



Original Article

Kin selection and allocare in sperm whales

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Cooperative care and defense of young are hypothesized to be foundational to the societies of several species, including the sperm whale (*Physeter macrocephalus*). However, the extent of allocare among sperm whales and the mechanisms driving it have not been well-characterized. Sperm whale social units are matrilineally based, making kin selection a likely key driver of allocare, but the relationship between kinship and calf care is essentially unknown. We investigate calf care in the context of kinship, by combining association and interaction data with genetic profiles for 16 calves from 7 eastern Caribbean social units. Mothers were the primary associate for 62.5% of calves, and the primary nurse for 87.5%, so behavioral observations are not always sufficient for assigning maternity. Babysitting and allonursing were frequent in some cases, particularly for calves less than a year old. Within social units, babysitting rates were correlated with relatedness ($r_s = 0.4$, $P < 0.05$), and allonurses were, on average, closer maternal relatives of the calves they nursed than were available females who were not allonurses ($\Delta r = 0.14$, $P = 0.054$). Exceptions to the overall positive relationship between allocare and kinship suggest that additional factors influencing allocare among sperm whales may include reciprocity, group augmentation and gaining maternal experience.

Key words: alloparental care, allosuckling, babysitting, kinship, sperm whale.

INTRODUCTION

Among species that have few offspring, each offspring typically receives high levels of investment, which sometimes includes care from individuals other than its genetic parents (Riedman 1982). Typically, such alloparental care (also called allocare), defined as “any behavior by a non-parent which benefits the young and which would not be carried out if the young were not there” (Woodroffe and Vincent 1994), occurs in species that live in groups that are highly social, cooperative, or related (Riedman 1982). Within groups of related individuals, kin selection and inclusive fitness benefits (Hamilton 1964a, 1964b) likely contribute to why individuals behave in this seemingly altruistic manner (Clutton-Brock 2002). Within groups that are unrelated, however, the costs of providing care may be compensated by other factors, including gaining parental experience (Lancaster 1971), receiving reciprocated altruistic behaviors (Trivers 1971, 2006) or benefiting from increases in group size (Kokko et al. 2001; Kingma et al. 2014). These other mechanisms may also reinforce selection for allocare among relatives.

Allocare is thought to be foundational to the evolution the complex, cooperative social system of sperm whales (*Physeter macrocephalus*) (Best 1979; Gero et al. 2013). Female and juvenile sperm whales

live in social units that are stable across years (Christal et al. 1998; Gero et al. 2014) and are matrilineally-based, in that females typically stay with their mothers, though social units can also contain unrelated or distantly related individuals (Christal 1998; Ortega-Ortiz et al. 2012; Konrad et al. 2018a). Males disperse from their natal units before sexual maturity and are thought to have only fleeting interactions with other social units after that (Best 1979; Whitehead 1993). Instances of communal defense of calves against predators have been reported in sperm whales (Weller et al. 1996; Pitman et al. 2001), as has “babysitting” (remaining with the young during the absence of the mother; Kleiman and Malcolm 1981), in which calves are serially accompanied by other unit members while their mothers forage at depth (Gero et al. 2009). Babysitting likely increases the calves’ safety in the case of an attack by predators (especially as calves typically do not dive to the depths or for the durations of their mothers; Whitehead 2003), and appears to often result from a behavioral change by the babysitters, not just association driven by the calves’ following behavior, so that babysitting is a form of allocare (Whitehead 1996). However, the fitness cost of babysitting is likely low (Whitehead 1996). Sperm whales may also provide more costly allocare in the form of allonursing. Best et al. (1984) showed that when whole groups of sperm whales were killed by whalers, there were consistently considerably more lactating females than suckling calves (e.g., 14 calves and 41 lactating females in Japanese whaling data). In studies of living animals, there have been frequent observations of individually identified

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calves appearing to perform peduncle dives (indicating suckling) alongside more than one female, whereas others only do so with their biological mother (Gordon 1987; Gero et al. 2009, 2014).

Lukas and Clutton-Brock (2018) show that among social mammals the mean relatedness within groups of females is closely related to several major aspects of sociality. When groups have low mean relatedness, there tend to be high rates of aggression and dominance. In contrast, groups with high mean relatedness are more likely to have division of labor and reproductive suppression, as well as female infanticide and alloparental care. The mean relatedness within sperm whale social units ($r = 0.14$ for our study population; Konrad et al. 2018a) is towards the lower end of the range for social mammals (Lukas and Clutton-Brock 2018). Sperm whales, as predicted by Lukas and Clutton-Brock's (2018) analyses, have produced no evidence of female infanticide, reproductive suppression or division of labor (see Whitehead 2003). However, there is also little evidence for the female–female aggression predicted by Lukas and Clutton-Brock's (2018) model, and alloparental provisioning is unusual for a social mammal with the sperm whales' degree of within-unit relatedness. It is this apparent anomaly that we address by investigating potential drivers of allocare.

