

Best wishes

Peter Tyack

MALE COMPETITION IN LARGE GROUPS OF WINTERING HUMPBACK WHALES

by

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(With 7 Figures)
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Introduction

In all oceans, humpback whales, *Megaptera novaeangliae*, make seasonal migrations of several thousand kilometres (DAWBIN, 1966). The exact routes taken by individuals are not known, but the end points are frequently marked by areas of remarkably high seasonal humpback density. In summer the whales feed in low Arctic and Boreal waters on fish and plankton where the densities and movements of the whales are clearly related to the distributions of their prey (WHITEHEAD et al., 1980). However the most striking concentrations of humpbacks are found on banks or near islands in the tropics where most of the whales winter, but there is no equally obvious cause for these concentrations: little food is

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available, and humpbacks feed very rarely in winter. Not only do humpbacks congregate during the winter but a conspicuous part of these concentrations are very active fast moving groups of three to more than fifteen adults. Previous speculations as to the functions of these groups have included feeding, mating and migration. This paper presents the results of our observations of these groups.

It is in winter that the males have enlarged testes, the females ovulate (CHITTLEBOROUGH, 1955, 1958, 1965), and mating presumably occurs, although we know of no reports of observed copulation. The gestation period is about one year and only one calf is produced at a time. Most births take place in January to March in the Northern hemisphere, which must also be the peak months for mating. Although post-partum oestrus sometimes occurs, most females fail to conceive until the following year, and therefore produce one calf every two years (CHITTLEBOROUGH, 1958). Calves suckle for approximately ten months (CHITTLEBOROUGH, 1965). Throughout lactation, but especially in the first few weeks after birth, the mother-calf bond is very tight: they are rarely separated by more than ten metres (Fig. 2) and another humpback is almost never seen between them.

Humpback song can almost always be heard in those areas where humpbacks congregate in winter, for example near the West Indies in the Western North Atlantic, and off Hawaii in the North Pacific. Humpback song has also been heard in open ocean and off Bermuda while humpbacks are migrating. The songs, whose structure was analysed by PAYNE & McVAY (1971), are a complex series of vocalizations performed by one animal covering a wide frequency range and cycling with a period of 6-25 minutes. Those singing whales for which sex has been determined have been males (WINN, 1973; HUDNALL, 1976; GLOCKNER, pers. comm.). Studies by one of us (TYACK, 1981) off Maui during the winter of 1979 showed that the songs are sung almost invariably by lone humpbacks, which stop singing when they join other whales. These interactions strongly suggested that the song acts as an advertisement display similar to that of songbirds. TYACK's (1981) conclusions have been reinforced by observations of singing whales during our two 1980 studies from which this paper is drawn, off Maui in the Hawaiian Islands (TYACK) and on Silver Bank in the West Indies (WHITEHEAD). The two study sites will be referred to as Hawaii and Silver Bank in the rest of this paper.

As our two studies used different methodologies we present the methods of each study separately, and draw on both in presenting the results and discussion of inter-male competition for females. The Silver

Bank study consisted of sessions in which single groups of whales were followed closely for several hours and during which most of the individuals in the group could be identified; it therefore provides the best information on group structure and stability. On the other hand, off Hawaii, several groups were monitored simultaneously, positions were accurately determined, and underwater observations were frequently made. Thus, the reaction of groups to one another and the nature of aggressive interactions within groups were much more clearly apparent.

Methods

The observations of Whitehead took place on Silver Bank (20° N., 70° W.) between 16 January and 5 April 1980. The research was carried out by a crew of four or five on board a ten metre ocean-going sloop. The Bank is very poorly charted so that we were only able to work at times of good visibility, when coral heads could be seen and avoided. This normally allowed a maximum of eight hours of whale-watching per day.

Groups of humpbacks were followed visually and, in the case of singers, acoustically from the boat for as long as possible in sessions called watches. In general the group nearest to the boat was selected for a watch, although we attempted to follow all different kinds of groups at different times through the study. The individual members of the group were identified as soon as possible by the shapes and marks of their dorsal fins or the patterns on their flukes (KATONA *et al.*, 1979). We attempted to keep the boat approximately 70 m from the whales, although ranges varied between five and 300 m. At each surfacing of the group we recorded its direction and speed of movement through the water, the relative positions and distances between members of the group, and any observed activities such as rolls, underwater bubblestreams or breaches (leaps from the water). The factors that caused us to halt the watch were no positive identification of the group for 30 minutes, confusion due to an overabundance of whales, bad light, bad weather, or lack of fuel.

The acoustic equipment consisted of a Gould hydrophone CH-17UT, Barcus-Berry standard preamplifier and Sony CD320 cassette tape recorder. During watches the hydrophone was lowered every half hour to ascertain whether the observed whales were singing. When we watched a group containing a singer, the hydrophone was continually monitored whenever the boat was not moving. Surfacing of the singer could generally be predicted by changes in the volume and tone of the song. There were a total of 90 watches totalling 235 hours, and averaging 156 minutes per watch.

Humpback whales were observed by TYACK and other members of a large research team off the leeward coast of Maui, Hawaii near the town of Lahaina. Humpbacks are seen in these waters from December to May and this study team covered most of each season in 1978-79, 1979-80 and 1980-81. Most of the results discussed here were obtained between 17 January 1980 and 9 April 1980. During this time, we coordinated observations of whales made from a station on land with those made by observers on boats, a technique which has been described in detail by TYACK (1981). Observers on a hilltop 80 m above sea level with an excellent view, were able to pinpoint the locations of surfacing whales using a surveyor's transit or theodolite (a Lietz TM-1A, accurate in our practice to less than five seconds of arc). They were able to follow many groups of whales at one time and could consistently follow individuals to more than ten km away.

Observers in boats (5.2 and 4.7 m Boston Whalers or 4.9 m Zodiac) followed one group of whales at a time. They identified individual whales by photographing distinctive natural markings on the flukes (KATONA *et al.*, 1979), stopped and listened regularly using

a hydrophone to hear whether any of the whales in the group were singing, and noted both the number of whales within each group and activities performed by members in the group. When conditions permitted, observers in boats watched whales underwater either by leaning over the side of the boat or by diving.

