

## Interactions Between Singing Hawaiian Humpback Whales and Conspecifics Nearby

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**Summary.** Interactions of singing humpback whales, *Megaptera novaeangliae*, with conspecifics nearby were studied during the breeding season off the west coast of Maui, Hawaii. On 35 occasions singing humpbacks were followed by boats (Table 1). The movement patterns of these singing whales and other conspecifics nearby were recorded by observers on land using a theodolite.

Thirteen of 35 singers stopped singing and joined with nonsinging whales either simultaneously or within a few minutes after ceasing to sing. Another 15 also stopped singing while under observation and were not seen to join with another whale, but all singing whales that joined with other whales stopped singing. Singing whales often pursue nonsinging whales, while nonsinging whales usually turn away from singers (Figs. 4, 5).

When a singer joined with a female and calf unaccompanied by another adult, behavior tentatively associated with courtship and mating was observed (Fig. 7). Such behavior also occurred during several interactions between singers and individuals of unknown sex. Aggressive behavior was observed during three interactions between singers and individuals of unknown sex (Fig. 4) and it predominated whenever more than one adult accompanied a cow and calf. During the other occasions when a singer joined another whale, we could not determine the nature of the interaction. Many times the singers and joiner would surface together only once and would then separate. However, on several occasions the singer and joiner would remain together for as long as we could follow them, up to 1.5 h.

The roles of singer and joiner can be interchangeable. For instance, on two occasions a singer joined with a whale that either had been singing or started singing later in the day (Fig. 3). Furthermore, on several occasions, a nonsinging whale appeared to displace the singer. Individual singing humpbacks are

not strictly territorial, although singers appear to avoid other singers.

As the breeding season progressed, singers sang for longer periods of time (Fig. 2). In addition, the probability of a whale joining with the singer decreased by 42% from the first half of the observation period to the second half. Furthermore, this increase in duration of song bouts occurred during that section of the season when female reproductive activity as measured by rate of ovulation is reported to be decreasing in other areas.

Our observations support the hypothesis that humpback song plays a reproductive role similar to that of bird song. Humpbacks sing only during the breeding season. If, as seems likely, most singing humpbacks are male, then singing humpbacks probably communicate their species, sex, location, readiness to mate with females, and readiness to engage in agonistic behavior with other whales.

### Introduction

Animals as diverse as crickets, songbirds, and gibbons all appear to sing for the same basic reasons (Alexander 1960; Armstrong 1963; Marshall et al. 1972). Generally, it is the male which sings, mostly during the breeding season, to communicate such information as species, sex, age, location, individual identity, readiness to mate with females, and readiness to engage in agonistic behavior with other males (Marler 1956). Song can act as a spacing mechanism since males often avoid conspecifics that are singing (Krebs 1977). Females in reproductive condition often approach singers and may even use song as a criterion in mate selection (Brockway 1969; Kroodsma 1976).

The songs of humpback whales (*Megaptera novaeangliae*) are the longest and most complicated

songs known (Payne 1970; Winn et al. 1970; Payne and McVay 1971). What little is known about humpback song fits the pattern outlined above as do the newly discovered interactions of singing humpbacks with conspecifics reported in this paper.

Humpbacks sing during the winter and spring near their tropical breeding and calving grounds (Schevill 1966; Payne and McVay 1971). Even though the mating of humpback whales has never been directly observed, winter must be the mating season for three reasons. First, the vast majority of female humpbacks bear their calves in the winter (Matthews 1937). Since the gestation period is about one year (Chittleborough 1958), mating must occur during the same season. Second, humpbacks ovulate in the winter (Chittleborough 1965). Third, mature male humpbacks show an increased testis weight and increased spermatogenesis during the winter (Chittleborough 1955). One singing humpback sexed by cytological means (Winn et al. 1973) and four sexed by visual identification (Glockner, personal communication; Hudnall 1977) proved to be males.

### Methods

A combination of excellent weather, good underwater visibility, vantage points on shore, and a high concentration of wintering humpbacks makes the leeward or western coast of Maui, Hawaii, a superb site for observing humpback behavior. Humpbacks were observed from a shore station on a hill as well as from two to three boats, which followed groups of humpbacks in the waters near the shore station (Fig. 1). Shore-based observations of humpbacks were made from an 80-m hill named Kilea near the town of Olowalu. During our observation period, from 26 January 1979 to 12 March 1979, many humpback whales were visible every day from the hill. It was easiest to follow whales that were less than 10 km from Kilea, a distance that thus delineates the approximate boundaries of our study area as shown on Fig. 1, but we were able to follow whales up to 20 km away. Whales were only visible to shore observers when they blew or when part of their bodies emerged from the water. Most whales surfaced at 5–15 min intervals. Since whales move slowly and their density was low, we were usually able to follow the same whale between surfacings. Each lone whale or group of several whales that was followed for more than one surfacing was assigned an identification letter. Since no other species of baleen whale were sighted, 'whale' means North Pacific humpback, *Megaptera novaeangliae*, in this paper unless otherwise stated. 'Singer' indicates a whale only while it is singing. An ex-singer is a humpback that has stopped singing.

