

Social organization of sperm whales off the Galapagos Islands, February–April 1985

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Between February and April 1985 sperm whales (*Physeter macrocephalus*) were tracked visually and acoustically in the waters west of the Galapagos Islands. Individuals were identified and measured photographically. Using statistical criteria the female and immature whales encountered were clustered into 13 groups with closed membership during the study period. These groups had a median estimated population of 19.5 animals each, and associated with one another at different times. The groups showed no significant immigration into or emigration from the study area during the study. Seven large males were identified. These associated with each other and the groups of females and immatures for periods lasting approximately 6 h. Individual males were found with different groups of females and immatures at different times. A simple model suggests that a male employing a "searching" strategy should encounter more oestrous females than the traditionally accepted "harem" holder when the interval between encountering groups of females is less than the duration of the females' oestrus. Neither the groups of females nor the mature males appeared to possess territories or preferred ranges within the study area. The number of large males encountered was considerably less than that expected if all large males were present on the breeding grounds, suggesting that males may not breed every year.

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L'observation et l'audition des cris ont permis de suivre des cachalots (*Physeter macrocephalus*) de février à avril 1985 dans les eaux situées à l'ouest des îles Galapagos. Des photographies ont servi à identifier et à mesurer les individus. D'après des critères statistiques, les femelles et les individus immatures ont été rassemblés en 13 groupes et les liens entre les individus étaient très forts au cours de l'étude. Le nombre moyen d'individus dans les groupes a été estimé à 19,5 et les groupes étaient associés les uns aux autres à différents moments. Il ne s'est pas produit d'immigration ou émigration significative hors de la région d'étude durant la période d'observation. Sept mâles de grande taille ont été reconnus. Ils s'associaient entre eux et avec les groupes de femelles et de petits pour des périodes d'environ 6 h. Les mâles s'associaient avec différents groupes de femelles et de petits à différents moments. Un modèle simple a démontré qu'un mâle qui utilise une stratégie de « recherche » a plus de chances de rencontrer des femelles en période d'ovulation que ne le laisse croire le concept du « maître de harem » lorsque l'intervalle entre ses rencontres avec des femelles est plus court que la durée du cycle oestral des femelles. Ni les groupes de femelles, ni les mâles à maturité ne semblaient posséder de territoire ou préférer certains endroits dans la région étudiée. Le nombre de mâles de grande taille était beaucoup plus faible que prévu selon l'hypothèse qui veut que tous les grands mâles soient présents dans les aires de reproduction, ce qui permet de croire que les mâles ne se reproduisent peut-être pas chaque année.

[Traduit par la revue]

Introduction

Best (1979) summarized knowledge of the social organization of sperm whales, *Physeter macrocephalus*. Sperm whales show considerable sexual dimorphism, with large males, at 45 t, reaching approximately three times the mass of mature females. The primary social units are thought to be stable groups composed of females, calves, and juveniles, each of which contains approximately 20–30 animals. Males, and possibly females as well, leave these "nursery" groups at approximately 4–15 years of age to form "juvenile" or "bachelor" schools. Larger males are found generally in smaller aggregations (Gaskin 1970) and at higher latitudes. The largest males are often single and may frequent polar waters. This is in contrast to nursery groups which, in most oceans, principally inhabit tropical and subtropical waters (Best 1979).

Hitherto, it has proved impossible to provide a reliable description of the sperm whales' presumably polygynous mating system (Gaskin 1982). It was usually supposed that a large male holds a group of females as a "harem," controlling access to oestrous females (Tomilin 1967). However, Tormosov and Sazhinov (1974) have proposed that males may act in consort to monopolize one or more groups of females, and

D. W. Rice (Caldwell *et al.* 1966), suggested that smaller males may perform much of the mating, with the larger males becoming "outcasts." In their recent reviews, Best (1979) and Gaskin (1982) tend to favour a system including male coalitions. Although most previous workers believed that males maintain control of one or more groups of females for at least one breeding season, Best (1979) presents evidence, primarily from the investigation of cyamid infestations, that large males may remain with groups of females for shorter periods, "possibly only a matter of days."

