The behaviour of mature male sperm whales on the Galápagos Islands breeding grounds

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The behaviour of mature male sperm whales (*Physeter macrocephalus*) was observed off the Galápagos Islands between 1985 and 1991. The abundance of males peaked in April and May at 3% of the population. Only 1 of the 18 photographically identified males was sighted off the Galápagos in two different years. In their residency periods off the Galápagos and their lack of preferred ranges, and in many aspects of their behaviour, males were similar to females. However, unlike females, males were sometimes seen alone and never performed any aerial behaviour. Although they were occasionally seen or heard together, there are indications that males avoided one another, perhaps by listening for the "slow click" vocalizations made by males approximately 75% of the time. One incidence of possible aggression between males was observed, and many males possessed parallel scars on their heads, presumably made during aggressive encounters. Males moved between groups of females, spending very approximately 8 h with each group. Groups of females were often revisited by particular males over periods of a few days but never over more than 1 week. Males showed no obvious preference for particular groups, although a few close associations between individual males and individual females were noticed over intervals of a few days. When males were present, females showed increased rates of making spyhops and sideflukes (indicating manoeuvring) and codas (a communicative vocalization). Copulation was not observed. The evidence is consistent with males' maximizing their expected reproductive success by roving between groups of females.

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Le comportement de mâles adultes du Cachalot macrocéphale (*Physeter macrocephalus*) a pu être observé au large des îles Galápagos de 1985 à 1991. L'abondance des mâles atteignait son maximum en avril et en mai et représentait 3% de la population. Un seul des 18 mâles reconnaissables par photographie a été vu deux années de suite. Les mâles se comportaient généralement comme les femelles lors de leur séjour au large des Galápagos; ils ne manifestaient aucune préférence pour des sites particuliers. Contrairement aux femelles cependant, les mâles étaient quelquefois seuls et n'exécutaient jamais de déploiements aériens. Bien que des mâles aient été aperçus ou entendus en compagnie d'un autre mâle, il semble que les mâles s'évitaient, peut-être en écoutant les vocalisations de type « clic lent » que les mâles émettent 75% du temps. En une occasion, une présumée agression entre mâles s'est produite; d'ailleurs, de nombreux mâles portaient des cicatrices parallèles sur la tête, probablement le résultat d'affrontements entre mâles. Les mâles allaient d'un groupe de femelles à un autre, passant grosso modo 8 h avec chacun. Certains groupes de femelles recevaient des visites répétées d'un même mâle sur une période de quelques jours, mais cela ne se prolongeait pas au-delà d'une semaine. Les mâles ne semblaient pas manifester d'attachement particulier pour un groupe ou un autre, bien que des associations entre un mâle et une femelle aient été observées à des intervalles de quelques jours. En présence de mâles, les femelles augmentaient leur nombre de sauts de reconnaissance et de coups de nageoire latérale (des comportements de positionnement) et produisaient des codas (des vocalisations de communication). L'accouplement n'a pu être observé. Il apparaît donc que les mâles maximisent leur succès reproducteur potentiel en allant d'un groupe de femelles à un autre.

[Traduit par la rédaction]

Introduction

Despite a considerable body of knowledge on many other aspects of the biology of the sperm whale, *Physeter macrocephalus*, (e.g., Berzin 1971), the mating system is not well understood (Gaskin 1982). Interest is growing in the relationships between mating systems and other aspects of the ecology and natural history of species (e.g., Clutton-Brock 1989). The sperm whale is remarkable for its size, sexual dimorphism, diving behaviour, social organization and ecological success (e.g., Ridgway and Harrison 1989). Thus, the nature of the sperm whale's mating system, and how it may fit into models developed with other groups of mammals, is of particular interest.

Assumptions regarding the form of the mating system have been made when constructing models of the population biology of the sperm whale (International Whaling Commission 1980). Recent whaling has concentrated on mature males, so these assumptions have considerable influence on the expected response of populations to exploitation (May and Beddington 1980; Whitehead 1987). It has been suggested that pregnancy rates have declined in some areas because of a lack of males (Clarke et al. 1980; Whitehead 1990*a*). Thus, information on the mating system of the sperm whale has immediate practical significance.

Female sperm whales (which reach physical maturity at about 10.7 m; Rice 1989) are usually found at latitudes less than 40° and are most common in tropical waters (Berzin 1971; Gaskin 1982). In contrast, the much larger mature males (which reach physical maturity at about 15.7 m; Rice 1989) are generally encountered in cold waters (Berzin 1971; Best 1979; Gaskin 1982). However, on occasion, large males can be seen accompanying the social groups of females at low latitudes. It has traditionally been assumed that these are males who migrate to warmer waters for the mating season and associate with a group of females as a "harem" for the duration of the mating season (e.g., Berzin 1971).

There is evidence of fights between mature males, from head scarring (Best 1979; Kato 1984) and broken teeth (Clarke and

Paliza 1988), and from observation (Caldwell et al. 1966). These fights were generally thought to be for control of a harem. Sometimes, however, more than one male is seen with a group of females, suggesting the existence of coalitions between males (Best 1979). A harem-based mating system was used in the International Whaling Commission's models of sperm whale population dynamics (International Whaling Commission 1980).

However, Best (1979) presented evidence, primarily based on cyamid infestations, that males may spend only short periods, "possibly only a matter of days," with groups of females. From observations and photographic identifications of both female and male sperm whales off the Galápagos Islands in 1985, Whitehead and Arnbom (1987) concluded that the mature male sperm whales were moving independently between groups of females spending periods of only a few hours with each group. Further data collected off the Galápagos in 1987 confirmed these patterns (Whitehead and Waters 1990), as did observations off the Seychelles in 1990 (Kahn 1991).

In this paper I reexamine the 1985 and 1987 data from the Galápagos Islands, as well as the data from studies in 1988, 1989, and 1991, and describe in greater detail the behaviour of mature males on the Galápagos grounds. The topics addressed include the numbers and residency patterns of mature males around the Galápagos, interactions with groups of females, individual females, and other males, the behaviour of the males, and changes in the behaviour of females when males are present.