Observers at Kilea could pinpoint the location of a surfacing whale by means of a theodolite or surveyor's transit (a method developed by R.S. Payne). The transit technique allows one to follow in detail the movement patterns, spatial distribution, and interactions of whales. The observer aligns the cross hairs of the transit reticle with the water line of the surfacing whale, and takes both vertical readings for range and horizontal readings for azimuth. The distance from the transit station to the whale equals the altitude of the transit above sea level times the tangent of the vertical bearing plus a correction for the curvature of the earth. A correction for refraction of light was found to be unnecessary. Our Lietz TM-1A transit was accurate in parallax to 10'' of arc, measured by repeated readings of a buoy 2.25 km from

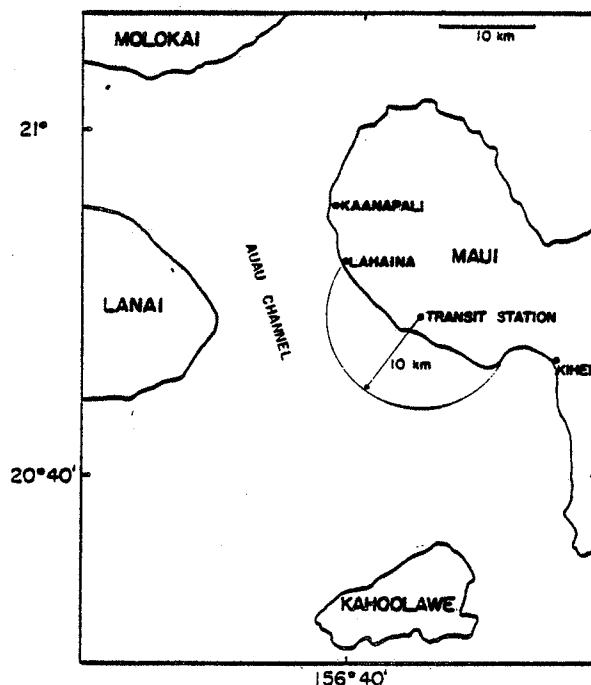


Fig. 1. Map of the study area off the shore of Maui, Hawaii. Shore-based observations of humpback whales were made from a surveyor's mark, named Kilea, on a hill 80 m above sea level. Whales could be sighted from as far away as the coast of Lanai, but few singing humpbacks were first sighted further than 10 km from Kilea.

the transit site. There were negligible errors in azimuth measured clockwise from true north. The horizontal zero of the transit was repeatedly checked throughout each day, and was reset if it was off by more than 3'' of arc.

A major source of error in range was uncertainty in measurements of the altitude of the transit above sea level. Since the amplitude of the tide off the west coast of Maui was less than 30 cm during most transiting periods, we calculated ranges on the basis of mean low tide. Other sources of error, such as ocean waves, indicate that our altitude estimates may be accurate only to  $\pm 50$  cm leading to uncertainties of range at 10 km of  $\pm 68$  m or approximately four whale lengths. The maximum error of measured distance between interacting whales will be much less than the error of range from the distant transit station. Fortunately the relative positions of interacting whales are the important points for interpreting behavior and these errors in relative position were always less than one whale length.

Operation of the transit station required a minimum of two people and was optimal with at least four. The transit operator aligned the transit, took transit readings, kept track of the location of most of the whales being followed at any one time, and communicated with the boats by radio. Another person took notes. With additional observers using binoculars, it was possible to follow many whales at a time, and to make up to six transit readings of separate whales in one minute. The transit bearings were converted into rectangular coordinates using an iterative correction for curvature of the earth developed by J. Wolitzky (Würsig 1978). The rectangular coordinates of selected whales were plotted using a computer plotter and these were traced to make the finished figures.

Observers in boats coordinated their observations by radio communications with the transit station to locate singers, to record

the songs, to identify individual whales, and to observe behavior not visible from the shore. Singers were monitored and recorded using Gould UT-19 or Aquadyne AQ-17 hydrophones, Barcus-Berry 1330 preamplifiers, and Nakamichi 550 cassette tape recorders. Singers could only be monitored while a boat was stopped, for the hydrophones had to be pulled up when a boat was underway.

Singers were found by nonsystematic search. Starting each day near the transit station, the boats would slowly cover the area near the station stopping every 10–20 min to listen for song. Usually within an hour observers in boats found a song loud enough to indicate that the singer was less than a kilometer away. They would then wait for a particular section of the song after which singers often surface (Winn and Winn 1978). As a singing whale surfaced, the loudness of the song would diminish, especially a few seconds before surfacing. While the singing whale was at the surface, the song remained faint, but when the whale would dive after the last of several surfacings, the song immediately became loud again. Observers in boats attempted to approach the whale whose surfacing correlated with the reduction in song intensity and resumed listening. If they were successful, song intensity was much higher after approach, often being audible through the hull of the boat. After following a whale through several surfacings and their correlated periods of faint song, the observers could be sure that they were following the singer. Nonsingers were rarely confused with the singer even on the first surfacing.

Variations in the pattern of pigmentation of the ventral side of the flukes and in the notches on the trailing edge of the flukes allow one to identify individual humpbacks with confidence (Kato et al. 1979). Whenever possible, photographs of the natural markings were taken and were later used to check how long a given whale had been followed. However, not all whales followed were identified, for whales do not show their flukes on every surfacing nor is it easy to maneuver to the right position for photographing flukes even when they are exposed.

## Results

### *Song Stops when Other Whales Join Singers*

As Winn and Winn (1978) have reported, singing humpbacks are usually alone. Out of 95 singing humpbacks, which we sighted in Hawaii from 1977 to 1979, 91 were alone, three were in pairs and one was in a trio. During the spring of 1977 in Hawaii, a fixed pattern was adopted of approaching every whale or group of whales seen, regardless of the size or behavior of the group. I would then listen with hydrophones to determine if any animal in the group was singing. Of the whales thus sighted 38% (49/129) were alone; 59% (29/49) of these lone whales were silent while 41% (20/49) of them were singing. No song was heard from the 25 pairs of adults sighted in this season nor from the 25 mothers and calves (with or without another accompanying adult). One of the 14 trios of adult whales sighted contained a singing whale, but none of the 16 groups of more than four whales contained a singer. Two singing humpbacks were never seen in the same group.

