Sperm whale social units: variation and change

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Abstract: Sperm whale (*Physeter macrocephalus*) photoidentification data spanning 12 years of study around the Galápagos Islands were examined to investigate the size, variability, and stability of social units. Adult females and immature whales of both sexes have two types of associates: “constant companions,” which are members of an individual’s “stable” social unit, and “casual acquaintances,” which are temporarily associating members of different units. We analysed long-term association patterns and calculated that individuals have a mean of 11.3 constant companions. Estimated social unit size ranged from 3 to 24 individuals. Evidence of splitting and merging of units and of transfer of individuals between units is presented. The estimated overall frequency of these unit-membership changes is 6.3% per individual per year. These forms of unit dynamics are rare in species with male dispersal and matrilineally related social groups, and cannot be easily explained in this species. There is considerable variation in unit size (perhaps caused by demographic processes), suggesting that the benefits of remaining in a social unit usually outweigh selection for some optimal unit size. However, the occurrence of merging and transfers suggests that the ecological or social cost/benefit of leaving one’s matrilineal unit may sometimes outweigh the cost/benefit of staying.

Résumé : Des photographies individuelles de cachalots (*Physeter macrocephalus*), recouvrant une période d’étude de 12 ans dans les Galápagos, ont servi à étudier la taille, la variabilité et la stabilité des groupes sociaux. Les femelles adultes et les individus immatures des deux sexes s’allient à deux types de compagnons : ils ont des « compagnons constants », qui sont des membres du même groupe social « stable », et des « connaissances d’occasion » qui sont des membres d’autres groupes auxquels ils s’associent temporairement. Nous avons procédé à une étude à long terme de ces associations et avons calculé qu’un individu a en moyenne 11,3 compagnons constants. Un groupe social contient de 3 à 24 individus. Nous avons observé des séparations et des fusions au sein des groupes, de même que des transferts d’individus d’un groupe à un autre. La fréquence globale de ces changements d’appartenance a été estimée à 6,3% par individu par année. Ce type de dynamique au sein des groupes est rare chez des espèces dont les mâles se dispersent et où les groupes sociaux sont formés par affiliation maternelle, et il est impossible à expliquer chez cette espèce. Il y a une variation considérable de la taille des groupes (peut-être causée par des processus démographiques), ce qui semble indiquer que les bénéfices d’appartenir à un groupe social dépassent généralement les bénéfices de la sélection pour la taille optimale d’un groupe. Cependant, les fusions et transferts qui se produisent au sein des groupes indiquent que les coûts/bénéfices écologiques ou sociaux reliés au fait de quitter son groupe d’affiliation maternelle dépassent parfois les coûts/bénéfices reliés au fait d’y rester.

[Traduit par la Rédaction]

Introduction

One of the fundamental issues in any study of social species is the size and stability of social groupings. Among mammals, female grouping behaviour is thought to be directly related to resource acquisition and predation avoidance (Wrangham and Rubenstein 1986), so the pattern of social groups gives us insight into the ecology of the species. Female grouping behaviour is a strong determinant of male social behaviour (Wrangham and Rubenstein 1986), and therefore strongly constrains mating strategies and systems. The size and stability of social groups may vary with the types of interactions and strengths of relationships between individuals. Where group members are related and (or) are long-term associates, there is the potential for kin selection (Hamilton 1964) and reciprocal altruism (Trivers 1971). Information on the nature and duration of bonds between individuals can aid in assessing the value of sociality for a species (Myers 1983).

Group size and membership may be recorded instantaneously for some species in some circumstances. However, in many situations this information is difficult to obtain, perhaps because not all members of a social group are found together at one time, or some individuals, although present, are obscured from the observer’s view. In cases where group size cannot be determined visually, and instantaneously, measures of association must be developed to investigate the strength of relationships between individuals. Measures of association may be behavioural, spatial, or temporal, but must always be selected with reference to the individual animal’s experience, and at appropriate scales. It is then important to define rigorously what is meant by a group (Whitehead and Dufault 1998). For any thorough analysis of social organisation or group dynamics, it is necessary to be able to identify animals individually.

The study of group membership and dynamics in cetaceans is complicated by the environment in which they live.

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Sperm whales (*Physeter macrocephalus*) dive to feed, and hence foraging individuals are unavailable for surface counts to determine group size. Individual sperm whales are identifiable from photographs of their tail flukes (Arnbom 1987). Typically, the tail flukes are raised only at the start of a foraging dive, and since the dive-cycle time of sperm whales is approximately 50–60 min (Papastavrou et al. 1989), each individual is available for identification only roughly once every hour. Since individuals cannot usually be distinguished at the surface (except when the tail flukes are raised), behavioural or spatial measures of association cannot be collected routinely, and temporal measures, based on identification times, are the only readily available data for investigating social associations. Past research has used a 2 h association criterion, so two individuals are considered associates if they are photographically identified within 2 h of each other (e.g., Whitehead et al. 1991, 1992). We wished to test a range of temporal association criteria to determine whether the 2-h period most appropriately reflects the association patterns of individuals.