Given the kin-based social system of sperm whales, a likely functional driver of allocare is kin selection. Within social units, association generally correlates with kinship (Konrad et al. 2018a), but whether provision of allocare is related to kinship has only ever been examined for a single calf, in which case the primary babysitter was the mother's closest relative (Gero et al. 2008).

Studying allocare requires the ability to distinguish between parents and non-parents. In the absence of genetic information, mother identity is often assigned based on social observations, under the assumption that the adult that the calf spends the most time with is its mother (Gordon 1987). The reliability of this assumption in sperm whales, however, has only ever been validated for one calf (Gero et al. 2008), and it is not strictly valid among all odontocetes (Augusto et al. 2017).

In this study, we explicitly examine patterns of kinship and social behavior using well-studied sperm whale social units from the eastern Caribbean, to test two primary hypotheses: (1) whether genetic mothers can be identified based on behavioral data, and (2) whether rates of allocare within units are correlated with kinship.

METHODS

Field methods

We collected data on the sperm whales off the western coast of Dominica, in the Caribbean Sea (15.5°N; 61.5°W) between 2005 and 2016. Field seasons lasted between 2 and 4 months between January and June, using various research platforms (Gero et al. 2014). During these studies 518 days were spent at sea.

Groups of sperm whales were located and tracked for periods of hours to days using both visual and acoustic methods (Whitehead 2003). Photoidentification used the flukes of juveniles and adults (Arnbohm 1987) and the dorsal fins of calves (Gero et al. 2009). We recorded observations of peduncle dives and of associations of individuals in clusters (Gero et al. 2014). In sperm whales, peduncle dives are short (ca. 14 s) shallow dives made by a calf, immediately beside (usually <3 m) the peduncle of an adult, during which the calf performs what appear to be mammary bumps, which are thought to stimulate milk letdown (Gero and Whitehead 2007; Johnson et al. 2010). Clusters were defined to be sets of individuals

at the surface in close proximity (<40 m) to their nearest neighbor with coordinated behavior (Whitehead 2003).

We collected sloughed skin opportunistically from the diving slicks of individual whales or clusters of whales (Whitehead et al. 1990) and biopsy skin samples using a 90-lb draw weight crossbow and bolts with 2.5 cm long tips with 0.5 cm circumferences (see Kowarski et al. 2014). Skin samples were stored in either ethanol (at a concentration of $\geq 70\%$), or 20% Dimethyl sulfoxide (DMSO) solution saturated with salt (Seutin et al. 1991).

Identifications, age class and defining social units

Individual identification primarily used photoidentification from high-quality photographs as described by Gero et al. (2015). In some cases (~6% of adult/juvenile identifications) well-known adults and juveniles that could not be photographed but whose flukes were observed by S. Gero were recorded as having been identified. Patterns of association are essentially unchanged when these field-identifications are included (Gero et al. 2015). Similarly, well-known calves who were readily identifiable due to distinct dorsal markings that were visible or because they were known to be the only calf in the social unit (there was generally only one social unit in the study area; Gero et al. 2014) were also recorded as having been identified (25% of calf identifications).

Individuals were classified as adult females, juveniles or calves, based on their size, as well as observations of nursing (Gero et al. 2014), and molecular-genetic sex assignments (see below). Juveniles were noticeably smaller than adult females, but not nursing. Mature males are notably larger than adult females (Best 1979; Best et al. 1984), so individuals that were sexed as male but indistinguishable from adult females were classified as juveniles. Calves were small individuals that we observed nursing. Some individuals that were initially classified as calves were later re-classified as juveniles if they were no longer seen nursing.

Social units were delineated as in Gero et al. (2014), so that they reflect long-term, stable social relationships: two whales that were identified within two hours of each other in at least two different years were assigned to the same unit.

