competitive behaviour in the presence of a female, both are considered escorts (Herman & Tavolga 1980). In this

study, we took genetic samples from whales in known behavioural roles to confirm genetically the sex of individuals in these behavioural roles. Thirteen singers and six escorts were all genetically determined to be males and four whales closely associated with a calf were found to be females, supporting previous genetic studies. Our assumptions concerning the sex of unbiopsied animals in these behavioural roles therefore followed these precedents.

In this study the term 'calf' refers to calves of that year. It was not possible to differentiate reliably between immature or subadult and adult whales, therefore the term 'whale' refers to all noncalf whales.

Statistical Analysis

We carried out all statistical analyses using Statview 5.0 (SAS Institute, Inc., Cary, North Carolina, U.S.A.). We restricted analyses of interactions and associations involving singers to sightings within a 10-km visual and acoustic limit as we considered this the limit of satisfactory visual and acoustic detection and tracking of whales. We determined the accuracy of group compositions recorded from land-based visual observations by comparing group compositions determined by observers on the boat with those from the land-based station prior to the boat tracking the groups, for the same groups of whales. In 19% of cases ($N = 42$) group composition was incorrectly determined, although most errors (50%) were due to an underestimation of group sizes for groups of three or more whales and were for groups farther offshore (>5 km). Singers typically did not interact with large groups and we excluded these from the analysis owing to small sample sizes, and the majority of interactions occurred within 5 km of the land-based station.

We used unpaired *t* tests to determine whether singers that associated with other whales, compared to lone singers, differed in either the average time they were observed by land-based observers in the study area or the average time they spent singing. We restricted analyses to data from singers that associated with the following group types: mother-calf pair, mother-calf and one other escort, a lone whale, and two whales (not a mother-calf pair). We excluded larger group types because of small sample sizes and the unreliability of group size estimation from land. The data were not normally distributed and were tested with nonparametric statistics.

To test whether singers interacted and associated with other whales because there were more groups of whales to interact with, we compared the numbers of different group types that were available to singers that did and did not associate with other whales. We used only the first interaction of each singer in the analyses to avoid non-independence of observations. We defined groups available to singers as groups within 5 km of the singer at any time while he was singing, as this was the maximum distance at which whales were observed to alter their course of travel and join with other whales. We calculated the numbers of available groups of each group composition for each singer and then averaged across all singers. We compared differences in the numbers of groups of each

group composition available to singers between the two categories of singers using Mann–Whitney *U* tests.

To determine whether there were differences between the types of groups that joined singers and those that singers joined, we used a chi-square contingency test. We categorized data into groups containing a mother–calf pair and groups not containing a mother and calf owing to small expected values of some group compositions. To then determine whether singers were observed interacting with certain group compositions more than expected at random, we tested each group composition separately using a chi-square goodness-of-fit test. We calculated expected values based on the numbers of groups that were available for singers to interact with while singing and assumed that singers joined with nearby groups randomly. We calculated expected proportions by dividing the numbers of available groups of each group composition by all available groups. We then used these to calculate the numbers of groups of each type that singers would have interacted with if they had interacted with groups randomly; we compared these expected values with the observed values.

For singers that did interact with conspecifics, we tested differences among group compositions in both the association times of singers and the proportions of time singers spent singing within groups using the Kruskal–Wallis test and Mann–Whitney *U* test for further pairwise testing. We applied both conservative and relaxed criteria when testing durations of associations because singers were often already with other whales when first observed or still with others when last observed in the study area. The conservative criterion used only group associations of known start and end times, whereas the relaxed criterion included durations of open-ended associations measured as the total time that a singer was observed with another whale within the study area. There were clear differences in singers' association times

with different group types that were consistent between the two approaches, and thus we used the relaxed criterion to increase sample size. We calculated the proportion of time a singer spent singing within a group for each group composition by dividing the time observed singing within the group by the duration of the entire association. We then averaged the proportions of time singers spent singing within each group across all singers to obtain an overall proportion of time for each group composition.