The bearings of whales measured by the transit were transformed into rectangular coordinates by computer. These coordinates were used to compute the velocities of different groups and to calculate the distances between two groups. The speeds of whales calculated in this way are not measures of the whales' speed through the water, because we did not correct for water currents. Since the bearings of two different groups could not be measured simultaneously, a process of linear interpolation was used to estimate the location of a group whose sightings flanked a sighting of the other group of interest.

Results

Structure of large groups.

Groups containing three or more adults frequently possessed a very definite structure. One animal could often be identified as a *Nuclear Animal (NA)*, by its centrality, its lack of obvious responses to the approach of another adult, and, when the speed and direction of movement of the group were fairly constant, its consistent proximity to another adult, called the *Principal Escort (PE)*. Although sometimes the *NA-PE* structure was readily apparent, on other occasions, particularly during short watches in bad weather, no *NA* or *PE* could be identified in a group of three or more adults. Table 1 catalogues the 22 watches on Silver Bank during which some elements of the *NA-PE* structure were observed. The watches averaged 271 min, during which there were three or more adults in the group for an average of 185 minutes. In 13 watches the full *NA-PE* structure was clearly recognized. It is quite possible that some groups containing three or more adults did not possess this structure, but such groups were relatively rare on Silver Bank.

Column 7 of Table 1, entitled "Centrality", shows that the *NA* was among the 50% of whales closest to the center of the group 73.8% of the time. As column 8 entitled "Closest Pair" shows, the *NA* was part of the most closely spaced pair in the group 91.2% of the time. *PEs* could be replaced but the *NA* never was. The *NA* was never part of the numerically smaller segment when the group split; in this sense it defined the group. Other adult members of the group were termed Secondary Escorts (*SEs*). *SEs* occasionally replaced *PEs*, or more often left the group. We will refer to groups which conformed to this pattern as having the *NA-PE* structure, which is illustrated in Fig. 1A.

This *NA-PE* structure was most easily identified when the group was moving slowly and steadily. The *NA* and *PE* usually stayed in the centre of the group, separated by about 3-8 m (Fig. 2), coordinating

movements. The *SEs* surrounding the *NA* and *PE* usually maintained individual stations (such as "to the right and in front of") relative to the central pair. They were usually scattered around the central pair at ranges of 5-15 m, showing some coordination with the central pair, and less with each other.

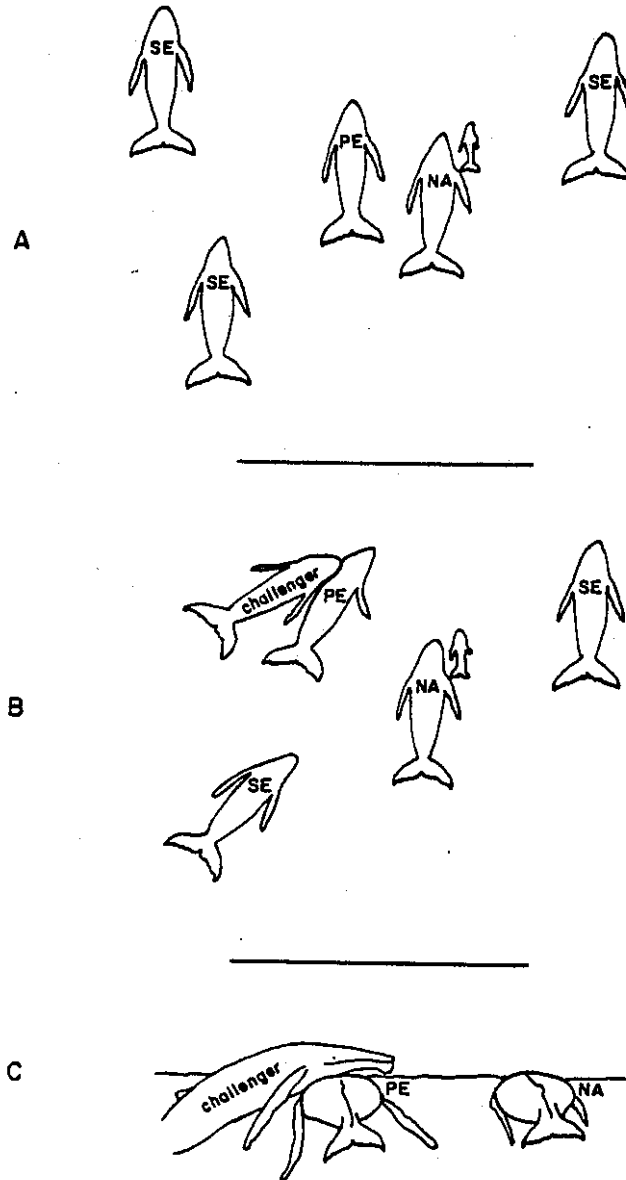


Fig. 1A) Structure of large groups: *NA* — Nuclear Animal, *PE* — Principal Escort, *SE* — Secondary Escort. 1B) Challenge in large group. 1C) Physical contact between Principal Escort and challenger.

If a calf was in a large group, then the mother was always the *NA*. Only twice was more than one calf observed in any group at one time. Once on Silver Bank, two calves were seen together during the apparently accidental merging of two groups which happened to be in the same place at the same time, but soon diverged. Once in Hawaii, two calves were seen in a group of seven whales that was stable for over an hour.

In Hawaii, some groups of more than three adults appeared to lack the *NA-PE* structure. Whales in these groups seemed to tolerate the approach of any other members of the group. Surfacing were much more relaxed in these groups, unlike the lunging surfacings seen in more active groups.

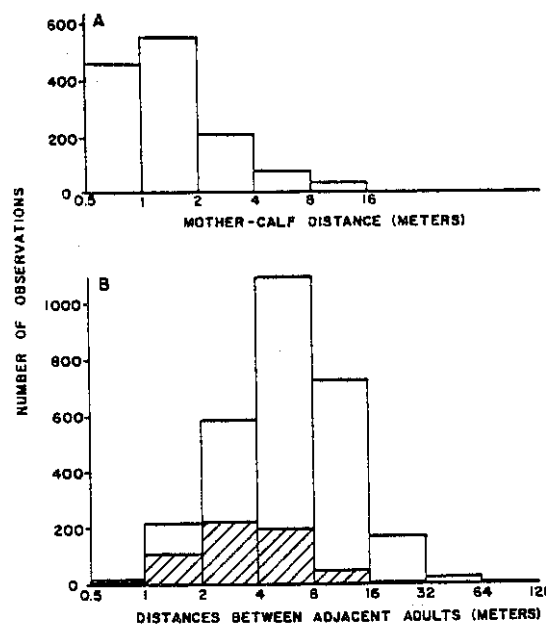


Fig. 2. Mother-calf distances, and distances between adjacent grouped adults on Silver Bank. Distances between Nuclear Animals and Principal Escorts are hatched. Distances estimated by eye during individual watches.