To develop a realistic model of the population dynamics of sperm whales, and to investigate their reaction to exploitation, information on the behaviour of sperm whales is of vital significance (Anonymous 1980; Best *et al.* 1984; Gambell 1972). The form of the sperm whales' social organization is especially significant when considering the effects of relative male depletion on female fecundity.

To obtain a reasonable understanding of the sperm whales' social system, protracted observations of the whales in the wild are needed (Best 1979). Although this was thought to be "almost impracticable technically and economically" (Ohsumi 1971), Whitehead and Gordon (1987) have developed techniques for

studying the behaviour of living sperm whales from small vessels. From data collected using these methods off the Galapagos Islands in early 1985, we are able to describe the general social organization of the sperm whales in this region.

Definitions and methods

In this paper we use "aggregation" to mean any general extended association of whales, "group" to mean a set of animals with closed membership over periods of at least days, and "cluster" to mean whales swimming in a reasonably coordinated manner, within 100 m of one another (cf. Best 1979). We were able to distinguish visually three size classes of sperm whale: "large males" which appeared much larger than the other animals present (this discontinuity in size was later confirmed by measurements, see below), "females and immatures" which constituted the majority of the animals observed, and 1st-year "calves," which were considerably smaller than other animals.

The field research took place in the waters west of the Galapagos Islands, Ecuador. We used a 10-m sloop with a crew of five to track sperm whales. We sailed when conditions permitted, otherwise motoring. The tracking was continuous during day and night, apart from six breaks each lasting from 1 h to 7 days. A total of 716 h were spent in visual (daylight) or acoustic (night or fog) contact with aggregations of sperm whales between 23 February and 20 April 1985. This is thought to be the height of the breeding season for North Pacific sperm whales (Best *et al.* 1984), although it is not clear whether the sperm whales off the Galapagos, which lie on the equator, are part of northern or southern hemisphere stocks, or whether such designations are even appropriate (Rice 1977).

Virtually all the tracking was of female and immature sperm whales, although large males were sometimes present. We attempted to remain with particular aggregations of sperm whales, although sometimes we found ourselves with an apparently different set of whales as suggested in real time by observations of individually marked animals, and later confirmed photographically.

While we were tracking, recordings of the whales' sounds were made through a hydrophone for 5 min each hour. As large males have vocalizations distinctively different from other sperm whales, a "slow click" which they make with reasonable regularity (L.S. Weilgart and H. Whitehead, manuscript in preparation), their presence could be presumed from these recordings and other monitorings of the hydrophones.

During the study, 210 female or immature sperm whales and 7 large males were identified individually from high quality photographs of marks and scars on their flukes, with 63 of the females or immatures and 4 of the large males being identified from photographs taken on more than 1 day (Arnbom 1986). From an examination of the high quality fluke photographs taken that did not allow positive individual identification, Arnbom (1986) has shown that a maximum of about 9% of the whales in our study area were not identifiable by this technique. Additional identifications of the large males, and of six calves, were obtained from photographs of marks and patterns on their dorsal fins.

Whales were measured using a photographic method described by Gordon (1985). We photographed whales from 9.2 m above the water surface in such a way that the horizon was visible in the same frame as the whale. A measurement of the distance between the image of the whale and the image of the horizon on the negative allowed an estimate of range, and thus scale, to be calculated. Gordon's (1985) formulae were slightly altered to remove rounding errors when the calculation was performed in single precision.

