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Kinship and association do not explain vocal repertoire variation among individual sperm whales or social units

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Vocal learning often results in distinct dialects among individuals or groups, but the forces selecting for these phenomena remain unclear. Female sperm whales, *Physeter macrocephalus*, and their dependent offspring live in matrilineally based social units, and the units associate within sympatric clans. The clans have distinctive dialects of codas (patterns of clicks), as do, to a lesser extent, the units within clans. We examined the similarity of coda repertoires of individuals and units from the eastern Caribbean and related these to patterns of kinship and social association. Similarity in coda repertoires was not discernibly correlated with close kinship or association rates for either individuals or units (matrix correlation coefficients <0.12 for all tests using whole repertoires and data from all units). This supports the prevailing hypothesis that these vocalizations are culturally transmitted. The lack of correlation also indicates that vocal learning may occur broadly within clans, rather than preferentially from close kin or close social associates within social units, or that biases in vocal learning at lower levels of social structure are diffused by clan-level processes, such as conformity. Finally, an absence of signals of kinship in vocalization patterns suggests that a different mechanism, perhaps familiarity through repeated association, mediates kin selection among sperm whales.

Vocal learning has been documented in a range of taxa, but its phylogenetic distribution is uneven. Outside humans, it is best known in birds, especially oscine species and parrots (Kroodsma & Baylis, 1982). Vocal learning has also been demonstrated in some lineages of mammals, including elephants (Poole, Tyack, Stoeger-Horwath, & Watwood, 2005), great apes (Crockford, Herbinger, Vigilant, & Boesch, 2004), bats (Boughman, 1998), pinnipeds (Reichmuth & Casey, 2014) and cetaceans (Janik & Slater, 1997). Socially learned vocalizations likely serve several important functions in animal societies (Tyack, 2008), including sexual selection (Janik, 2014), signalling individual identity (Tyack, 1997) and maintaining social bonds (Poole et al., 2005). While vocal learning in birds has attracted a broad range of research, spanning social enhancement (e.g. Chen, Matheson, & Sakata, 2016), genomics (e.g. Pfenning et al., 2014) and speciation (Mason et al., 2017), there has been much less work on nonhuman mammals, especially wild populations. With some important exceptions (e.g. King, Harley, & Janik, 2014; Lemasson, Jubin, Masataka, & Arlet, 2016; Stoeger & Manger, 2014), most research on vocal learning in nonhuman mammals has had a primary aim of showing that vocalizations are socially learned. Thus, the functions of vocal learning and the social processes by which it occurs have been assessed in few mammalian species.

Cetaceans are a mammalian taxon for which vocal learning has been relatively well documented. In bottlenose dolphins (*Tursiops* spp.), for example, the function and process of vocal learning have been examined extensively (Janik, 2014). Among sperm whales, *Physeter macrocephalus*, vocal learning is less understood, but repertoire variation has been identified at several levels of sperm whales' well-characterized hierarchical social structure, suggesting such variation functions to signal identity at these nested levels of social organization (Gero, Whitehead, & Rendell, 2016). However, studies of vocal learning in sperm whales remain few. Thus, there is still much of interest to learn from sperm whales about the variation, cultural transmission and function of learned vocalizations.

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Female and juvenile sperm whales live in social units that have stable membership across years (Gero et al., 2014; Whitehead, 2003), and from which males disperse before sexual maturity (Best, 1979). Within social units, there is communal care for calves (Gero, Engelhaupt, Rendell, & Whitehead, 2009; Gero, Gordon, & Whitehead, 2013; Whitehead, 1996). Social preferences, as indicated by nonrandom behavioural coordination in close clusters at the surface between dives, exist among individuals within units (Gero, Engelhaupt, & Whitehead, 2008) and between social units in the formation of temporary affiliations, termed groups (Gero, Gordon, & Whitehead, 2015). Social units can contain unrelated individuals, but the units are generally matrilineally based (Christal, 1998; Konrad, Frasier, Gero, & Whitehead, 2018a; Mesnick, 2001; Ortega-Ortiz, Engelhaupt, Winsor, Mate, & Rus Hoelzel, 2012). Association preferences within units, including patterns of alloparental care, loosely reflect kinship, although association preferences among social units generally do not (Konrad et al., 2018a; Konrad, Frasier, Whitehead, & Gero, 2018b).