Furthermore, the very rapid rate of travel which characterizes large active groups did not occur. In general, levels of activity seemed to be proportional to group size. Groups of three or four whales had higher overall display rates than groups of one or two whales, but had much lower rates than groups of five or six whales.

During four of the earlier watches (nos 4, 20, 24, and 38) on Silver Bank there appeared to be two animals acting simultaneously as *PE*, flanking the *NA*, one on either side. They showed no aggression towards one another, but defended the *NA* from challenges by other escorts.

Competition between escorts.

The orderly arrangement of *SEs* around a central pair was sometimes punctuated by challenges directed towards the *NA* and fended off by the *PE*. In contrast to the *NA* which was notably nonresponsive to the approach of other whales, the *PE* deliberately and energetically interposed its body between the *NA* and any *SEs* approaching it. When defending its proximity in this way the *PE* and its challenger often engaged in a wild series of charges, sudden turns, stops, and lunges from the water for 0.5-10.0 minutes. Occasionally a challenger would manage to come between the *NA* and *PE*, and it then became the new *PE*. *SEs* joined or left the group from time to time, usually singly or in pairs. Usually only one *SE* would challenge a *PE* at a time. Several times in Hawaii, one of us (P.T.) observed that a *SE* starting a challenge would strike or fend off another *SE* if both were approaching the *PE*. This may have kept one *SE* from slipping into the *NA* while another *SE* was challenging the *PE*.

Table 1 notes the number of replacements of the *PE* during each watch on Silver Bank, as well as the approximate number of challenges for this position by *SEs*. In particularly large and active groups it was often impossible to tell where one challenge ended and another began — hence the uncertainty as to the number of challenges in Table 1. But the figures suggest that challenges to *PEs* were made approximately every 48 minutes and that about 9% of these were successful.

The object of the challenge appeared to be to come between the *NA* and *PE*. The methods employed in attempting to intervene included sudden increases in speed, turns, stops, dives and surfacings. The *PE* usually defended by paralleling every move of the challenger a few metres closer to the *NA*. The view from the surface was confused but the two animals could be seen turning, lunging (sometimes with jaws partially open) and diving side-by-side, as illustrated by Fig. 1B. Violent sideways thrashes of the tail were frequently made, often by whales swimming on their sides, perhaps as a result of trying to turn fast, perhaps as a threat or form of attack. TYACK (1981) has called these "tail thrashes" and "tail slashes", and he associates them with agonistic behaviour. In the Silver Bank study these thrashes are included in the category "side-flukes" which, together with lunges and bubblestreams, had striking and significant increases ($p < 0.01$) in the rates of performance with group size (above two animals) shown in Fig. 3.

On occasions when there was no all-out challenge, but when we felt tension existed within the group, the *PE* often blew a stream of bubbles

TABLE 1. Watches on Silver Bank during which elements of the Nuclear Animal-Principal Escort structure were recognized

Watch No.	Total time (min.)	Time with 3 or more adults	With calf?	Group size (No. of adults)	Certainty of Nuclear Animal?	Centrality	Closest pair?	Certainty of Principal Escort?	Challenges	Takeovers
4	359	344	No	3-1-3	Poor	17/18	20/20	(2)	0	0
11	213	213	Yes	4-3-4-3	Good	22/28	17/20	—	?	?
20	178	178	No	3-4-5-2	Poor	3/3	3/3	(2)	?	?
24	391	391	No	4-3-4-3-4	Good	49/52	45/46	(2)	2	0
26	72	40	No	1-3	Medium	1/1	—	Poor	?	?
34	474	3	Yes	2-3-2	Good	—	—	Good	1	1
38	170	147	No	3-2-3-2	Good	15/15	19/19	(2)	1	0
39	247	159	Yes	5-6-5-4-2	Good	11/21	26/27	Good	18	0
46	124	98	No	5-6-7-1	—	—	—	Medium	?	?
55	249	224	Yes	3-2-3	Good	3/17	9/14	Good	0	0
57	126	36	No	1-4-3-4	Good	1/3	1/2	Good	5	0
60	111	40	No	2-3-2-4-3-2	Poor	4/7	6/6	Poor	2	0
63	41	41	No	4-5	Good	7/11	9/10	Good	2	0
72	491	89	Yes	1-2-3-2-3-2-3 4-3-2-1-3-1-2	Good	3/6	8/8	Good	5	3
73	227	17	Yes	2-3-2	Good	—	—	Good	0	0
75	223	28	Yes	2-3-4-3-2-3-2	Good	0/7	2/7	Good	4	1
77	600	600	No	7-6-5-4-5-4 7-6-5-4-3-4	Good	63/99	89/92	Good	16	3
78	355	355	No	7-6-5-6-5-6-7 8-7-8-9-10-9 10-9-8-9-8-7-6	Good	80/92	68/76	Good	11	1
83	210	77	Yes	4-3-2	Good	0/4	0/4	Good	2	0
85	221	221	No	11-10-11-9 8-9-10	Poor	14/19	—	Medium	16	0
86	353	353	No	7-8-7-8-9-8 9-8-7-9-10-8	Good	22/24	—	Good	16	0
90	425	425	No	5-4-7-4-6 4-5-6-4	Good	65/93	81/88	Good	8	1

Column 6 gives the certainty with which the Nuclear Animal was recognized. Column 7, Centrality, gives the number of recorded instances when fewer than 50% of the other members of the group were closer to the center of the group than the Nuclear Animal: "a/b" means that of the "b" times on which such information was recorded, on "a" of them the Nuclear Animal was closer to the center of the group than more than 50% of the members of the group. Column 8, Closest pair?, similarly gives the proportion of recorded instances that the Nuclear Animal was part of the closest pair in the group. Column 9 gives the certainty with which the Principal Escort was recognized; "(2)" indicates that there were two animals simultaneously behaving like Principal Escorts. Column 10, Challenges, gives the approximate number of challenges on the Principal Escort, and Column 11, Takeovers, the number of changes of Principal Escort.