There was a clear temporal correlation between the time a singing humpback stopped singing and

**Table 1.** Summary of sightings of singing humpback whales in 1979. This table lists all occasions when a singing humpback was observed both from a boat and from the transit station and was observed closely enough that observers in boats knew when and if the singer stopped. The observed song duration is a minimum value, for we only found singers after they had started singing

No.	Date	Observed song duration (min)	Whale stops singing?	Another whale joins singer?	Latency of joining after singer stops (min)
1	7 February	178	yes	yes	8
2	8 February	164	no	no	—
3	12 February	33	yes	?	—
4	12 February	38	yes	no	—
5	14 February	67	yes	?	—
6	15 February	60	yes	?	—
7	16 February	33	yes	no	—
8	16 February	23	yes	yes	0
9	16 February	135	yes	no	—
10	16 February	6	yes	yes	0
11	17 February	20	yes	yes	28
12	17 February	55	yes	yes	0
13	17 February	76	yes	no	—
14	17 February	134	yes	no	—
15	20 February	58	no	no	—
16	22 February	58	yes	yes	21
17	23 February	33	yes	no	—
18	24 February	135	yes	yes	12
19	24 February	126	yes	yes	0
20	26 February	22	yes	yes	1
21	27 February	119	yes	no	—
22	27 February	24	yes	no	—
23	27 February	267	no	no	—
24	28 February	51	yes	no	—
25	1 March	287	yes	no	—
26	1 March	5	yes	yes	4
27	4 March	83	yes	?	—
28	5 March	118	no	no	—
29	5 March	422	no	no	—
30	6 March	172	no	no	—
31	6 March	88	no	no	—
32	7 March	23	yes	yes	2
33	7 March	198	yes	?	—
34	10 March	380	yes	yes	0
35	11 March	124	yes	yes	7

when a nonsinging whale joined the singer. Table 1 presents a summary of all cases from the 1979 season in which we followed a singer and in which it was clear whether a singer stopped singing, joined another whale, or both. We adopted the criterion that a whale joined a singer if both whales surfaced together, separated by less than a whale's length. We could not determine whether two such whales had come together before surfacing. There was a great variation in the duration of singing recorded from the boats (range = 5–420 min;  $\bar{x}$  = 107 min;  $n$  = 35). Our observations of seven whales out of 35 (20%) were ended before the whales stopped singing, because of a storm, nightfall, or because we pursued another singer. We were usually unable to follow a singer for long after it stopped

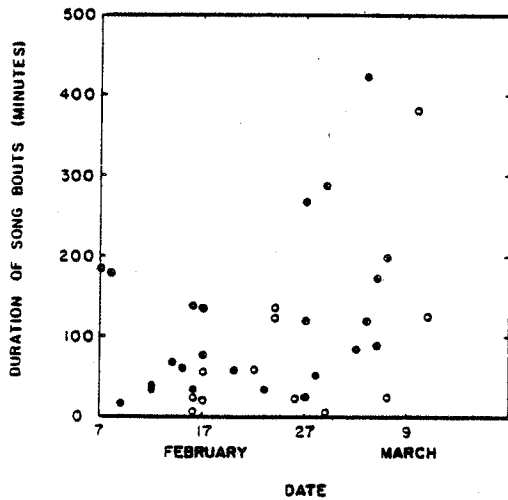


Fig. 2. Observed song durations on various dates in 1979: since we found singing humpbacks only after they had started singing, actual durations were longer. Pearson's  $r=0.38$ ,  $P<0.05$ . Open circles: song bouts that ended when the singer joined with another whale. Filled circles: singer not seen to join with another whale

0912	0926	1100-1300	1359	1511	1516	1520-1550
Singing adult Ⓐ sighted	Non-singing adult Ⓑ sighted	Ⓑ swims slowly away from Ⓐ	Ⓐ Stops singing, turns and races towards Ⓑ who is...	Found to be singing at 1511	Ⓑ stops singing	Ⓐ and Ⓑ swim rapidly NW side by side

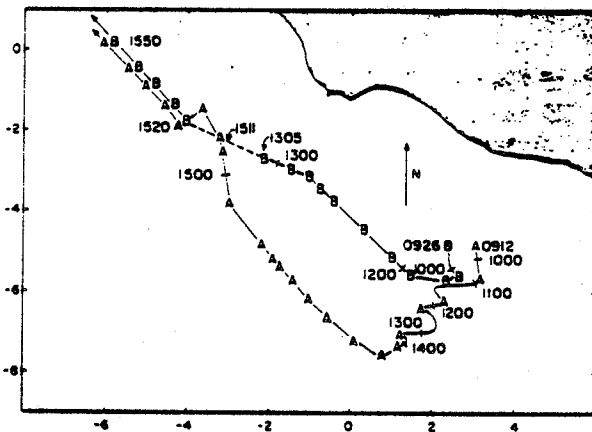


Fig. 3. An interaction between two humpback whales, each of which sang during different periods of the interaction (occurred on 1 March 1979). The numbers on the borders of the plot mark the distance to the transit station in km. For example, the 1520 surfacing of A and B together is 4 km west of the transit station and 2 km south of it. The plots presented in this paper are simplified from more detailed data

singing, but distinctive natural markings sometimes made this possible. Thirteen of the 28 singers that stopped singing while under observation, joined with another whale within 30 min of stopping (range=0-28 min;  $\bar{x}=6.4$  min). No singer joined with another whale without ceasing to sing. Five of the 13 singers

that joined stopped singing and surfaced with another whale at the same time. The intervals between stopping and joining are maximum values, because the time of joining could only be scored as the time when the singer and joiner surfaced together.

#### Seasonal Changes in the Duration of Song Bouts

The data presented in Fig. 2 suggest that song bouts become longer in duration over one segment of the singing season. In fact, the correlation between date and song duration is 0.38 ( $P<0.05$ ). This correlation is apt to be an underestimate of the magnitude of the effect, since the starting time of the sessions is unknown (we found singers only after they had started singing).

