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Who Cares? Between-group variation in alloparental caregiving in sperm whales

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Although the details of the various systems of allocare in primates, rodents, and carnivores have been well described, little is known about the existence of alloparental care in cetaceans. It is believed that the matrilineal social organization of the sperm whale functions to provide vigilant allomothers for calves at the surface while mothers make deep dives for food. Sperm whale females do have a system of allocare, but details are unknown. This study aimed to elucidate sperm whale allocare, in particular: who escorts whose calf and whether or not calves suckle from nonparent females. Using photo identification and behavioral calf follows, we examined patterns of adult–infant interactions for 23 sperm whale calves in the Sargasso and Caribbean Seas. Although multiple individuals of both sexes escorted the calves, the system of escorting differed between the 2 sites. For all calves studied in the Caribbean, we found that 1 female provided most of the allocare but did not nurse the calf, whereas in the Sargasso, multiple females provided care for, and nursed, the young. We discuss differences between populations that may have resulted in the observed differences in these 2 systems of allocare and how these findings fit with current hypotheses on the roles of kin selection and reciprocal altruism in cooperative care in mammals. *Key words:* alloparental care, allosuckling, cetaceans, escort, mother–calf, *Physeter macrocephalus*, social structure, sperm whale. *[Behav Ecol 20:838–843 (2009)]*

Parental care of offspring is so common among mammals that it is the exceptions and variations that attract our attention. Because many mammals bear only 1 offspring at a time, its survival is critical to the fitness of its parents. In the vast majority of mammals, mothers provide virtually all the care for the young (Reeve and Shellman-Reeve 1997). In a few species, paternal care is present (Kleiman and Malcolm 1981), and in very few, alloparental care is provided by animals other than the parents (Jennions and MacDonald 1994).

Alloparental care can be defined as any behavior by a nonparent which benefits the young and which would not be performed outside the presence of the young (Woodroffe and Vincent 1994; Whitehead 1996a). Alloparental behaviors within mammalian groups vary along a continuum of investment by the alloparent. At the lower end are behaviors categorized as indirect, in which the alloparent does not interact directly with the young (e.g., territorial defense, herding movements, and protection via increased vigilance over young). Direct allocare behaviors, in which the alloparent actively interacts with the young (e.g., carrying, grooming, babysitting, provisioning, and adoption), are at the opposite end of the spectrum (Lewis and Pusey 1997). Alloparental care of both types is widely known and has been described in primates (Nicolson 1987), rodents (Mayer 1983), and carnivores (MacDonald and Moehlman 1982); however, little is known about the existence of alloparental care in cetaceans (Anderson 1969; Haenel 1986; Johnson and Norris 1994; Whitehead 1996a; Mann and Smuts 1998; Simard and Gowans 2004).

Sperm whales (*Physeter macrocephalus*) are large, sexually dimorphic toothed whales, which have a sexually segregated social structure. Mature males are found alone or in impermanent "bachelor groups" when not breeding and rove individually between groups of females when breeding (Whitehead 2003). In contrast, female and immature sperm whales live in stable social groupings, called units, characterized by long-term social relationships between individuals (Christal et al. 1998; Whitehead 1999), which are often, but not always, matrilineally related (Mesnick 2001). Individual social units may associate for periods of a few days with other units to form what are called "groups" (Christal et al. 1998). Sperm whales make long (ca., 40 min) and deep (ca., 600 m) dives to forage for squid. Calves do not dive deep to forage with their mothers and group or unit members (Whitehead 2003). As a result, each calf associates with several adults or subadults at the surface while their mother is submerged during lengthy foraging dives (Best et al. 1984; Gordon 1987; Arnbom and Whitehead 1989; Whitehead 1996a).

Whitehead (1996a) found that the dive behavior of group members changes when a calf is present, such that there is more frequently an adult at the surface than would be expected given the synchronicity of dives in sperm whale groups without calves. Whitehead (1996a) pointed out that this form of alloparental care is not necessarily altruistic because subtle changes in the scheduling of foraging dives are unlikely to have much effect on foraging success.