Two other factors complicate the study of sperm whale sociality. Maximum longevity of female sperm whales exceeds 60 years (Gambell 1972), yet it is possible for research vessels to follow groups for a maximum of a few days at a time. Therefore the data collected can form only short-term “snap-shots” in relation to an individual’s lifetime experience of sociality. Sperm whales are not territorial, and females may have ranges in the order of 1000 km (Best 1979; Dufault and Whitehead 1995). As a result, particular individuals are infrequently and unpredictably available for study.

Male sperm whales disperse from their natal groups prior to attaining sexual maturity (Rice 1989) at an estimated mean age of 6 years (Richard et al. 1996), returning to the tropical and subtropical waters inhabited by females and immature animals in their late twenties to breed (Best 1979). Female sperm whales and their offspring live in a fission–fusion society, with observed groups representing temporary associations between permanent social units (Whitehead et al. 1991). These units associate for periods of only hours to days (Whitehead et al. 1991). Thus, at any time a particular individual may have two sets of associates: “constant companions” and “casual acquaintances” (Whitehead et al. 1991). Constant companions are members of an individual’s own unit, and are “permanent” associates. Casual acquaintances, however, are members of a separate, associating, unit.

Although female philopatry is thought to be the norm, there are indications of some female dispersal from stable units (Best 1979; Richard et al. 1996), and of long-term association between members of different matrilines (Richard et al. 1996). Genetic studies have indicated that a group may consist of one or more matrilines (Richard et al. 1996). The most obvious interpretation is that each constituent unit within a group constitutes a single matriline. However, the study of genetic relationships within known units indicates that units may not all represent perfect matrilines, and that some may include individuals with different mitochondrial haplotypes (J. Christal, unpublished data).

The “stable units” model of sperm whale sociality was developed from a relatively short data series, including sightings of sperm whales in the Galápagos Islands in 1985, 1987, and 1989. This model has consequences for all aspects of sperm whale research, from behaviour, genetics, and population modeling to theories on the evolution of sociality. With a longer data set available (1985–1996), we felt that it was important to test the model. In this paper we consider the different temporal-association measures that can be used in analysing sperm whale sociality, and determine which is the most appropriate. We estimate the numbers of constant companions of known individuals, examine the possibility of preferred companionships within units, and calculate the frequency distribution of unit sizes and overall mean unit size. We also investigate unit membership and consider evidence for the stability and dynamics of sperm whale social units.

Methods

Field methods

Identification photographs of adult females and immature sperm whales of both sexes were collected during field research aboard sailing vessels in a study area around the Galápagos Islands (1°30´S–1°30´N, 89°–92°30´W) during 1985, 1987, 1988, 1989, 1991, 1993, 1994, 1995, and 1996, and off the western coast of mainland South America from Panamá (7°N, 80°W) to Peru (19°S, 72°W) during 1985, 1991, 1993, and 1995.

Identification

Analysis of fluke photographs followed the methods devised by Arnbom (1987) with later refinements by Dufault and Whitehead (1993). Each black and white negative was assigned a quality (Q) grade from 1 (poor) to 5 (excellent), based on the focus and resolution of the image, the angle of the fluke relative to the negative plane, and the proportion of the fluke visible within the frame (Dufault and Whitehead 1993). Individuals were identified from negatives of $Q \geq 4$ and assigned identification numbers. A black and white print of the best negative available for each individual was digitised (using a *Calcomp* digitising tablet) into a computer catalogue that stores details of the locations and types of markings along the trailing edge of the fluke (Whitehead 1990). Each new set of individuals was compared with the past catalogue, both visually and using a computer matching program (Whitehead 1990).

Selection of key individuals

Sightings records for all individuals were searched in order to identify animals that had been seen during at least three identification periods, with each period separated from all others by a gap of at least 30 days. This interval was selected to ensure that any associates common to two separate identification periods were likely to be constant companions (as determined by Whitehead et al. 1991). Any individual with a sighting history that conformed to these criteria was designated a “key individual.”

To identify the most appropriate temporal association criterion for use in this study, a number of different association intervals were analysed. Past work has used a 2 h association criterion (e.g., Whitehead et al. 1991, 1992). Clearly, the longer the time interval being considered, the greater the proportion of the total number of constant companions that will be identified. Our aim was to find the association interval or range of association intervals that allows the most accurate estimation of individuals’ true numbers of constant companions. The following association criteria were tested: 10 min, 30 min, 1 h, 2 h, 4 h, 6 h, and 12 h. Since light conditions in the study area are suitable for photoidentification from almost exactly 6 a.m. to 6 p.m., an association criterion of 12 h is equivalent to “being identified on the same day.”

At this point, the original photographs of the key individuals and all their associates (those identified using the 12-h criterion) were scrutinised to check for incorrect or missed matches. Only two errors were found, both involving missed matches (i.e., a previously identified whale was not recognised as such and was given a new ID number on a second or subsequent sighting). Although it is impossible to rule out the possibility that errors remain, the use of only $Q \geq 4$ identifications, and the scrutinisation process, should mean that they are very few.

A QuickBasic^{TM} program was written to investigate the associates of each of the key individuals. Once the association criterion is specified, the program outputs list (for each key individual) the first and last dates of each identification period, the numbers and identities of all associates during each identification period, and the identification numbers of all individuals that were associates during at least two identification periods.

