Humpback whale (*Megaptera novaeangliae*) singers in Hawaii are attracted to playback of similar song (L)

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The use of playback experiments to study humpback whale song was assessed. Singers clearly detected playback song while singing and with other singers in the distance. Singers approached or joined song similar to their own from as far as 800 m but did not do so for a different (foreign) song. In one compound trial, on the playback of different song, the singer moved away and continued singing; when the playback was changed to similar song, it stopped singing and joined the playback speaker. Song playback experiments on the breeding grounds are viable and may provide insight into song function. © *2012 Acoustical Society of America*.
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I. INTRODUCTION

Humpback whales emit a repetitive series of sounds known as song (Payne and McVay, 1971). The song's composition, that is, the use and arrangement of different sound units, progressively changes, yet all singers in a population tend to sing the same version at any one time (Payne *et al.*, 1983). Singing is a male behavior that typically leads to brief, non-agonistic interactions between the lone singer and other males; at times, a male may sing while escorting a female (Darling and Berube, 2001; Smith *et al.*, 2008). The purpose of these behavior patterns, as well as the function of the song overall is unknown. The objectives of this study were (1) to assess the use of song playback experiments in the investigation of humpback whale song function and (2) examine the idea that song characteristics may play a role in the interactions of males during the breeding season (Darling *et al.*, 2006).

Whether or not playback methodology was viable for the study of song function on a breeding ground was a question for two reasons. First, the song playback would occur into an environment of multiple natural songs with a high density of interacting whales. There was little understanding of the "reach" of the song, attention of whales to individual song, or if whales would discriminate between electronic simulated and natural song. Second, results of two earlier playback studies (Tyack, 1983; Mobley *et al.*, 1988) in Hawaii raised the possibility that playback of song may not typically elicit a response from nearby whales (for either simulation or behavioral reasons).

The second objective of this study was to investigate whether song characteristics (e.g., composition) might be a factor determining the interactions between neighboring singers. Darling *et al.* (2006) described variability in natural interactions between neighboring singers in Hawaii ranging from joining to approaching (but not joining) to none apparent. If specific song characteristics played a role in this variability, playbacks of songs with different characteristics should elicit different responses from a target singer.

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II. METHODS

Simulated songs, either similar to, or substantially different from, current song were broadcast to singers on the Hawaiian breeding grounds and their responses documented. For the purposes of this study, "similar" song was defined as a current song in the study area. Initially, to ensure similarity, songs were obtained from the target singer ($n = 6$) just prior to playback (i.e., its own song was played back), then later from a different singer ($n = 3$) from a current time frame (within 3 days) in same general location. All of these current songs had the same fundamental composition (see Payne *et al.*, 1983). To ensure a difference in playback stimuli, a foreign song from the South Atlantic in 2002 was used (see Darling and Sousa-Lima, 2005). This song had the same structure and timbre as any humpback song but with a different composition (and potentially other qualities) not familiar to the Hawaiian whales. Two trials of non-whale sounds, a church bell and human song, were also conducted.

The playback system used to simulate the song was a Lubell - LL9162 underwater acoustic transducer (frequency range 240 Hz to 20 kHz) with Lubell amplifier Model CA-160. The calibrated source level of the playback was a maximum of 163 dB re. 1 μPa at 1 m rms, which falls within the range of natural song source-level measurements 151–173 dB re. 1 μPa at 1 m (Au *et al.*, 2006). The LL9162 transducer had a fairly uniform response from 700 Hz to 18 kHz; however, the song frequencies below 700 Hz were attenuated compared to actual song.[1] Because of this, we term the playback stimuli "simulated song." It is important to note that all playback songs, in all trials, were differentially attenuated in the same way. Also, audio recordings made within 10 m of the target singer during playback trials confirmed that all units of the playback song reached the target—that is, the attenuation was not such that sound units were lost in the transmission.

Before a playback, the target singer was located, photo-identified, its song recorded and position determined by GPS. One boat observed the singer; a second boat 600–800 m distant conducted the playback. The observation boat audio-recorded the singer, so that the start of the playback was recorded along with the target individual's song. During a 30 min playback trial, the acoustic and physical reactions

of the singer were documented through the monitoring of sounds, underwater video (when feasible) and GPS measurement of its movements. A whale's movements were measured by recording the time of a surfacing, then a boat moving to the whale's location (as determined by its fluke print) and taking a GPS position. Relative orientation and distance between playback speaker and the target whale, and changes in these due to response of the whale during the playback trial and/or drift of the playback boat were plotted using OXIEXPLORER V 3.09 GPS mapping software.