There was also a clear change during our observation period of the frequency with which other whales join with singers. Five of the singers that we followed from 7 February 1978 to 11 March 1978 cannot be used to study the frequency of joining because we were not sure whether they joined other whales or not. The first 15 of the remaining 30 singers (observed from 7 February 1978 to 24 February 1978) joined seven times in 18.15 h of observation, yielding a joining rate of 0.386 times/h. During the last 15 of these 30 interactions (from 24 February 1978 to 11 March 1978), a singer joined six times in 37.07 h of observation, yielding a joining rate of 0.162 times/h. The probability that another whale would join a singer in the first half of our observation period was twice as great as that in the second half. The correlation between date and the duration of the 13 song bouts that were ended by joining is 0.31 ( $P<0.10$ ), almost equal to the correlation for all song bouts.

#### Interchange of the Roles of Singing and Joining

An interaction that occurred over a 6.5-h period on 1 March 1979 will be discussed in detail to demonstrate how the boats and transit station worked together (Fig. 3). During this interaction, a whale changed role from singer to joiner. Shortly before 0912, observers in the boats sighted and identified a singing humpback called whale A and the transit station took a bearing of this whale. At 0926, a non-singing whale, B, was sighted near the singer. Both whales moved along a parallel course for over an hour. Between the 1019 and 1037 surfacings, whale B slowed down and turned towards the singer A. Between its surfacings at 1047 and 1110, the singer A turned towards B, and at 1111 the whales were separated by only 150 m. By 1145 both whales had moved off to the west but by 1200 A had turned to the south while B had established a course to the

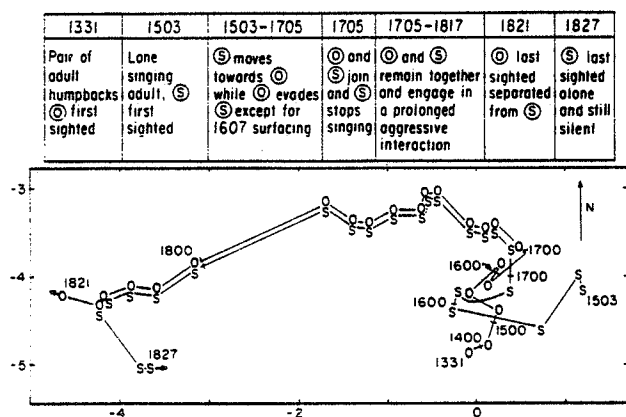


Fig. 4. An interaction from 24 February 1979 involving aggressive behavior after a lone singing humpback joined a pair of adult humpbacks (symbols as in Fig. 3)

northwest. B moved off steadily to the northwest and was not followed by the transit station between 1305 and 1510. By 1215 the singer A was being followed by two boats, one to record its song and one to identify the singer and any whales nearby. The singer slowly moved southwest until 1410 when it stopped singing, several hundred meters from a lone adult, which was spotted by observers in both boats but not transited. The ex-singer A then abruptly changed course and swam rapidly northwest on a course that paralleled the earlier passage of B. While moving northwest, A was identified several times from the boat following it. At 1507 the boat following A stopped to listen for song. Observers on the boat heard very loud song indicating a singer close by, but when A surfaced near the boat the intensity of the song did not attenuate, indicating that A was not the singer. Several minutes later, a different whale surfaced to the west of both A and the boat. Attenuation of the song did correlate with this surfacing. At 1516 the song stopped and the two whales surfaced, separated by 100 m and converging. By 1520 the two whales had joined and were transited together. The pair then moved off to the northwest followed by the boat, which was able to identify both whales. Fluke identification photographs indicated that one of the whales was indeed the original singer A and the other whale, which was singing at 1507, turned out to be B, the whale which had nearly joined A while it was singing in the morning.

On another occasion (16 February 1979) a whale that joined with a singer started to sing after separating from the singer. The original singer, which had stopped singing as soon as it was joined, moved rapid-

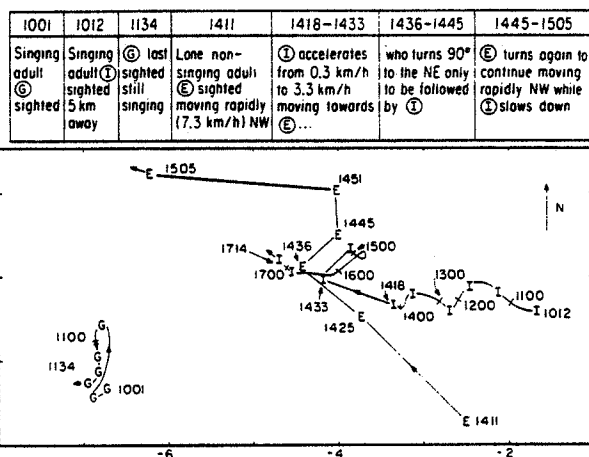


Fig. 5. An interaction from 5 March 1979 in which a singer pursued a nonsinging whale that evaded the singer. This plot also depicts the movements of two singers that were followed simultaneously (symbols as in Fig 3)

ly away from the joiner. The joiner remained near the location where it had joined with the singer and started to sing. In this case, it appears that the joiner displaced the original singer.

#### *Pursuit of Nonsinging Whales by Singers*

In most of the interactions accompanied by joining, singing humpbacks turned towards other whales. Nonsinging whales often moved away from singers in these interactions. For example, during the first 2 h of an interaction between a singer, S, and a nonsinging pair, 0 (Fig. 4), 0 turned away from S in all but one surfacing from the time S was sighted (1503) to when 0 and S joined (1705), while S turned toward 0 during every surfacing. The rest of the interaction, which took place after 0 and S joined, is described in later section 'Agonistic Encounters'.