from a depth of roughly five m. These bubblestreams consisted of very roughly 30 bubbles in a 30 m horizontal line. They appeared to be placed as a screen between the *NA* and a potential or active challenger. As Fig. 3 demonstrates, bubblestreams were seldom observed in groups of less than three adults. We seldom observed bubblestreams in groups without elements of the *NA-PE* structure. Bubblestreams were the activity most characteristic of *PEs*, and most observed bubblestreams were produced

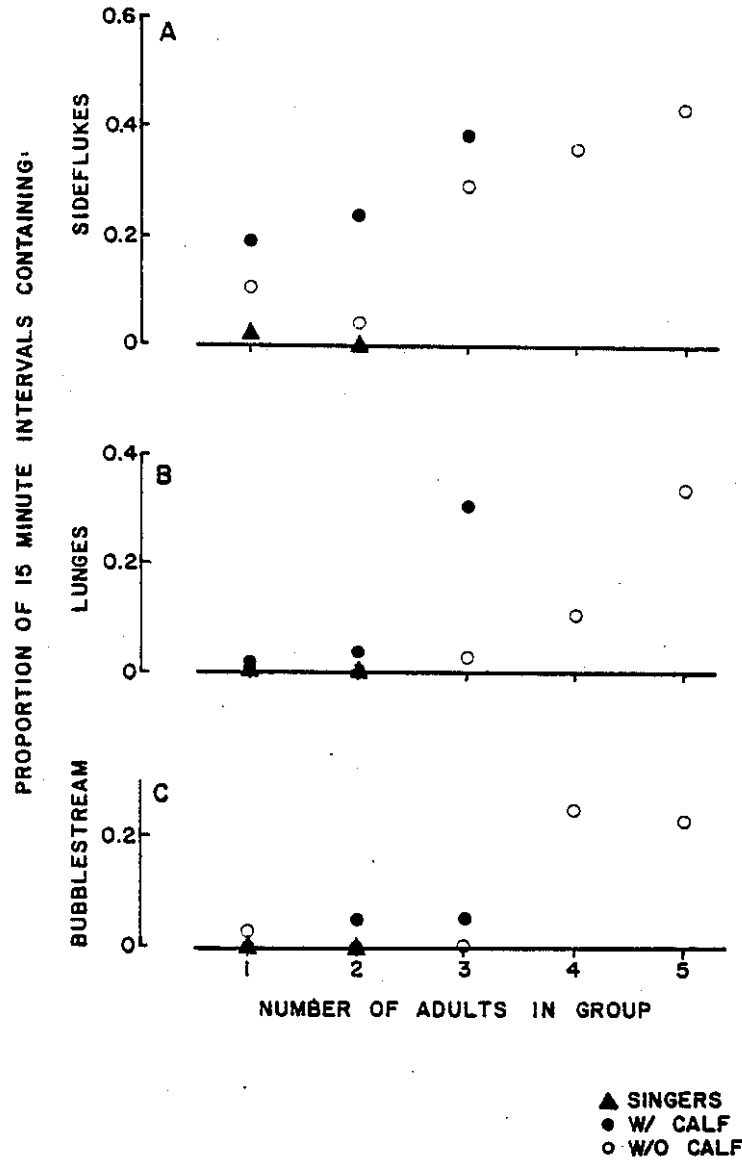


Fig. 3. Frequencies of sideflukes (A), lunges (B), and bubblestreams (C) with group size for singers (▲), groups with calves (●), groups without calves (○) on Silver Bank.

by them. On Silver Bank, we were able to tally which whales produced bubblestreams in groups with the *NA-PE* structure. Of 88 bubblestreams observed in these groups on Silver Bank, 55 (62%) were produced by *PEs*, 6 (7%) were produced by *SEs*, 1 (1%) was produced by a *NA*, and 26 (30%) were produced by whales of unknown status. For example, during watch no. 77 on Silver Bank which lasted ten hours and had at least four animals in the group for all of this time (the *NA* H_e , and three escorts H_f , H_w and H_c), 18 bubblestreams were observed. Two were blown by H_w and 13 by H_c , while for the other three the producer was unidentified. During the watch, H_w and H_c alternated as *PE*, replacing each other three times. The 15 bubblestreams were only blown from whichever of H_w or H_c was *PE* of the moment.

Several other displays were also common in large groups. Graeme ELLIS, a member of the research team in Hawaii, has made detailed observations of apparent displays, in which an escort in a large group lunged with its jaws open. These whales occasionally had distended pleats, which may have functioned to increase the apparent size of the escort (a suggestion made by Karen MILLER, another member of the research team in Hawaii). Humpbacks in large groups also frequently exhaled in a manner which produced a loud sound clearly audible to us both in air and underwater.

Both these open mouth displays and loud exhalations may have played a role in aggressive interactions but they were not as direct as other forms of aggression in which whales struck each other. Several times physical contact was observed between the competing escorts, usually when the challenger tried to swim over the *PE*, who rose underneath to "beach" the challenger, as shown in Fig. 1C. In addition, in Hawaii, several humpbacks have been observed to beat another one violently with their flukes. To our knowledge this behaviour was first seen by DARLING and SILBER in 1979 (DARLING *et al.*, in press) and subsequently observed by several members of the research team in Hawaii including one of us (PT). This behaviour has only been observed in groups of three or more whales which were moving fast and in which other types of aggressive behaviour were observed.

One of us (PT) observed one whale beating another on 20 February 1980 in a group of six to eight whales. This occurred when two *SEs* made a simultaneous rush from the periphery of the group towards the center. The lead whale of this pair was one to two m ahead, and both were moving rapidly, side by side, with powerful thrusts of the flukes. Three times in a row, the lead animal rotated its flukes as it was finishing a

downward stroke and slammed them against the tail stock of the following whale. This motion was very different from that used in normal locomotion. The rotation and lateral motion of the flukes were pronounced before impact and were strong enough that the flukes were parallel to the lateral surface of the tail stock of the attacked whale. The impact of the flukes sent waves along the tail stock of the following whale and produced a sharp slapping sound which was almost painfully loud. The lead whale then slid its flukes along the tail stock of the following whale, creating a loud rasping sound (intermediate between "shhh" and "sss") and scraping skin from the following whale. Both whales appeared to be slowed by this aggression and the lead whale accelerated after finishing the attack. This kind of attack may prevent more than one *SE* from challenging the *PE* at one time, but most attacks occur between a *PE* and a *SE*.