In sperm whales, escorting has been hypothesized to allow foraging freedom for the mother while providing protection at the surface for the calf (Gordon 1987; Whitehead 1996a). The best data on sperm whale escorting originate from the first study on the behavior of living sperm whales (Gordon 1987). Gordon (1987) followed a total of 6 calves off the coast of Sri Lanka over several days and found that the calves were each escorted by 7–12 different adults. In one case, the calf appeared to make peduncle dives (a type of behavior defined below which is typically associated with suckling behavior; Gero and Whitehead 2007) alongside 2 different adults. Similar observations were made off the Galapagos Islands (Arnbom and Whitehead 1989) and off the island of Dominica in the West Indies (Gordon et al. 1998).

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Kin selection (Hamilton 1964), or reciprocal altruism (Trivers 1971), has been suggested as evolutionary mechanism behind the existence of alloparental behavior in mammals. Both could have a role for sperm whales. Kin selection might be more important for sperm whales which spend the majority of their time in small groups usually containing just 1 small (perhaps <10 individuals) unit with closely related members, whereas reciprocation may be favored in larger social groups, where the increased group size makes it likely that mothers are able to find allomothers with dependent calves with whom to enter into a reciprocal relationship. Here, we compare patterns of adult–infant interactions for 23 sperm whale calves in the Sargasso and Caribbean Seas. We determine the identity of the caregivers, their relationships to the calves, and gain some insight into whether the explanations of kin selection or reciprocal calf escorting are sufficient to explain the evolution and maintenance of this form of allocare in sperm whales.

MATERIALS AND METHODS

Field methods

Groups of female and immature sperm whales were located and followed both acoustically, using a directional hydrophone and towed hydrophone array, and visually by observers on a dedicated 13-m auxiliary sailing vessel. Fieldwork occurred at 2 sites. The first (5 May to 20 June 2004; 38 days effort) was located in the Sargasso Sea in an area of open ocean in international waters that covered approximately 200 000 km^2. The 2005 fieldwork (14 January to 13 April 2005; 58 days effort) was completed off the leeward shore of the island of Dominica in an area that covered approximately 1500 km^2 along the entire west coast of the island, in waters sheltered from the trade winds. An encounter with sperm whales began from the time they were first detected, acoustically or visually. Acoustic contact with the animals was maintained 24 h a day until the encounter ended when there was no visual or acoustic contact for more than 2 h.

During daylight hours, clusters of whales breathing at the surface were approached and photographs were taken for identification of individuals. If calves were present in a given cluster, priority was given to taking dorsal fin pictures of the calves from alongside the animals before moving behind the cluster in order to photograph distinct markings on the trailing edge of their flukes that are raised as adult individuals initiate deep dives (Arnbom 1987). During the 2004 field season, photographs were taken using a Canon EOS Elan II SLR camera with a Canon EF fixed 300-mm lens (Canon Canada, Ontario, Canada) and Ilford HP5 400 black and white film (Ilford Imaging, Marly, Switzerland). For the 2005 field season, a Canon D10 digital SLR base was used. Digital pictures were taken in full color at a resolution of 3072 × 2048 pixels and were saved in JPEG format. Slough skin samples, for genetic determination of sex, were collected in the slicks of individuals after they dove (Amos et al. 1992).

Focal-calf follows

Focal-animal follows (Altmann 1974) conducted on calves were completed within the larger group follows of the sperm whales (Whitehead 2004). Behavioral data were collected using continuous sampling for all calf behaviors (Altmann 1974). As in Cowie et al. (1951), we use "suckling" to refer to the behavior of a calf whose aim is to ingest milk from an adult female, whatever those actions may be. The term "nursing" is used to describe the behavior performed by the adult female who is presumably providing the milk during this adult–calf interaction. We defined "allosuckling" as a situation in which the calf was attempting to suckle from a female who was not its presumed mother; and "allonursing" as the acts performed by an adult female who appeared to be providing milk to a calf other than her own.