Genetic laboratory methods and analysis

Each sample was analyzed at a series of molecular markers to develop individual-specific genetic profiles. These included molecular sex determination (Konrad et al. 2017), sequencing 346 bp at the 5' end of the mtDNA control region using the primers t-Pro and Primer 2 (Yoshida et al. 2001), and genotype analysis at 18 microsatellite loci. Further information on these molecular methods is given by Konrad et al. (2018a): details of the microsatellite loci are listed in Table S2 of the supporting material of Konrad et al. (2018a), and unit assignment, sex, mtDNA haplotype, and microsatellite genotypes for all unique genetic individuals have been archived in Dryad (doi:10.5061/dryad.63464hf). Genetic identities were then linked to photo-identities (see Konrad et al. 2018a).

These data were then used to estimate pairwise relatedness, using the R package *related* (Pew et al. 2015) with Wang's (2002) estimator, and to infer maternity of calves through a full maximum-likelihood method for polygamous diploids as implemented in Colony 2.0.6.2 (Jones and Wang 2010). Details are given by Konrad et al. (2018a). There was one ambiguous assignment: even though in all runs Colony assigned Lady Oracle as Aurora's

mother, both Lady Oracle and Rounder were genetically consistent with being the mother of Aurora (both share at least one allele at every locus with Aurora, and their estimated relatedness with Aurora was $r = 0.51$ and 0.50 , respectively). In the statistical measures and tests, we assumed Lady Oracle for Aurora's mother, as this was best supported by the genetic data and observations in 2018 indicated Rounder as giving birth to a calf in late 2017 (Gero S, personal observation), which would have been very unlikely if she was also the mother of Aurora likely born in the second half of 2015. However, assigning Rounder as Aurora's mother had little effect on the results.

Measuring association

We defined association as individuals identified in the same cluster (<40 m apart and coordinated behavior), because this fine spatiotemporal scale is presumably the most relevant for defense and care of calves. Across our study period, social unit compositions were affected by births and deaths. Therefore, we used an association index, "both identified," that minimizes the bias of these demographic changes on association measures (Whitehead 2008). To examine the effect of temporal resolution, we calculated association rates using two sampling periods: 2 h and 1 day. Two hours corresponds to approximately two dive cycles in sperm whales (Christal and Whitehead 2001; Gero et al. 2015). Daily sampling periods minimize autocorrelation in cluster composition and will include (as not associated) any pairs that were both identified in the same day, but not in the same 2-h period. We calculated association rates between calves and the adults and juveniles within their social units. We only included each calf up until the last year it was observed making peduncle dives.

Approximating nursing

We used observations of peduncle dives as a proxy for nursing, because nursing cannot be directly observed from above water. We classified all adult or juvenile females on which each calf was observed performing peduncle dives as nurses of that calf. However, we acknowledge this may include some individuals from whom the calf did not receive milk; variation in factors such as suckling ability and the female's ability to produce and release milk can uncouple suckling and milk intake, such that observing the behavior of suckling does not correlate with milk intake (Cameron 1998). Nonetheless, each sperm whale calf, despite having a wide range of associates, only peduncle dives on one or a few females, and never on males (Gero et al. 2007), suggesting that the behavior is performed when necessary, or in circumstances when gaining access to milk is likely. We also acknowledge that we never saw (nor could have seen) milk transfer. Yet, sucking that does not lead to milk letdown may still have social or emotional benefits (Cameron 1998), such as among African elephants (*Loxodonta africana*), where allonursing appears to relate more to providing comfort than nutrition (Lee 1987).

Maternal calf care

For all calves that had a genetically determined mother or a genetically sampled primary caregiver, we examined whether the genetically determined mothers were their calves' primary caregivers. We assessed whether genetically determined mothers had the highest association index with their calves of any unit member, and if they were the female unit member most often observed receiving peduncle dives from their calves.

Maternal relatedness and allocare

We compared babysitting rates and presence or absence of allonursing to the caregiver's pairwise relatedness to the calf's mother. We used pairwise relatedness to the mother, rather than to the calf, to focus on the effect of maternal relatedness and because relatedness is harder to distinguish against background noise when there are more generations between the related individuals. These analyses were restricted to include only calves from well-sampled social units (i.e., units with genetic data for all adult females and at least 70% of all unit members).

To determine babysitting rates, we standardized the association indices (described above) to account for differential identifiability of calves, in two different ways. For one method, we standardized association indices by dividing each babysitter's index with the calf by the mother's index with the calf. For the second method, we standardized association indices and pairwise relatedness values by ranking the values for the unit members of each calf, and then scaling the ranks to fall between 0 and 1. This method also removes the effect of differences between calves in the relative level of allocare received and focuses on whether, for each given calf, ordinal ranks of babysitting rate and of maternal relatedness correlate (i.e., whether the closest relatives of a given calf are that calf's most frequent babysitters).