Social units can be clustered at a higher level of social organization, called vocal clans, based on patterns of association and shared dialects (Gero, Bøttcher, Whitehead, & Madsen, 2016; Rendell & Whitehead, 2003). Clans differ in nonvocal behaviour, but are defined based on repertoires of codas (Rendell & Whitehead, 2003), which are stereotyped patterns of broadband clicks (Watkins & Schevill, 1977) that appear to be used for communication (Schulz, Whitehead, Gero, & Rendell, 2008; Whitehead & Weilgart, 1991). Models show that social learning, with a bias towards learning common codas from individuals with similar repertoires, can drive the evolution of sympatric vocal clans (Cantor et al., 2015). However, this theoretical result is not dependent on the social level (within social units, within clans, or populationwide) at which social learning occurs (Cantor et al., 2015). Therefore, ambiguity remains about which individuals vocal repertoires are learned from, the details of which will, to a large extent, determine how coda repertoire variation emerges among units and individuals.

The information that we have about the development of sperm whale coda repertoires is from observations, inferences and correlations. Males are believed to mate across wide geographical areas, in different social units from their natal families, and likely, at least sometimes, with members of other clans (Whitehead, 2003). In the Pacific, clans have distinct, but overlapping, distributions of mitochondrial haplotypes (Rendell, Mesnick, Dalebout, Burtenshaw, & Whitehead, 2012). Off Dominica, in the Atlantic, social units within clans have characteristic coda type repertoires (Gero, Whitehead et al., 2016). All this supports social learning, rather than genetic determination, as driving the ontogeny of coda repertoire, and that the social learning occurs primarily within clans, and perhaps within social units. But it leaves the nature of the social learning pathway open.

Coda repertoires or specific coda types may be preferentially learned from closer social associates as found in several bird species, such as crossbills, *Loxia curvirostra* (Sewall, 2009). Alternatively, or additionally, coda repertoires or particular coda types could be preferentially learned from kin. These codas could then serve as a kin recognition signal, and thus mediate kin-driven patterns of association and calf care in sperm whale social units (Konrad et al., 2018b, 2018a).

To investigate how social association and kinship relate to the vocal repertoires of individual sperm whales and their social units, we compared social affiliations, genetic relatedness and vocal repertoire similarities, at both the individual and unit levels, using data from a longitudinal research project on sperm whale behaviour off Dominica (Gero et al., 2014). These relationships can inform us about potential pathways for the development of coda repertoires. For instance, if coda repertoire similarity between individuals is strongly correlated with kinship, this might indicate that coda repertoire is preferentially learned vertically from the mother and from other close kin. Alternatively or additionally, should within-unit coda repertoire similarity be strongly correlated with association rate, this might support a role for horizontal social learning. In contrast, if coda repertoire similarity is not strongly correlated with either kinship or within-unit association rate, but is unit and clan specific (Gero, Whitehead et al., 2016; Rendell & Whitehead, 2003), this would suggest that the repertoire is socially learned widely from unit and clan members, perhaps being standardized at the unit and/or clan level by conformism (Cantor et al., 2015). Similar inferences are possible at the level of the social unit. Correlations between repertoire similarity and between-unit kinship could indicate stable repertoires substantially informed by a history of unit fissions, while a correlation of repertoire similarity with association rates between units would suggest a role for horizontal convergence of dialect, as seen in killer whales, *Orcinus orca* (Deecke, Barrett-Lennard, Spong, & Ford, 2010). Finally, we examine relatedness among animals from different clans with distinct coda repertoires. If clans represent separate matrilineal clades, then the separation in coda dialects could be a consequence of vertical social learning plus drift. However, matrilineal kinship across clans would indicate transfer of individuals or units between clans, and thus horizontal social learning, and probably conformism.

METHODS

Field Methods

From 2005 to 2016, social units of sperm whales were located and followed using acoustic and visual methods (Gero et al., 2014), in an area of approximately 2000 km^2, off the leeward, western coast of Dominica, in the Caribbean Sea (15.5°N, 61.5°W). Annual field seasons took place between January and June and lasted 2–4 months in duration aboard a variety of research platforms. The total effort at sea was 518 days.