Previous work on sperm whales (Gordon 1987; Gordon et al. 1998) assumed that suckling was occurring based on above-water observations of repeated short dives underneath the peduncle of an escort, referred to here as "peduncle diving." It is important that such behavioral observations be treated with caution as we are unable to determine if milk is being transferred while the calf is below the surface, as even confirmed mouth-to-nipple contact is not always indicative of milk transfer in other mammals (Cameron et al. 1999). Gero and Whitehead (2007) discuss alternative hypotheses for the function of peduncle diving and supporting evidence for each. They conclude that peduncle diving is likely an indication that suckling is occurring.

Analyses

Identifications

A quality rating (Q) between 1 and 5 was assigned to each fluke photograph, where 1 indicated a very poor photograph and 5 indicated a very high-quality photograph (Arnbom 1987). The Q value was a function of the attributes of the photograph but not the quality of the markings on the fluke (Arnbom 1987). Only pictures with $Q \geq 3$ were used for the analyses. The best fluke picture for each individual within each encounter was assigned an identification number and then matched between encounters using a computer-based matching program (Whitehead 1990).

The shape of the dorsal fin and distinct markings on the dorsal fin and body were used for individual identification of young calves (which rarely lift their flukes). The criteria used to assign quality ratings to the photographs of calf dorsal fins were similar to those for adult fluke pictures (focus, exposure, angle of dorsal fin relative to the negative plane, percentage of the dorsal fin not submerged, and the proportion of the frame filled by the dorsal fin). The best picture for each individual calf within each encounter was then matched between encounters by eye.

Defining groups

All individuals identified on any 1 day were assumed to be from the same group (Christal et al. 1998; Whitehead 1999; Coakes and Whitehead 2004; Whitehead and Rendell 2004). In order to determine whether groups were the same on different days, we used the same methods as in previous work (Whitehead 1999); the cut-off similarity was set such that the group being followed on each of 2 days was classified as the same if at least 50% of animals identified on the day with the fewest identifications were identified on the other day.

Group size for a particular day was estimated using the photo identification data. Observed group size was determined by dividing a given day's identifications into 2 sets and then using a Petersen mark–recapture estimator to estimate the number of individuals present (Coakes and Whitehead 2004). Mean typical group size was then derived from those estimates as in Coakes and Whitehead (2004). "Typical" group size is an approximation of group size as experienced by a randomly chosen member of the population as opposed to the outside observer (Jarman 1974).

Defining associations

To identify intragroup associations, individuals were deemed to be associating if they were within the same cluster of animals at the surface. Individuals were considered to be in the same cluster if they were within approximately 3 adult body lengths from any other cluster member (~40 m "chain rule") and were coordinating their behavior (Whitehead 2003). A standard 2-h sampling interval was used along with the "half-weight index" (HWI) to measure relationships between pairs of animals. Further distinction was needed when defining associations with calves. We defined 3 hierarchical levels of association: 1) "associates," any individual identified on the same day as the calf but was not observed in association with the calf; 2) "escorts," any individual identified within a cluster which contained the calf (Gordon 1987; Mann and Smuts 1998); and 3) "mother," determined genetically, or, in the absence of genetic data, the mother was assumed to be the mature female escort with which the calf spent the majority of its time and thus had the highest HWI value (Gordon 1987; Whitehead 1996a).

Escorts were considered to have had a preferred association with a calf when their association index was more than twice the mean index of all dyads in the group being considered for the analysis (Durrell et al. 2004). An escort was considered to have an avoidance with the calf if their association index was below half the mean. These threshold values were chosen because they were approximately twice (in the case of preferred associations), or half (in the case of avoidances), the value that would be expected if associations were completely random.