Results

Groups of females and immatures

Aggregations of female and immature sperm whales sometimes appeared to merge, and usually were separated into a number of clusters which might be scattered over several square kilometres of ocean; thus visual observations of spatial organization are unreliable guides to overall social structure (Ohsumi 1971). We attempted an objective description of the social

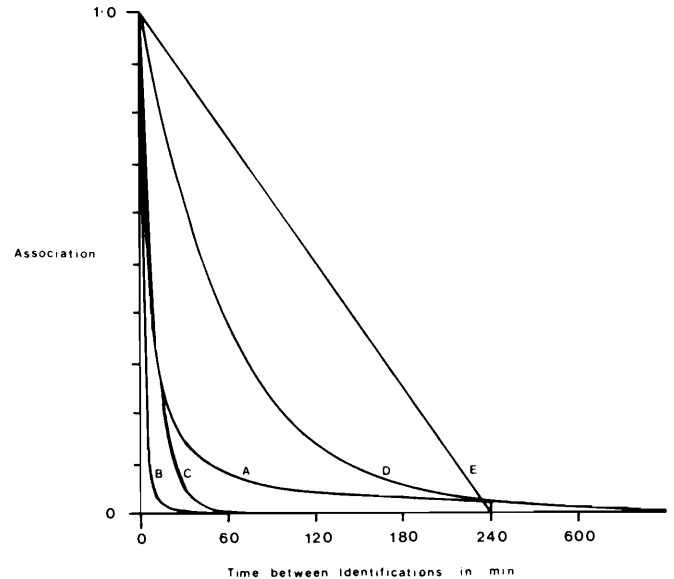


FIG. 1. Original function used to compute the association, R , between pairs of identified whales (A), compared with four alternative functions (B–E). The mathematical formulae for these functions are given in the text.

organization of the female and immature sperm whales off the Galapagos using photographic identifications of particular animals.

A coefficient of association, $R(x,y)$, was calculated between each pair of identified female or immature whales x and y :

$$[1] \quad R(x,y) = \sum_i 5/(5 + t(i)) \cdot ((1/N(x)) + (1/N(y)))/2$$

where the summation is made over i , the number of occasions on which x and y were identified less than 240 min apart (240 min was chosen as the cutoff, as there appeared to be occasional changes in the primary aggregation being followed over intervals of approximately this duration); $t(i)$ is the time interval in minutes between the identifications of x and y on occasion i (times recorded to nearest 5 min); and $N(x)$ and $N(y)$ are the total number of identifications of x and y . Thus if two whales were each identified once on several days, always within 5 min of one another, then $R = 1.0$; if they were never seen within 240 min of one another then $R = 0.0$. The shape of the association function is given by the curve marked A in Fig. 1. Of the 22 155 pairs of whales ($210 \times 209/2$), 1079 had values of R greater than 0.01, and 382 had values of R greater than 0.1.

The association matrix, $\{R(x,y)\}$, was used as input to a group average hierarchical cluster analysis (Everitt 1974). The resulting dendrogram is shown in Fig. 2. Groups were merged using this clustering technique until a likelihood ratio test showed a significant (at $P < 0.05$) decrease in the fit of the data (of the days on which individuals were identified) for the resultant group to a model of closure (with no individuals entering or leaving the group during the study period) compared with its two constituent groups. At each junction in the clustering tree, we calculated the likelihoods of the two original groupings of whales and their concatenation, under the multinomial model, using the formula given by Darroch (1958). High values of the likelihood function suggest that the data fit the model well, low values, that they do not. The likelihood ratio test, described by Silvey (1975), tests whether the two discrete groupings fit the model significantly better than their union. The



FIG. 2. Dendrogram showing the results of a group average hierarchical cluster analysis on associations between identified whales. The 210 identified female and immature whales are arranged vertically. Vertical lines indicate the level of association (R) at which pairs of clusters were linked. Links represented by bold lines did not significantly decrease the fit of the data to a model of closure; fine lines indicate that the linkage of the two clusters significantly (at $P < 0.05$) reduced the fit of the data to a model of closure. The primary groups obtained by this procedure are indicated at the left.

groups formed by this technique, whose members are joined by bold lines in Fig. 2, are the largest that do not significantly violate closure.

There were 13 "primary" groups with more than six identified whales each, which are listed in Table 1, and 10 other groups with from one to three identified members; the latter may have been unidentified members of the larger primary groups. The identification data for these groups were subjected to tests for "equal catchability" (that all individuals were equally identifiable) and for fit to the multinomial model (that no animals joined or left the groups during the study) (Seber 1982). Only one significant (at $P < 0.05$) failure was found: the data for group G4 (as in Table 1) showed a significant departure from the multinomial model; in particular a new set of whales appeared to join the group on 11 March.