Additionally, certain whales may preferentially associate with the calf's mother, and by extension the calf, but not associate with the calf when the mother is not present. To account for this possibility, we repeated the above calculations of association indices excluding any clusters with more than one adult (or juvenile) present, such that this index reflects clusters where the individual was the sole babysitter.

For all measures of association, we calculated Spearman's correlation coefficients between association indices of each calf with each adult and juvenile in their social unit (excluding the calf's mother and juveniles that were previously classified as calves) and the pairwise relatedness estimates of the unit members to the calves' mothers. To test the statistical significance of these correlations, we randomly permuted (50,000 times) the adult-calf association rates for each calf, recalculating the correlation with relatedness to generate a distribution of correlations. One-sided *P*-values were calculated as the proportion of simulations where a correlation greater than or equal to the true correlation was generated.

We also tested whether allonurses were closer maternal relatives of the calves they nursed than were the available females who did not nurse the calves. Female unit members from which the calf did not nurse were classified as "available" if they were observed in the same year that the calf was observed suckling, and were not calves themselves. Sperm whales can begin lactating at least as young as 5 years old (Best et al. 1984), but whether this is typical is unknown, as were the ages of most juvenile females in this study. Thus, in an attempt to exclude females that were immature and not lactating, females that transitioned from calves to juveniles in the study period were only considered "available" after being observed as the recipient of peduncle diving.

For each calf, we obtained the pairwise relatedness to the calf's mother for each allonurse for that calf and each available female that was not an allonurse for that calf. We calculated the difference between the average relatedness values for all nurses and for all non-nurse available females. To estimate the probability of this difference being achieved by chance, we randomly permuted the classification of nurses and available females for each calf, while

maintaining the number of each class of female for each calf. We ran 50,000 permutations (which stabilized P -values) and recalculated the relatedness difference each time, to generate a distribution of differences. A one-sided P -value was calculated as the proportion of simulations where a difference greater than or equal to the true value was generated.

RESULTS

Assignment of genetically determined mothers

Out of 18 sampled calves, 15 had genetically determined mothers among the sampled candidate mothers. All individuals were scored at no fewer than 16 microsatellite loci, and all maternity assignments were consistent across runs, and had a mean probability across runs greater than 90%. Maternity assignments were supported by agreement in the mtDNA haplotypes of mothers and their offspring, when both were known.

Social indications of genetic mothers

In all cases, calves associated with and nursed from their genetically-determined mothers, and in most cases, genetically-determined mothers were their calves' closest associates and primary nurses (Table 1). Of all clusters with a single adult or juvenile present with calves, the associate was the calf's mother 71.0% of the time. Other adult females were the next most common class of sole non-calf associates in clusters with calves (14.1%), followed by juvenile females (10.2%), and juvenile males (4.6%).

For each sampling interval that was used in the calculation of association indices, 62.5% of genetically determined mothers unambiguously had the highest association indices with their calves (Table 1). In two cases the mother was not the calf's closest associate, whereas in three cases the association rate of the calf with another adult was equal to the mother's value (Table 1). Two of the ties were resolved when associations were calculated within

2-h, rather than daily, sampling periods – one resolved in favor of the mother, and the other in favor of the other associate (Table 1). About half of the calves suckled on one or two adult females in addition to their mother. For all but two calves (87.5% of calves), the genetically determined mother was the female most often observed receiving peduncle dives from their calf (Table 1), and one of these exceptions was the calf Aurora for whom the primary target for peduncle dives was Rounder, another potential mother (see Methods). Additionally, another calf (ID: Distinct), for whom a genetic mother was not identified, was only identified associating with and suckling on one individual who was not the calf's mother (pairwise relatedness = 0.14).

Calf associations and interactions correlated with maternal relatedness

The rates at which the 14 calves from well-sampled units associated with non-calf members of their own units were positively correlated with the relatedness between the calf's mother and the potential associate (Table 2). However, the effect size and statistical significance of the correlation depended on the parameters of the analysis (Table 2). No correlations were significant when intra-calf rank values of association and relatedness were used, and the effect sizes of most of these correlations were quite small (Table 2). When associations were scaled relative to the mother's association rate with the calf, effect sizes were generally greater, particularly for the restricted dataset and the daily sampling period, and three of the correlations were statistically significant at $P < 0.05$ (Table 2).