Photographs of the trailing edge of flukes of juveniles and adults (Arnbom, 1987) and of the dorsal fins of calves (Gero et al., 2009) were taken for individual identification. We recorded associations of identified individuals in clusters (Gero et al., 2014). Clusters were defined as groupings of individuals at the surface in close proximity to each other (<40 m) with coordinated behaviour (Whitehead, 2003).

We used dip-nets opportunistically to collect sloughed skin from the diving locations of individual whales or clusters of whales (Whitehead, Gordon, Mathews, & Richard, 1990). In 2015 and 2016, we also collected biopsy skin samples from specific individuals, to fill known gaps in our sample set (for details, see Konrad et al., 2018a).

Acoustic Sampling

Using a towed hydrophone array, codas were recorded when clusters of whales initiated dives and while whales were socializing at the surface (Gero, Whitehead et al., 2016; Rendell & Whitehead, 2003). In 2014 to 2016, codas were also recorded using third-generation Dtags (Digital Acoustic Recording Tags; Johnson & Tyack, 2003). See Appendix 1 for numbers of codas recorded across years and details of recording systems.

Codas were assigned to individuals and units (see Gero, Whitehead, et al., 2016). For Dtag recordings, codas were assigned to the unit in which the tagged whale was a member if no other units were identified on the tagging day. At the individual level, Dtag codas were only assigned to the focal tagged whale based on consistent interpulse interval, and for which angle of arrival was consistent with tag placement.

Social Units and Defining Social Association

Social units were delineated by Gero et al. (2014), and reflect long-term stable social relationships. One pair of social units (Units F and U) that merged across the study period (Konrad et al., 2018a) were treated as separate units, because much of the acoustic data were collected before the merger was complete.

For our analysis, we used two definitions of association. First, as a fine spatiotemporal scale of association, we considered individuals in clusters at the surface. Clustered individuals often interact vocally (Schulz et al., 2008), and thus association at this scale may influence the coda repertoires of individuals. Second, we defined association more broadly as individuals identified within 2 h of each other, as such individuals are almost always close enough (ca. 7 km) to be in acoustic contact.

To assess the influence of both short- and long-term association preferences on acoustic similarity, we used two different sampling periods to calculate association indices with our finer definition of association (i.e. clusters). The shorter period used was 2 h, which corresponds to approximately two dive cycles in sperm whales and has been applied in other studies of this species (Christal & Whitehead, 2001; Gero et al., 2015). With this sampling period, we aimed to maximize the number of samples while minimizing autocorrelation in cluster composition. The longer period used was ‘year’, which has also been previously applied in this species (Gero et al., 2015) to highlight long-term association preferences. With our broader definition of association (i.e. both identified within same 2 h), we used a daily sampling period to calculate an association index of intermediate temporal scale.

To calculate association indices for these three combinations of association definition and sampling period, at both the individual and unit level, we used half-weight indices (HWI) of association (Cairns & Schwager, 1987). This index best corrects for the types of biases in identification rates that are typical of cetacean photo identification (Cairns & Schwager, 1987; Whitehead, 2008). For unit level associations, if at least one member from each of two social units were associated in a sampling period, then those individuals’ social units were considered associated in that sampling period.

Genetic Laboratory Methods and Analysis

For detailed genetic laboratory methods, analysis of microsatellite genotypes, genetic sexing and mitochondrial DNA (mtDNA) sequence data, see Konrad et al. (2018a). To estimate relatedness between individuals, we used the R package ‘related’ (Pew, Muir, Wang, & Frasier, 2015). Performance of different relatedness estimators varies depending on the relatedness structure of the population, and no single estimator performs best across all relatedness structures (Csilléry et al., 2006; Van De Casteele, Galbusera, & Matthysen, 2001). For our analysis, we selected the estimator of relatedness that performed the best in a comparative function in ‘related’ that used our population allele frequencies to generate pairs of individuals with known relationships and to estimate the relatedness of these pairs using four different relatedness estimators (Li, Weeks, & Chakravarti, 1993; Lynch & Ritland, 1999; Queller & Goodnight, 1989; Wang, 2002). The estimator with the highest correlation between observed and expected relatedness values was Wang's (2002) estimator. We used this estimator to calculate pairwise relatedness values for all pairs of individuals, based on genotypes of 18 microsatellite loci and population allele frequencies determined by Konrad et al. (2018a). To calculate mean relatedness values between social units, we averaged the pairwise relatedness values between all genetically sampled pairs of individuals across each pairwise combination of social units.