Estimation of numbers of constant companions

At any given time, the set of associates of a key individual will consist of a number (N) of companions who remain with it constantly, plus a variable number of casual acquaintances (Whitehead et al. 1991). The key individual and its constant companions together form a permanent unit of size $N + 1$. As casual acquaintances remain with an individual for up to a few days (Whitehead et al. 1991), and the population is large (Whitehead et al. 1992), we assume that individuals associating with a whale during two or more periods separated by at least 30 days were constant companions.

For each whale we wished to estimate the number of constant companions, N. Suppose a particular whale, I, was observed during three periods, t_1, t_2, and t_3, then let n_{12} be the number of associates common to t_1 and t_2, n_{13} the number of associates common to t_1 and t_3, n_{23} the number of associates common to t_2 and t_3, and n_{123} the number of associates common to t_1, t_2, and t_3. The three periods are separated by sufficient time that all individuals associating with I in two or more periods are likely to be constant companions. So, if p_1, p_2, and p_3 are the probabilities that constant companions were identified in periods t_1, $t_{2,}$ and $t_{3,}$ respectively:

$$n_{12} \simeq N \times p_1 \times p_2$$

$$n_{13} \simeq N \times p_1 \times p_3$$

$$n_{23} \simeq N \times p_2 \times p_3$$

$$n_{123} \simeq N \times p_1 \times p_2 \times p_3$$

Therefore an estimator for N is

$$N = \frac{n_{12} \times n_{13} \times n_{23}}{n_{123}^2}$$

This estimator is biased infinite if $n_{123} = 0$. Therefore, following Chapman's (1952) modification of Petersen's mark–recapture estimate, we used the following estimate of the number of constant companions of I:

$$[1] \qquad N = \frac{(n_{12} + 1) \times (n_{13} + 1) \times (n_{23} + 1)}{(n_{123} + 1)^2} - 1$$

Simulation showed that this estimator is approximately unbiased when n_{123} is greater than 2, but has a negative bias when n_{123} is smaller. N was estimated for all key individuals for each association criterion. For key individuals with four or more identification periods, N was calculated using each set of three identification periods. The median value of the multiple estimates of N was then used as the estimate of N for that key individual.

Unit delineation

Units were delineated by identifying sets of individuals that had been associated during several identification periods. The following working definition of unit membership was used: a set of individuals of which each was associated with at least two of the others during at least two identification periods. Where a unit was represented by only one key individual, all animals associated with that key individual during two identification periods were considered to be members of its unit.

Preferred companionships

If individuals have a subset of their constant companions with which they associate preferentially, and either these preferred companions show a greater degree of synchrony in their dive cycles and (or), at least on some occasions, these sets of companions separate off as scattered subgroups, then preferred companions would be likely to be identified close together in time but other unit members may not. Hence, preferential associations of this type would result in artificially small estimates of the number of constant companions when the shorter association intervals are used. To investigate this possibility the data were examined for indications of preferred companionships.

For each key individual, the associates for each successive pair of identification periods for both the 12 h association criterion and for shorter association criteria were considered. K is the set of associates (using the 12 h criterion) common to t_1 and t_2; K_1 is those associates (using a shorter criterion) present at t_1; K_2 is those associates (using a shorter criterion) present at t_2; K_{12} is those associates (using a shorter criterion) common to t_1 and t_2.

If the set of constant companions that was identified within the shorter time interval of a key individual is simply a random assortment of the total number of constant companions present, then the expected value of K_{12}, $E(K_{12})$, can be calculated as

$$[2] \qquad E(K_{12}) = \frac{K_1 \times K_2}{K}$$

If preferred companionships do occur, the extent to which the number of constant companions common to two periods, K_{12}, exceeds that expected by chance, $E(K_{12})$, will be greater for intervals closer to, rather than further from, identifications of a key individual. To test for evidence of preferred companionships, K_{12} and $E(K_{12})$ were calculated for each key individual, for each successive pair of identification periods, for two different shorter association criteria: "less than 10 min" and "more than 10 min but less than 20 min" from identifications of the key individuals. To reduce problems of non-independence of the data, only values corresponding to the largest $E(K_{12})$ value for each individual were selected for analysis. The distributions of $K_{12} - E(K_{12})$ values (i.e., the extent to which numbers of associates differed from those expected by chance) for these two data sets were then compared using a Mann–Whitney U test.

Unit stability/dynamics

The long-term association patterns of the key individuals were searched for indications of unit membership change. Three forms of unit dynamics were investigated: splitting: defined as the division of a previously cohesive unit into two or more smaller units; merging: defined as the union of two previously distinct units; and transfer: the movement of one or more individuals from one unit to another. Estimates of rates of the three different types of unit membership change were calculated as the total number of changes for all individuals divided by total animal-years (where total animal-years equals the sum, for all individuals, of the number of years between first and last identification). For mergers and splits, each member of all affected units was considered to have undergone

Fig. 1. Comparison of mean estimates of the number of constant companions for all 91 key individuals for the seven temporal association intervals. Error bars depict 1 standard error about the mean.