Almost all individuals spent at least some time associated with the calves in their social units (Figure 1a), but fewer individuals were observed in clusters where they were the sole non-calf individual in the cluster (Figure 1b). The average sole babysitting rate of likely first-degree relatives of the mother ($r \geq 0.35$; likely grandmothers or maternal half-siblings to the calf) was roughly double that of more distant relatives ($0.1 \leq r < 0.35$), which was in turn double that of

Table 1
Calf care in sperm whale social units

Unit	Calf ID	Mother ID	Mother rank		Babysitters		Allonurses	
			Asso.	Nursing	Avail.	N	Avail.	N
A*	Allan	Lady Oracle	1	1	5	5 (2)	5	1
	Aurora	Lady Oracle/ Rounder ^a	2/1	3/1	3	2	3	2
	Soursop	Fruit Salad	1 (2)	1	5	4 (1)	5	0
	Snowman	Oryx	1 _T (1)	1	3	2 (1)	3	0
	Crake	Oryx	1	1	5	4 (1)	5	2
	SLBC	Atwood	1 _T (2)	1	5	5 (2)	5	1
D	Distinct	—	—	—	1	—	1	
F*	Thumb	Fingers	1	1	5	5 (3)	4	0
	Tweak	Pinchy	1	1	4	4 (3)	3	0
	Enigma	Mysterio	1	1	4	4 (3)	3	1
J*	Jonah	Sophocles	3 (2)	1	2	2	2	1
	Oedipus	Jocasta	1	1	2	1	2	0
R*	Routine	Raucous	1	1	4	3 (0)	4	0
	Rema	Rita	1	1	4	2 (1)	4	2
T	Tusk	Tooth	1 _T	1	—	1 (0)	—	0
U*	Spoon	Fork	1	1	2	2 (1)	2	0

"Mother rank" is relative to other available unit members; a tie is indicated by "_T". Association was defined as identification in the same cluster, with a daily or 2-h sampling period, using "both identified" as the association index. For mother rank, parenthesis indicate her rank based on the 2-h sampling period, if it differs from her rank based on the daily sampling period. For babysitters, parenthesis indicate number (N) of available unit members observed associating with the calf while associated with no other adults or juveniles, if it differs from the number when all clusters are included. Only calves from well-sampled social units (indicated by an asterisk) were included in calculations of mean relatedness values and in permutation tests.

^aBoth Lady Oracle and Rounder were genetically possible as the mother of Aurora.

individuals who were not close relatives ($r < 0.1$) (note: these are post hoc observations and so cannot be tested statistically). These trends were regardless of whether the raw association values or the mother-standardized values were used. Consequently, much of the sole babysitting (51.2%) was carried out by likely grandmothers or maternal half-siblings to the calf (Figure 1b). Likely second- or third-degree relatives of the mother were also sole babysitters more often (29.3% of occasions) than unit members who were not close relatives (19.5%; Figure 1b).

Overall, females who nursed calves that were not their own were more closely related to the mothers of those calves than were the available females who did not nurse them ($\Delta r = 0.14$, $P = 0.054$, 50,000 simulations; Figure 2). The mean relatedness of nurses to

the mothers of the calves they nursed was 0.287, compared with 0.147 for the other available females in the calf's unit who did not nurse the calves.

DISCUSSION

We found positive correlations between maternal relatedness and two forms of alloparental calf care: babysitting and nursing. These suggest that kin selection has a key role in the evolution of the sperm whale's system of cooperative breeding.

We also demonstrated that the commonly practiced – but previously untested – assumption that mothers can be correctly determined based purely on social data is not always valid. Although in most cases the genetically determined mother was the same individual as would be inferred from the social data, assigning maternity based exclusively on social data is likely to be particularly unreliable if based on rather few behavioral observations.

Different levels of care likely have different costs to the caregiver, which appears to affect which individuals are willing to provide care. Associating with calves while other adults or juveniles are also present would include occasions when the whole unit is socializing, and likely has little or no cost to the participating individuals, whereas being the sole escort of a calf may be costlier. The former is practiced by almost all unit members (Figure 1a), and the positive correlations between babysitting rates and kinship with the mother can be seen as a partial consequence of a general correlation between association and kinship among unit members (Konrad et al. 2018a). Being the sole babysitter is more specific, and was typically done only by those individuals who were at least third-degree relatives of the mother ($r \geq 0.125$) and most often by those who were first-degree relatives, and so a sibling or grandmother of the calf ($r \approx 0.5$; Figure 1b). Similarly, nursing, assuming milk is being provided

Table 2
Correlations between association rates and maternal relatedness across all calf-babysitter pairs

	Sampling period	Rank-standardized		Mother-standardized	
		r_s	P	r_s	P
All clusters	Day	0.253	0.051	0.240	0.049*
	2 h	0.063	0.35	0.147	0.330
Just one adult/juvenile	Day	0.066	0.34	0.403	0.019*
	2 h	0.078	0.28	0.374	0.048*

One-sided P -values for Spearman's rank correlation coefficient (r_s) were calculated based on 50,000 simulations. Associations and relatedness values for each calf were ranked and scaled to values from 0 to 1, or association rates were standardized relative to the mother's association rate. Association indices were calculated using all clusters, as well as excluding clusters with more than one adult or juvenile.