We also classified social units’ mtDNA haplotypes as the same or different, based on 346 bp sequences at the 5′ end of the mtDNA control region, using the haplotype assignments for social units in this population determined by Konrad et al. (2018a). As only two haplotypes were found, and all members of each unit possessed the same haplotype, same/different is a fully descriptive measure of relative haplotype similarity.

Mother–offspring relationships for the individuals in this study were determined by Konrad et al. (2018a), including both relationships between mothers and dependent calves and genetically determined mother–offspring relationships between adult females for which the relative generations of the adults were unknown.

Testing for Kin Relationships Between Vocal Clans

To test for instances of close kinship between individuals in different vocal clans, we used the program ‘ML-Relate’ (Kalinowski, Wagner, & Taper, 2006). Based on microsatellite genotypes across 18 loci, we tested whether the relationship between any pair of individuals in different vocal clans was likely to be parent–offspring, half-sibling/grandparent–grandoffspring, full sibling or unrelated. We determined which of these four relationships was consistent with the genetic data at the 0.05 level of significance by calculating likelihood ratios and using simulations to reject unlikely relationships. If multiple relationships were consistent with the genetic data, this method was also used to identify the most likely relationship.

Measuring Similarity Between Coda Repertoires

To quantify coda repertoire similarity among individuals or units, we employed the continuous measure of similarity of Gero, Whitehead, and Rendell (2016) based on the absolute interclick intervals (ICIs), which are the times between the onsets of each sequential click in a coda. ICIs were extracted using two different programs. Prior to 2014 codas were analysed using Rainbow Click (Leaper, Gillespie, & Papastavrou, 2000), after which we used a custom-written MatLab R2015b script (Mathworks, Natick, MA, U.S.A.) and LabVIEW program (National Instruments, Austin, TX, U.S.A.). The various recording systems used over the years, including Dtags, all had flat (±2 dB) frequency responses across ranges of at least 2–20 kHz and sampling rates of 44.1 kHz or higher (see Appendix 1). Importantly, differences in our recording systems did not affect our ability to record clear signals of coda clicks and, therefore, did not affect the calculation of ICIs used in this analysis. For pairs of codas with the same number of clicks, we calculated the multivariate similarity of the codas using the Euclidean distance between the ICI vectors of those codas. Codas with different numbers of clicks were assigned a similarity of zero. Using custom-written routines in MATLAB v.7.12 (Mathworks), we averaged these multivariate similarities to calculate a measure of similarity between pairs of coda repertoires, for both individuals and social units, following the equation in the electronic supplementary material of Gero, Whitehead, et al. (2016).

For an analysis of ‘whole repertoire’ similarity at both the unit and individual level, we included all codas with a length up to and including 10 clicks (as codas with more than 10 clicks are rare and may not be easily distinguishable from sequences of rapid echolocation clicks). We also determined the multivariate similarity of four-click coda repertoires at the unit level and the multivariate similarity of 5R1 codas (five regularly spaced clicks with a total duration of ca. 0.35 s) at the individual level. These coda types were selected because unit variation in four-click coda repertoires and individual variation in 5R1 codas suggest that four-click coda repertoires and 5R1 codas may function as unit-level and individual-level identity cues, respectively, based on the results of Antunes et al. (2011) and Gero, Whitehead, et al. (2016).

Unit-level Matrix Correlations

In this analysis, we included social units for which genetic data were available for at least three individuals, and for which at least 250 codas had been recorded. Discovery curves have demonstrated that coda sample sets of this size should be representative of a unit's repertoire, including all but very rare coda types (which combined make up <2% of a unit's coda production; see supplementary material Figure 3 in Gero, Whitehead, et al., 2016). For tests of four-click coda similarity, we restricted our analysis to social units for which at least 25 four-click codas had been recorded, which is a minimum sample size that has been applied in other studies of unit coda usage in this species (Rendell & Whitehead, 2005).