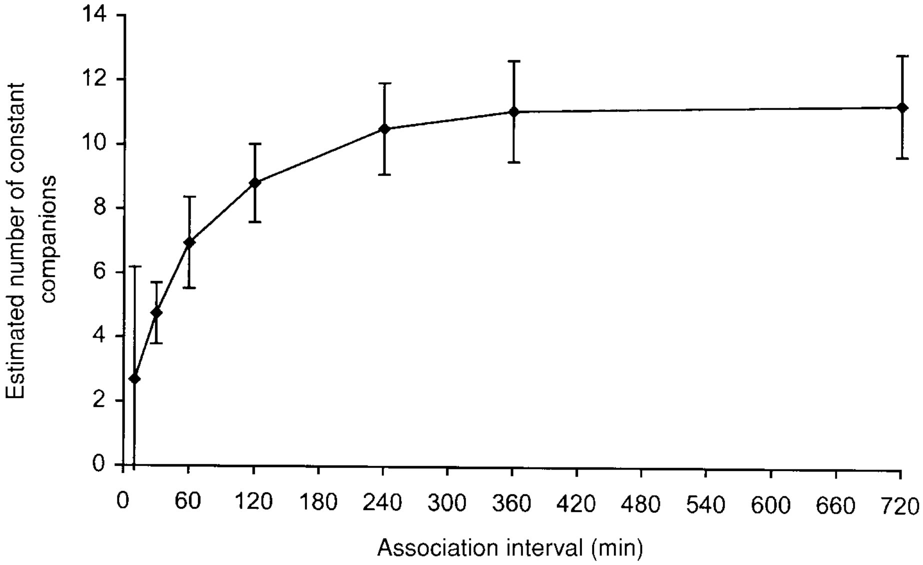


Table 1. Numbers of individual whales (key individuals) identified in three or more identification periods ($Q \geq 4$).

No. of identification periods	No. of individuals
3	57
4	24
5	10
Total	91

unit-membership change; for transfers, however, only those individuals directly involved were counted.

Results

Identifications and key individuals

Our data base includes 5129 photographic identifications of $Q \geq 4$, representing 1809 individual sperm whales (excluding mature males). Of these, 91 individuals satisfied the requirement of having been photographically identified during at least three periods separated by at least 30 days and so were designated key individuals (Table 1). With the exception of eight individuals (members of a single unit) for which one identification period occurred off the coast of Ecuador, all identifications of the key individuals occurred within the Galápagos study area. In the vast majority of cases, because of the seasonal nature of the research, identification periods were separated by at least 1 year. These 91 key individuals and their associates formed the basis of this study of unit membership.

Estimation of number of constant companions

The analysis of constant companion numbers was performed for the 91 key individuals for each of the seven temporal association criteria. Estimated numbers of constant companions (N) ranged from 0 to 59. The mean estimates of key individuals' numbers of constant companions increased with increasing association interval (Fig. 1). Clearly, the longer the time interval being considered, the greater the proportion of the total number of constant companions that will be identified, and thus the larger n_{123} will be. Therefore, the trend towards an increase in the estimated mean number of constant companions with an increasing association interval would be expected, given the properties of our estimator, although some of the increase could be due to preferred associations within units (see below). The rate of increase slows as the association interval increases, and the estimated means appear to be approaching an asymptote, which represents the true mean number of constant companions. There is no significant difference between the estimated mean numbers of constant companions for the 6 and 12 h association intervals (Welch's approximate t test, $p > 0.05$), but the estimate for the 12 h association interval is significantly higher than those for the 4 h and 2 h association intervals (Welch's approximate t test, both $p < 0.05$). Since the bias in our estimator will be least for the longest association interval, the estimated mean number of constant companions for the 12 h association interval, 11.3, is our best estimate of the true value. Unit size is simply a key individual's number of constant companions, plus the key individual itself (i.e., $N + 1$); thus, this analysis provides an estimate of mean unit size of 12.3.

Unit delineation

Units were delineated as described above. The number of units into which the key individuals and their associates were delineated decreased with increasing association interval (Table 2). This is a result of the artificial splitting of some larger units caused by small numbers of associates being identified during the shorter association intervals. Estimates of the number of constant companions for animals allocated to the same unit were significantly less variable

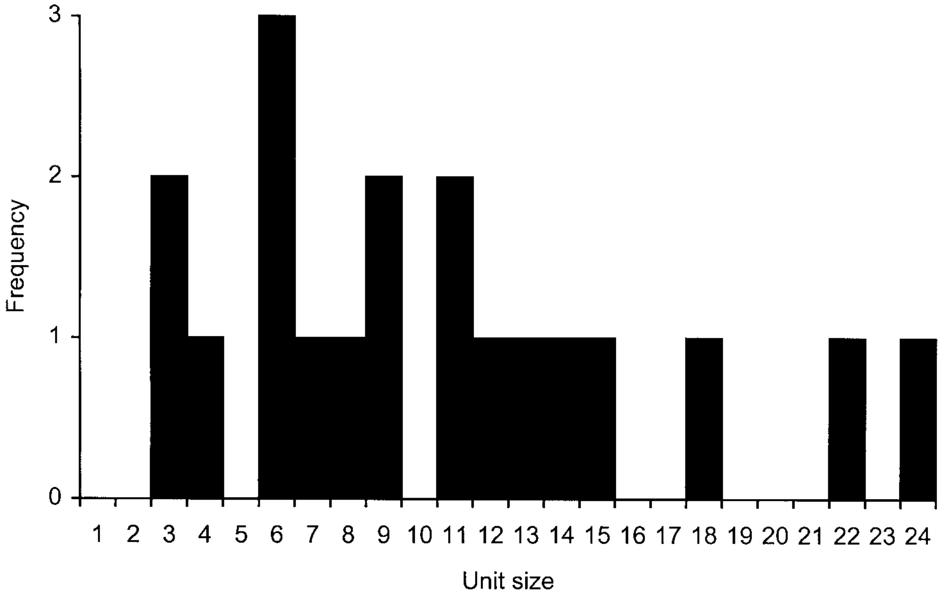
Table 2. Unit delineation and statistical significance of within-unit correlation of estimated numbers of constant companions for the seven temporal association intervals.