A permutation test, as in Bejder et al. (1998) with modifications as in Whitehead et al. (2005), in which observed associations among individuals are permuted within 2-h sampling periods, was used to test whether calves had preferred/avoided associations with adults against the null hypotheses that calves associate randomly with all adults except the mother. A rectangular portion of the association matrix (calves on 1 axis and adults on the other) was randomized 40 000 times with 100 flips per permutation for each analysis as this stabilized the P values. The calculation of the HWI and the permutation tests were carried out using SOCPROG 2.2 (H. Whitehead, Dalhousie University, Nova Scotia, Canada) in MATLAB 6.5 (The Mathworks, Inc., Natick, MA).

Feeding success

Feeding success affects the activity budget of individuals and therefore may be a factor that could determine escorting behavior. Feeding success was compared between study areas using defecation rate (defecations observed divided by the number of fluke-ups recorded) as a measure of feeding success (Whitehead 1996b; Whitehead and Rendell 2004). When identification photographs were taken as whales began a fluke-up dive, it was noted whether a defection (indicated by a brown patch in the water) was or was not observed or whether it was unknown due to sea state or distance to the whale. Justification for, and possible limitations of, this methodology are discussed by Whitehead (1996b).

Gender determination

Whole-cell DNA was extracted for use in subsequent polymerase chain reactions from sloughed skin samples by a standard phenol/chloroform extraction technique (Hoelzel 1998). Gender determination was performed, according to conditions described in Engelhaupt (2004), using odontocete-specific primers (ZFYX0582F, ZFY0767F, and ZFX0923R) that amplify the ZFX and the ZFY sequences (Bérubé and PalsbØll 1996). Females were defined as having only 1 band at approximately 383 bp, whereas males possessed a characteristic 227 bp fragment in addition to the 383 bp fragment. It is this 383 bp fragment that acts as a positive control verifying that the amplification reaction has taken place. Four controls, consisting of 2 confirmed male and 2 confirmed female samples taken from stranding events in the North Sea and Gulf of Mexico, respectively, were run with each set of unknown samples to insure that both proper amplification had occurred as well as to provide a means of gender verification. A negative control, composed of the stock solutions only, was run to check for potential cross-contamination. Each individual sample was molecularly sexed using the ZFY/ZFX method a minimum of 2 times to verify the results.

RESULTS

Encounters off Dominica were dominated by the nearly continuous presence (41 out of 58 days) of one particular social unit, "the group of seven" (GOS; Gero 2005), which contained a single male calf. There were fewer data (ranging between 1 and 9 days) for the remaining 22 calves (10 Caribbean and 12 Sargasso) in 11 groups (6 Caribbean and 5 Sargasso).

Patterns of allocare

Group of seven

Associations among members of the GOS unit were heterogeneous, such that individuals formed preferred associations and avoidances (Gero et al. 2008). The GOS calf only made peduncle dives alongside one particular adult, its genetically identified mother (#5722). The GOS calf was escorted by all 6 other unit members (Table 1) but was escorted significantly more by 1 nonparent adult female, the preferred escort #5561 (HWI $= 0.48$ compared with 0.13–0.29 for the other nonparent females). If not with the mother or the preferred escort, the calf was most likely to be escorted by the only juvenile in the group, followed by the remaining adult females in the social unit.

Caribbean calves

As in the detailed follow of the GOS, potential allosuckling (in the form of peduncle dives beside non-mothers) was not observed during any follows of the other 10 calves off Dominica. Patterns of association are also consistent with the GOS. Calves were observed making peduncle dives alongside a single adult by whom they were most often escorted (Table 1). They were otherwise generally escorted by a single particular escort. Other presumed mothers in the group and their calves (if more than 1 calf was present) and other adult females were secondary and tertiary escorts, respectively. Table 1 summarizes escorting patterns for all Caribbean calves.