Methods

Definitions

In this paper, I will use the following terms.

Male: a distinctively large (>12.5 m) sperm whale, assumed to be mature. Female sperm whales off the Galápagos rarely reach 11.0 m (Waters and Whitehead 1990*b*).

Calf: a distinctively small (<6.5 m) first-year calf.

Medium-sized whales: whales other than large males and small calves; mainly sexually mature females, although some immatures of both sexes are included.

Cluster: several whales swimming at approximately the same speed in the same direction and within 100 m of one another (Whitehead and Arnbom 1987).

Unit: a permanent association of medium-sized whales over periods of years, containing very approximately 12 members (Whitehead et al. 1991).

Group: very approximately 20 medium-sized sperm whales, about two units, travelling together and moving in a coordinated fashion over periods of days (Whitehead et al. 1991). Pairs of medium-sized whales identified together on 2 or more days were assigned to the same group.

Clustered: two whales were "clustered" at a particular time if they were observed swimming together in the same cluster.

Associated: two whales were "associated" if they were photographically identified within 2 h of one another (Whitehead et al. 1991).

Fluke-up: flukes (tail) raised above the water surface, usually at the start of a deep dive.

Breach: leap from the water (Waters and Whitehead 1990*a*).

Lobtail: flukes lifted above the water and then thrashed onto the water surface (Waters and Whitehead 1990*a*).

Spyhop: slow raising of the whale's head above the water surface (Whitehead and Weilgart 1991).

Sidefluke: one fluke seen oriented vertically, but moving horizontally, above the water surface (Whitehead and Weilgart 1991).

Coda: short patterned sequences of clicks used in social circumstances (Watkins and Schevill 1977).

TABLE 1. Summary of identifications of mature males in each year, with photographically estimated lengths, number of different days on which the whales were identified, first and last identification dates, and intervening time span

Year	Male No.	Length (m)	No. of days	Identification date		Span (days)
				First	Last	
1985	500	15.1	3	04-17	04-19	2
	501	16.4	1	02-12	02-12	—
	502	14.0	1	03-31	03-31	—
	503	13.7	2	04-14	04-15	1
	504	—	1	04-19	04-19	—
	505	—	2	04-11	04-12	1
	506	14.4	2	03-08	03-11	3
	507	—	1	03-11	03-11	—
1987	510	12.8	3	04-16	05-13	27
	511	13.4	2	04-28	06-03	36
	512	13.9	1	04-16	04-16	—
	513	12.8	3	04-16	04-19	3
	514	—	1	01-03	01-03	—
	520	—	1	03-22	03-22	—
1989	530	15.0	3	04-29	05-05	6
	531	14.4	5	04-17	05-21	34
	532	15.0	3	03-05	05-14	70*
1991	507	—	1	04-13	04-13	—
	535	13.3	1	04-06	04-06	—

*Male 532 was identified off the Galápagos Islands on 89-03-05 by T. Lyrholm (unpublished data), as well as on 89-05-05 and 89-05-14 during our studies.

Creak: a series of clicks made at high repetition rates (>60 clicks/s) (Norris and Harvey 1972).

Slow click: a distinctive series of clicks with interclick intervals of about 6–8 s, made by mature males (Weilgart and Whitehead 1988).

Period of contact with male: a period of tracking during which there were no breaks of longer than 2 h between consecutive determinations of the presence of one or more males, either visually, or acoustically from recordings of the slow click. The period had to be initiated with at least 2 h in which recordings were made but no males were sighted or heard. Periods followed by at least 2 h in which recordings were made but no males were sighted or heard were considered to have been *concluded*.

Location and tracking

Field studies were carried out off the Galápagos Islands (2°S–1°N, 89–93°W) in February–April 1985, January–June 1987, May 1988, April–May 1989, and March–April 1991. Together with a crew of about four, I used 10- to 12-m auxiliary sailing vessels which spent 6–16 days at sea between port calls.

Groups of sperm whales were tracked acoustically using a directional hydrophone specially built for the project by Dev-Tec Inc. (Pasadena, Calif.). This allowed us to locate groups of sperm whales and follow them for periods of days, staying within about 2 km of them during most of the tracking time. Groups principally consisted of female sperm whales and their young, but these were sometimes accompanied by mature males (Whitehead and Arnbom 1987; Whitehead and Waters 1990).

Because of the tendency of the sperm whales to aggregate (Whitehead and Weilgart 1991), several different groups might be tracked consecutively or, occasionally, simultaneously. During tracking periods, the aggregation of whales being followed on 2 consecutive days might have some, but perhaps not all, members in common, or might be composed of completely different individuals.

Individual identification and associations

During daylight we approached clusters of sperm whales discreetly to photograph the flukes of the animals as they dived. We use fluke photographs to identify individual whales (Arnbom 1987). We made special attempts to photographically identify the distinctively large mature males. The individual identification photographs were pro-

cessed as described by Arnbom (1987) and Whitehead et al. (1991). Only high-quality photographs (Arnbom's (1987) $Q = 4$ or 5) were used in the analysis. Mature males were given identity numbers between 500 and 535 (Table 1).

Visual data

During the 1985 and 1987 studies we recorded, every 5 min during daylight, the ranges, bearings, and composition (maximum number of large males, first-year calves, and medium-sized whales observed) of all visible whale clusters, together with the number of occurrences of any observable behavioural activities (including fluke-ups, breaches, lobtails, spyhops, and sideflukes). In addition, we estimated the speed (from comparison with the mechanically measured speed of the research vessel) and heading (in degrees magnetic, using compasses) of clusters when they were sufficiently close for these to be determined with reasonable accuracy. From the records of headings we calculated a measure of the consistency of the headings of clusters seen at the same time (Whitehead and Weilgart 1991).

In all studies, for each cluster for which we took fluke photographs, we recorded the numbers of first-year calves, adult males, and medium-sized whales present.