	10 min	30 min	1 h	2 h	4 h	6 h	12 h
No. of units[a]	46	37	31	28	24	21	19
n^b	92	94	95	95	94	93	96
p	0.088	0.000	0.008	0.013	0.021	0.045	0.029

[a] Number of units delineated using the following working definition: a unit equals a set of individuals each of which was associated with at least two of the others during at least two identification periods.

[b] Number of key individuals (some key individuals, with four or more identification periods, were assigned to more than one unit on the basis of their sets of associates, for some association criteria. As a result, these individuals were included twice in ANOVAs to investigate the relationship between unit membership and estimated number of constant companions (therefore n ranges from 92 to 96).

Fig. 2. Frequency distribution of unit sizes delineated using the 12 h association criterion.



(ANOVA, $p < 0.05$) than those between units, for all association criteria greater than 10 min (Table 2) as would be expected, since all members of a single unit have the same true number of constant companions.

When the frequency distribution of delineated units is examined (Fig. 2; in this case using the 12 h association criterion) it is clear that there is considerable variation in unit size. The estimated mean size of the delineated units (using this association criterion) is 10.4 (range = 3–24, SD = 6.23, CV = 0.60). This value represents the mean size of units from the observer's perspective. A measure of unit size that is more relevant to the whales' experience of sociality is the size of unit in which the average individual found itself. This can be derived by summing the size of unit in which each individual found itself and dividing by the total number of individuals, to find the "typical unit size" (Jarman 1974). Using the data shown in Fig. 2, the typical unit size is 13.9.

Preferred companionships

The distributions of K_{12}–$E(K_{12})$ for the 10 min association interval and the greater than 10 min but less than 20 min association interval did not differ significantly (Mann–Whitney U test, $p = 0.142$), suggesting that there were no preferred companionships among unit members. For the 10 min association interval, the observed number of associates common to two periods (K_{12}) exceeded that expected by random assortment ($E(K_{12})$) by a mean of only 0.10 companions. The fact that this value is double that for the greater than 10 min but less than 20 min association interval (mean K_{12}–$E(K_{12})$ = 0.05) may indicate that, in fact, a very slight degree of preferred companionship is occurring. The limited extent of any preferred companionship makes it unlikely to be a major contributor to the trend shown in Fig. 1.

Unit stability/dynamics

Although the delineated units generally appear to have closed membership (allowing for birth and death of unit members), an examination of the patterns of long-term association does provide evidence for some variation about this norm. There are examples of splitting of units, merging of units, and transfer of individuals between units.

The data set provides some evidence for the splitting of a unit, although unfortunately the permanence of this split cannot be assessed. In 1995, a set of five individuals were identified together (in association with another unit). These five animals had previously been identified as members of unit A (Fig. 3*a*), the largest unit delineated in this study, with 24 members. The set of five animals seen in 1995 was followed continuously for 7 days, yet none of the other 19 members of unit A were seen during that week, or even during that field season. Because these 19 individuals have not been identified since 1991, and the set of 5 animals has not been seen since they were identified in 1995, it is not possible to determine whether this separation represents a temporary dissociation or a permanent division of the unit.

To demonstrate merging, which we define as the union of two previously distinct units, a considerable amount of information is required. Both of the original units must have been seen at least twice for delineation of those units to be possible (so that merging can be distinguished from transfers) and to ensure that the "merged" unit is not simply a later sighting of all members of an original unit, not all of which were identified initially. In addition, the merged unit must have been sighted at least twice, so that merging of units can be distinguished from casual association. Given these requirements, and the small number of individuals that have been sighted in four or more periods (Table 1), it is perhaps not surprising that there is no clear-cut example of merging in our data set. There is, however, a case that exemplifies either merging or transfer (Fig. 3*b*). In 1987, 2 whales (793 and 795) were identified in association with 13 other whales. Two months later a separate unit of approximately 15 whales (unit B in Fig. 3*b*) was identified, and this pair was not seen. However, when unit B was identified in 1988, 1994, 1995, and 1996, whales 793 and 795 were present. That these two whales had permanently joined a new unit is clear. What is not so clear is whether this is a case of merging or transfer. If, at their initial identification in 1987, whales 793 and 795 were a unit of two individuals and their associates were simply casual acquaintances, then the joining of this pair with unit B represents the merging of two units. Alternatively, if whales 793 and 795 were members of a larger unit in 1987, and then left that unit to join unit B, then this is a case of the transfer of two individuals between units.