Estimates of the populations of female and immature whales in those groupings seen on more than 1 day (G1–G10) were calculated using Schnabel mark–recapture censuses (Seber 1982) and are given in Table 1 together with their estimated standard errors. These population estimates may be biased to the low side by up to 9% if some members of the population were not identifiable by our methods (Arnbom 1986).

To investigate the robustness of this clustering technique, the analysis was repeated with different functions for the coefficient R . Instead of the original $5/(5+t)$ as the determinant of relatedness (eq. 1), we used four alternative functions: $125/(5+t)^3$, $e^{-t/10}$, $e^{-t/60}$, $1-t/240$ ($t < 240$ min). These alternative functions, represented by curves B, C, D, and E, respectively, are compared with the original function, curve A, in Fig. 1. These functions allocated 0–6 of the 214¹ whales to the "wrong group," and merged 0–2 of the "original" groupings. The first and second alternative functions, B and C, which emphasize short time intervals, left 14 whales ungrouped (in groups of size 1), as opposed to 2 in the original analysis. When the analysis was repeated (3 times) but with identifications chosen randomly on each occasion that a whale was actually identified, the whales were quickly clustered into one "super group." These tests suggest that the clustering technique is reasonably robust to the choice of R , and produces meaningful groups.

Further evidence of the authenticity of the derived groupings comes from an examination of the contexts in which calves were identified. Three calves were identified on more than one day: calf C5 was with group G1 on both days that it was identified; calf C6 was with group G8 on both days that it was identified; calf C4 was identified with members of group G1 on 2 days, and simultaneously with members of both groups G1 and G10 on a 3rd. Thus these calves seemed to remain with particular groupings of adults.

Our data therefore are consistent with the generally held view that female and immature sperm whales travel in groups possessing a reasonably stable composition over periods of at least several weeks. The estimated population sizes of the groups given in Table 1 are also consistent with the literature: our median estimated group size was 19.5 female and immature animals, which can be compared with Best's (1979) "median

¹The investigations of the robustness of the clustering technique were carried out on an original data set with six errors in the identification data, giving 214 identified animals rather than 210. Because of their use of computing resources, and unlike the rest of the analysis in this paper, these simulations were not repeated with the corrected data set. The conclusion that the clustering technique is reasonably robust and meaningful should not be changed by small alterations in the data set being tested.

TABLE 1. Derived groupings of whales, with the number of animals identified, a population estimate, its estimated standard error, the number of days on which the grouping was identified, the time span between its first and last sighting in days, and associations (members of both groups identified within 120 min of one another) with other groups

Group ID	No. of whales identified	Population estimate (SE)	No. of days group was identified	Time span of identifications, days	Associations*
G1	14	14.1 (1.0)	7	46	G2,G8,G9,G10(4)
G2	20	29.8 (6.9)	4	13	G1,G3,G9
G3	18	18.3 (1.0)	6	43	G2,G5(2),G8(2)
G4	18	20.9 (2.8)	5	36	G5,G8,G10
G5	20	22.5 (2.8)	7	40	G3(2),G4,G6(3),G8(2),G9
G6	19	28.2 (6.9)	5	41	G5(3)
G7	17	20.7 (4.0)	2	14	—
G8	14	17.8 (3.5)	5	36	G1,G3(2),G4,G5(2),G10
G9	9	10.6 (2.4)	4	48	G1,G2,G5,G10
G10	12	13.7 (2.6)	6	23	G1(4),G4,G5(2),G8,G9
G11	10	—	1	1	—
G12	8	—	1	1	—
G13	7	—	1	1	—

*The number of days pairs of groups were associated is given in parentheses if greater than one.

figure" of all previous estimates of the size of "groups of mixed sexes," 25 animals.