Furthermore, in several interactions a singer appeared to pursue a whale that was successful in avoiding the singer. The interaction between I and E on 7 March 1979 provides a good example (Fig. 5). While a singing whale I was followed for 7 h, there was only one obvious interaction between I and another whale, a nonsinging lone adult, E. E was first sighted at 1411 during a period when whale I was moving very slowly, 100 m in 19 min. E on the other hand was moving rapidly (3.5 km/h), for between 1411 and 1425 it moved 1.7 km. At its 1425 surfacing, E had moved to within 400 m of the 1418 surfacing of I. Singer I then accelerated to match E's velocity. By the next surfacing of I at 1433 and of E at 1436, the gap between the two had closed to 260 m. Both whales

0918	0919	0919 1220	1208	1217	1219	1225	1230 - 1347
Mother and calf sighted	Singing adult sighted	⊙ remains in 1 km <sup>2</sup> moving slowly	Lone non-singing adult first sighted moving towards	⊙ stops singing	⊙ and ⊙ join and one whale flippers several times	One whale breaches and the other belly flippers for ~ 5 mins.	⊙ and ⊙ swim off rapidly side by side

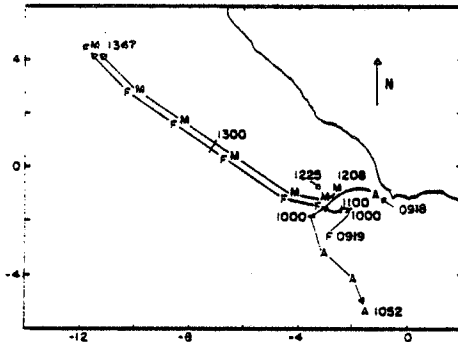


Fig. 6. An interaction from 7 February 1979 in which one whale joins a singer (symbols as in Fig. 3)

then made a right-angle turn after which whale I surfaced even closer to E, but E then turned back to its original course and moved over 2 km in 20 min, a very rapid pace for a humpback. The singer, I, did not follow at this point but slowed down dramatically, moving 300 m in the next 35 min. It is clear that singer I was pursuing nonsinger E during this interaction.

In several cases when a nonsinging humpback approached a singer, they joined so quickly that we could not detect the approach of the nonsinger even when the singer was stationary. For example, a nonsinger, M, whose movements are plotted in Fig. 6 was only transited once before it joined a stationary singer F. These events took place so close to the transit station that any surfacing of a whale within 2 km of F should have been sighted, so M must have moved rapidly towards F from a considerable distance. The movements of a mother and calf A, which appeared to avoid the singer, were much more thoroughly documented even though no boat was following A.

Singers seldom turned away from a nonsinger nearby, and never repeatedly turned away as the nonsinger E did in the I-E interaction discussed above. This was one of the few consistent patterns in the interactions of singers and other whales and it contributes additional evidence that singers are motivated to join other humpbacks.

*Singing Humpbacks Are Not Strictly Territorial, but Seem to Avoid Other Singers*

Singing humpback whales differ from many other animals that sing in that individual singers do not seem to remain in particular areas during the breeding

season. Individually identified singers were never sighted in the same place on different days. The few identified singers that were resighted were seen in locations tens of kilometers apart, a distance much greater than the average separation of neighboring singers. Furthermore, on most days during the 1979 observation period, a singing humpback was sighted within 5 km of the location of a different singer followed the day before. In fact, most of the whales sighted off Maui seem to be moving through, for the number of individual whales resighted within a season is remarkably low (Darling, personal communication).

Surveys of humpbacks in Hawaii (Shallenberger 1976; Herman and Antinaja 1977) indicate that there are dense clusters of whales in the Auau Channel off Maui and in the Penguin Banks off Molokai. However, within the Auau Channel, singing humpbacks seem to avoid each other and may be spacing themselves evenly. We have never observed a singing humpback to join another singing humpback while both are still singing. In the course of three seasons of acoustic recording off Maui, it became apparent to us that singing humpbacks seldom were separated by less than 5 km and seemed to be evenly spaced. When we stopped recording a singing humpback we usually had to move 5-10 km before finding another. At this distance, song is probably the only cue available to a singing humpback about the position of other singers nearby. Thus, humpback song probably functions to maintain between singers if singers are evenly distributed.

On two occasions during our 1979 study period, we were able to follow two singers simultaneously, providing the first precise data on the spacing of singing humpbacks. On 27 February 1979, a first singer, D, was sighted at 0855. The second singer, L, was sighted approximately 6 km away at 0938, and both whales were moving away from each other. The largest separation, 10 km, occurred when D stopped singing at 1131. The second example occurred on 5 March 1979 (Fig. 5). While singer G was followed, singer I was slowly moving in its direction at a distance of 5.2 to 4.8 km. At 1123 the boat that had been monitoring singer G left to attempt to identify whales near the other singer, I. The importance of using boats to follow whales, particularly at this range of almost 8 km from the transit station, is apparent in this case, for G was lost after only one more surfacing at 1134.

*Interactions Involving Behavior Associated with Sexual Activity*

Details of the interactions between singers and the whales that joined with them were difficult to ob-

serve and interpret. Several patterns of behavior did recur, however, and one of these patterns has been associated with courtship and mating in several species of baleen whale, as will be discussed later. The kinds of behavior tentatively associated with courtship or mating are flippering, belly flippering, head-up, and rolling, whose manifestations visible above water include flipper extension and vertical flukes. A whale flippers when it raises one flipper (pectoral limb) out of the water and then slaps the water with the flipper. A whale that is belly flippering, lies ventral side up and slaps the water with both flippers, alternating one flipper then the other. A head-up occurs when a whale, lying horizontal to the water surface, raises the dorsal part of its head out of the water, then sinks back down into the water without forward motion. Flipper extension occurs when one of the flippers of a whale appears above the water but does not slap the water surface. The behavior called vertical flukes occurs when the flukes of a whale are extended out of the water vertically rather than with the usual horizontal orientation.