RESULTS

Associations between Singers and Conspecifics

In total, we obtained reliable visual and acoustic tracks for 114 singers; 48 did not associate with other whales, whereas 66 were involved in 63 associations (Table 1). Singers associated with nonsinging lone whales ($N = 27$), unescorted mother–calf pairs ($N = 20$), mother–calf pairs with one escort ($N = 4$), groups of two whales ($N = 7$) or four whales ($N = 2$) that did not include a mother and calf, and other lone singers ($N = 3$). There was no significant difference (unpaired *t* test: $t_{112} = 0.944$, $P = 0.346$) in the amounts of time that we observed singers that did not associate with other whales ($\bar{X} \pm SD = 155 \pm 74$ min) compared to singers that did ($\bar{X} \pm SD = 169 \pm 83$ min) in the study area. There was also no significant trend ($t_{112} = -1.721$, $P = 0.088$) for males to sing for longer when they did not associate with other whales ($\bar{X} \pm SD = 116 \pm 72$ min) compared to singers that did associate ($\bar{X} \pm SD = 95 \pm 57$ min). Comparisons of the numbers of groups of each composition that were available for singers to interact with showed no significant differences between lone singers that did not associate with other whales and singers that did.

Table 1. Frequency of interactions between singers and other whales categorized by singing behaviour

Type of interaction/association	Group composition						Total
	1 Whale	2 Whales	4 Whales	Mother–calf pair	Mother–calf and ♂ escort	♂ Singer	
Singer stopped singing							
Singer joined other whale(s) and stopped singing	3	3	1		4	3 (3 ♂)	14
Singer joined by other whale(s) and stopped singing	17 (10 ♂)	1				2 (2 ♂)	20
Singer started or continued singing							
Whale joined other whale(s) and started to sing				4			4
Singer joined other whale(s) and continued to sing	1	1		6			8
Singer joined by other whale(s) and continued to sing	2	1				1 (1 ♂)	4
Singer was singing while associating with other whale(s) when first observed	4	1	1	10			16
Total	27	7	2	20	4	6	66

The numbers in parentheses represent the numbers of males whose gender was determined either genetically or behaviourally. The group composition columns do not include the focal singers and in the case of singer–singer interaction, data on the interaction of both singers were included although there was only one association (i.e. there were six singer–singer interactions although only three associations).

Interactions between Singers and Conspecifics

Of the 63 associations between singers and other whales there were 50 interactions in which it was clear that the singer either joined other whales ($N = 26$) or was joined by other whales ($N = 24$) (Table 1). The frequency at which singers interacted with the various group compositions depended on whether the singer joined or was joined by the other groups (chi-square test: $\chi^2_1 = 22.2$, $P < 0.0001$; Fig. 2). Based on the numbers of groups available for singers to interact with, singers joined groups containing a mother and calf significantly more often than expected and joined adult-only groups significantly less often than expected ($\chi^2_1 = 4.03$, $P = 0.0447$; Fig. 3a). In contrast, singers were joined by groups comprising only adults ($\chi^2_1 = 9.94$, $P = 0.0016$) significantly more often than expected and were never joined by groups containing a mother and calf (Fig. 3b). In particular, singers joined unescorted mother–calf pairs in 10 of the 26 interactions (39%) when they joined other whales and were joined by lone whales in 22 of the 24 interactions (92%) when a singer was joined (Fig. 2).