Seven of the primary groups listed in Table 1 were identified over periods of time longer than 1 month, and tests similar to those performed for the single animals suggested no significant immigration or emigration of groups to or from the area in which we were carrying out our study. However, there is evidence that at least some females migrate substantial distances through the general region of the Galapagos Islands: over a 10-month period, a 9.8-m female, which was marked with a stainless steel "Discovery" tag about 400 km northwest of the Galapagos, migrated to the Peruvian coast, 1500 km to the southeast, where it was killed (Ivashin 1978).

The positions at which groups were first identified on each day are given in Fig. 3. There is no indication that particular groups possessed territories or preferred ranges within the area in which we were studying them.

Table 1 gives associations between primary groups. On 11 of the 31 days on which at least two whales were identified, members of different groups were seen within 2 h of one another. These associations were sometimes very close, with up to 52 animals visible at the surface in one compact aggregation of less than 200 m across.

Large males

Attributes of the seven identified large males are listed in Table 2. The five that were measured photographically had lengths between 13.7 and 16.4 m. This supports Best's (1979) contention that "prime breeding bulls" are those over 13.7 m. The two unmeasured males were judged by eye to be a similar size to those measured. Thirty-two high quality images of whales accompanying large males, or near them, were measured. The mean estimated lengths of the whales producing these images was 9.66 m, with a range of 7.69–11.97 m. These are approximately the lengths of immature and female sperm whales recorded in the literature (e.g., Best 1979).

Only two of the males were identified over periods longer than 4 days, and the proportion of large males to other animals that were sighted less than 300 m from the research vessel increased from 0.0024 in late February to 0.0206 in April. Thus

there seems to have been immigration during the study period. The positions in which the males were first identified on each day are given in Fig. 3. There is no indication that particular males possessed preferred ranges or territories within the area in which we were studying them.

Males frequently associated with one another. On 4 days, two males were sighted within the same 5-min interval, and on one occasion three males were sighted simultaneously. Particular males were seen to associate with a variety of other males at different times (Table 2). No behaviour that could obviously be interpreted as agonistic was observed.

Associations between large males and groups of females

Using the recordings of slow clicks as a guide, we estimate that for 16% of the time during which we were following groups of females and immatures, they were attended by one or more large males. Our 21 encounters with large males varied in duration from 5 min to over 19 h, although it was often difficult to tell exactly when a male joined or left a group. Description of the duration of contacts between large males and specific groups of females was also hampered by the associations between groups of females and those between large males, so that often it was impossible to establish a one to one correspondence between them. However, during 14 encounters with males, the association between one male and one group of females was clear (i.e., only the one group was identified immediately before, during, and just after the encounter). These encounters had a mean duration of 5 h and 40 min, and a standard deviation of 5 h and 30 min.

Four of the seven identified males were seen in association with more than one group of females at different times, and four of the groups of females were attended by more than one identified male at different times (Table 2). There were three repeat associations between particular males and groups of females on different days, but two of these (G3 with 500, and G6 with 503) were on consecutive days.

Using just those times when members of only one primary group were identified within 240 min, the mean number of males visible less than 300 m from the research vessel (recorded each 5 min, and averaged over 30 min) showed no significant