Measurement

Sperm whales were measured by taking, from a position 9–11 m above the sea surface, a photograph that included the horizon with the whale approximately parallel to it and with the whale's snout, blowhole, and dorsal fin visible above the surface. Knowing the height of the camera, its focal length, and the relationships between different dimensions on sperm whales, the lengths of the sperm whales can be estimated from such photographs using the methods of Gordon (1990) and Waters and Whitehead (1990*b*). As in Waters and Whitehead's (1990*b*) study, errors were minimized by not using this technique in substantial swells and by excluding from the analysis photographs in which the angle between the whale and the horizon was greater than 30°. Estimates of length from different photographs of the same whale were averaged.

Acoustic data

During the 1985 and 1987 studies, we recorded the underwater sounds of the sperm whales on a regular schedule, 5 min per hour beginning on the hour, although some sessions were missed because of poor weather or technical problems (Whitehead and Weilgart 1990). The codas and creaks in the first 4 min of each session were counted and the presence or number of "slow click" series was noted.

Rate of making slow clicks

During a 5-min recording session, let the probability that a male (within range of the hydrophone) is heard making slow clicks be p, and, given that one male is present, let the probability that another male is present be q. Then, given that a male is visible, the expected proportion of times that

0 slow clicks heard are heard: $(1 - q)(1 - p) + q(1 - p)^2$

1 slow click is heard: $(1 - q)p + 2qp(1 - p)$

2 slow clicks are heard: qp^2

More than 2 slow-click series were never definitively heard. This model was fitted to the data on the number of 5-min acoustic sessions, within 30 min of the sighting of a male, in which 0, 1, and 2 slow clicks were heard in order to estimate p and q.

Behavioural and acoustic measures

Following the methods described by Whitehead and Weilgart (1991), the records of visually observed behaviour (only for those whales seen within 500 m of the research vessel) and acoustic variables were agglomerated by hour. To reduce potential seasonal effects, only the data from April and May (when mature males were most abundant) were considered when these behavioural data were examined. To remove autocorrelation, only records for selected hours of the day (e.g., 08:00 and 16:00 for measures significantly autocorrelated at lags of 6–8 h) were used when carrying out statistical tests (Whitehead and Weilgart 1991).

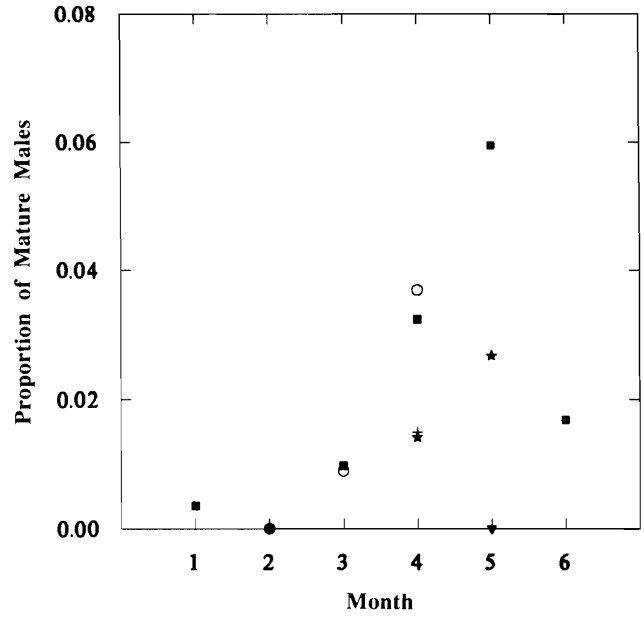

FIG. 1. Relative abundance of mature male sperm whales according to calendar month in 1985 (○), 1987 (■), 1988 (▼), 1989 (★), and 1991 (+).

Results

Numbers, seasonality, and identity of large males

Overall, there were 99 mature males in the 5369 sightings of whales (1.85%) in clusters (excluding calves) for which fluke photographs were taken. Furthermore, 18 individual males were photographically identified out of a total of 1320 different individuals (1.36%). Males were clearly very scarce.

Their abundance did, however, appear to vary seasonally within the 6 months of our studies, rising to about 3% of the population in April and May (Fig. 1). As an exception, males were not sighted in April 1988, but only 5 days were spent at sea with sperm whales during that year. Males were considerably scarcer, but not absent, in January, February, and March. This pattern of relative seasonal abundance based on visual sightings (Fig. 1) generally agrees with the rates at which slow clicks were heard during the regular hourly recordings in 1985 and 1987, which also peaked in April and May (Weilgart 1990).

The identified males had estimated lengths between 12.8 and 16.4 m (Table 1), which, using Ohsumi's (1977) age–length key for the North Pacific, suggests ages of 21–40 years.

Residency and range

One male, No. 507, of the 18 that were photographically identified (5.5%), was identified in the Galápagos in two different years, 1985 and 1991 (Table 1); none of the other 17 males were identified in more than one year. For comparison, 158 of 1302 medium-sized whales (12.1%) were identified in more than one year.

Mature males were identified on a mean of 2.6 different days during a year, the distribution being significantly (likelihood ratio G-test, $G = 11.68$, df = 3, $p < 0.005$) from that of the medium-sized whales, who were identified on a mean of 1.4 different days during a year. However, there was no significant difference between males and medium-sized whales

