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Social organization of female sperm whales and their offspring: constant companions and casual acquaintances

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Summary. Associations among female sperm whales, *Physeter macrocephalus*, and their dependent offspring, off the Galápagos Islands were studied between 1985 and 1989. The whales were found in groups containing about 23 individuals, with each individual having approximately 12 constant (over years) companions. These permanent units associated with one another for periods of ~6.5 days, although the rate and duration of these associations seemed to vary between years, perhaps because of differences in the food supply. The principal function of the closed units may be care of the offspring, and units in the same general area may derive benefit from feeding in a coordinated manner.

Introduction

Sperm whales, *Physeter macrocephalus*, are remarkable among the mammals for a number of reasons. Among these are their ecological success (Kanwisher and Ridgway 1983) and their highly developed society (Caldwell et al. 1966). It is likely that such distinctive characteristics may have been linked through evolution, and, thus, the survival value of sperm whale sociality is of particular interest.

Adult female sperm whales are much more gregarious and altruistic than adult males (Caldwell et al. 1966; Caldwell and Caldwell 1966). At about 4–5 years of age, males leave the social groups of females, which principally reside in tropical and subtropical waters, and begin a gradual movement into higher latitudes with increasing age, returning again to breed when about 27 years old (Best 1979). Best proposes two principal functions for sociality in female sperm whales: cooperative foraging, and the communal care of calves. Important evidence in assessing the value of sociality in a species can come from an examination of the nature and duration of bonds between individuals (Myers 1983).

Female sperm whales, together with their young, can sometimes be seen clustered at the surface, with each individual a few metres from its nearest neighbour, either moving steadily or lying still (Caldwell et al. 1966), but more frequently individuals are observed apparently foraging in a dispersed but coordinated fashion (Caldwell et al. 1966; Ohsumi 1971; Whitehead 1989). Four pairs of female sperm whales marked together in the North Pacific were also killed together 5–10 years later (Ohsumi 1971). This suggested to Best (1979) that the groups of females might constitute stable units. More recently, consistent associations between photographically identified female sperm whales have been found over periods of months and years off Sri Lanka and the Galápagos Islands (Gordon 1987; Whitehead and Arnbom 1987; Whitehead and Waters 1990). We have used cluster analyses on several thousand identifications from the Galápagos to allocate identified individuals to groups, and likelihood ratio tests did not reject the hypothesis that, within years, groups with a mean size of about 20 individuals were closed in membership (Whitehead and Arnbom 1987; Whitehead and Waters 1990). This mean group size of 20 is in approximate agreement with most previous estimates which have been summarized by Best (1979), who suggested a median group size might be 25 whales, and Caldwell et al. (1966), whose own observations suggested 12–50 animals per group. Part of the considerable variation in estimates of mean group size is likely to be due to differences in definitions as to what constitutes a group (Best 1979). Many authors were unable to do more than count whales at the surface, which, for a deep-diving cetacean, can severely underestimate group size. On the other hand, groups may sometimes associate at the surface (Whitehead and Weilgart 1990), leading to overestimates from visual counts.

As the time period of individual identifications from the Galápagos grew to 4 years, apparent anomalies started to appear (Whitehead and Waters 1990; Whitehead et al. in press). A few "transient" individual whales, and pairs of whales, appeared to move between groups over periods of weeks, and over periods of years the

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groups we thought to have stable membership appeared to sometimes lose or gain members, or to have split. The data certainly fit a model of closed groups significantly better than the null hypothesis of random associations (Whitehead and Arnbom 1987), but this does not necessarily mean that the groups were completely closed.

In this paper we develop an empirical approach, similar to those of Underwood (1981) and Myers (1983), for examining social organization from time-series of individual identifications. The results suggest a model of social organization for female sperm whales. We estimate parameters for the model and test its assumptions.

Methods

Field methods. Identification photographs of *Physeter macrocephalus* were taken during five field projects (23 February–20 April 1985; 3 January–28 June 1987; 4–20 April 1988; 27 October 1988–5 April 1989; 13 April–21 May 1989) off the Galápagos Islands, Ecuador (0° N; 91° W). Virtually all research was carried out within 100 km north, northwest, west and southwest of the major Galápagos Islands (Whitehead et al. 1989b). We located and tracked groups of sperm whales acoustically and visually; this enabled us to stay in continuous contact with sperm whales (perhaps of different groups) for periods of several days (Whitehead and Gordon 1986). During daylight, we would discreetly approach sperm whales lying at the surface to photograph their flukes as they dived.

Identification. Sperm whales can be identified individually from good photographs of their flukes (Arnbom 1987). Photographs from all years were identified and catalogued with assistance from a computer matching routine (Whitehead 1990). Each identification was assigned a quality grade from 1 (poor) to 5 (excellent), depending on how well an individual could be recognized with certainty from the identification (Arnbom 1987). All the identifications for all years were checked at least twice.