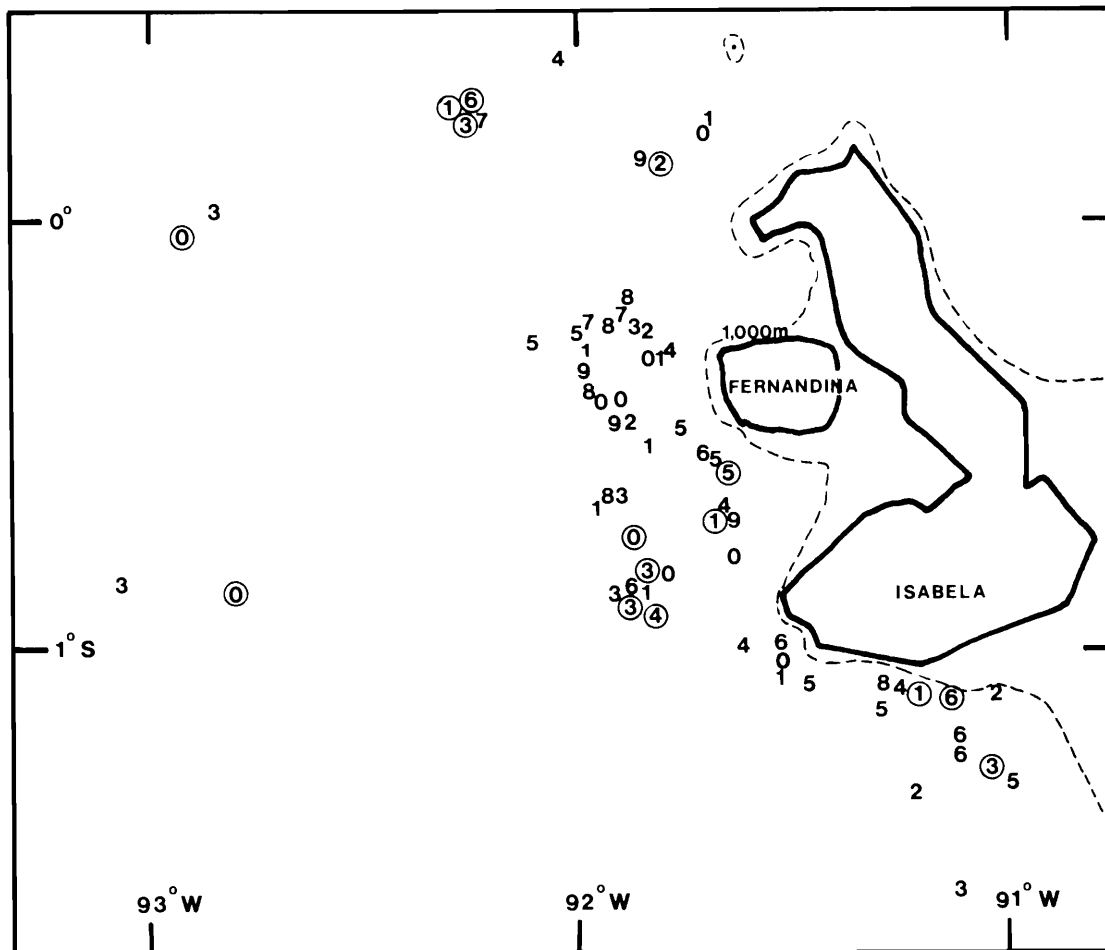


FIG. 3. Positions in which primary groups, represented by uncircled numbers, and large males, represented by circled numbers, were first identified on each day. Each first identification is represented by the last digit of the identification code (e.g., G3 = "3", G10 = "0" for the groups; 506 = ⑥ and 503 = ③ for the males). The broken line indicates the 1000-m depth contour.

TABLE 2. Identified large males (identity numbers: 500–506), with estimated lengths (mean of one to six photographic measurements per individual), number of days identified, span of days over which identified, and associations (identified within 120 min of one another) with other males and groups of females

ID No.	Length, m	No. of days male was identified	Time span of identifications, days	Associations with:*	
				Males	Groups
500	15.05	3	3	—	G3(2)
501	16.38	3	36	503,506(2)	G4(2),G5,G9,G10
502	14.03	1	1	—	G1,G9,G10
503	13.74	4	36	501,506	G1,G6(2)
504	—	1	1	—	—
505	—	1	1	—	G4,G5
506	14.39	2	4	501(2),503	G4

*The number of days males were associated with other males or groups is given in parentheses if greater than one.

variation with identity of the primary group present ($F_{11,383} = 1.243, P = 0.256$). Thus, there was no tendency for some groups to be attended by males more frequently than others.

There was no indication from our observations that large males were "corralling" females or immatures, or in any other way forcing their actions. We observed females and immatures,

while at the surface, to alter course and speed so that they could join a large male a few hundred metres away, and males to do the same so that they could approach females or immatures. The different sexes swam together for several minutes, then dived together or separately. There was also one occasion on which it appeared that a large male and a female avoided one another. In

their movements, associations, and other behaviour at the surface, the males behaved much like the smaller whales with which they were associating.