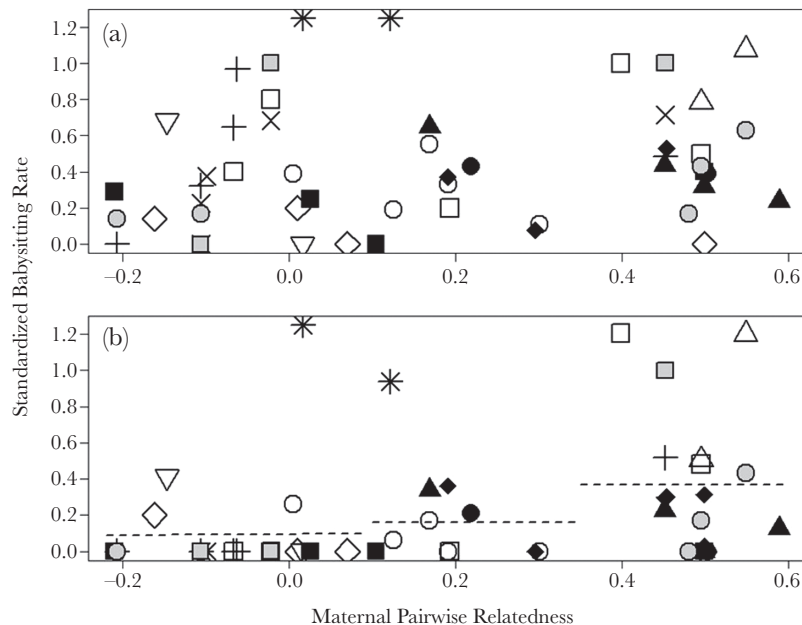


Figure 1

Maternal relatedness between calves and non-calf unit members correlates with babysitting rate. Relatedness values were calculated using Wang's estimator (Wang 2002). Babysitting rate was based on "both identified" association indices, with a daily sampling period, and scaled by the calf's association rate with its mother, (a) with all clusters, and (b) excluding clusters with more than one adult or juvenile. Shape and shade indicate calf identity. Dashed horizontal lines indicate mean babysitting rates for likely first-degree relatives of the mother ($r \geq 0.35$), more distant relatives ($0.1 \leq r < 0.35$), and individuals who were not close relatives ($r < 0.1$).

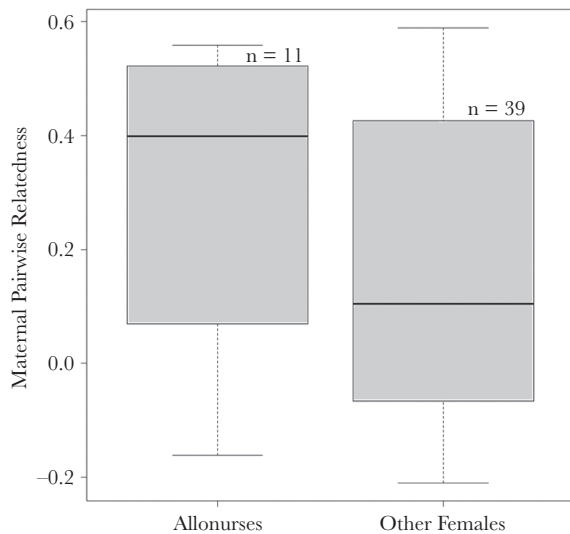


Figure 2

Relatedness of allonurses and other available females to the mothers of the calves they nursed, or were available to nurse. Relatedness values were calculated using Wang's estimator (Wang 2002).

to the calf, is likely costlier than simply associating with a calf, and it was mostly performed by close relatives of the mother ($r \geq 0.4$; Figure 2). For example, allonursing was prevalent in Unit A, which is composed of two strict matriline (Konrad et al. 2018a), and observed allonurses were exclusively from the same strict matriline as the calves they nursed. The mean relatedness between allonurses and the mothers of the nursed calves, $r = 0.287$, is at a level where, if this is the mean kinship within groups, alloparental provisioning is common among social mammals (Lukas and Clutton-Brock 2018). Thus, our examination of allonursing and kinship partially resolves the paradox that we noted in the Introduction whereby the mean kinship within sperm whale social units is lower than typically found in groups of mammals with alloparental provisioning.