The data set also provides evidence for three definite transfers (without the complication of the possibility of merging). In each case a single individual transferred between units. Whale 236 was identified during four periods between 1985 and 1989 (Fig. 3*c*). It had approximately 20 associates during each of these periods. Only two associates were common to the first two identification periods, indicating that whale 236 was a member of a fairly small unit at this time. There were no associates in common between the second and third periods, but of the associates identified in the third period (all of which were new, i.e., none in common with the first or second period), 14 were also identified in the fourth period. Our interpretation is that whale 236 transferred from its original, small unit to a completely separate, larger unit at some time between the second and third identification periods. Whale 902 provides a second example of a transfer. Although its unit affiliation is unknown from its first sighting in 1987 (at which time it was associated with a unit that was resighted in 1989 and 1996), it had no associates in common between 1987 and later sightings. In 1989 and 1993 it was identified as a member of a unit of 11 individuals. Whale 2942 was first identified in 1994 with a previously sighted unit (unit E; Fig. 3*d*). When this individual was seen again, in 1995 and 1996, it was associated with a different unit (unit B), and none of its associates from 1994 were identified.

Who transfers? Of the three individuals that definitely transferred (Figs. 3*c* and 3*d* and whale 902) and the two individuals that either merged or transferred (Fig. 3*b*), three animals are known or presumed to be female. Whales 795 and 2942 were sexed using a molecular technique (Richard et al. 1994). Whale 793 was photographically measured (Gordon 1990) at a size that is inconsistent with it being a male, given the number of years for which the animal has been known (using growth curves in Best 1970). Whales 793 and 795 were both measured in 1995 at lengths that correspond to an age of at least 20 years (Best 1970), therefore they were both at least 14 years of age, and thus sexually mature (Best 1968), at the time of unit membership change. Whale 2942 was also photographically measured in 1995, at which time its length corresponded to an age of 5–6 years. Thus, at the time of transfer it was an immature female 4–6 years old. No information is available on the sex or age of whales 236 and 902. Hence, of the animals that moved between units, two were adult females, one was an immature female, and two were of unknown age and sex.

Rates of unit-membership change were calculated separately for each type of change over the 537 animal-years encompassed by the data. It should be recognised that the following values are simply estimates, provided in order to indicate the order of magnitude of changes. The rates of unit-membership change per individual each year were as follows: 0.026 for mergers, 0.028 for splits, 0.009 for transfers. These values indicate that there is roughly a 6.3% chance that a given individual will be involved in merging or splitting of a unit, or will transfer between units, within any given year.