In Hawaii, we have been unable to watch these large groups underwater long enough to be able to estimate from direct observation how often one whale strikes another. But the sounds these whales make when they beat one another are loud and distinctive. If these rasping and slapping sounds are scored with caution from recordings made near large groups, they allow one to indirectly estimate the rate of beating.

We have no evidence that the peculiar rasping sound, produced when one whale forcefully slides its skin against another whale, occurs in any other context. But the slap which is produced upon impact sounds similar to that produced when a whale lifts its flukes or a flipper out of the water and slams it on the water surface. Sounds caused when a whale slaps the surface of the water should thus be disregarded in attempts to monitor impacts by listening. Rasp and slap sounds not correlated with slaps of the water surface have only been heard in large groups. Since these groups usually move rapidly and since we could only record underwater sounds while the boat was stationary, we seldom could record them for more than a few minutes at a time. But the groups occasionally slowed down and even circled in one area for up to 30 minutes. In recordings from two such groups in Hawaii, there were 20 rasping and slapping sounds produced when one whale hits another in 54 minutes, an average rate of 0.37 impacts/minute. However, these rates of impact may be atypical, for we were only able to record their sounds when the whales were circling and moving slowly.

There was undoubtedly more physical contact than we saw — perhaps much more, for in two watches (nos 85 and 86) of particularly active groups on Silver Bank, the dorsal fins and tubercles (bumps) on the heads

of the competing escorts were noticeably worn and bloody. Moreover in watch no. 86 the fins of some of the animals grew more ragged and bloody as the day wore on. We have made similar observations for many whales in large groups in Hawaii. In watch no. 85 on Silver Bank the *NA* was not certainly identified, but in no. 86 its body and fin were unmarked. In general, escorts had scratched and scarred dorsal fins, while *NAs*, with or without calves, had relatively smooth unmarked fins.

Single challenges on Silver Bank lasted from 30 seconds to over ten minutes, but the precise time was difficult to pinpoint in larger groups as several escorts appeared to join in challenges. The *SEs* varied considerably in their rates of challenging; in watch no. 77, of the three escorts who remained in the group throughout the watch, H_f challenged approximately ten times, always unsuccessfully, H_w twice both successfully, and H_c made one challenge which was also successful. Generally replacement of the *PE* made little change in the overall structure of the group: a *SE* that swam behind and to the left of the central pair would still be found there, if it had not left the group or become the new *PE*.

We observed ten replacements of the *PE* on Silver Bank. After six of these the displaced animal left the group within 30 minutes, one left after 46 minutes, and the other three (all in watch no. 77) remained within the group until the end of the watch. In Table 1 it can be seen that the *PE* usually fended off challenges for there were many more challenges than takeovers. During three of the five replacements where such information was recorded, smaller animals displaced larger, and during the other two larger displaced smaller. The success of a challenge appeared to depend on the relative stamina of the two contestants. Both challengers and the defending *PEs* were often visibly tired after long or energetic clashes — they would frequently lie at the surface blowing frequently and heavily. The drain on the *PE* of fending off challenges from *SE* H_f and others may partially explain why in watch no. 77 H_c and H_w were able to replace one another after periods of 90 and 194 minutes. *PEs* maintained their position for an average of 7.5 hours before replacement.

Movement of large groups.

The observed speeds of different classes of group on Silver Bank are given in Fig. 4. It is apparent that speed increases very dramatically with group size. An analysis of the tracks taken by groups showed them to have no obvious goal or preferred direction (WHITEHEAD & MOORE, in press); they doubled back and forth, often turning at the edge of the Bank. Larger

groups had relatively straighter tracks, but there was no obvious relation to the supposed migratory direction: in the final watch of the season (no. 90) on 5 April, when whales might be expected to be returning north, we followed a group 50 km from the northern edge of Silver Bank southward until after it had crossed the southern edge.

Group stability.

The stability of groups of different sizes on Silver Bank is shown in Fig. 5 by the rates at which animals joined groups of different sizes and the rates

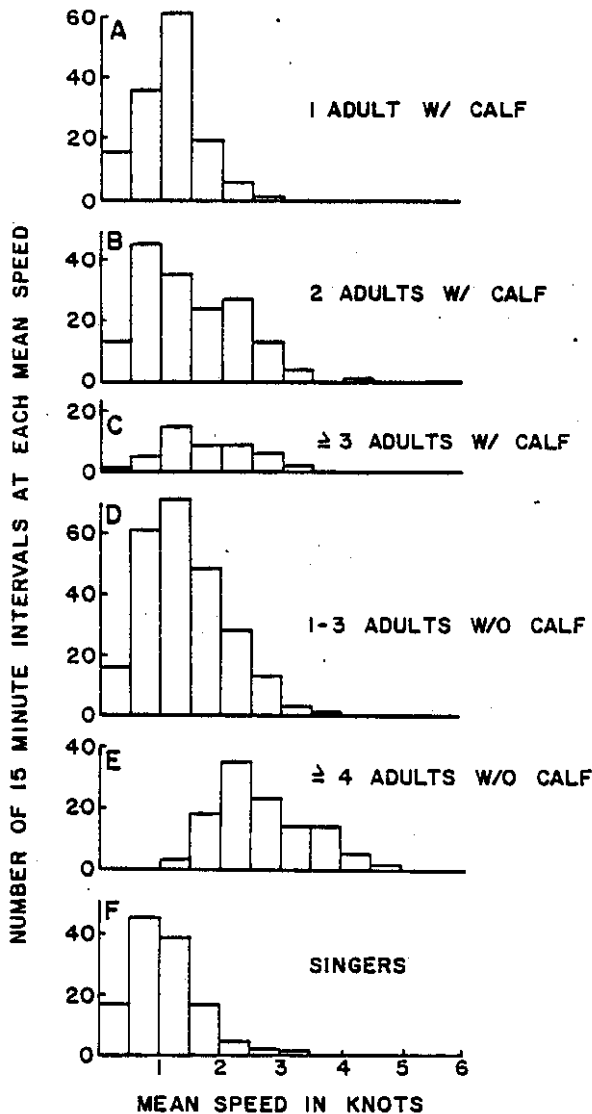


Fig. 4. Speeds (in knots) of groups of humpbacks watched on Silver Bank.

at which groups split. Large groups very rarely maintained a stable group size for longer than one hour. Larger groups split more frequently than smaller ones ($P < 0.01$). The relationship between group size and the rate of joining was only significantly ($P < 0.05$) higher for the groups without calves.