For subsequent analysis we only used those identifications of quality grade 4 or 5 which were accompanied by an accurate record of the time the photograph was taken. We omitted identifications of mature males and 1st-year calves. In the resulting data set there are 3414 high-quality photographs of 1295 whales, 364 of which were identified on more than 1 day.

Statistical methods. Independence in contingency tables was tested using the likelihood-ratio G-test (Sokal and Rohlf 1981). A curve was fitted to the standardized reassociation rates using the "nonlinear estimation" quasi-Newton procedure in SYSTAT (Wilkinson 1987) with least-squares error and weighting by the number of pairs of known associates in each time interval (different weighting procedures produced very similar results).

Portraying social organization. We define the *associates* of a given individual whale at any time as those individuals potentially able to be photographed within 2 h of it, and the *known associates* as those that actually were.

Let $g(d)$ be the probability that two associates on a particular day are still associates d days later [as in Fig. 3 of Underwood (1981) and on the time axis of Fig. 2 of Myers (1983)], and let M be the mean number of associates an individual has at any time. Then, if whale X has $N(X,t)$ known associates when photographed at time t and $N(X,t+d)$ known associates when photographed at time $t+d$, the expected number of repeated known associations with this whale on these two occasions is $N(X,t)\cdot g(d)\cdot N(X,t+d)/M$. Then, the expected total number of repeated known associations d days apart is:

$$C(d)=1/2\sum_{X,t} N(X,t)\cdot g(d)\cdot N(X,t+d)/M, \tag{1}$$

where the summation is over all whales X identified d days apart (a particular whale might be entered more than once if it was photographed on more than one pair of days separated by d days). (The "1/2" is because each reassociation will be counted twice, from the perspective of both individuals.) As M is unknown we cannot directly estimate $g(d)$, but $g(d)/M$, which might be called "the standardized reassociation rate," can be found from:

$$g(d)/M=2\cdot C(d)/\sum_{X,t} N(X,t)\cdot N(X,t+d). \tag{2}$$

If a whale was photographed more than once on the same day, only the first identification was considered. As an exception to this, $g(d\approx 0.25)/M$ was estimated for reidentifications of a whale on the same day but at least 4 h apart (in this case we used the first identification on each day and the first reidentification at least 4 h later). Time intervals (d) were grouped (<1 day, 1 day, 2, 3, 4, 5, 6–10, 11–20, 21–40, 41–160, 161–1550 days) so that $C(d)>100$ for each interval, giving some precision to the estimates of $g(d)/M$.

Results

Social organization in female sperm whales

The standardized reassociation rates, $g(d)/M$, are plotted against d, time in days, in Fig. 1. Confidence intervals cannot be easily added, as a tendency for individuals to be found in stable groups would make the data not independent (if whales X and Y are associated, and Y and Z are associated, then X and Z are also likely to be associated). However, the points for different d, being obtained from different pairs of days, are less confounded.

The general pattern suggested by Fig. 1 is that female sperm whales and their offspring possess two types of associates: some who stay associated for about 4–20 days, and others who are constant companions for a

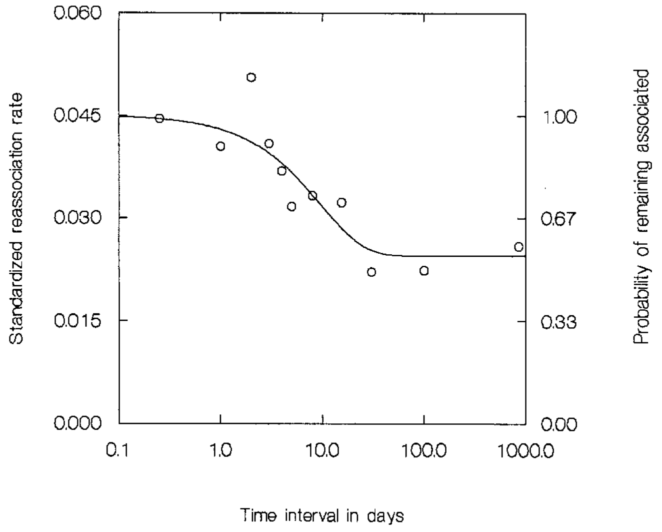

Fig. 1. *Physeter macrocephalus.* Estimated standardized reassociation rates (probability that associates remain together divided by the mean number of associates), $g(d)/M$, over different time intervals, d, together with fitted curve and derived estimated probabilities that associates remain together (*right axis*)

year or more. We now try to fit a model with these characteristics to the sperm whale data.