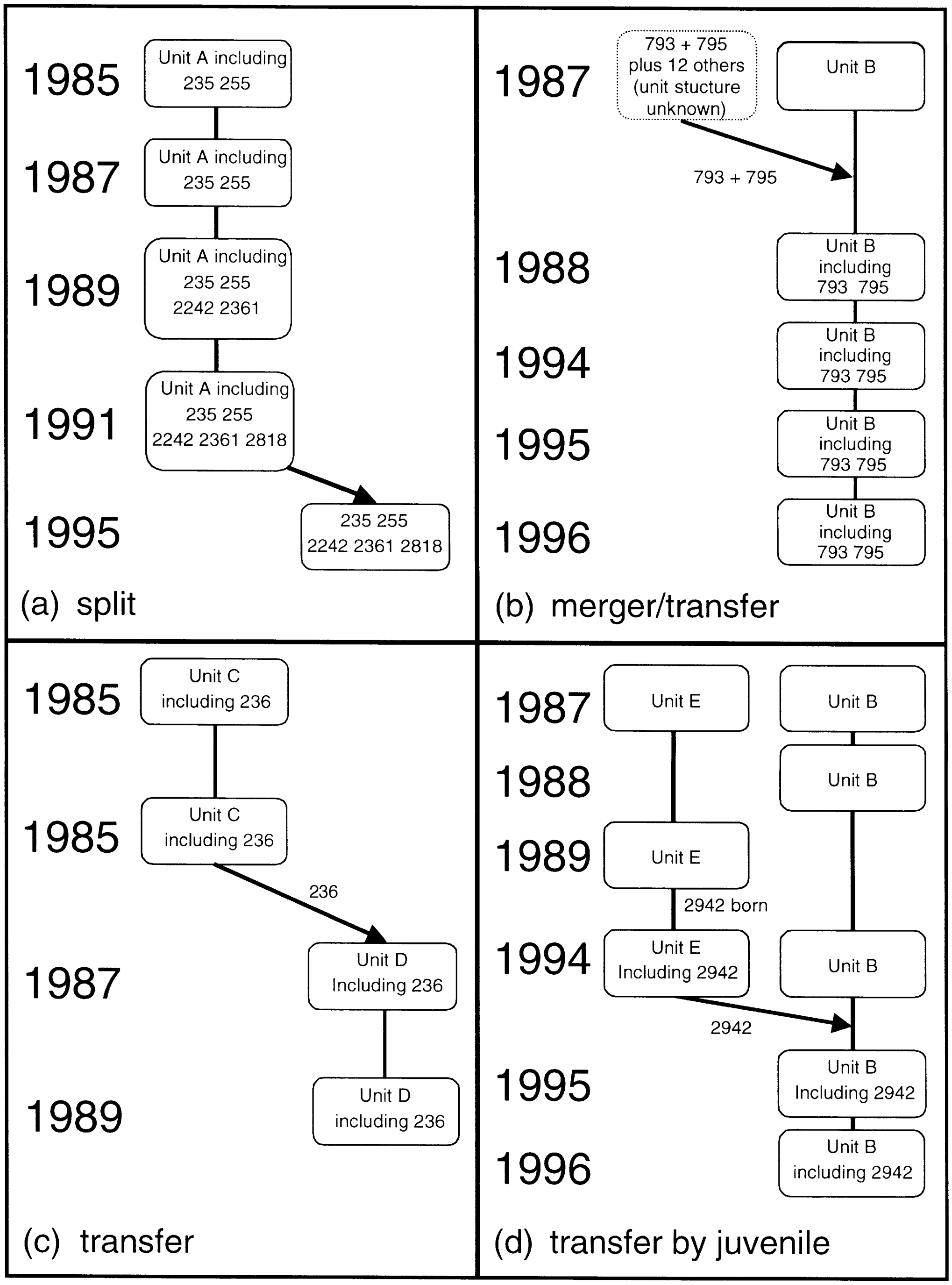
Discussion

Use of the shorter association intervals (less than 2 h) artificially reduced the estimated numbers of constant companions (Fig. 1) and artificially increased the number of units delineated (Table 2). While preferred companionships among unit members might partially explain these results, the extent of any preference was too limited to be detected statistically, and preferred companionships are unlikely to have had a considerable effect on results. The asymptotic nature of the curve of estimated mean numbers of constant companions (Fig. 1), with no significant differences between the values for the 6 and 12 h association criteria, indicates that at these time intervals, the estimated means approach the true mean numbers of constant companions.

Since our analyses of potential biases in the estimates indicated that the extent of any bias would be least significant for the 12 h association criterion, we consider the estimated mean number of constant companions using this criterion, 11.3, to be our best estimate of the real mean number of constant companions. Since the estimated means for the 2 and 12 h association criteria are significantly different, past work using the 2-h interval (e.g., Whitehead et al. 1991) may have slightly underestimated the true numbers of associates.

Using "number of constant companions + 1" as the unit size, the mean unit size is estimated at 12.3. This agrees

Fig. 3. Diagrams of unit-membership dynamics. Units are represented by boxes, which are linked between years to indicate stability of unit membership. Notations such as "unit B" are used to represent all original members of that unit, except in *a*, where "unit A" is used to denote members of the original unit for which individual identification numbers are not shown. (*a*) Long-term association patterns of members of an original unit "A." Five members of the unit were identified in 1995, in the absence of the rest of the unit, indicating a split of unknown duration within the unit. (*b*) Two individuals (793 and 795) transferred into, or merged with, unit B between 1987 and 1988. (*c*) Transfer of individual 236 from its original unit, C, to a second unit, D. (*d*) Whale 2942, photographically measured (Gordon 1990) and estimated to be 5–6 years old in 1995, was first identified as a member of unit E. Between 1994 and 1995, it transferred permanently from its original unit, E, to unit B.



with "about 13" estimated by Whitehead et al. (1991) using lagged association rates calculated from data from 1985–1989. Although the mean size of the units delineated (using the 12 h association criterion) is 10.4, the unit size experienced by the average individual (Jarman's (1974) "typical group size") is 13.9. There is considerable variation around these estimated mean unit sizes. Delineated unit sizes ranged from 3 to 24 individuals. De Vore and Hall (1965) suggest that a wide range of social group sizes in an apparently uniform environment indicates that social factors are more important than ecological factors in determining social group size. Unit size may be determined to some extent by demographic stochasticity, through such factors as individual fecundity and sex ratios of offspring. The situation in sperm whales is complicated by the social structure, which involves association of units to form groups. Although no data are available, it is possible that small units avoid some of the ecological costs of small group size by associating with other units more frequently than do larger units.

Unit dynamics

Cases of unit membership change can be documented reliably only for individuals that have been identified on a number of occasions (generally at least three); thus, only the 91 key individuals in this study could provide evidence for unit dynamics. The fact that one split, one possible merger (or two individuals transferring together), and three separate transfers by single individuals were identified during the 12 years of the study indicates that unit-membership change is not a particularly rare phenomenon. Our rough estimates of unit-membership change indicate that the average individual has a 6.3% probability per year of being involved in unit splitting, merging, or transfer. Since the maximum longevity of female sperm whales may exceed 60 years (Gambell 1972), there is clearly the potential for considerable nondemographic change in unit membership during an individual's life. The evidence for unit merging and transfers agrees with results from genetic studies of sperm whales that suggest long-term associations between different matrilines and possible dispersal between groups (Richard et al. 1996).

Splitting

Splitting of social units, although rare, has been reported for several species that live in stable, female-bonded matrilineally related groups (e.g., rhesus monkey (*Macaca mulatta*), Chepko-Sade and Sade 1979; baboon (*Papio* sp.), De Vore 1965; African elephant (*Loxodonta africana*), Moss 1988), including one other large odontocete (killer whale (*Orcinus orca*), Ford et al. 1994). Fission of formerly cohesive social groups in these species was contingent on one or more of the following factors: above average group size, loss of the matriarchal female and therefore the bonds holding her daughters' subgroups together, and disruption of the group due to the simultaneous death of several group members. Splitting of social groups usually occurred along lines of maternal relatedness (Chepko-Sade and Sade 1979; Moss 1988; Ford et al. 1994). Such patterns of matrilineal splitting can theoretically have profound micro- and macroevolutionary consequences by accelerating genetic differentiation of social groups (Melnick and Kidd 1983). The sperm whale social unit within which splitting is documented in this study (Fig. 3*a*) was the largest of the 19 units delineated. We have no information on the pattern of maternal relatedness within this unit, so it is not known whether this split followed matrilineal lines. The proximate cause is also unknown. The ultimate cause presumably relates to group-size effects. As Moss (1988) suggests for elephants, at a certain group size, a loss in feeding efficiency may outweigh the social benefits of large group membership.