Sargasso calves

In the Sargasso Sea, allosuckling was observed in follows of 7 different calves (#3002, #3005, #3006, #3012, #5862, #3016, and #3009; Table 2). In the case of "group 5," 2 of the calves were observed making peduncle dives from 3 different adults; 2 of which were common to both calves. Calf #3005 suckled from the assumed mother of #3002 but #3002 was not seen to suckle from the assumed mother of #3005 (Table 2). All other females were observed to nurse only 1 calf, even if more than 1 calf was present in the group (Table 2).

General patterns in the strength of associations with escorts in the Sargasso Sea were similar to those in the Caribbean. Due to a lack of genetic data and multiple nursing escorts, it is difficult for us to know which female was the calf's mother. However, with the exception of calf #3006, nursing escorts were the individuals with the strongest association with the calves, followed by nursing escorts of other calves, other calves, and finally other adult females in the group (Table 2).

Clusters with calves present were significantly larger in the Sargasso Sea (mean $= 2.96$) than in the Caribbean (mean $=$ 1.96; $t = -5.25$; degrees of freedom $= 165.2$; $P < 0.0001$). On average, calves in the Sargasso were escorted by 2 individuals, whereas only 1 was present in the Caribbean. Typical

Table 1

Escorts of each sperm whale calf in the Caribbean Sea listed in order of descending strength of dyadic HWI with the calf

Unit	Calf	Mother	Escorts	Associates	
GOS Days: 41 Individuals: 7	5703_{M}	5722_{F}^{a*} (N:95)	5561_{F}^{a*} 5727_{M}^{*} 5560_{F}^{*} 5130_{F}^{b*} 5563_{F}^{b*}	None	
S Days: 9 Individuals: 6	5725	5724^{a*} (N:13)	5726^{a} 4001 5759	5742	
	4001	5759^{a*} (N:5)	5725 5724	5726 5742	
A Days: 3 Individuals: 11	4002	5723^{a} (N:7)	5586^{a*} 5720^{a} 5719^{a}	5710^{b*} 5711 5712	5713 5714 5721
	5719	5720^{a} (N:3)	5586^{a} 5723^{a} 4002^{a}	5710^{b*} 5711 5712	5713 5714 5721
T Days: 3 Individuals: 4	5701	5163^{a} (N:9)	5698	5699^{b*}	
A-O Days: 1 Individuals: 6	5718	5138^{a} (N:3)	5716^{a}	5137 5715 5717	
B Days: 1 Individuals: 9	4003	5745^{a} (N:3)	5744^{a} 4004^{a}	5743 5746 5747	5748 5749
	4004	5746^{a} (N:1)	5748^{a} 4003^{a}	5743 5744 5745	5747 5749
	5747	5748^{a} (N:2)	None	4003 4004 5743 5744	5745 5746 5749
R Days: 1 Individuals: 8	4005	5733^{a} (N:2)	None	5728 5729 5730	5731 5732 5734

Nursing females are marked with an "N" and the number of bouts of peduncle diving observed with each adult is given. If known, sex of the whale (F or M) is noted in subscript after the ID number.

[a] Preferential association (coefficient of association > twice the mean HWI).

[b] Avoidance (coefficient of association < half the mean HWI).

[*] Statistically significant ($P < 0.05$) based on permutation tests.

Table 2

Escorts of each sperm whale calf in the Sargasso Sea listed in order of descending strength of dyadic HWI with the calf