Arrival and departure of escorts.

In general, groups on Silver Bank appeared to ignore one another, although those with calves occasionally made small changes of course or speed, apparently to avoid large groups. With the very high whale

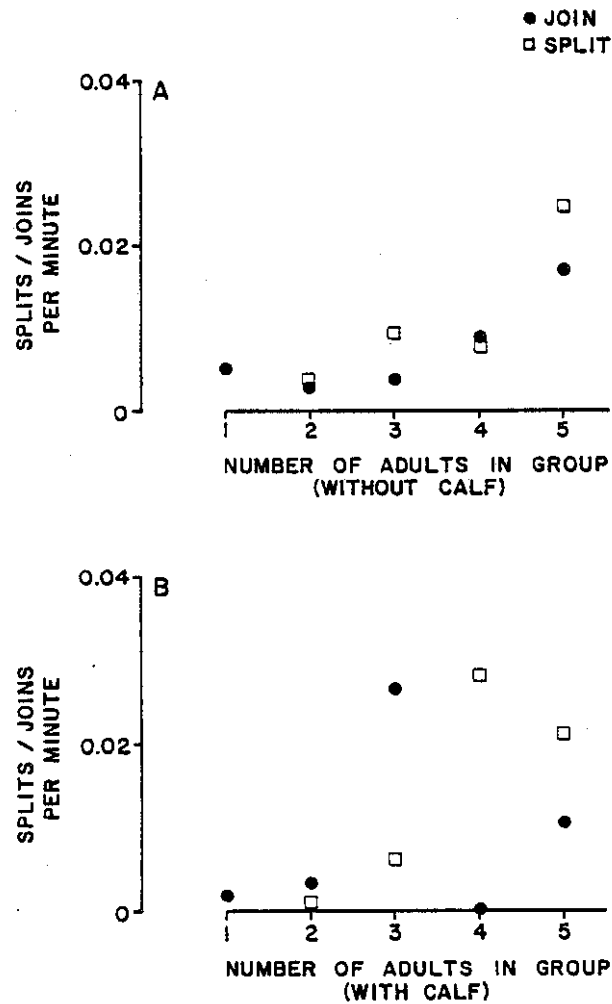


Fig. 5. Splitting (□) and joining (●) rates of groups of different sizes on Silver Bank. Figure 5A (above) includes groups without a calf, figure 5B (below) includes groups with a calf.

densities on Silver Bank, two groups frequently found themselves in the same place at the same time. Generally there was little sign of interaction and both groups left the encounter without change in composition or behaviour. But on three occasions we observed an escort transfer between the two groups. One of these animals was the sole escort to a mother and calf, which it deserted for another mother and calf already surrounded by three escorts, suggesting differential desirability of *NAs*.

No group with a calf in it was seen to join with a large group. Pairs of whales or single whales, particularly those that had recently stopped singing, were most likely to join large groups. Single whales joined groups containing two or more adults on Silver Bank on nine occasions. Three of the six whales that had been single for at least 20 minutes before joining groups of two or more were singing before joining the large group. Five single escorts and three pairs were followed away from large groups on Silver Bank. Of the five single whales followed away from large groups, three started singing. Thus singers will stop to become escorts in large groups, and escorts that leave large groups sometimes start singing.

Singing humpbacks interact with large groups.

The technique used in Hawaii, combining observations from boats and land, made it possible to follow two groups of humpbacks simultaneously, and thus to follow interactions between distant groups. Singing humpbacks stopped singing and swam rapidly towards large active groups from distances as large as nine km. An example which occurred on 26 February 1980 is plotted in Fig. 6. In this case, the singer (labelled F) milled about from 1130 to 1336 at an average speed of 2.3 km/hr. From 1336, when F stopped singing at a distance of nine km from a large active group (labelled H), to 1407, when it was last seen alone, F swam directly towards group H at an average speed of 10.9 km/hr. It appeared that group H turned towards the exsinger F as F approached, although this was not as clear as the response of F to H. We believe that F joined H, although we were unable to take identification photographs to confirm the observation.

We have observed singing humpbacks to join a large active group soon after joining a lone adult and ceasing to sing. They occasionally joined a large active group as a pair of adults, but singers and the lone adults which joined them often split up a few minutes after joining. Soon after such a pair split up, we have followed either exsingers or their joiners to join a large active group.

Not only have we heard singing humpbacks stop singing and seen them move great distances apparently to join large groups of whales, but we have also seen singing humpbacks seem to ignore large groups which were very close to them. For example, on 8 April 1979, J. DARLING (pers. comm.) saw a group of seven or eight whales pass less than one km from a singing humpback that he was recording in Hawaii. The singer did not

1130	1208	1241	1245	1255	1336	1407	1416	1551
Singing adult (F) sighted	Group (H), in which 3 adults are chasing a pair, is sighted	(H) now contains 8+ adults	(F) stops singing	(F) starts singing	(F) stops singing and accelerates from <3km/hr to >10km/hr towards (H), 9km away	(F) last seen alone	(F) has probably joined (H) by now. (H+F?) contains 5+ adults	(H+F?) last sighted