We performed Mantel tests (Mantel, 1967), with 10 000 random permutations (which stabilized *P* values), using SOCPROG2.7 (Whitehead, 2009) to test for matrix correlations between each measure of acoustic similarity (whole repertoire similarity and four-click coda similarity) and each association index (clusters in 2 h, clusters in a year, 2 h in a day), as well as each measure of genetic similarity (mean pairwise relatedness and mtDNA haplotype sharing). We repeated the 'whole repertoire' analysis with the single unit from the EC2 vocal clan (Unit P) excluded to examine variation between units exclusively within the EC1 vocal clan. Similarly, we performed Mantel tests of matrix correlations between social units' clan membership (same = 1, different = 0) and the two measures of genetic similarity. For all analyses, we conducted two-sided tests, because units or individuals may learn repertoires that are more like their kin or associates, or that are dissimilar, such as has been observed among bottlenose dolphins (*Tursiops* spp.), for which females' whistles were unlike those of their mothers (Sayigh, Tyack, Wells, Scott, & Irvine, 1995).

Individual-level Acoustic Analysis

For our analysis of whole repertoires of individuals, we included individuals from known social units for which genetic data were available, and for which at least 25 codas had been recorded. Discovery curves have demonstrated that coda sample sets of over 75 should be representative of an individual's repertoire (see supplementary material Figure 3 in Gero et al., 2016, and supplementary material Figure 2 in Gero, Bøttcher, et al., 2016), so we repeated these analyses after removing individuals that did not meet this more stringent sample size criterion. As in a past study that identified individual differences in 5R codas (Antunes et al., 2011; later split into subtypes 5R1 and 5R2 by Gero, Whitehead et al., 2016), we restricted our analysis of 5R1 codas to individuals with at least five 5R1 codas recorded. We also repeated this analysis with a more stringent sample size cutoff of 25 to remove possible effects of undersampling individual variation.

Across all adequately sampled individuals, as well as within social units that had at least three adequately sampled members, we performed Mantel tests (Mantel, 1967), with 10 000 random permutations, using SOCPROG2.7 (Whitehead, 2009) to test the significance of matrix correlations. We tested for correlations between each measure of acoustic similarity (whole repertoire similarity and 5R1 coda similarity) and each of two association indices: association in a cluster in a 2 h sampling period and association in a cluster in a yearly sampling period. Across all individuals, we also tested for a correlation between social unit (same or different) and each acoustic similarity measure. Likewise, we tested for matrix correlations between these acoustic similarity measures and three measures of kinship: pairwise relatedness, mtDNA haplotype sharing and whether the pair of individuals had been genetically identified as a mother–offspring pair or not. We did not include mtDNA haplotypes as a predictor in the within-unit analyses because haplotypes were uniform within social units (Konrad et al., 2018a). Analyses were repeated with calves omitted to account for differences between repertoires of calves and adults, which have been reported in this species (Gero, Whitehead et al., 2016; Schulz, Whitehead, Gero, & Rendell, 2011).

Power Analysis of Individual-level Analysis

To assess the power of our data to detect small effects of relatedness on individual-level acoustic similarity, we repeated Mantel tests of matrix correlations between pairwise relatedness and whole repertoire similarity across all individuals ($N_{\text{ind}} = 20$; so $N_{\text{pairs}} = 190$) with modifications to the acoustic similarity matrix based on kinship. To simulate a situation where mothers and their offspring have more similar repertoires, we boosted the acoustic similarity of all known mother–offspring pairs ($N_{\text{pairs}} = 8$) by adding to these values a percentage of the mean acoustic similarity value, ranging from 10% to 400%. To simulate a situation where all close relatives have more similar repertoires, we boosted the acoustic similarity of all pairs with a relatedness value of at least 0.2 (i.e. roughly including first- and second-degree relatives; $N_{\text{pairs}} = 27$) by adding to these values a percentage of the mean acoustic similarity value, ranging from 10% to 200%.