The only interaction that we observed between a singer and a cow and calf unaccompanied by another adult belong to this set, as do five interactions between a singer and an adult of undetermined sex observed in previous years. In 1979, only one interaction fitted the patterns of the five similar interactions observed in 1977 and 1978 (Fig. 6). This occurred on 7 February 1979 between two whales of unknown sex, a singer, F, and a lone nonsinging adult, M. F was first sighted at 0919 and was identified with ease since it spent the next 3 h within approximately 1 km<sup>2</sup>. F stopped singing at 1217 and surfaced with M at 1219, at which time one of the whales flippered several times. At 1225 one of the whales breached and the other one belly flippered for approximately 5 min. The two whales then moved rapidly off to the northwest surfacing simultaneously within a whale's length of each other.

On 24 February 1979 we observed a singer join a mother and calf unaccompanied by another adult (Fig. 7). Observers in the boats were unable to identify any whales on this day, so that the only evidence supporting the connections between surfacings are the movement patterns themselves. However, these were convincing to both boat and shore observers. The large number of boats present on this day may have affected the behavior of the whales. Singer F joined the mother and calf, H, sometime after 1220 and before being sighted at 1234. At the time when the two groups joined, one of the whales performed a half breach - a motion like a breach except that only half of the body emerges from the water. At 1238 one of these three whales rolled 90°, showing vertical

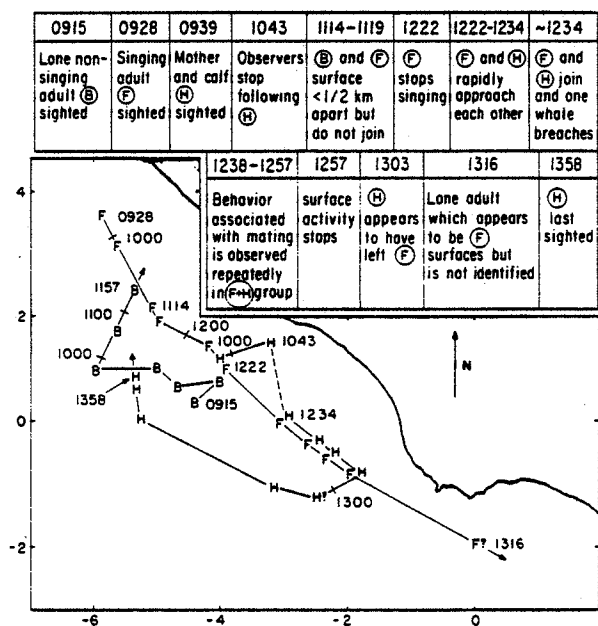


Fig. 7. Plot of an interaction from 24 February 1979 in which behavior associated with sexual activity was seen after a female humpback with a calf joined a singing humpback (symbols as in Fig. 3)

flukes, while at 1245 one of the whales flippered several times. From 1248 to 1252, we observed vertical flukes eight times in this group. At 1252 either a flipper or a vertical fluke was observed above the water but it did not slap the water in the normal flippering movement. At 1253 two vertical flukes and a head-up were seen and observers at the transit station noted that the water around the group appeared to be boiling with activity. At 1254 the calf performed a tail lob and at 1255 we observed a flipper out of the water followed by vertical flukes at 1256. This activity stopped at 1257. By 1303 we thought the mother and calf, H, might have split off from the ex-singer, F. At 1316 a lone whale was sighted 3.4 km from the mother and calf, H. This whale could have been the ex-singer F, but we were neither able to identify it nor to be sure if any other whales were with the mother and calf, H, after 1303 because the whales in H were not surfacing simultaneously.

#### Agonistic Encounters

The types of behavior visible above the water surface that we have found to occur specifically in agonistic interactions are rear body thrashes and horizontal tail lashes. A rear body thrash occurs when a whale powerfully throws the rear third of its body out of the water, then slams it sideways and downwards against the water surface. A horizontal tail lash occurs when a whale lashes its flukes sideways through the

water. Lobtailing also frequently occurs during agonistic interactions although it may also occur in other contexts as well. A whale lobs tails when it lifts its flukes out of the water and then slaps the water surface with the broad side of its flukes. Lobtailing differs from rear body thrashing in that there is no sideways motion of the flukes. One of the few ways by which a baleen whale can damage an opponent is by lashing out with the flukes. The horizontal tail lash, rear body trash, and tail lob are all powerful fluke movements, and all three have not only been seen in interactions between conspecifics, but are also responses of baleen whales towards predators.

The most dramatic agonistic encounter we observed occurred on 24 February 1979 (Fig. 4). At 1331 two whales, 01 and 02, or together, group 0, were sighted by the transit station moving northwest very slowly. At 1503 a lone singer, S, was sighted and identified little more than 1 km from the pair 0. For the next 2 h, the singer repeatedly approached the pair 0. During this time, the pair moved away from the singer at every surfacing with one exception between 1552 and 1608. Sometime between 1659 and 1705, 0 and S finally joined and S stopped singing. Before the joining, all surfacings of all three whales consisted of quiet blows but at 1708, during the first surfacing of all three whales, a violent rear body trash was performed by one of them.

For the next hour all three whales remained close together. During this period, was observed 25 tail lobs, 13 rear body thrashes, and 9 vertical flukes. Three examples of breaching and head-ups, two examples of belly flipping, and one flipping motion, spy hop, and horizontal tail lash were also observed. The spy hop motion occurs when a whale lifts its head vertically out of the water at least to the level of its eyes. In all cases when observers in boats could identify the thrasher or lob tailer, it was 01. Several of the rear body thrashes appeared to be directed towards the ex-singer, but often we were unable to determine the location of the other whales while one whale was thrashing. During this interaction, we also observed one of the two examples of horizontal tail lashing seen during the entire season. The interaction was the most prolonged aggressive interaction I have ever observed in whales, and included many more performances of aggressive behavior than the interactions we have seen between killer whales, *Orcinus orca*, and either humpbacks or southern right whales, *Eubalaena australis*. Even more striking was the sudden cessation of agonistic behavior when the ex-singer left this group at 1817.