In 34 of the 50 interactions (68%) the singer stopped singing at the onset of the interaction (Table 1). Singers were typically joined when they stopped singing and were predominantly joined by lone whales (59%) in these cases. The sex of the lone whale was determined for 12 of the 20 joiners and all were male. Singers that were joined by other whales had a significantly shorter latency period between when the singer stopped singing and when the association began ($\bar{X} \pm \text{SE} = 1.05 \pm 0.6$ min) compared to singers that joined other whales ($\bar{X} \pm \text{SE} = 12.6 \pm 4.7$ min) ($U = 67.5$, $N_1 = 20$, $N_2 = 12$, $P = 0.046$). There were two cases in which a singer was escorting a mother–calf pair while singing and stopped singing shortly after being joined by other males ($\bar{X} \pm \text{SE} = 2.5 \pm 0.5$ min). In one of the cases the original singer started singing again while still escorting the mother and calf after two males that had joined left the group. Singers that joined mother–calf groups in which another male escort was present also always stopped singing shortly after joining ($\bar{X} \pm \text{SE} = 4 \pm 4.7$ min, $N = 4$).

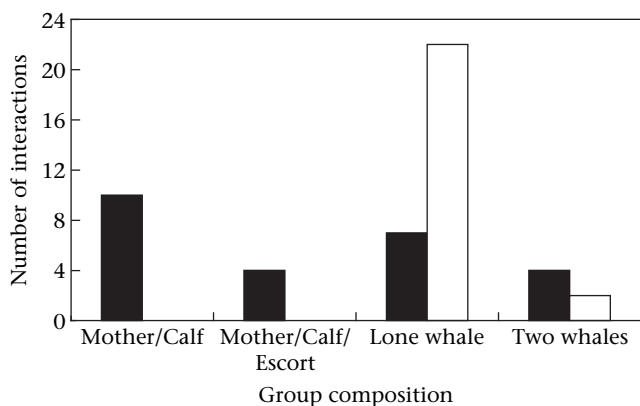


Figure 2. The number of interactions in which singers were observed to either (■) join or (□) be joined by other whales of the four different group compositions.

Singers interacted with other singing whales in six of the 50 interactions, although both singers were never singing at the same time within the same group. The initial singer stopped singing at the onset of the interaction in all three cases, whereas the second singer stopped in two of the three interactions and continued singing in the other interaction. The mean duration of singing by the three initial singers before the interactions was 118 ± 56.1 min ($\bar{X} \pm \text{SD}$), with the overlap of songs (before the singers joined) ranging from 2 to 25 min ($\bar{X} \pm \text{SD} = 12 \pm 11.6$ min). The initial singer joined the second singer in two of the three interactions, resulting in associations of 6 and 82 min, and in the second of these interactions the second singer continued singing in the presence of the ex-singer. In the remaining interaction the initial singer was joined by the second singer, resulting in an association lasting 46 min.

Effect of Group Composition on the Duration of Associations

The durations of singers' associations with other whales differed significantly with group composition (Kruskal–Wallis test: conservative criterion: $H_3 = 12.73$, $P = 0.0052$;