TABLE 2. Associates of males seen on more than one day

Male No.	Date	No. of associates photographed	Associates common to other days	
			Date	Number
500	85-04-17	9	85-04-18	1
500	85-04-18	7	85-04-17	1
500	85-04-19	2	—	
503	85-04-14	3	—	
503	85-04-15	2	—	
505	85-04-11	2	—	
505	85-04-12	12	—	
506	85-03-08	0	—	
506	85-03-11	2	—	
507	85-03-11	2	—	
507	91-04-13	7	—	
510	87-04-16	7	—	
510	87-05-12	11	87-05-13	2
510	87-05-13	8	87-05-12	2
511	87-04-28	6	—	
511	87-06-03	11	—	
513	87-04-16	15	87-04-18	2
			87-04-19	5
513	87-04-18	6	87-04-16	2
			87-04-19	3
513	87-04-19	20	87-04-16	5
			87-04-18	3
530	89-04-29	17	89-04-30	2
			89-05-05	2
530	89-04-30	8	89-04-29	2
			89-05-05	5
530	89-05-05	15	89-04-29	2
			89-04-30	5
531	89-04-17	6	—	
531	89-05-02	15	89-05-03	5
			89-05-06	3
531	89-05-03	15	89-05-02	5
			89-05-06	5
531	89-05-06	11	89-05-02	3
			89-05-03	5
531	89-05-21	9	—	
532	89-03-05	22	—	
532	89-05-07	12	—	
532	89-05-14	4	—	

seen on more than 1 day in the distribution of time spans between first and last sightings within a year (likelihood ratio G-test, $G = 1.80$, df $= 2$, $p > 0.05$). These results suggest that males and medium-sized whales spend approximately the same time periods within the study area, but because of sampling bias or behavioural differences (which, however, seem to be small (see later), males are more likely to be identified than medium-sized whales.

There was no evidence that individual males had preferred ranges within the Galápagos study area in 1985 and 1987 (Whitehead and Waters 1990). In 1989, the only other year in which individual males were sighted on more than 1 day, again there was no tendency for individual males to remain in particular subareas within the area of general sperm whale distribution around the Galápagos.

Associations of mature males with females

Associations of identified mature males with identified medium-sized whales are summarized in Table 2. Ten mature males were identified on more than 1 day. In the post-1985 studies, 5–15 whales were usually photographed associating with each male on every day that it was identified. (In 1985 we had less expertise in obtaining identification photographs.) Of the 35 associations between individual males and individual medium-sized whales that were repeated over more than 1 day, all were of less than 6 days' duration, and 12 were on consecutive days.

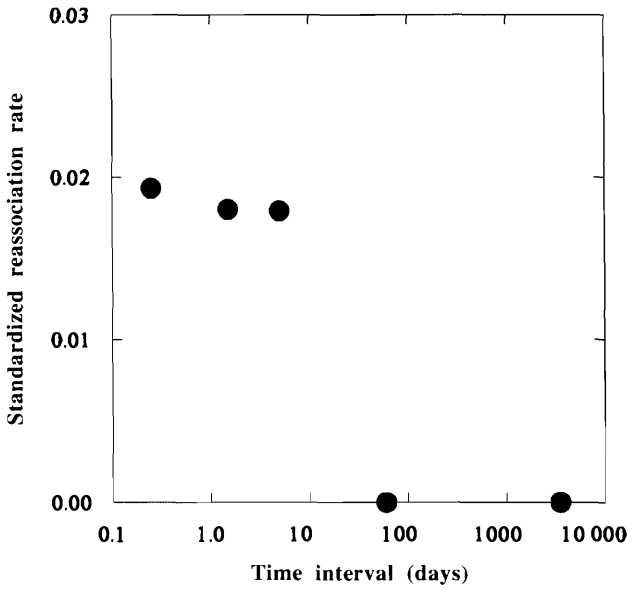

FIG. 2. Standardized reassociation rates of mature male sperm whales with medium-sized whales over different time periods, i.e., the probability of an associated male and medium-sized whale remaining together divided by the mean number of associates of a male.

TABLE 3. Durations of periods of contact with males

Interval (L)	Number of periods: concluded	not concluded
<0.5	1	0
0.5–1.5	2	0
1.5–5.5	4	0
5.5–10.5	4	2
10.5–20.5	4	1

These associations are summarized in Fig. 2, which gives the "standardized reassociation rates" (Whitehead et al. 1991) between mature males and other identified whales for a range of time intervals. These are the probabilities that an animal photographed associating with a mature male at a certain time was also in a photograph of an associate of that male at various intervals later on. The time periods covered range from 4–12 h to 6 years (from male 507). The plot in Fig. 2 suggests that males associated with medium-sized whales either for less than 4 h or very approximately 7 days, but never for more than a month.

Associations of groups of females with mature males

Because of the fission–fusion nature of the social organization of female sperm whales, and the sporadic and irregular identification of individuals, it is difficult in most cases to ascertain even the approximate duration of associations between

TABLE 4. Identification histories (within a year) of those groups of medium-sized sperm whales that were seen on at least 2 days, on 1 of which they were associated with a male

Group	Date	No. of medium-sized whales identified	Identified with group: Male No.	Identified with group: Number of associates
A	85-03-09	7	—	
	85-03-10	8	—	
	85-04-12	7	501	7
			505	3
B	85-03-29	3	—	
	85-04-12	6	501	6
			505	3
C	85-03-27	4	—	
	85-03-31	5	502	4
D	85-03-28	4	—	
	85-04-17	7	500	6
	85-04-18	5	500	3
E	85-03-26	3	—	
	85-04-18	3	500	3
F	87-02-07	4	—	
	87-02-08	5	—	
	87-02-09	6	—	
	87-02-11	5	—	
	87-02-12	5	—	
	87-05-12	4	510	4
			518	4
	87-05-13	6	510	6
G	87-01-03	7	514	4
	87-04-16	10	510	7
			512	6
			513	6
	87-04-17	10	(Male seen but not identified)	
	87-04-18	19	513	6
	87-04-19	21	513	16
H	87-06-02	8	—	
	87-06-03	8	511	8
I	89-04-26	3	—	
	89-04-29	6	530	6
	89-05-01	6	—	
J	89-04-30	6	530	5
	89-05-05	7	530	7
K	89-04-27	9	—	
	89-04-29	9	530	9
	89-05-02	7	531	1
	89-05-04	9	—	
	89-05-17	8	—	
L	89-04-28	10	—	
	89-05-02	12	531	10
	89-05-03	19	531	14
	89-05-06	16	531	15
	89-05-07	14	532	10
M	91-04-13	4	507	4
	91-04-14	4	—	

mature males and groups of females. Table 3 is a very rough guide to the distribution of durations of periods of contact of our research vessel with males in 1985 and 1987. These periods of contact had a mean duration of 9 h before they concluded, although they lasted sometimes less than an hour and sometimes more than 15 h.