To minimize interference by surrounding whale activity, playback trials were (1) conducted late in the Hawaiian season (April) when numbers of whales were reduced from peak times (Mobley *et al.*, 1999; Au *et al.*, 2000), (2) not initiated when other whales were sighted within 2 km or if loud singing was heard using a hydrophone near the target, (3) aborted if other whales approached the target whale during the trial, and (4) conducted in calm seas (<Beaufort 3) to minimize boat drift and maximize observation.

III. RESULTS

The study was conducted in Hawaii on 32 days from 2005 to 2007. Encounters with 67 singers led to 23 playback trials with 18 used in analyses.

A. Objective 1: Viability of playbacks on breeding ground

Results, summarized in Figs. 1–3 and in the following text, indicate the target singers perceived the playback signal within seconds of its introduction, and a measurable physical and/or acoustic response occurred in 78% (14/18) of trials. The majority of the responses to playbacks was overt and clearly occurred within the context of the playback song rather other whales that may have been present in the vicinity. This was especially obvious when target singers stopped singing and swam directly to the playback boat (as far as 800 m distant). This movement to within a few meters of the speaker occurred in five of nine similar song playbacks.

B. Objective 2: Song characteristics a factor in singer interaction

This analysis consisted of whether the target singers approached the playback song source, moved away from it, or did neither (neutral response) as shown in Fig. 1.

The results are summarized in four points.

1. Playback of similar song led to the singer approaching and joining the playback speaker in a majority of cases [examples Fig. 2(A) and 2(B)].

Seven of nine (78%) playbacks of similar song led to the singer approaching the playback speaker, five of these seven (71%) actually "joined" (that is, hovered within a few meters of) the speaker. The responses in the other two trials were neutral. The approaches occurred both directly, with no surfacing between playback start and appearance under the speaker, or with up to four surfacings between the beginning of the response and close approach. Of the five singers that "joined" the speaker, three did so when played back their own song and two when played-back similar current Hawaii song.

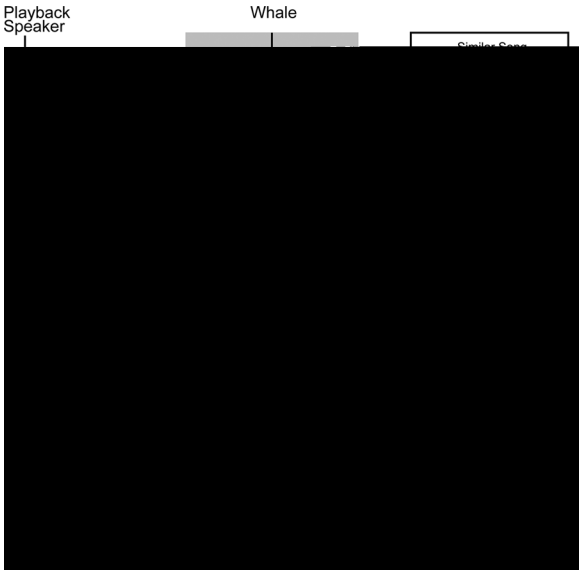

FIG. 1. Physical responses of singers to playbacks. This figure illustrates the maximum change in the singer's distance from the playback speaker during each of 18 trials (e.g., 100% "decrease" means the singer joined the PB speaker, 116% "increase" means the singer more than doubled its distance from the PB speaker). The shaded area gives a rough indication of the neutral response distance. That is, up to a 34% increase or decrease in the distance from playback cannot necessarily be attributed to the playback stimuli. This is estimated from the mean distance (250 m) subject singers moved between the final dive after one surfacing to the final dive after the next surfacing prior to playback ($n = 37$), and the mean starting distance (700 m) between the playback boat and the whale. In the similar song playbacks, the top six trials involved the subject's own song played-back to it; the last three were a current Hawaii song but from another singer. All singers were stationary when playback started.

2. Different song (and non-whale sounds) did not result in the singer approaching the playback

All seven trials of playback of the different song led to the singer either increasing its distance (5/7, 71%) from the playback [examples Figs. 2(C) and 2(D)] or a neutral response. The same occurred with two playbacks of non-whale sounds. The difference in response to similar and different song was statistically significant (two-tailed Mann–Whitney $U = 4.14$, $n = 14$, $P < 0.001$).

3. Same singer changed its response with change in playback stimuli

In one trial, illustrated in Fig. 3, circumstances allowed the playback of different and similar song to the same singer. On broadcast of a different song, the singer moved away (increased distance 78%) but continued singing. The playback was stopped and the singer stopped moving. A similar song (in this case current but not the subjects own song) was then broadcast to the same singer. The singer stopped singing 2 min 35 s into this second playback, surfaced once, then "joined" the playback speaker. The opportunity did not arise to repeat this type of compound trial.