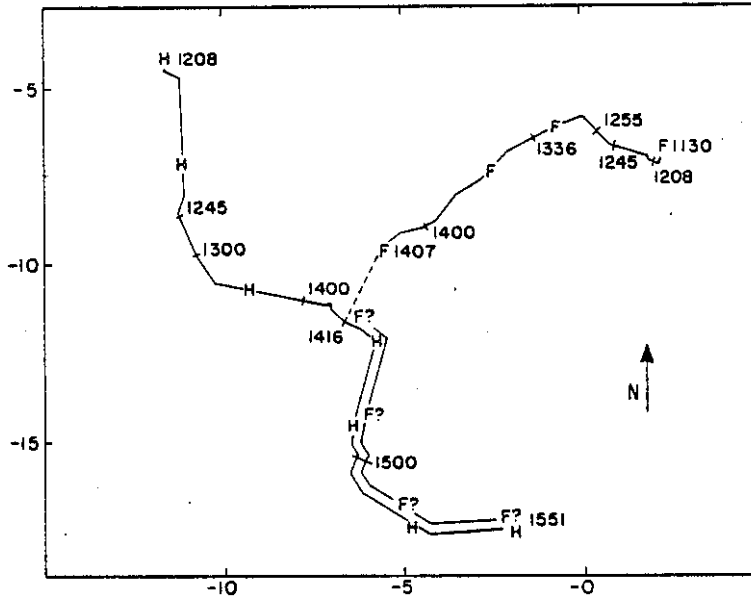


Fig. 6. Plot of an interaction which occurred on 26 February 1980 in Hawaii in which a singing humpback, F, stops singing and joins a large group of humpbacks, H, more than 9 km away.

stop and did not join the group. While monitoring the hydrophones, DARLING noted that the underwater sounds of blows and flipper slapping from this group were very loud. On 19 April 1979, DARLING observed a similar lack of interaction between a singing humpback off Maui and a group of three or four humpbacks which also passed less than one km away.

TABLE 2. Distances between lone singers and those groups of 3 or more adults in which aggressive behavior was seen and when both were followed simultaneously

Date (1980)	Singer	Paired large group	Initial distance (km) between groups	Distance (km) between groups when last seen or when singer stopped	Singer's motion re group	Group's motion re singer
Singer joined the large group						
2/12	S	T	5.5	1.1	to	to
2/18	M	W	2.7	1.8	to	to
2/20	E	F	4.8	4.8	to	—
2/26	D	C	7.3	6.0	to	away
2/26	F	H	14.0	9.2	to	—
3/4	II	B	6.6	6.0	to	—
Singer joined another group						
1/20	R	T + U	9.7	13.0	—	away
2/2	B	E + F	8.8	11.5	—	—
2/19	B	U	13.5	16.6	—	away
(2/26	F*	C	9.4	10.7	—	—)
2/26	P**	H	2.8	2.6	to	—
2/29	A	E	3.6	3.3	—	to
3/4	U	S	6.6	7.0	away	to
4/9	F	G	16.5	18.9	to	—
Singer joined no other whale						
1/20	X	T + U	5.4	7.1	—	—
1/27	K	G	8.1	9.6	—	away
1/30	G	A	7.7	11.6	to	away
2/4	C	E	10.2	14.3	—	—
3/1	AA	DD	10.2	9.9	—	—
3/2	X	R	11.8	12.0	—	—
3/15	A	D*	10.1	10.4	away	—

* Singer F joined large group H rather than C. ** Singer P left large group C just before starting to sing.

The distance between the singer and group increased or decreased monotonically except in three cases where the distance first decreased and then increased: Groups F and C on 2/26 went from a 9.4 km separation to 9.3 km before moving farther apart, groups P and H on 2/26 moved as close as 2.4 km before moving farther apart, and groups F and G on 4/9 approached to a minimum separation of 14.6 km before moving farther apart.

Table 2 lists those occasions during the 1980 season when singing humpbacks in Hawaii were followed both by boat and by the transit station at the same time as a group of three or more adult whales in which aggressive behaviour was observed. Of these 20 singers, six joined a large

group that was followed simultaneously, seven joined another kind of group, while the other seven were not seen to join any other whales. Singer F, which joined the large group H, stopped singing while still 9.2 km from H (Fig. 6). The other five of the six singers that joined large groups were never more than 7.5 km from the group which they joined. Eleven of the 15 singers that did not join the paired large group under observation were always further than 7.5 km from the large group. This seems to indicate that there may have been a critical distance of approximately 7.5 km beyond which singers were unlikely to join a large group.

All singers that joined a large group approached that group while singing. Only for three of the 15 singers that did not join the paired large group did the distance between the two groups diminish, and only three of these singers clearly moved towards the large group. Two factors may have led to this. Singers appear to have approached or avoided large groups while singing depending on whether they joined the large group after ceasing to sing. In addition, large groups may head for singers, and this may affect the likelihood of a singer joining the group.

Involvement of singers in the formation of large groups.

Not only did singing humpbacks join and leave large groups, but large active groups also formed when a singer joined a smaller group of whales. When a singer joined two adults with or without a calf, a pronounced aggressive interaction usually ensued between the exsinger and one of the two whales (the escort if the group was a mother, calf, and escort). One example of this kind of interaction in which a singer joins a pair of adults without a calf is plotted in Fig. 4 of TYACK (1981). Another example of a singer joining a mother, calf, and escort was observed on 26 February 1979 in Hawaii. As soon as the singer joined the other group, the mother and calf accelerated, moving away from the other two whales. The exsinger and escort then chased after the mother and calf, each one seeming to try to get closest to the mother. The speed of this group, over 12 km/hr, was remarkably high, and we were unable to keep up with it for long.

This kind of rapid chase also occasionally occurred after a mother and calf or lone adult joined a singer. Sometimes other whales in the area would start chasing after such a newly formed group. The chasing whales often converged into a group of up to 8-10 whales which swam rapidly after the lead group. When the rear group caught up with the lead group, the more typical *NA-PE* structure was established.

Seasonal variation in the number of large groups.

On Silver Bank large groups were most often found towards the end of the season, in late March when overall whale densities were lower (Fig. 7). At this time the humpback song bouts off Hawaii were longer, which TYACK (1981) relates to the different periods of sexual activity of individual males and females: females are receptive for a short period generally during February, whereas males are sexually active until they migrate North, some weeks after most nonlactating females (CHITTLEBOROUGH, 1958, 1965; DAWBIN, 1966). NISHIWAKI (1960) found that towards the end of the winter season at the Ryukyu Islands (at latitudes a few degrees North of Silver Bank and Hawaii), males increasingly predominated in the humpback catches.