However, as we were not necessarily following the same medium-sized whales before, during, and after the period of contact, the distribution given in Table 3 can only be considered a rough guide to the duration of interactions between groups of medium-sized whales and males. In five instances, two or more medium-sized whales were identified both before and after a period of contact (and during the period if it lasted more than 2 h). These periods had durations of 11, 1, 8, 15, and 4 h, the mean being 8 h. Thus, it seems that periods of contact of medium-sized whales with one or more males lasted, on average, about 8−9 h, although they were very variable in duration, and might include breaks of up to 2 h.

Specific patterns of association between groups of medium-sized whales (identified on 2 or more different days, during at least 1 of which they were identified associating with a male) and males are summarized in Table 4. Each group (containing at least three members) is listed, together with the days on which members of it were identified and the males with which it was associated. All except 3 of the 13 groups were identified without males on 1 or more days. Six groups were identified associated with males on more than 1 day, six groups were identified associated with more than one male, and five groups were identified with the same male over periods of 2−5 days. However, even when a group was identified with a particular male on consecutive days, the male does not seem to have always remained with the group. For instance, 6 members of group G were identified associated with male 513 during the earlier part of 87-04-18, and 16 members were identified associated with him on 87-04-19. However no male was seen or heard between 12:00 and 21:00 on 87-04-18, during which time 15 members of group G were identified. These included 4 of the 6 whales photographed associated with No. 513 earlier on 87-04-18 and 8 of the 16 associated with him on 87-04-19.

TABLE 5. Associations of medium-sized whales identified with males on at least 2 days in April or May (numbers in parentheses show the binomial distribution)

Year	Identified associated with male: on neither day	on 1 of 2 days	on both days
1985	2 (3.5)	9 (6.0)	1 (2.5)
1987	12 (12.0)	14 (13.9)	4 (4.0)
1989	45 (41.3)	32 (39.3)	13 (9.3)

Associations of individual females with mature males

To investigate whether some medium-sized whales were more likely than others to accompany males, I examined the association patterns of those medium-sized whales identified on more than 1 day during April and May, when mature males were most common. For those medium-sized whales identified on more than 2 days during this period, only the data from the first 2 days were used. In Table 5, these are broken down into those medium-sized whales identified with mature males on both days, on just 1 day, or on neither day. If all medium-sized whales were equally likely to associate with males on any day they were present, these frequencies should be binomially distributed. The expected binomial frequencies given in Table 5 are not significantly different from those observed for any of the 3 years (1985, 1987, 1989) for which sufficient data were

TABLE 6. Medium-sized whales identified clustered with a male on 2 or more days; the number of medium-sized whales in the cluster is given, and whether the male or the medium-sized whale dived first, or they dived simultaneously (=)

Date	Time	Medium-sized whale No.	Male No.	No. in cluster	Dived first
89-04-28	16:15	1002	—	1	
89-05-03	6:25	1002	—	1	
	7:10	1002	—	2	
	13:50	1002	531	2	♀
89-05-06	7:10	1002	531	1	♀
	15:50	1002	—	3	
89-04-29	13:40	854	530	12	♂
	14:10	854	530	6	♂
	14:40	854	530	8	♂
	15:20	854	530	7	♀
89-05-05	8:40	854	530	2	♀
	9:20	854	530	4	♀
	10:05	854	530	3	♀
	11:15	854	530	4	♀
89-04-30	17:40	1957	530	7	♀
89-05-05	6:50	1957	—	1	
	9:20	1957	530	4	♀
	10:00	1957	530	3	♀
	10:35	1957	530	4	=
89-05-06	9:55	1957	—	1	
89-05-20	15:20	1957	—	1	
89-04-30	17:45	145	530	7	♀
89-05-05	11:15	145	530	4	=
	17:50	145	—	1	

available to make such a test valid (likelihood ratio G-tests, $p > 0.05$ for all 3 years). These tests are not strictly valid because the long-term associations occurring between medium-sized whales mean that individuals are not independent in their associations with males. However, there is clearly no substantial tendency for certain females to preferentially associate with males and others not to.

On 27 occasions males were seen clustered with one or two medium-sized whales. Ten of these companions in small clusters were photographically identified. One individual, No. 1002, was photographed clustered with the same male, No. 531, in a small cluster on 2 different days, 89-05-03 and 89-05-06 (Table 6). However, these two whales were photographed apart on several occasions (Table 6) and male 531 was sighted alone at 06:20 on 89-05-06 between the repeat clusterings. Three other medium-sized whales were identified while clustered with males on more than 1 day: No. 854 was always seen clustered with male No. 530 on 89-05-29 and 89-05-05, whereas Nos. 1957 and 145 were clustered with No. 530 on both 89-04-30 and 89-05-05, but not consistently so (Table 6). Except on 89-04-29 and 89-04-30, there were four or fewer medium-sized whales in the clusters containing these animals. Thus, there is some evidence of persistent close relationships between particular males and particular medium-sized whales over periods of a few days. Except for No. 854 on 89-04-29, the male dived after his medium-sized whale companion in these instances (Table 6). This might suggest that the male was generally maintaining contact with the female rather than vice versa.

Males were sometimes observed to alter course to join medium-sized whales, medium-sized whales sometimes appeared to join males, and, on one occasion (85-04-17), a male and a medium-sized whale, 300 m apart, both altered course to swim toward one another. After meeting, they swam together as a cluster for about 5 min before diving together.

On 85-03-21 a male was briefly observed swimming upside down beneath a medium-sized whale, one of the mating postures described by Berzin (1971). However, they did not appear to touch.