The model

We assume that a given individual whale at any time has two types of associate: "constant companions" stay associated with the individual throughout the period of our study, whereas "casual acquaintances" remain associated with the individual for a random length of time distributed according to the negative exponential distribution with parameter μ. After leaving, casual acquaintances never reassociate with the given whale. Suppose that a whale at any time is associated with a mean of n constant companions and m casual acquaintances, so that $M=n+m$. The probability that a given associate of a particular whale is a constant companion is $n/(n+m)$, and that it is a casual acquaintance $m/(n+m)$. Then:

$$g(d)=n/(n+m)\cdot 1+m/(n+m)\cdot e^{-\mu[(t+d)-t]} \tag{3a}$$

and

$$\begin{aligned} g(d)/M &= [n/(n+m)\cdot 1+m/(n+m)\cdot e^{-\mu((t+d)-t)}]/(n+m) \\ &= [n+m\cdot e^{-\mu\cdot d}]/(n+m)^2. \end{aligned} \tag{3b}$$

The results of fitting this curve to the estimated standardized reassociation rates are shown in Fig. 1, and parameter estimates (for n, m and μ) with their standard errors are presented in Table 1. The curve in Fig. 1 gives the expected values of the standardized reassociation rates at any time interval. The results suggest that at any time an individual was associated with about 12 constant companions, who remained with it for periods of two or more years, and about an equal number of casual acquaintances, who remained in association for periods of about 6.5 days (half-life for negative-exponential distribution with parameter 0.106). As this model is for all individuals in the population, this implies that each individual is a member of a "unit" (about 13 constant companions), and that at any time a mean of about two of these units are temporarily associated.

We can use the estimate for $M(n+m=22.0)$ to convert the standardized reassociation rates $[g(d)/M]$ into probabilities that associates remain together for different time periods $[g(d)]$. These probabilities are given on the right-hand axis of Fig. 1.

Table 1. Estimates of parameters of model of social organization in female sperm whales (*Physeter macrocephalus*) off the Galápagos Islands

Parameter	Interpretation	Estimate	SE
n	No. of constant companions	12.0 individuals	1.5
m	No. of casual acquaintances	10.0 individuals	0.8
μ	Rate of departure of casual acquaintances	0.106/day	0.038

Is the model realistic?

Although the model appears to fit the data on the estimated standardized reassociation rates, it is certainly not the only one which could do so. There are a number of assumptions in the model which should be examined critically:

1. Are constant companions constant? We would expect that these groups of constant companions would show some attrition as individuals die or emigrate. This would eventually lead to a drop in $g(d)/M$, the standardized reassociation rate, as d, the time interval, increased. However, there is no sign of such a drop over time periods of 40–1000 days in Fig. 1. Therefore there seems to be no substantial attrition over the time periods of our studies. Constant companions could conceivably also separate temporarily from time to time for periods of days or more. This is investigated in the next paragraph.

2. Do associates never reassociate after splitting up? Either constant companions or casual acquaintances could leave each other for periods of days or more, and then reassociate. If this behaviour were frequent, in our observations of pairs known to be associates over several days we would expect sequences of time during which a particular pair was not sighted together. We looked at sequences of days during which one of a pair of certain associates was sighted ("certain" because the pair was photographed associating both before and after the sequence). Over intervals of less than 3 days two identifications of one of the whales not associated with the other followed one another about as many times as would be expected if the sequence were random (75 times observed, 71.9 expected, $G(1)=0.440$, $P>0.5$). Therefore, there is no evidence in our data of associates leaving each other temporarily.

3. Are constant companions and casual acquaintances equally likely to be photographed as associates? It is feasible that, within our definition of association, constant companions might be more likely to be photographed associating with a given whale than casual acquaintances. If this is the case, considerable complexities are added to the model. To examine this possibility we looked at the sighting rate of certain associates. We compared known "long-term" associates, which had been photographed as associates on two occasions at least 40 days apart (which will almost entirely consist of constant companions), and known "short-term" associates, which had been photographed as associates at a maximum of 3 days apart (which will include both constant companions and casual acquaintances). On days between their first and last identification as associates, short-term associates had a standardized reassociation rate of 0.054, whereas long-term associates had a rate of 0.046. There is no significant difference between these rates $[G(1)=0.5624, P>0.25]$, and the short-term rate is higher – the opposite trend to that which would be expected if casual acqaintances were less readily photographed.