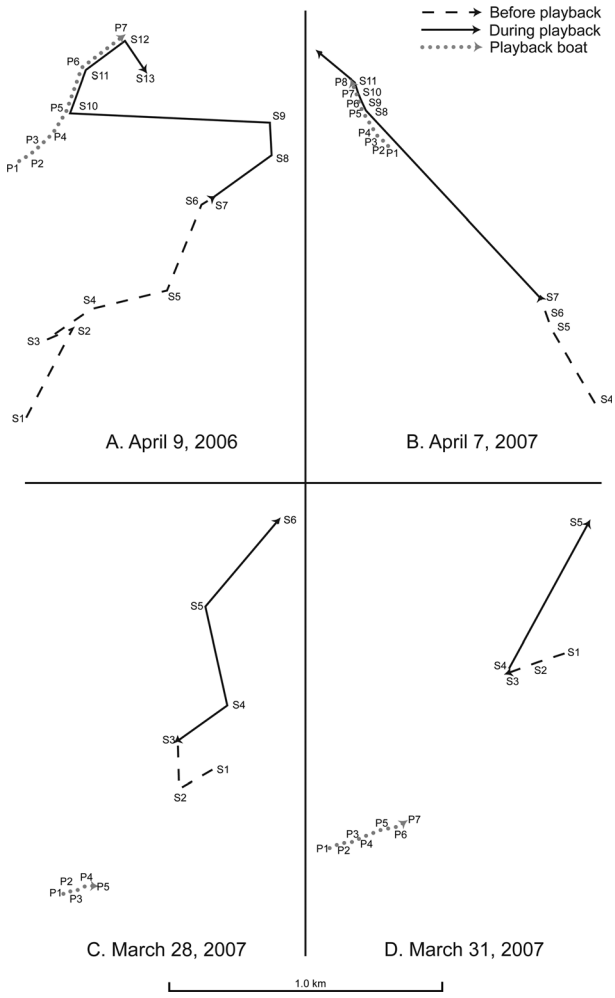

FIG. 2. Examples of responses to playback of similar and different songs. Similar song: (A) April 9, 2006—singer stopped singing 6 min 2 s into playback and surfaced twice before joining playback speaker. (B) April 7, 2007—singer stopped singing 7 min 57 s into playback and next seen at PB speaker. [In the example, the heading of the singer when breathing on the surface was toward playback boat (786 m away); it was stationary when singing. When it responded to the playback, it stopped singing and increased its speed 5 ×, swimming directly to the speaker.] Different song: (C) March 28, 2007—singer increased distance from PB (116%) but did not stop singing; (D) March 31, 2007—singer increased distance from PB (38%), and stopped singing after full song (17 min).

4. Variability in response

Responses to the playbacks varied in detail within both the similar and different song trials. As illustrated in Fig. 1, in "similar" song trials, some target singers remained in neutral zone, others approached but did not join the playback source and others swam straight to the playback speaker; in the "different" song trials, some remained in neutral zone while others substantially increased their distance.

Response time, as indicated by the target whale stopping singing, ranged from near immediate (<30 s from start of playback), to stopping after several minutes, to stopping after a full song was complete and on surfacing, to not stopping at all. Singing stopped during 70% of playback trials. The target singer stopped singing in eight of nine similar song playbacks, four of seven different song playbacks, and one of two non-whale song playback trials. The time between start of a similar song playback and the target whale stopping singing

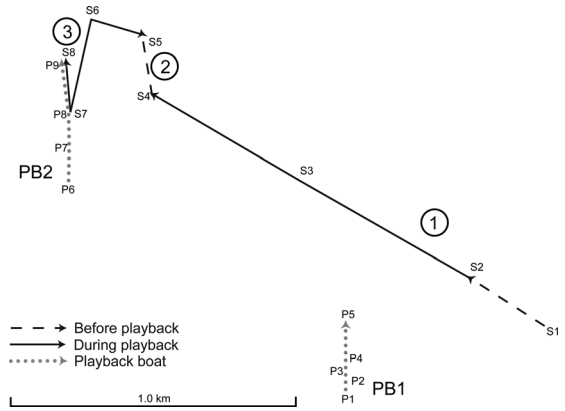

FIG. 3. Compound trial: Different song led to repulsion; similar song led to attraction. 1. On broadcast of the different song (PB1), the singer moved away (increased distance 78%) but continued singing. 2. The playback was stopped and the singer stopped moving. 3. A similar song (current Hawaii song but not singers own song in this case) was then broadcast to the same singer (PB2). The singer stopped singing 2 min 35 s into playback, then joined playback speaker.

ranged from 0:27 s to 8 min 53 s (Me: 2 min 30 s), different song playback from 0:28 s to 17 min 06 s (Me: 11 min 30 s).