TABLE 7. Distribution of numbers of different slow click series heard in each 4-min session, together with the expected numbers, given the Poisson distribution (random associations between males), and the results of tests for differences between observed and expected values (lumping sessions in which two or more slow clicks were heard)

No. of slow clicks heard	1985		1987	
	Observed	Expected	Observed	Expected
0	139	146	205	210
1	65	51	70	61
2	4	9	6	9
≥3	0	1	0	1
G-statistic	8.58 (1 df), $p < 0.005$		3.08 (1 df), $0.05 < p < 0.1$	

Associations between mature males

On eight occasions two males were seen clustered together, or near one another, at the surface, and on 85-03-11 three males were briefly seen together. Even more frequently, the slow clicks of two males could be heard together. Of 85 recording sessions made 30 min or less after a male was observed at the surface, one "slow click" series was heard in 56, and two "slow click" series from two males were heard in 10. Using the model described in the Methods, q, the probability that, given the presence of one male, another male was also present, was estimated to be 0.218.

If males acted independently as they moved between medium-sized whales, the number of males present at any time should show roughly a Poisson distribution. The distribution of the number of slow click series heard at any time, and the expected numbers, given the Poisson distribution, are presented in Table 7 for the months of April and May, when males were most abundant. In both 1985 and 1987, the numbers of slow clicks heard do not seem to show a Poisson distribution; two or more slow clicks were heard less often than expected. This suggests that, to a certain extent, males avoid one another, although this effect could be partially the result of two series of slow clicks being heard within one 4-min session, not overlapping and thus being considered to be one.

On only one occasion did we see possibly aggressive interactions between two males. Between 10:30 and 10:45 on 87-04-16, males 512 and 513 were observed side by side a few metres apart, with much thrashing of flukes at or beneath the surface. They both dived, together with the other nine members of their cluster, at 10:45. Two males were observed together at the surface at 11:30, No. 512 and an unidentified male. Previous to this incident, Nos. 512 and 513 had been observed together at 08:40 the same day.

A number of the males that we were able to observe closely possessed series of parallel scars on their heads (e.g., Fig. 3), presumably received during contests with other males (cf. Kato 1984).

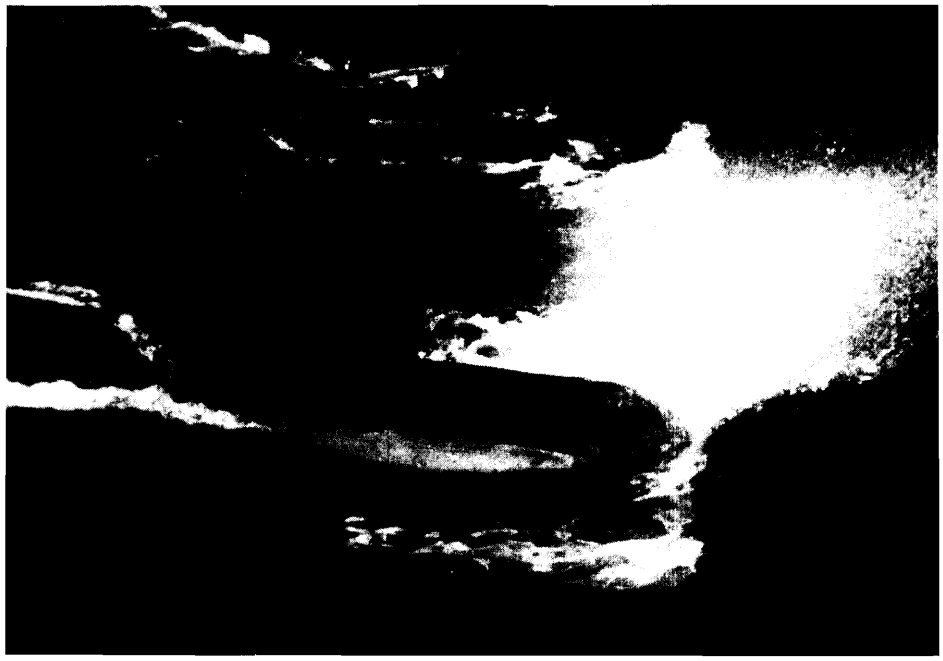

FIG. 3. Parallel scars on the head of a mature male sperm whale.

Behaviour of mature males

Using the model described in the Methods, p, the probability that a male, when present, had its slow clicks recorded, was estimated to be 0.735, which suggests that males make slow clicks roughly 75% of the time. However, as found at high latitudes (Mullins et al. 1988), they also appear sometimes to make the "usual clicks," with repetition rates of about 2/s, heard from females (Weilgart and Whitehead 1988): during the period of observation of a male alone on 87-06-26 only usual clicks were heard.

In some respects the behaviour of the mature males was similar to that of the females with which they were associating. For instance, they moved at similar speeds, dived to comparable depths for similar periods of time (Papastavrou et al. 1989), and were found in similar sized clusters. The mean cluster size (for individuals in clusters sighted less than 200 m from the boat) in April and May 1985 was 8.1 individuals for medium-sized whales and 8.2 individuals for males. In April and May 1987, the means were 13.6 for medium-sized whales and 12.2 for males.

There was no particular tendency for males to dive before or after medium-sized members of the same cluster that dived during the same 5-min interval (Table 8).

Males were sighted in a cluster by themselves on a total of 20 days, usually within 1000 m and 10 min of an observation of a cluster of medium-sized whales. However, at 09:20 on 85-04-19, male 500 was sighted alone (no medium-sized whales being observed until 09:55). He was also sighted between 10:00 and 10:05 about 1100–1800 m from the nearest cluster of medium-sized whales. At 11:30 on 87-04-18, a male was observed moving away from a large cluster of medium-sized whales to a distance of at least 1200 m. On 87-06-26, a male was observed alone (no medium-sized whales being observed for 50 min before or afterwards) between 10:40 and 10:50 and again between 13:05 and 13:15.