Aggressive behavior predominated during this interaction, but some behavior associated with sexual activity was also observed. This combination is simi-

lar to that observed whenever more than one adult is escorting a cow and calf. The 14 escorting adults that have been sexed have been male (D. Glockner, personal communication). We have several times observed singing humpbacks to join a cow, calf, and escort, after which this combination of behavior has been observed. In all of these interactions, most of the aggressive behavior occurs between escorts. J. Darling (personal communication) has observed escorts underwater and has seen them to beat each other with their flukes. In one such case, the first escort left the group, while the joiner remained as the only escort of the cow and calf. The interaction plotted in Fig. 4 is a slightly atypical example of these interactions because no calf was present, the level of aggressive behavior visible above water was as high as we have seen, and the speed of the whales was lower than is often seen in these groups (we have observed such groups moving faster than 12 km/h). However, since many of the rear body thrashes were directed by 01 towards the ex-singer S, I am tempted to conjecture that S intruded upon a male-female pair and that 01 was the male.

## Discussion

### *Comparison to Earlier Studies*

Winn and Winn (1978) found that all but three of more than 100 lone humpbacks observed in the Caribbean were singing and they concluded that almost all lone humpbacks are singing. This stands in marked contrast to my finding that over half of the lone whales that I approached in 1977 were silent. While differences in the size or behavior of groups of whales may have affected the likelihood of my sighting them, I believe that I was equally likely to sight lone whales whether singing or silent. On the other hand Winn and Winn used a passive directional sonar to find singing humpbacks and obviously were much more likely to encounter singing humpbacks than silent ones.

Winn and Winn (1978) state that humpback whales sing 24 h a day for several months while on the tropical breeding grounds in the Caribbean. This is very different from our finding that 80% of the whales we followed stopped singing. This discrepancy between the Winns' data and those reported in this paper may result from variation in the rate at which whales join singers, since whales stop singing when joined by another whale. Seasonal or geographic variation in the duration of song bouts may also occur independent of changes in the rate of joining. In only a few cases may the discrepancy result from the fact that singers sometimes stop when approached by a



boat, as noted by Payne and McVay (1971) and Winn and Winn (1978).

#### *Does Singing Facilitate Joining?*

While the abilities of baleen whales to locate sound sources have not been studied, humpbacks can almost certainly locate singing humpbacks over much greater distances than silent ones. The proposition that song in humpbacks facilitates joining, at least by advertising location, is supported by the fact that many of the singers that we followed joined with another whale, while only a few nonsinging whales were seen to join with other nonsinging whales. However, it was difficult to follow the silent lone adults, which were most likely to join with a singer, much less determine exactly when they joined other whales. Because of this difficulty, we were unable to determine the probability that lone nonsinging adults would join with other nonsinging whales. Furthermore, a statistical association between singing and joining would suggest but not prove that singing facilitates joining. The nonsinging whales that we followed were more likely to avoid singers than to approach them, while singers never moved away from nearby whales. Thus singing may inhibit joining with some classes of whales. Even if there is an association between singing and joining, this may be due to an increased motivation to join on the singer's part rather than an increased tendency for nonsinging whales to approach singers. Playback experiments would provide an important test for causation.

#### *Song Bouts Are Shortest During What Appears to Be the Peak of Ovulation*

One interpretation of the increase in the length of observed song bouts as the season progressed is that the motivation for singing increased during our observation period. For example, in songbirds both the frequency and duration of song bouts increases with the concentration of testosterone in circulation (Eisner 1960). The duration of song bouts is thus linked to the annual reproductive cycle in songbirds by a direct physiological mechanism. Mature male humpbacks have larger testes and spermatogenesis occurs at a higher rate during the winter breeding season than during the summer feeding season. However, there are no systematic changes in testis weight or rate of spermatogenesis during the breeding season (Chittleborough 1955). Male humpbacks are thus probably capable of sexual activity throughout the breeding season, but there is little indication of variation in the reproductive state of males throughout the breeding season.

Since other whales can stop singers by joining them, the duration of song bouts is not due to the motiva-

tional state of the singer alone, but is also affected by the behavior of other whales. The probability of a singer being stopped by joining might simply be a function of the number of whales nearby. However, this does not appear to be the case, since we found singers joining and stopping more rapidly in the first half of the period when fewer whales are present off Maui (Shallenberger 1976; Herman and Antinoya 1977).

The observed increase in song bout duration occurred during that phase of the breeding season when a decline in the frequency of ovulation has been reported for female humpbacks from other areas. Nishiwaki (1959, 1960, 1962), who studied ovaries from female humpbacks taken in the Ryukyuan Islands in the North Pacific (25°–30° N latitude), states that the peak of ovulation occurs after the beginning of January and before the end of February. Chittleborough (1954) studied the ovaries of female humpbacks caught off Western Australia (25°–35° S latitude) and found a sharp peak in the number of females with ruptured follicles indicating recent ovulation in late July and early August. This season corresponds to late January and early February in the northern hemisphere, the same time as the peak of ovulation reported by Nishiwaki. Chittleborough does report that even though there was a marked peak in ovulation, he found female humpbacks ovulating throughout the breeding season. Female humpbacks often ovulated for a second or even third time in one season if conception did not take place after the first ovulation. If the songs are indeed an important part of the mating system of humpbacks, then one might expect the largest number of interactions between singers and other whales to occur at the peak of ovulation. The duration of song bouts should be shortest when the rate of those interactions in which a singer stops (e.g., joining) is highest. Thus the observation that song sessions are shortest during the probable ovulatory peak, when the largest number of receptive females are present, supports the hypothesis that singing behavior is related to reproductive behavior in humpbacks.