Discussion

Form of social organization

The principal difference between our observations and the traditional assumptions about the social organization of the sperm whale concern the interactions between large males and groups of females. These were labile and of only a few hours' duration. Also, the data are not consistent with long-term coalitions between large males. Rather, they fit the "searching bull strategy" described for African elephants (*Loxodonta africana*) by Barnes (1982), in which males move between groups of females searching for oestrous females. Barnes (1982) considered the advantage to a male adopting this searching strategy as compared with the originally accepted "herd bull" strategy (similar to the traditional harem mating system of sperm whales). He showed that, while in most circumstances the searching bull would have a higher probability of associating with an oestrous female, at very low elephant densities the herd bull might expect greater success.

Following Barnes (1982), we made a simplistic comparison of harem holding and searching as strategies for male sperm whales. If there is a mean of f mature females per group, the breeding season lasts M days, with each female coming into oestrus for q days once every C years, then the expected number of oestrous females, $E(h)$, encountered each breeding season by a harem-holding male is

$$[2] \quad E(h) = f/C \text{ females per season}$$

For a searching male (taking a mean of G days between encountering groups) the expected number of oestrous females encountered, $E(s)$, is

$$[3] \quad E(s) = (\text{no. of groups encountered}) \cdot (\text{oestrous females per group}) \\ = (M/G) \cdot (f \cdot q/(C \cdot M)) \text{ females per season} \\ = f/C \cdot q/G \text{ females per season} \\ = E(h) \cdot q/G \text{ females per season (from eq. 2)}$$

If $E(h) > E(s)$ then harem-holding males will have greater access to oestrous females than searching males, and vice versa. But, from eq. 3, $E(h) > E(s)$ if $G > q$. Therefore a male does better to search if the time between schools of females (search time plus time in attendance) is less than the length of oestrus.

West of the Galapagos, we travelled a mean distance of 103 km before finding a group of females acoustically, and the mean speed of whales during our study was about 4 km/h. It is likely that sperm whales are more sensitive to each others' sounds than our hydrophones are, and searching males, by transferring from one group of females to another as they encounter one another, should be able to reduce travel time. The presence of males, as indicated by their clicks, might induce female groups to converge: in our study a male was twice as likely to be present when two or more groups were identified within 2 h. Therefore the mean time for males to find groups of females off the Galapagos was probably less than 26 h. The length of oestrus for female sperm whales is unknown. If it is longer than a day, then groups of female sperm whales would have to be more dispersed than in our study area, where they averaged about 0.0005 groups/km², for harem holding to be a more profitable strategy for males than searching.

This model may have more general application in populations in which males have the option of either searching for groups of females or staying with a particular group. However the model is simplistic, and various factors could modify or invalidate its conclusions: females might eject males from groups, "resident" males might possess an advantage during encounters with other males, or a female might show signs of approaching oestrus which could be monitored by males.

The proportion of large male sperm whales encountered during our study was low, peaking at about 2.1% of the total at the end of the study. Best (1979) gives the proportion of sexually mature, large males (over 13.7 m long) to sexually mature females in the population as 1:2.6, and estimates 40% of the members of groups of females and immatures are not mature females. Therefore the proportion of large males in a population consisting of large males and groups of females and immatures is 22% ($1/(1 + 2.6 + 0.4 \times 2.6)$). This is considerably greater than the peak proportion of 2.1% that we observed. Observations from other tropical breeding areas also suggest proportions of large males in the range 0–4% (Whitehead 1986). Although there has been a general relative depletion of male sperm whales in the most recent phase of whaling, it is unlikely to have changed the ratio of mature animals of each sex by a factor of 10. Perhaps, because of energetic or other limitations, males might not breed every year, remaining instead in the colder waters where they normally feed.

The results presented in this paper, especially the low proportion of large males on the breeding grounds, the apparently labile and assortative mating system, and site fidelity of groups of females, have considerable implications for the assessment and management of sperm whale populations. These are discussed in a separate paper (Whitehead 1986).

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