Group	Calf	Escorts and nursers	Associates		
5 Days: 4 Individuals: 32	3002	5808^{a*} (N:2) 5810^{a} (N:2) 5807^{a} (N:1) 5809_{M}^{a} 5823^{a} 5806^{a} 3005^{a}	3006 5811 5812 5813 5814 5815 5816 5817	5818 5819 5820 5821 5822 5824 5825 5826	5827_{F} 5828 5829_{F} 5830 5831 5832 5833 5869
	3005	5817^{a*} (N:1) 5808^{a} (N:1) 5819^{a} 5807^{a} (N:1) 3002^{a}	3006 5806 5809_{M} 5810 5811 5812 5813 5814 5815	5816 5818 5820 5821 5822 5823 5824 5825 5826	5827_{F} 5828 5829_{F} 5830 5831 5832 5833 5869
	3006	5828^{a} 5827_{F}^{a} (N:2) 5830^{a} (N:1) 5824^{a} 5832^{a}	3002 3005 5806 5807 5808 5809_{M} 5810 5811 5812	5813 5814 5815 5816 5817 5818 5819 5820 5821	5822 5823 5825 5826 5829_{F} 5831 5833 5869
	5818	5814^{a*} (N:3)	3002 3005 3006 5806 5807 5808 5809_{M} 5810 5811 5812 5813	5815 5816 5817 5818 5819 5820 5821 5822 5823 5824 5825	5826 5827_{F} 5828 5829_{F} 5830 5831 5832 5833 5869
10 Days: 4 Individuals: 10	3010	5857_{F}^{a} (N:1)	3012 5852^{b*} 5853	5854 5855 5856	5858_{F} 5859
	3012_{F}	5856^{a} (N:2) 5855^{a} (N:2) 5857_{F}^{a} (N:1) 5854^{a} 5858_{F}^{a} 5859^{a} 5852^{a}	3010 5853		
11 Days: 3 Individuals: 11	3015	5791^{a} (N:2) 5864^{a} 5862^{a} 5789^{a}	3014 5791 5792	5860 5861^{b*} 5863	
	5862	5864^{a} (N:4) 5792^{a} (N:1) 3015^{a} 5791^{a}	3014 5789 5790 5860	5861^{b*} 5862 5863	
12 Days: 3 Individuals: 14	3016	5865_{F}^{a} (N:2) 5801^{a} (N:1) 5800^{a} 5894_{F}^{a} 5898^{a} 5867	5793 5795 5796 5797	5799 5866 5868	
	5800	5868^{a} (N:2) 5866^{a} 5798^{a} 5865_{F}^{a} 3016^{a}	5793 5794_{F} 5795 5796	5797 5799 5801 5867	

group size estimates were twice as large in the Sargasso as compared with the Caribbean (Table 3). Values were similar using 2 different levels of precision of cut-off for group sizes to be included (coefficient of variation <0.25 or <0.40) and when the data were divided using 2 different methods (at midday or half of the identifications on a given day; Coakes and Whitehead 2004). Finally, defecation rate, used here as a proxy for feeding success, was almost twice as high in the Caribbean as in the Sargasso (Caribbean = 29.8%, Sargasso = 16.2%).

DISCUSSION

This study is the first to elucidate the identity of sperm whale caregivers and their relationships to the calves. The findings suggest that sperm whales have alternative systems of escorting and that some females potentially provide direct care to another's calf in the form of allonursing. The 2 systems differ in the

Table 2 (continued)

Group	Calf	Escorts and nursers	Associates
8 Days: 1 Individuals: 6	3008		5482_M
	3009		5842_M

Nursing females are marked with an "N" and the number of bouts of peduncle diving observed with each adult is given. If known, sex of the whale (F or M) is noted in subscript after the ID number.

[a] preferential association (coefficient of association > twice the mean HWI).

[b] avoidance (coefficient of association < half the mean HWI).

[*] statistically significant ($P < 0.05$) based on permutation tests.

identity and number of escorts, as well as the nature and quality of the relationships between the mother–calf pair and the caregivers. In the Caribbean system, specific preferred escorts shared strong social bonds with and provided the bulk of the allocare to the calves, although all or most individuals in the group escorted the calves at some point (Table 1). In contrast, in the Sargasso Sea, multiple nursing escorts provided alloparental care for the young, but overall, a smaller proportion of the group escorted the calves (Table 2). These 2 different systems appear to be consistent within study areas.