Mergers

The evolutionary force for sociality in sperm whales remains uncertain. Although cooperative foraging may occur (Best 1979; Whitehead 1989), most authors suggest that alloparental care and protection of calves, with consequent inclusive fitness benefits, were important factors in the evolution of stable matrilineal units (Best 1979; Gordon 1987; Arnbom and Whitehead 1989; Whitehead 1996). Our finding of a possible merging of two social units (Fig. 3*b*) is unexpected in light of these theories. If sociality evolved because of benefits to related individuals that stayed together, how do we explain the merging of two separate units?

One explanation that seems reasonable in this context is optimal group size. Whatever the ultimate cause of sociality among female sperm whales, whether it be protection from predation, communal calf-care, cooperative foraging, etc., there is clearly some benefit to individuals from being a member of a unit. If the extent of this benefit increases with unit size, and is not entirely due to inclusive fitness benefits from association with related unit members, then individuals that are members of small units may gain by joining another unit, even if it is unrelated. If a small unit joins a larger unit (as in the case of whales 793 and 795 joining a unit of approximately 15 members), the benefits to the members of that larger unit, if any, are unclear. Perhaps the newcomers benefit their adopted unit by transmitting culturally gained information such as the location of good feeding grounds?

It should be remembered that the unit membership change involving individuals 793 and 795 cannot be confirmed as an example of unit merging, since their original unit affiliation is unknown. This change may actually have been a transfer of the two animals from one unit to another. The distinction between these two forms of unit-membership dynamics has consequences for our understanding of sociality in sperm whales. The merging of units may make sense simply in terms of optimal group size (whatever the ultimate cause), particularly where one unit is particularly small. The causes of transfers are less easy to imagine. Why should one or more whales elect to leave their set of (presumably closely related) constant companions, to join another (presumably less closely related) unit?

Transfers

Many cases of intergroup transfer are explained in terms of access to nonrelated mates. However, in species where males disperse from natal groups at or before puberty, female transfer between established groups is unusual (Greenwood 1980; Moss 1988; Clutton-Brock 1989). Proximate causes for adult female intergroup transfer vary within and between species and may include infanticide avoidance, female–female aggression, oestrus, and reproductive failure (Moore 1984; Pusey and Packer 1987). Infanticide is not known to occur in sperm whales, and seems unlikely given the short tenure of breeding males with social units. Aggression between females has never been reported. Since female sperm whales in all reproductive states have been found together in groups (Best 1968), social-unit membership generally seems to endure for far longer than the reproductive cycle, and access to males is unlikely to be affected by unit membership, the latter two factors also seem unlikely to be important in this case. Adult female intergroup transfers occur in a variety of contexts, and a variety of ultimate causes have been suggested: reduction of intragroup competition, access to superior habitat, and access to superior mates (Rutberg 1990). Again, with the possible exception of the first, these causes seem to have little relevance to sperm whale sociality.

The social and ecological costs of transferring between units are expected to limit its occurrence (Watts 1996). Individuals that move from their natal units will lose their affiliative relationships with familiar, related associates (Gouzoules and Gouzoules 1987), and any inclusive fitness benefits which they could have gained in the future by helping relatives. These social costs will be ameliorated to some extent if animals transfer with members of their original unit. However, the three definite cases of transfers in this study involved lone individuals. Ecological costs, such as increased predation risk during transfer, will be low if, as is expected for sperm whales, direct transfer between units is possible (Watts 1996). Since sperm whales, other than mature males, are never found singly or in very small groups (Whitehead and Weilgart 1991), we believe that transfers probably occur when two units are associated. Benefits to members of the new unit could relate to group-size factors, or perhaps to transmission of cultural information (as is suggested for mergers). In each case of possible or definite transfer, the unit into which the individual transferred was reasonably large (at least 11 members in each case) and it is thought that the group-size benefits, or costs, conferred by one or two additional, unrelated unit members are unlikely to be great.

Given the high social costs for transferring sperm whales, the lack of obvious proximate or ultimate causes, and the apparent lack of benefits to members of their new units in the cases documented, we are unable to provide a functional explanation for the occurrence of transfers.

The fact that merging of units and transfer of individuals between units occur has a number of consequences, both for the structure of the units concerned and for our understanding of sperm whale sociality. Both these forms of unit-membership dynamics result in units containing some unrelated individuals. Thus, a unit may consist of two or more separate matrilines. Since these relationships will be unaffected by future reproduction, because all male genetic input is external to the unit, these distinct levels of relatedness within the unit will persist. Although the observed variability of social-unit sizes suggests that the benefits of remaining in a unit usually outweigh ecological benefits for optimal group size, the occurrence of merging and transfers suggests that the ecological or social cost/benefit of leaving one's matrilineal social unit may sometimes outweigh the cost/benefit of staying. Overall, our analyses demonstrate considerable variability in the social structure of female and immature sperm whales.

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