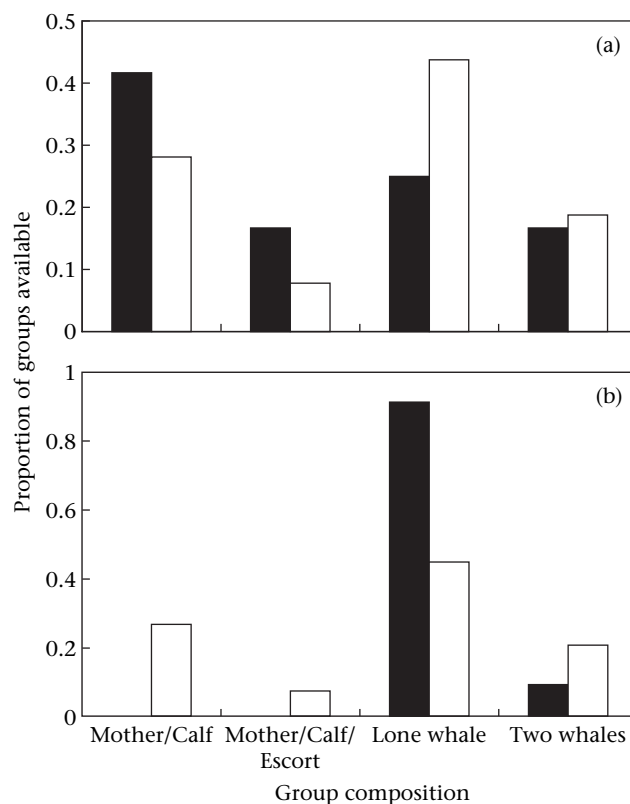


Figure 3. (a) (■) The proportions of groups of each composition that singers were observed to join compared to (□) the proportions of these group types that were within 5 km of the singer and available for the singer to interact with. (b) (■) The proportions of groups of each composition that were observed to join singers compared to (□) the proportions of these group types that were within 5 km of the singer and available for the singer to interact with.

relaxed criterion: $H_3 = 13.96$, $P = 0.003$; Fig. 4a). Association periods were significantly longer when singers were escorting only a mother–calf pair than when they were associating with lone whales (Mann–Whitney U test: relaxed criterion: $U = 127.5$, $N_1 = 20$, $N_2 = 29$, $P = 0.0009$) or groups of two other whales (relaxed criterion: $U = 22$, $N_1 = 20$, $N_2 = 8$, $P = 0.003$), which was consistent when applying both sets of criteria. All other pairwise tests were not significant. Singers associated with a mother and calf pair for the greatest duration of time, followed by mother–calf pairs escorted by other males, although there was no significant difference between the two groups. However, singers showed the greatest variation in their association durations when with mother–calf groups escorted by other males (Fig. 4a).

Singing during Associations

In 32 of the 63 associations (51%) and 16 of the 50 interactions (32%), the singers sang after the onset of interactions in the presence of other whales (Table 1). Singers sang with other whales in four different contexts: four singers started singing immediately after joining a group, four continued singing after being joined by another group, eight continued singing after joining another group and 16 were already singing as part of a group when first observed. Singers that were singing when escorting

a mother–calf pair with no other male escorts present comprised 67% of the observations, followed by singers with one other whale (24%) or two other whales (9%). Regrettably, it was not possible to determine the sex of the adults involved in the interactions when a mother and calf were not present except for one singer–singer interaction, in which the second singer continued singing in the presence of the ex-singer.

Singers spent significantly different proportions of time singing when with different group compositions (Kruskal–Wallis test: $H_3 = 19.91$, $P = 0.0002$; Fig. 4b). They sang for a significantly greater proportion of time when escorting a mother–calf pair compared to when associating with a mother and calf pair escorted by one other male (Mann–Whitney U test: $U = 0.0$, $P = 0.0019$), a lone whale ($U = 102$, $P = 0.0001$) or two other whales ($U = 23.5$, $P = 0.0041$). All other pairwise tests were not significant. The only group type that singers started to sing with after joining was unescorted mother–calf pairs (Table 1). In contrast, singers never sang during associations with mother and calf pairs that were escorted by another male (Fig. 4b).

DISCUSSION

Our results on the interactions of singers and nearby conspecifics provide the highest reported occurrence in humpback whales of males singing when escorting females and support an intersexual function of song in this species. Until now, the occurrence of males singing in the presence of females has been believed to be low. Our observations show that male singers preferentially joined and escorted mother–calf groups. Singers also associated longer with mother–calf pairs with no other males present and sang for a significantly greater proportion of time in these groups than in any other. Parallels in the complexity of song between those of humpback whales and those of birds strongly suggest that song is a male acoustic display aimed towards females. An intersexual function of humpback whale song for attracting potential mates has been a long-standing hypothesis in the literature (Winn & Winn 1978; Tyack 1981). However, evaluating the success of male mating tactics and particularly the use of song has been difficult because copulation has never been observed in this species. Despite the early hypothesis that song functions to attract females, there has been little direct evidence to support an intersexual function for song.