The social structure of the population in which the mother–calf pair resides likely plays a large role in determining the system of alloparental care that is observed. Although it is clear from the long-term resighting of the GOS (Gero et al. 2007) that this and other Caribbean groupings likely consisted of just 1 stable social unit, it is difficult to say what level of social organization was present in the Sargasso Sea. In the Pacific, the mean typical unit size is about 14 individuals (Christal et al. 1998). The difficulty in determining the level of social organization in the Sargasso derives from uncertainty in whether the groupings observed were composed of 2 or more units with a typical unit size of 6–7 individuals, as observed in the Caribbean, or if these groupings in the Sargasso were single units similar in size to those found in the Pacific.

This distinction becomes important when considering how kin selection and reciprocal altruism might explain these differing patterns of escorting. If escorts are group members, but not necessarily long-term unit members, the larger number of group members makes it likely that mothers are able to find allomothers with dependent calves with which to enter into a relatively short-term reciprocal relationship (Trivers 1971). Escort reliability (the likelihood of reciprocation), however, may be low among group, but not unit, members as group stability is only short term (a few days), thus making reciprocation unlikely between females who are not rearing calves concurrently. Concurrent reciprocation of escorting may explain the patterns of escorting observed in the Sargasso study area as several presumed mothers were observed alone with several different calves. It is also likely that the larger group sizes in the Sargasso allow for concurrent reciprocal allosuckling as several females in the groups were nursing at the same time.

Conversely, the smaller numbers of females in the long-term stable units observed in the Caribbean Sea make it unlikely that several of the females would be nursing dependent calves (sperm whales give birth to single offspring at about 5-year intervals; Best et al. 1984). As a result, if calf escorting is restricted to members of the mother's unit, as it appears to be in the Caribbean, the matrilineal structure of sperm whale social units would suggest that kin selection likely plays a role in the identity of escorts. Given that Gero et al. (2008) found that pairwise genetic relatedness correlates with patterns of association and that the preferred escort is the mother's closest relative in at least one of the units in the Caribbean (GOS), it is likely that kin selection can explain the patterns of escorting observed in the Caribbean Sea. However, Gero et al. (2008) also showed that this correlation was stronger if the calf was excluded. This would suggest that less related individuals associate with the calf out of obligation to the unit or mother rather than a direct preference based on genetic relatedness. It is possible that for unrelated unit members, escorting a calf is a cost of being a member of the unit. These costs might be very small (Whitehead 1996a) and could be alleviated by other benefits such as by-product benefits while foraging in a group (Whitehead 1989), interchange of behaviors (reciprocation of different acts; Hemelrijk 1990), or delayed reciprocation of escorting. Because of the long-term bond between unit members, escort reliability will be high, and as a result, individuals may escort nonkin with the expectation of reciprocation to their future offspring.

Thus, both kin-biased allocare and reciprocation of care may be required to explain the patterns of escorting observed in this study. It is possible that neither mechanism is sufficient on its own to explain the evolution and maintenance of the escorting systems observed in sperm whales. In addition, there may be other factors that affect the form of sperm whale allocare. For instance, increased prey availability (as the differences in feeding success between sites suggest) may affect the number and quality of escorts by decreasing the amount of time mothers spend away from their calves feeding. As a result, generalizing too widely about a mechanism's role would mask the complex combination of potential ecological, behavioral, and cultural differences between study areas that create the distinctive set of processes operating in each population.

Table 3

Estimates of typical group size (TGS) in the Caribbean and Sargasso Seas, calculated using Petersen mark–recapture methods with a day's identifications divided in half by 2 different methods and 2 levels of the coefficient of variation (CV) (as in Coakes and Whitehead 2004)

		Estimates with CV < 0.25		Estimates with CV < 0.40	
Splitting methodology	Location	*N*	TGS[*]	*N*	TGS[*]
Split at midday	Caribbean	32	6.63 (1.51)	35	6.82 (1.57)
	Sargasso	12	12.05 (6.56)	16	12.95 (6.96)
Split by half of identifications	Caribbean	45	6.37 (1.48)	48	6.62 (2.00)
	Sargasso	17	12.01 (6.52)	20	11.37 (6.37)

[*] Mean (standard deviation).

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