Unlike the females and immatures with whom they were associating, the mature males were never recorded breaching or lobtailing (Waters and Whitehead 1990*a*), although a breach from a male was reported in May 1989, when I was not on board the research vessel and formal records of behaviour were not being kept. Males did sidefluke and spyhop on occasion. One defecation from a male was noted from 17 recorded fluke-ups in 1989 and 1991 in which the presence or absence of an accompanying defecation was noted. This defecation rate is similar to that recorded from the medium-sized whales (Smith 1992). A lower beak of a cephalopod collected after this defecation was identified as coming from an *Ancistrocheirus leseuri* with a lower rostral length of 6.5 mm (Smith 1992). Beaks of this species were frequently found in collections made from the feces of medium-sized sperm whales off the Galápagos. The beak collected after the male's defecation was equal in size to the largest from this species collected after defecations of medium-sized whales (Smith 1992).

TABLE 8. Order of diving of male sperm whales when within a cluster

No. of whales diving within 5 min	No. of occasions	Order in which the male dived									
		1	2	3	4	5	6	7	8	9	10
2	15	9	6								
3	18	5	5	8							
4	10	3	2	1	4						
5	4	1	2	0	0	1					
6	5	0	0	1	1	1	2				
7	1	0	0	0	0	0	1	0			
10	1	0	0	0	0	0	0	1	0	0	0

Behaviour of females in the presence of mature males

Of the seven visual measures (speed, consistency of heading, fluke-ups, lobtails, breaches, sideflukes, and spyhops) and two acoustic measures (codas and creaks) considered, two, the rates of seeing sideflukes and spyhops, showed significant or marginally significant ($p < 0.1$) changes in the

TABLE 9. Changes in rates of observing sideflukes and spyhops and hearing codas during hours in which one or more males were sighted during April and May of 1985 and 1987

Max. no. of males observed during the hour	No. of sideflukes per whale observed		No. of spyhops per whale observed		No. of codas per 4 min session	
	Mean	*n*	Mean	*n*	Mean	*n*
0	0.051	205	0.024	205	6.28	183
1	0.082	66	0.055	66	14.54	59
2	0.154	3	0.093	3	48.0	3
Autocorrelation[a]	2		2		6	
Data used in test[b]	7, 11, 13, 15, 17		7, 11, 13, 15, 17		8, 16	
Significance (Kruskal–Wallis)	$p = 0.068$		$p = 0.022$		$p = 0.175$	

[a]Lag (in hours) at which significant autocorrelations were detected (from Whitehead and Weilgart 1991).
[b]Hours of the day used when testing for significant differences in the values of the measure with the presence of males.

presence of mature males. Both behaviours were observed substantially more frequently during hours in which males were observed (Table 9). Of the other measures considered, only codas, which increased in the presence of males, showed a major change, but in this case the difference was not significant (Table 9). (The high degree of autocorrelation in coda counts (Table 9) necessitated more radical pruning of the data set, smaller sample sizes, and therefore less powerful tests than were possible for sideflukes and spyhops.) Although a few of these sideflukes, spyhops, and codas were made by the males themselves, the great majority were not, and so, especially in the case of spyhops, it can be concluded that the presence of males was correlated with a change in the behaviour of the females.

Discussion

The remarkable scarcity of males during our research off the Galápagos Islands is echoed in other recent studies of sperm whales in tropical areas: off Sri Lanka (Gordon 1987), off the Seychelles (Kahn 1991), and near mainland Ecuador (Kahn et al. 1993). In the general area of the Galápagos, Rice (1977) found 2.6% large (>14 m) males during surveys between February and April 1975. The current incidence of mature males off the Galápagos (about 2% of the population) is about 1/10 of that in the catches of the Yankee whalers in the same area between 1830 and 1850 (Hope and Whitehead 1991). It is also about 1/10 of that predicted by models employing the natural history parameters for sperm whales used by the International Whaling Commission and assuming that all mature males take part in breeding (Whitehead 1990*a*). The Yankees may have biassed their catches toward males (Best 1983), and not all mature males may enter the breeding regions every year. However, the magnitude of the differences in relative male abundance between recent observations and what would be expected strongly argues for a real reduction in the relative abundance in males.

The selection for mature males by the modern whaling industry combined with the slow rate of maturation of male sperm whales led to a reduction in the proportion of males (>12.0 m) on the Peruvian whaling grounds (1000 km from the Galápagos) from 58% in 1958 to 14% in 1976 (Clarke et al. 1980). These catches would also seem to be the most likely cause of the scarcity of males off the Galápagos, as the Galápagos males likely migrate to areas of recent whaling. An important corollary is that if the relative abundance of male sperm whales off the Galápagos has been very much reduced below its natural (prewhaling) level, then the patterns of mating behaviour may also have changed. Thus, our observations today may not necessarily correspond to the behavioural patterns existing before human exploitation.

A number of lines of evidence suggest that, as believed by Colnett (1798), sperm whales do mate on the Galápagos grounds. Groups of females, which spend long periods in the region of the Galápagos, are seen there with small calves (Whitehead 1990*a*). The seasonality of the presence of large, mature males also argues for mating taking place in this area (Whitehead et al. 1989). Despite the suggestion of some whalers (Caldwell et al. 1966) that mating may be carried out by smaller males, it seems highly probable that the large males, such as those we see, are the ones doing the mating (Best 1979).

That we never saw copulation is not surprising. Although there are reports in the literature of sperm whales being observed copulating (e.g., Slijper 1962; Caldwell et al. 1966; Best et al. 1984; Ramirez 1988), these reports are few, somewhat contradictory, and not always convincing (Best et al. 1984). Groups that we followed contained approximately one first-year calf, suggesting that about one birth per group occurs each year. If all conceptions took place in April and May (likely a conservative assumption; Best et al. 1984), which we think is the principal mating season (Whitehead et al. 1989), then during the 65 days we spent following sperm whales in April and May, we might expect approximately one copulation leading to conception to have occurred. Thus, there is a strong probability that no copulations leading to conception occurred while we were following whales. Alternatively the few that did occur were not recognized as such.