#### *Behavior Associated with Sexual Activity*

The interpretation of the interactions described in Results under 'Interactions Involving Behaviour Associated with Sexual Activity' relies on the association of four types of behavior – rolling, belly flipping, flipping, and the head-up – with courtship or mating in humpbacks. Most reports of mating in baleen whales provide evidence to support this association, but few of these reports can prove that the behavior observed was indeed mating. Moreover, these reports are only anecdotal and do not address

such important questions as how often whales perform these types of behavior when not involved in sexual activity.

Mating groups of baleen whales can be positively identified only if intromission is clearly observed. Intromission has been seen and photographed in mating groups of right whales (Payne 1976, p. 332) and gray whales (Samaras 1974), but interpreting possible humpback reproductive behavior is difficult since mating has never been directly observed in these whales. Sexually active groups of baleen whales can be identified if they are seen to contain males with erect penises. Not all sexually active groups of whales are mating groups, for sexually active groups composed exclusively of male gray whales (Newman 1976) or male right whales (Payne, personal communication) have been reported. Rolling, belly flipping and flippering have been associated with mating in gray and right whales, and are also reported to occur during what has been interpreted as mating in humpbacks (Scammon 1874; Nishiwaki and Hayashi 1950; Dawbin 1956). However, these behaviors are performed by lone animals and during the feeding season (personal observation), when the rate of ovulation is very low. Thus, even if they are associated with sexual activity, they are not reliable indicators of mating.

Both Donnelly (1967, 1969) and Saayman and Tayler (1973) have reported that rolling, belly flipping, flippering and head-ups accompany mating in southern right whales, *Eubalaena australis*. Although both reports describe sexual activity, none of these investigators observed intromission in the whales reported to be mating. Roger Payne (1976, personal communication) finds intromission in mating groups of right whales associated with all four types of behavior. Gray whales are the only other species of baleen whale whose mating behavior has been well described by several authors. Reports by Houck (1962), Samaras (1974), and Sauer (1963) provide evidence that rolling, belly flipping, flippering, and head-ups are associated with sexual activity and mating in this baleen whale as well.

The only humpbacks that interacted with singers and whose sex we were able to determine were females sighted with their young calves. Most humpback females do not ovulate while lactating but wait for one year after giving birth until their calf is weaned before again becoming pregnant. Why then do we observe behavior associated with mating in humpback females with calves? The answer may lie in the fact that postpartum ovulation is not uncommon among humpback females. Chittleborough (1958) reports that 8.5% of the sexually mature female humpbacks that he examined were both pregnant and lactating and thus must have mated soon after giving birth.

### *Aggressive Behavior*

As mentioned earlier, J. Darling (personal communication) on several occasions during 1979 in Hawaii observed a humpback whale striking a conspecific with its flukes. The killer whale, *Orcinus orca*, is seen to attack baleen whales, and whales have been reported to strike this predator with their flukes. Chittleborough (1953) reports that a humpback struck attacking killer whales with its flukes. Right whales have also been seen horizontal tail lashing, rear body thrashing, and tail lobbing at killer whales (Donnelly 1967; Payne and Tyack, unpublished data).

Both humpbacks and right whales perform rear body thrashes and horizontal tail lashes towards animals or objects that are too far away from the whale to be struck. In this context, the behavior appears to be a threat. In several cases I observed in Argentina, approaching killer whales turned away from a group of right whales after one right whale performed a horizontal tail lash at least 5 m away from the nearest killer whale. When observers in boats approached right whales, particularly mothers and calves, R. Payne (personal communication) has observed that one whale in the group would frequently perform a gentle slow horizontal tail lash several times before performing the typical more violent tail slash motion.

Aggressive behavior was most commonly seen in groups of whales in which more than one adult was escorting a cow and calf. Most of the aggression occurs between escorts (which appear to be males, D. Glockner, personal communication). Since more than one escort seldom remains with a cow and calf for long, these escorts appear to be competing for the escort position. This conclusion is strengthened by the observation of displacement of escorts (J. Darling, personal communication). It seems likely that males can increase their chance of mating with a cow by becoming an escort, and presumably this is the focus of the competition.

### *Why is Humpback Song so Complex?*

The song of the humpback whale has been described as "the most elaborate single display known in any animal species" (Wilson 1975). The fact that distance-maintaining signals tend to be elaborate (Marler 1965) may be one reason for such complexity. Might other functions of the song also have spurred the development of such a remarkably complex signal? Several possibilities can be ruled out. For example, the complexity of humpback song cannot be due to the possible function of the song as a reproductive isolating mechanism, because humpbacks are the only cetacean known to sing. Nor is it likely that every variation in humpback song reflects a variation in what the

song communicates to other whales. The song of each population changes gradually throughout each breeding season, but at any one time most of the singing whales sing very similar songs. At the beginning of each new breeding season, humpback songs resemble those sung at the end of the previous season, and they continue the process of gradual song change (Payne, Tyack, and Payne, unpublished data). This process of change is rapid enough that songs recorded a decade apart from the same area seldom share any common elements. Once a particular song phrase was lost from the song, it never recurred over a 22-year sample of songs from Bermuda (Payne and Payne, personal communication). It is thus unlikely that humpback song is made up of many individual sounds each of which qualifies as a signal in its own right, for each sound is gradually modified into a completely different form or disappears from the song. It is only the rules of song structure that do not drift, implying that the song itself is the functional unit of this complex string of sounds.

The complexity of humpback song might have arisen through a process of sexual selection. Kroodsmma (1976) demonstrated that reproductive behavior in female canaries is stimulated more by large song repertoires (a complex song environment) than by small song repertoires (a simple song environment), although his findings might result from specific effects of the particular songs chosen as stimuli. If singers are indeed male, and if female humpbacks choose to mate with those male humpbacks that sing the most complex songs, then a powerful process of sexual selection is established. We may very well have to thank the choices of female humpbacks for the beautiful complexity of this strange song.

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