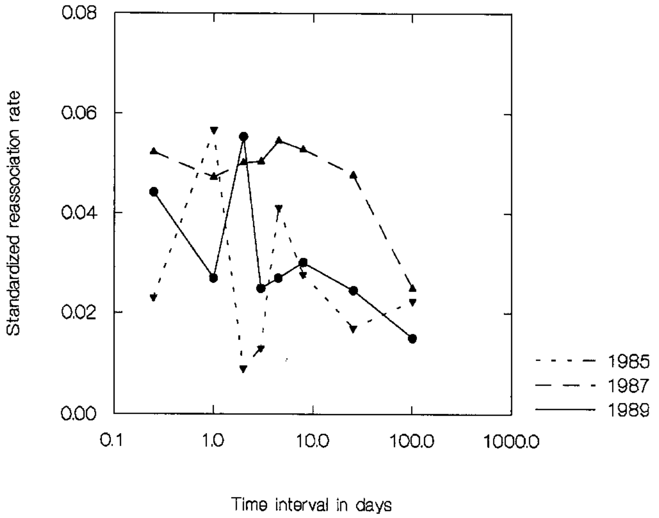

Fig. 2. Estimated standardized reassociation rates over different time intervals in 1985, 1987 and 1989

4. *Is "being photographed within 2 h of" a good measure of association?* Observing sperm whales in the wild is not especially easy so that, other than functions of the temporal proximity of identifications, it is hard to envisage measures of association between known individuals that could be collected systematically enough to provide data suitable for an examination of social organization. However, we repeated the analysis described above, using 1 h as the cut-off for whales to be considered associates. Results were similar, but less precise, as fewer identifications were considered ($n = 11.8$, SE 1.7; $m = 7.1$, SE 1.0; $\mu = 0.181$, SE 0.06).

5. *Are the association patterns invariant with time?* Figure 2 plots the standardized reassociation rate, $g(d)/M$, against time interval, d, for the three years during which substantial amounts of data were collected (1985, 1987 and 1989). There are insufficient data, especially over long time periods, to make useful estimates of the parameters of the model using the method described above for each year separately. However, the data points in Fig. 2 suggest that, compared with 1985 and 1989, in 1987 the mean number of associates was smaller [$g(d) \approx 1$ when $d \ll 1/\mu$, so that M approximately equals $1/g(d)/M$ at low d], and that casual acquaintances had more persistent associations [as $g(d)/M$ dropped at higher d in 1987 than in 1985 or 1989].

Discussion

In some respects the analysis presented here does agree with results of previous studies using both the same and different data. The estimated mean group size of *Physeter macrocephalus*, $m + n + 1 = 23.0$, is close to other modern estimates (Best 1979; Whitehead and Waters 1990), and the data show that female and immature sperm whales have constant companions for periods of at least several years, in agreement with other studies (Gordon 1987; Ohsumi 1971; Whitehead and Waters 1990). However, the crucial difference is that not all members of a group are permanent associates. A "group" seems to consist of an average of about two units, each with about 13 members ($n + 1$). It is these units that are stable in composition, and all whales are members of units. Associations between them last for periods of very roughly 6.5 days. During the period of association, as far as the tests performed on our data were able to show, members of the different units are well mixed.

It is likely that there is considerable variation in the sizes of groups, sizes of units, and the duration of associations between units. For instance, the "transient" individuals and pairs that Whitehead and Waters (1990) found to be moving between groups may constitute especially small units, whereas the 18 individuals that were found in the same group over a period of 2 years may constitute a particularly large one. It is quite possible that these stable associations of about 13 individuals are "family units," a term used for closely related females, plus male offspring younger than the age of dispersal, of other species. Such a matrilineal system might explain the tendency for morphometric similarity of whales within groups found by Arnbom and Whitehead (1989).

What is the principal function of these closed, possibly matrilineal, units of female sperm whales and their offspring? There is growing evidence that adults within groups cooperatively care for their young, principally protecting them from predators (Best 1979; Gordon 1987; Arnbom and Whitehead 1989). This may well be adaptive for females of a species in which adults make feeding dives to substantial depths for sufficiently long periods that their young calves cannot follow. The calves are then left vulnerable at the surface to potential predators like killer whales, *Orcinus orca* (Arnbom et al. 1987). There is also some evidence of communal nursing (Best 1979; Gordon 1987). Such a system of communal calf care is only likely to persist when members of altruistic groups are related, or the conditions for reciprocal altruism are met. Both selection mechanisms require that individuals stay together over considerable periods.

The associations between units, lasting only a matter of days, are less likely to have this calf-care function. Instead, they are perhaps most reasonably related to foraging. Whitehead (1989) found that female and immature sperm whales off the Galápagos generally foraged in structured formations, and concluded that this may have benefited individuals by providing information about prey densities and avoiding mutual interference from other whales feeding in the same place. For stable units of sperm whales feeding in the same general area for periods of days, it may be adaptive to form groups which can forage together in a fairly structured manner. If this were the major function for the grouping of units, we might expect that the dynamics of their fusion and fission would vary with the environmental conditions, as particular prey densities and distributions favour different rates and durations of association. This does seem to be the case. The analysis of the different years of our study in Fig. 2 suggests that units merged more frequently, and for shorter periods, in 1985 or 1989 than in 1987.

This may be linked to the "El Niño" oceanographic conditions of 1987 in which the sperm whales off the Galápagos appeared to have reduced feeding success (Whitehead et al. 1989a).

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