Consideration of allocare costs can also aid the identification of mothers based on social data. We found that calf care behaviors that were likely costlier were better indicators of maternity: peduncle diving was a more reliable indicator of maternity than social association, and restricting association data to clusters with one adult escort resolved maternal ambiguity in the association data in one case.

To generate hypotheses about what drivers, other than kinship, may be affecting cooperative calf care among sperm whales, it is informative to consider exceptions to these general trends, especially cases that are particularly deviant, and to compare results using different measures. Based on rank-standardized association values, we observed that, for a given calf, ordinal ranks of babysitting were not well-predicted by ordinal ranks of maternal relatedness (Table 2), meaning that a calf's closest maternal relative was not necessarily its primary babysitter. In contrast, correlations were greater and generally statistically significant when associations were standardized by the mothers' values. This difference suggests that perhaps it is not the rank of unit members' genetic relatedness that matters so much as their absolute genetic relatedness. For example, it may be unimportant that an individual is the calf's closest maternal relative if that individual is still not a particularly close relative. This idea is supported by the previously-mentioned approximate relatedness thresholds delineating which individuals provide certain

types of allocare. If the absolute level of relatedness is an important driver of babysitting, we would also expect social units with higher overall relatedness to have more prevalent babysitting. This was largely true among the well-sampled social units ($r = 0.86$ using all clusters; $r = 0.35$ using just clusters with one adult; $N = 5$ units).

Another important difference between the two standardized metrics of calf association is that standardizing associations by per-calf ranks ignores differences between calves in the relative level of allocare received. Younger calves likely require more care, and this could involve more care from their mother as well as from alloparents. Thus, scaling association rates by the mother's value could help control for this source of variation, reducing noise, and allowing a relationship between genetic relatedness and babysitting to be detected.

Calf age may also help explain why certain calves received especially high levels of babysitting. For example, Jonah (symbolized as the asterisk on Figure 1) a calf from the small Unit J, who was thought to be less than one year old, was babysat extensively by the only two other members of Unit J (besides its mother), neither of which were close maternal relatives. In the first year of their calves' lives, mothers are less gregarious and less socially connected, perhaps due to added energetic demands associated with lactating, which may require increased time allocated to foraging at depth (Gero et al. 2013). This may leave calves in need of particularly high levels of babysitting in their first year, especially because they are also likely the most vulnerable to predation at this young age. Two other calves (IDs: Aurora and SLBC) that also stand out as having received allocare that matched or exceeded the care provided by their mothers (Table 1) were also less than a year old. If very young calves indeed require more allocare, in small social units without close relatives, such as Unit J, the burden of this extra care may fall on distantly related or unrelated individuals.

We also observed deviations from the overall positive relationship between maternal relatedness and allonursing. For instance, a calf from unit R (ID: Rema) made peduncle dives on two adult females from her unit who were not close maternal relatives (maternal $r \leq 0$), yet the calf was not observed making peduncle dives on her mother's first-degree relative (maternal $r = 0.5$). These deviations may relate to sources of individual variation, such as physiological status (because we made assumptions about the availability of females to act as allonurses based on behavioral data and approximate age) and personalities of individual calves or potential carers (Sih et al. 2012). More gregarious individuals, for example, whether calves or babysitters, would be expected to have higher association rates. There might also be cultural differences in allocare behavior between units (Cantor and Whitehead 2015).

Reciprocal altruism could also be a driver of allocare patterns outside the expectations of kinship (Trivers 1971, 2006). Past studies have demonstrated concurrent mothers babysitting for each other, as well as a mother reciprocating babysitting after a delay of a year, when a calf was born to the past babysitter (Gero et al. 2009, 2013). Based on the observations of allocare reported in the present study, however, reciprocity is by no means a rule. For example, in 2010, there were two new calves in Unit A (IDs: Crake, and SLBC), but their mothers (IDs: Oryx and Atwood, respectively) were not observed babysitting each other's calves, except when other adults or juveniles were present in the cluster.