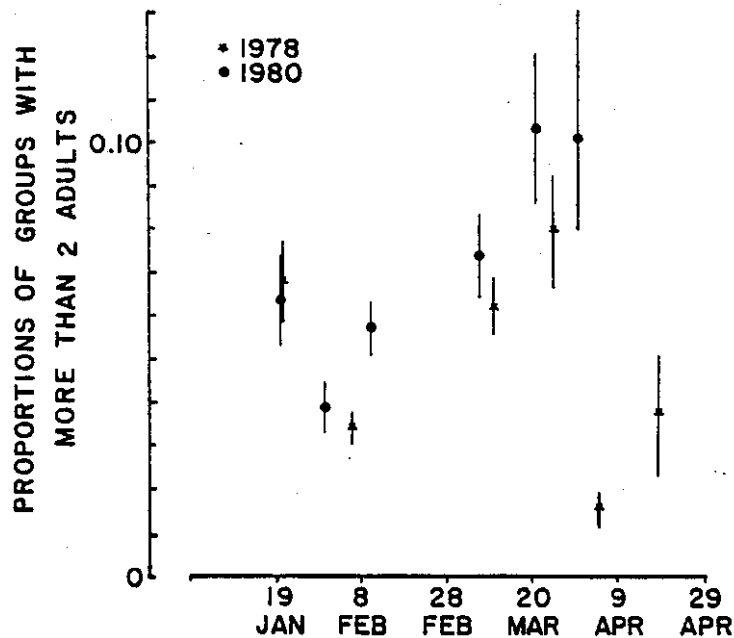


Fig. 7. Temporal changes in the proportion of large groups sighted on Silver Bank. The data is from surveys by *r/v Regina Maris*, including only groups within 1750 m of the transect line.

Discussion

Despite very different locations and methods we find that we substantially agree in our description of large groups of wintering humpbacks; the groups generally consisted of a number of escorts competing for proximity to a central Nuclear Animal. We believe that most, if not all, escorts

were males, and Nuclear Animals were females, for the following reasons:

1. Nuclear Animals were frequently the mothers of calves.
2. Cows and calves frequently have one adult escorting them.

Twenty one single escorts that have been sexed have been males (GLOCKNER-FERRARI & FERRARI, 1981).

3. Escorts frequently sang before or after escorting, and those singers to be sexed have been males.
4. Nuclear Animals never sang.
5. Escorts never had calves.

Since copulation has never been observed in humpbacks, we are not aware of any evidence which could directly link any increased access to a female by an escort to increased chances of mating. However, the level of competition between escorts was such that we find it hard to believe that becoming a principal or lone escort did not increase a male's chance of mating with the female *NA* at some point. Some sexual activity might occur in these large groups — the types of behaviour which TYACK (1981) tentatively associates with sexual activity in baleen whales are frequently seen in these groups. It is also possible that any sexual activity which might occur happens after all but one of the escorts have left the *NA*. The only humpback seen with an erect penis during either of our studies was the sole escort to a mother and calf (observation by G. ELLIS in Hawaii; the whale appeared to be urinating at the time of observation).

We believe that singing and joining a large group can be viewed as alternative strategies for gaining access to females. The relative usages of these strategies may depend on the absolute and relative abundances of males and females. Thus, at the end of the season when males would be expected to outnumber receptive females, the rate of formation of large groups increases.

In both studies there was evidence that all females were not equally desirable to potential escorts: escorts left one group to join another which already had more escorts, and unescorted mothers and calves were frequently ignored. This differential desirability is reasonably related to the stage of the females' oestrus cycle, with the unescorted mothers being those not showing or having finished a post-partum oestrus.

The humpback densities in the two study areas were very different, peaking at over 1.13 whales/km² on Silver Bank (WHITEHEAD, in press), and 0.17 whales/km² of Hawaii (HERMAN & ANTINOJA, 1977). These differences in density not only may have changed the patterns of interaction of the whales, but they also affected our ability to study interactions. On

Silver Bank where each group is usually within a few hundred metres of several others, the influences of groups on the movements and behaviour of other groups are very hard to determine. The humpback densities and methodology used off Hawaii have allowed these relationships to be carefully studied.

It is remarkable that singing humpbacks appear to sense and respond to large groups of whales up to at least nine km away. We believe that acoustic cues are likely candidates for those cues which humpbacks use to sense such distant groups. Both the sounds of the vocalizations which whales make in such groups and the sounds produced when one whale beats another can be quite loud. While we have not measured the source levels of these sounds, they occasionally appear to reach the source levels of humpback song (averaging 155.4 dB re one μPa at 1m, LEVENSON, 1972).

Given the probable sensitivity of singers to such distant sounds, we expect that the singers which did not join the large active groups less than one km away were still able to hear the sounds clearly audible to us through our hydrophones. This would indicate that not all singing whales hearing large groups joined them. However, we have no evidence to indicate what factors influence a particular singer to continue singing or to stop and join a particular group which it senses.

One of the most striking aspects of the large wintering groups is their speed through the water, for which there is no immediately obvious explanation. The evidence from Hawaii suggests that it is often the female that dictates the rapid movement, since a cow with calf or a *NA-PE* pair are often seen in the lead of a large group. She might do this to avoid unwanted matings, or to encounter more singers or other potential mates, thereby increasing the level of competition in the group, and eventually gaining a more fit mate. Alternatively it could be that sometimes the escorts increase group speed to shake off competitors.

Most of the aggressive behaviour we have observed which involves direct contact occurs as whales are jockeying for position to approach the Nuclear Animal, or as they make a challenge, attempting to manoeuvre past other escorts to the Nuclear Animal. However, the underwater observations of Hawaiian humpbacks show that an escort sometimes beats another escort in a way which interferes with locomotion and seems to be intended to hurt or deter it.

Summary

Fast moving groups containing three or more adult humpback whales are found in the winter on Silver Bank in the West Indies, and off Hawaii. Many of these groups have a definite structure: a central Nuclear Animal, with or without a calf, is surrounded by escorts who compete, sometimes violently, for proximity to the Nuclear Animal. This competition involves fluke thrashes, the blowing of bubblestreams, and physical contact, some of which appears designed to hurt an opponent: bleeding wounds are seen on the competing escorts. Escorts sometimes leave these groups and start singing, and singers sometimes stop to join large groups. The pattern of interactions strongly suggests that the escorts are males competing for access to a central female. Off Hawaii singers respond to such groups at ranges of up to approximately 7.5 km. On Silver Bank, Principal Escorts maintained a position of closest proximity to the Nuclear Animal for an average of 7.5 hours before replacement.

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