An immediate acoustic response did not necessarily correlate with a specific physical response. Of the three immediate acoustic responses of 0:27, 0:28, and 0:28 s, one whale joined the playback speaker, another eventually moved away from the speaker (increased distance 61%), and the third was in the neutral physical response category.

IV. DISCUSSION

A. Viability of song playback experiments on breeding grounds

Humpback whale song playback experiments on a breeding ground are viable but not without challenges. Singers clearly perceived and responded to playback song in measurable ways. The immediacy and accuracy with which singers recognized and pinpointed the location of a simulated playback song, at some distance, while they were singing themselves, with multiple natural background songs, was noteworthy.

Our results were surprisingly unequivocal considering earlier era playback studies, which left the impression that whales did not usually or predictably respond to song playbacks (Tyack, 1983; Mobley *et al.*, 1988—discussed further in the following text). In this study, the behavior elicited by the simulated similar songs was consistent with natural observations that a singer may stop and join a neighboring singer or indeed that males (singing or not) often join singers (Darling and Berube, 2001; Darling *et al.*, 2006). A recent humpback song playback study in Mexico breeding area also clearly demonstrated the singer's perception of, and variability in response to, song playbacks (Cholewiak, 2008).

A point worth emphasizing is that although viable, song playback experiments conducted on a breeding ground such as Hawaii are challenging. This is primarily due to the need to control for ongoing natural whale song and interactions in the experiment area and the need for calm seas. Substantially more effort/time was required to obtain a reasonable sample size of trials than was anticipated at the outset.

Considering the responses of the whales to the playbacks, the limitation of the transducer in replicating lower frequency portions of the song was, apparently, not a significant issue for at least the majority of targeted whales. If the whales had responded randomly to the playbacks, the quality of the simulation would be one immediate question. We presume all of the simulated songs, both similar and different, were affected in the same way by the transducer with a differential response still evident. However, we acknowledge that, ultimately, the effects, if any, of the attenuation of lower frequencies on the reactions of the singers are unknown. Work is ongoing to modify the playback system to more accurately broadcast the lower frequencies in humpback song.

B. Song characteristics a factor in singer interactions

In this study, the broadcast of a song similar and familiar to that of a target singer was likely to result in the singer stopping singing and approaching or joining the playback source. Playback of a song different or foreign to that of the target singer did not have the same effect. One explanation is that song characteristics are a factor in male interactions with male-male social connections facilitated by singing similar/familiar song.

However, this study design was intentionally simplified using only similar (current) song or very different (foreign) song to address the question of general viability of song playback experiments in this situation. Further, although the use of the same "different" song in all trials aided initial interpretation, it raised pseudo-replication issues limiting conclusions on response to this stimulus (Kroodsma *et al.*, 2001). While there was no question that songs similar to a singer's may attract it to the source, further studies are required to determine which characteristics of the song lead to such contrasting behavioral responses as observed in this study.

The results of earlier playback studies (Tyack, 1983; Mobley *et al.*, 1988) were somewhat the opposite of what is reported here. Although neither of these studies focused on song playbacks to singers, Tyack (1983), reported that three of four singers moved away from current (similar) song, while Mobley *et al.* (1988) reported that while 32 of 35 target singers did not respond at all to song playback, two of the three that approached the playback did so to non-current Hawaii song. (Non-current Hawaii song was not played-back in this study.) We have no explanation for the apparent difference between these earlier studies and this work.

The variability in response *within* one type of stimulus, particularly in the time between playback start and a reaction may be indicative of other, unmeasured, factors that may influence a response. For example, the target singers may differ in age and status or in the level of their engagement with distant song or social activity at the start of the trial or perhaps, even, some were less easily "tricked" by the simulated song than were others. Also in the playback of similar song, the "degree" of similarity between playback and target singer may vary (as our definition of similar song was broad). Relatively small differences in song presentation may occur within "current" song and even within one individual singer's song from one cycle to the next. Perhaps these minor (to us) differences affect the response.

In summary, while there were some clear limitations to this experiment, the results were strong and consistent enough to suggest the viability of playback experiments in this context and that these experiments may provide insight into how song mediates male-male interactions on the breeding grounds. Future playback studies using a variety of different songs both foreign and local, including those that range in degree of difference to that of the target singer, will be critical in assessing whether song characteristics govern male interactions.

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[1]This transducer was used initially because of the difficulty of obtaining a transducer with a flat response through full frequency range of humpback song, and this model had been used successfully in other playbacks experiments with cetacean sounds (Deeke *et al.*, 2002).

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