Another factor that may influence patterns of allocare is gaining maternal experience (Lancaster 1971). Rounder was a juvenile female whom we assumed to be nulliparous based on long-term field observations since the time she was a calf. She substantially

babysat three calves from her social unit and received peduncle dives from all of them (although it is possible she was the mother of the youngest one; see Methods). These three calves were all from the same strict matriline as Rounder, whereas two other calves in Unit A for whom Rounder did not act as the sole babysitter, were not. This suggests that if gaining maternal experience is indeed an important factor it may operate preferentially among close kin. Similarly, the only other likely nulliparous juvenile female, Canopener from Unit U, was the primary babysitter of the calf in her social unit. Both juvenile females babysat the calves in their units at a higher rate than the average for adult females, such that these two individuals accounted for 35.4% of sole babysitting observed across all calves, compared with the 22 adult females who accounted for 48.8%. There were also two juvenile males in our database, whose patterns of allocare were very different from each other. One juvenile male, Scar from Unit F, acted as a sole babysitter of all three calves in his social unit at higher rates than the average rate by adult females, whereas the other young male, Allan from Unit A, was never observed as the sole babysitter of any calves from his unit, despite being the maternal half-brother of one of them. Perhaps, the presence of a juvenile female in Unit A, but not in Unit F, could explain this difference in rates of babysitting rates by juvenile males. More robust assessment of the importance of gaining maternal experience will require investigation of whether individuals who provide more allocare as juveniles have higher reproductive success as adults.

The observation that allocare is typically found within highly social or cooperative groups of individuals (Riedman 1982) begs a question of causality: does allocare arise within these groups, or does dependence on conspecifics for the survival of young incentivize the maintenance of social relationships and provide opportunity for further cooperation? In the case of sperm whales, evidence suggests that their complex, cooperative social system is driven and maintained primarily by allocare, particularly the defense of calves (Best 1979; Gero et al. 2013), rather than the other way around. The same is believed to be true of African elephants (Lee 1987), which bear great socio-ecological similarity to sperm whales (Weilgart et al. 1996). The value of unit members in the communal defense of calves points to group augmentation (Kokko et al. 2001; Kingma et al. 2014) as another factor, beyond kin selection, which may strengthen allocare among both sperm whales and elephants.

Similarly, as an explanation of hyper-cooperation among humans, it has been suggested that cooperative breeding may promote further prosocial tendencies (Burkart et al. 2014). The robustness of this hypothesis has been disputed (Thornton et al. 2016), but it is commonly accepted that reducing predation risk, which often includes communal protection of offspring, motivates group living among numerous species (Alexander 1974). Groenewoud et al. (2016) argue that similar predation-driven selective pressures may have encouraged evolutionary transitions to more complex societies. In line with this idea, among lions (*Panthera leo*), defense of young against infanticide is thought to be the primary motivator behind groups formed by mothers, called crèches (Pusey and Packer 1994). Further, allocare that also occurs within crèches, namely allonursing, appears to be a by-product of this social system (Pusey and Packer 1994). Similar to what we observed among sperm whales, this allonursing was more common among close kin, suggesting that relatedness among female lions, as among sperm whales, contributes to the persistence of this potentially costly behavior (Pusey and Packer 1994).

The sperm whale population in the eastern Caribbean, which we reported on in this study, is in a state of critical decline, with a particularly clear decrease in the number of adults in social units (Gero and Whitehead 2016). A reduction in the number of adult social unit members will likely have implications for the quality and quantity of allocare that calves receive, which may, in turn, compound the rate of population decline if calf survival is negatively affected as a result. Thus, understanding the extent of allocare received by calves, and from whom they receive it, can improve our understanding of the trajectory of this declining population.

CONCLUSION

We identified a positive relationship between allocare and maternal relatedness, which points to kin selection as a driver of the evolution and maintenance of allocare among sperm whales. We also observed that while mothers typically provide the majority of care for their calves, allocare can be extensive in some cases, with some allocarers perhaps even exceeding the mother's contribution. Additionally, deviations from the overall trends may be partially explained by variation in factors like calf age, unit size and composition, individuals' gregariousness and personality, and sampling coverage, but we also suggest that some combination of reciprocity, group augmentation and gaining maternal experience may contribute to the observed patterns. Further longitudinal studies of allocare within well-known social units are likely to be the most fruitful avenue for elucidating the contributions of other factors. By studying the mechanisms that allow allocare to evolve, we increase our understanding of a process that may be foundational to many complex cooperative societies.

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Data accessibility: Analyses reported in this article can be reproduced using the data provided by Konrad et al. (2018b, 2018c).

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