Changes in behaviour by nearby conspecifics in response to song, as measured by avoidance or attraction to the singer, have often been used as indicators of song function (Andersson 1994; Bradbury & Vehrencamp 1998). Although singers were often joined by other males, it was evident that singers were never joined by groups containing a mother–calf pair, either with or without escorts (Fig. 2), which seems inconsistent with the mate attraction hypothesis (see Andersson 1994). There is currently little evidence from either behavioural studies (Darling & Bérubé 2001; Darling et al. 2006) or playback experiments (Tyack 1983; Mobley et al. 1988) for the attraction of females to singers. On the other hand, Medrano-Gonzalez et al. (1994) documented females

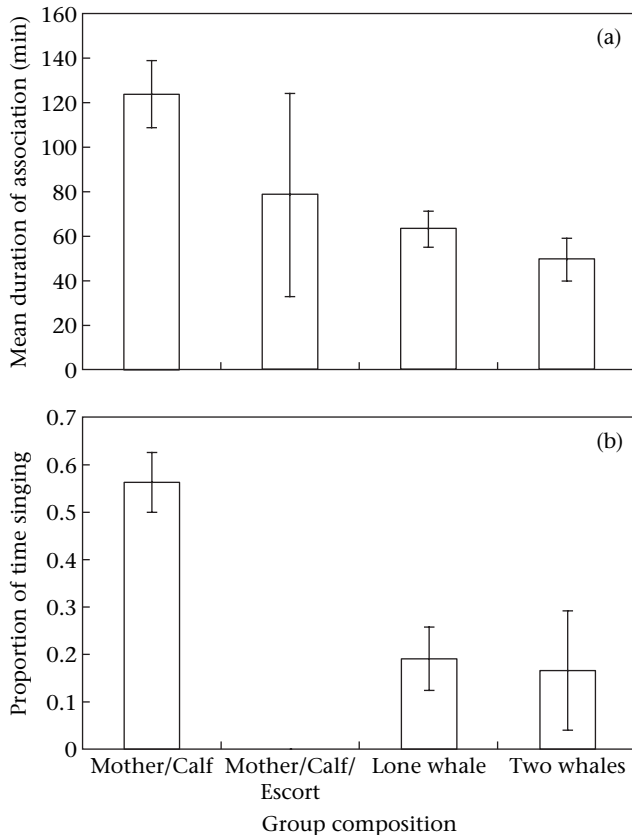


Figure 4. Effect of group composition on (a) the duration of time singers spent in association and (b) the proportion of time singers spent singing during associations. Shown are mean \pm SE values.

approaching singers on two occasions, and in our study the sex of all the whales that approached singers was not available, leaving open the possibility that some joiners were females. Certainly, singers were often observed associating with mothers and calves when singing, although further work is required to determine whether female attraction to singers occurs.

There was no significant difference in the numbers and types of groups that were available to singers that interacted with other whales compared to those that did not. Therefore, a singer did not interact with other whales simply because there were more whales to interact with. Consequently other factors may be involved in whether a singer associates with other whales. It could be hypothesized that a component of female choice based on song display may be involved in whether singers interact with females and also that females may solicit the approach of males, as suggested by Helweg et al. (1992). Adult females in competitive groups of males appear to use surface behaviours such as pectoral slapping to encourage competition from surrounding males (Deakos 2002). However, the role of surface behaviours and social sounds as acoustic cues for mediating social interactions and the extent that singers use such cues to join other whales are not known and require further work.

In the majority of interactions, singers stopped singing at the beginning of the associations (68%), although these associations predominantly involved other males (Table 1). In the remaining interactions, during which singers either started or continued singing after joining other whales, these singers predominantly interacted and associated with unescorted mother–calf pairs when singing (Table 1). Singers spent a significantly greater proportion of time singing while escorting mother–calf pairs than when associating with other whales and were observed starting to sing only after immediately joining a mother and calf. Furthermore, a proportion of the unsexed lone whales that joined singers and that singers associated with while singing (11% of associations) may have been females, given that male–female pairs are one of the most common group types found during migration (Brown & Corkeron 1995; Valsecchi et al. 2002) and singers typically stopped singing when interacting with lone males that joined singers (Table 1). In many other animals singing while associating with a female is a prominent component in courtship interactions (Ball & Dufty Jr 1998) and for many species of birds and some mammals, such as the male red deer, male song can have a direct effect upon a female's reproductive physiology and behaviour (Catchpole 1982; McComb 1987; Searcy 1992; Catchpole & Slater 1995; Ball & Dufty Jr 1998).