If the large males we saw off the Galápagos were there for mating purposes, it seems rather strange that in most ways their behaviour was indistinguishable from that of the females with which they associated. Their residency periods, grouping and diving behaviour were similar to the females': they made, at least some of the time, the usual click series commonly heard from females, and in their transitory associations with female units they behaved not unlike a unit of size 1. This may reflect the fact that the males, like the females, were spending much of their time foraging (a defecation from a male was observed), and that much of the behaviour that we saw was adapted to that purpose. In their diving behaviour, speed of movement, infrequent performance of aerial behaviour, and apparent lack of social organization, the males off the Galápagos

behaved similarly to comparably sized males studied using similar methods on the Scotian Shelf, where females are very scarce (Whitehead et al. 1992).

However, there were some differences in behaviour between the two sexes off the Galápagos. Males never breached or lobtailed, and, unlike the females, were occasionally seen alone, presumably in transit between different groups of females. Only one mature male has been identified in more than one year; it would be most interesting to know something of the long-term movement patterns of the males between and within low-latitude mating and high-latitude feeding grounds. This is probably best accomplished by satellite radio tracking.

The males seemed to move repeatedly between different groups of females, not favouring any particular group, spending about 8 h with a group at any one time, but often reassociating with one group over periods of a few days. A few close associations between certain medium-sized whales and mature males were repeatedly observed over periods of a few days, but it is not clear whether it was the males or the medium-sized whales that actively maintained this contact. There was some evidence that on some occasions males sought out females and on others females sought out males. The presence of males increased rates of spyhopping and sidefluking in the females. These are activities observed when whales manoeuvre near the surface, and their increased rate in the presence of males may indicate females taking action to change their proximity to the males. The tendency to increase production of communicative codas (Watkins and Schevill 1977) in the presence of males indicates that a greater degree of information is being exchanged. This might be expected, as the presence of a male likely adds significant complexity to the social environment of the females.

In our data there is no evidence of coalitions between males, as was considered to be the case by Best (1979). Instead the males seemed to move between the groups of females independently, perhaps even avoiding one another. Evidence of aggressive interactions between mature sperm whales is shown in the heavy scarring seen on many of their heads (Best 1979; Kato 1984) as well as in broken teeth and jaws (Clarke and Paliza 1988). Although there are recorded observations of fights between male sperm whales in the older literature (citations in Caldwell et al. 1966 and Clarke and Paliza 1988), recent observations of such behaviour seem to be scarcer (Best 1979), and during the studies reported in this paper we saw only one possible incidence of overt aggression, which appeared mild. Best (1979) attributes this apparent change in the rate of observing fights to the inhibitory effects of loud motors. As we often sail toward the whales and our motor is exceedingly quiet (we can make useful underwater recordings of the sounds of the whales while it is operating), this factor is unlikely to have greatly affected our observations. The lowering of the proportion of large males on the breeding grounds, caused by selection for males during the modern whaling period seems to be a more likely cause of any reduction in the rate of aggressive encounters. However, the scars on the heads of the males demonstrate that occasional fights, or at least ritualistic jousting, between males still do take place.

The breeding behaviour of the African elephant, *Loxodonta africana*, has much in common with that of the sperm whale (Best 1979; Best et al. 1984; Whitehead and Arnbom 1987), perhaps especially in the manner in which males move independently between groups of females. When one reads accounts of the results of research on the breeding behaviour of elephants (e.g., Moss 1983; Poole 1989), it is clear that, in comparison, our understanding of the mating system of the sperm whale is still rudimentary. However, we have made considerable progress during the last 10 years of research on living sperm whales, and although many details are unknown, a broad outline of the mating system, at least off the Galápagos Islands, has emerged.

The mature males may spend periods of a few days to a few months on the Galápagos grounds during any visit. It is clear that they do not usually defend spatial territories or accompany groups of females exclusively for periods of more than a few days. Instead, they move between groups of females, generally spending just a few hours with each, and appear to forage with the females sometimes. They may also forage alone on occasion. The slow click, which they make much of the time, may function to attract females or to repel other males, or both (Weilgart and Whitehead 1988). Certain females could appear to have more potential as mates, and be preferentially accompanied at certain times during periods of a few days. Contests between males may occur when two similar-sized males encounter a receptive female at the same time, or at different times, so that a dominance hierarchy is set up amongst the males in a particular area at any one time.

This scenario is consistent with previous observations of 0–4 males being found with groups of females, and the males sometimes being seen alone (Caldwell et al. 1966; Best 1979). Recent studies in other parts of the world also seem to conform to this general pattern. During a 3-month study off the Seychelles islands in the Indian Ocean, Kahn (1991) identified five males (1.5% of the identified population). Two of these were observed alone, but within 4 h of sightings of groups of females. The remaining three each spent 2–3 h with the groups of females that were being followed. During a 2-month study off mainland Ecuador (S. Dufault and H. Whitehead, unpublished data), four males were sighted (2% of the identified population). Three were identified on 1 day only, and one on 2 consecutive days. One of the males was observed alone over a period of 9 h making both slow click and usual click series, while the others briefly joined groups of females. During studies of sperm whales in the central tropical Pacific in 1992, four males were observed alone, separated by more than 24 h from encounters with groups of females, and two were sighted with groups of females (H. Whitehead, unpublished data). The rather more frequent observations of males alone in these studies may be attributable to the less aggregated distributions of females off the Seychelles and mainland Ecuador and in the central Pacific than off the Galápagos (Kahn et al. 1993).

Models of the mating strategies for males who do not defend territories predict that the "roving" behaviour of males observed off the Galápagos will be more successful (in terms of numbers of receptive females encountered) when the travel time between encounters with groups of females is less than the duration of oestrus (Whitehead 1990*b*). The oestrous period of a female sperm whale is unknown but it is likely considerably more than the few hours it would take a male to travel between groups of females in the relatively concentrated aggregations off the Galápagos.

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