Although male humpback whales commonly escort females during the breeding season, the purpose of escorting is poorly understood. Recent evidence, however, suggests that escorting and even singing while escorting mothers with calves may be related to mating opportunities. A molecular paternity study by Cerchio (2003) showed that a male that escorted a mother with a calf sired her next calf, indicating postpartum ovulation by the mother and successful copulation and fertilization by the male escort.

Furthermore, several males that sired multiple offspring in his study had sighting histories of commonly escorting mothers with calves. Successfully reproductive males were also observed across a range of behaviours, such as escorting mothers with calves and directly competing for females in competitive groups, and no one alternative mating tactic was predominant among males (Cerchio 2003; Cerchio et al. 2005). In addition to molecular paternity data, photographic identification studies and whaling data also show that females are capable of postpartum oestrus and conceiving offspring over consecutive years (Chittleborough 1958; Weinrich et al. 1993; Mikhalev 2000). Given the possibility that males escorting females with calves are capable of being reproductively successful, we suggest that song may play a role in the solicitation and coordination of mating behaviour of females, possibly by conveying certain attributes of a singer to a female such as fitness (Chu 1988).

In many taxa, male song also has an important function in deterring rival males in intrasexual competition over a mate or territory (see reviews by Andersson 1994; Gerhardt & Huber 2002; Collins 2004). In humpback whales, competition among males on the breeding grounds is more likely to occur over mates than territories as males do not appear to occupy or defend territories during the breeding season (Tyack 1981) and males commonly exhibit aggressive behaviour over access to females in competitive groups (Tyack & Whitehead 1983; Baker & Herman 1984; Clapham et al. 1992; Weinrich 1995). Contrary to the prediction that song should repel rival males, song seemed to attract nearby males in our study as shown by singers being joined predominantly by lone whales, of which 59% were sexed and were all male. If song were used for intrasexual competition, it might also be expected that males would continue to sing in the company of other males, as some songbirds do (Naguib & Kipper 2006). This study presents evidence to the contrary; in the majority of associations in which another known male was present, the singer stopped singing.

Recent observations of lone males frequently joining singers and exhibiting nonagonistic behaviour led to the proposal that song functions in male organization in humpback whales (Darling & Bérubé 2001; Darling et al. 2006). In the study by Darling et al. (2006), however, lone males joining singers comprised 80% of all interactions with singers, whereas they accounted for only 37% of interactions in our study owing to a higher frequency of singers joining other whales. This difference may be due to the studies having been undertaken at different locales (migration versus breeding grounds) or different times of the breeding season or to differences in study methodologies used, e.g. Darling et al. relied solely on boat-based observations. Due to the high proportion of singers interacting with other males, Darling et al. (2006) suggested that the song primarily functions to coordinate interactions between males and may aid in the formation of male coalitions.

Given that singers often join and continue to sing while escorting females, whereas lone males often join singers who then stop singing, we offer an alternative explanation for why males are seen joining singers. We propose

that the song may inadvertently act as a cue to other males about the potential presence of a female and that lone males that join singers may be prospecting for females. In the absence of other available cues, and given that singers often escort females, this would be an obvious and low-cost strategy for locating females. Prospecting males would disrupt the singing of singing escorts and may attempt to displace a singer as the principal escort. Singing might therefore be costly if it attracts competitors for mates, but also unavoidable if it is a reproductive display necessary in female–male interactions during courtship. It is also possible that singers may choose to sing alone, escort without singing or sing while escorting, depending on surrounding social factors such as the presence of other males.

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