Ethical Note

Data were collected from a population of approximately 280 sperm whales off Dominica containing females, juvenile males and calves (Gero & Whitehead, 2016). The field research was principally observational and all methods were designed to minimize impact on the animals. Some genetic material was collected using biopsy darts, and some acoustic data were recorded using temporary (ca. 8 h deployment) Dtags with suction-cup attachment systems. Our data and samples were collected in Dominica under scientific research permits from the Fisheries Division of the Ministry of Agriculture and Environment: SCR 013/05-02, RP-2/12 IW-1, RP-09/014 IW-1, RP-01/079 W-2, RP-03/059 W-4, P-122/4 W-2, P-40/2 W-7 and RP-16-04/88-FIS-9. Samples were transported through CITES permits for the import and export animal parts issued by Environment Canada and the Environmental Coordinating Unit of Dominica. The field protocols for approaching, photographing and recording sperm whales were approved by the University Committee on Laboratory Animals of Dalhousie University and the Animal Welfare and Ethics Committee of the University of St Andrews. Biopsy sample collection procedures were approved by the Saint Mary's University Animal Care Committee and the Animal Welfare and Ethics Committee of the University of St Andrews.

RESULTS

Unit-level Analysis

For 10 social units from the EC1 vocal clan (Units A, D, F, J, N, R, S, T, U and V) and one social unit from the EC2 vocal clan (Unit P), genetic data were available for at least three individuals per social unit (mean: 8.4, maximum: 12) from which at least 250 codas had been recorded (minimum: 296, mean: 579, maximum: 1443; Table 1). Four of these social units (Units A, F, N and V) had at least

Table 1
Acoustic and genetic data and sample sizes for eastern Caribbean sperm whale social units, delineated as in Gero et al. (2014)

Vocal clan	Unit	mtDNA hap	Unit members		Coda recordings	
			Known	With genetics	Whole repertoire	Four-click
EC1	A	BB	12	12	779	181
	D	A	7	4	336	–
	F	A	10	9	1443	256
	J	A	6	5	870	–
	N	A	9	8	296	74
	R	A	10	7	302	–
	S	A	4	3	464	–
	T	A	9	6	382	–
	U	A	4	4	737	–
	V	A	12	3	530	54
EC2	P	BB	9	3	388	–

Vocal clans are designated as in Gero, Bøttcher, et al. (2016) and Gero, Whitehead, et al. (2016). Only social units with at least 25 four-click codas recorded were included in the four-click coda analyses.

25 four-click codas recorded (minimum: 54, maximum: 256; Table 1).

No correlations between acoustic similarity and genetic or social predictors were statistically significant at $P < 0.05$, but for all three levels of analysis (whole repertoire, four-click coda repertoires, clan membership), the correlation between acoustic similarity and mtDNA haplotype sharing was large and positive ($\geq$0.58), with the lowest P values of any predictor, albeit still not significant (Table 2). The single social unit from the EC2 vocal clan for which genetic data were available (Unit P) had the rarer of the two mtDNA haplotypes observed in these social units, which was shared with only one other unit, Unit A. The contribution of Unit P to this positive correlation in the whole repertoire analysis is clear (Fig. 1), but this correlation was large and positive even with this unit excluded (Table 2). Thus, Unit A was also relatively acoustically dissimilar from the other social units in its vocal clan, in both its whole repertoire and its four-click coda repertoire (Fig. 1).

Individual-level Analysis

For analyses of whole repertoires, 20 individuals from five social units (Units A, F, J, S and U) had at least 25 codas recorded (minimum: 28, mean: 119, maximum: 300), with at least three individuals from each of these social units for intra-unit analyses. For 13 of these individuals, at least 75 codas were recorded, including at least three individuals from each of three of these social units (Units F, J and U) for intra-unit analyses. For analyses of 5R1 coda similarity, 13 individuals from five social units (Units A, F, J, S and U) had at least five 5R1 codas recorded (minimum: 7, mean: 35.2, maximum: 66), including at least three individuals from each of three social units (Units A, S and U) for intra-unit analyses. For eight of these individuals, at least 25 codas had been recorded but no intra-unit analyses could be conducted because no social unit had at least three individuals with this minimum number of 5R1 codas.

Table 2
Correlations between unit-level acoustic similarity and genetic and social predictors

Acoustic similarity	N	Predictor	Matrix corr.	P	No EC2	
					Matrix corr.	P
Whole repertoire	11	Mean rel.	−0.10	0.60	−0.11	0.62
		mtDNA	0.58	0.06	0.42	0.29
		Assoc.: clusters/2 h	0.07	0.51	−0.03	0.88
		Assoc.: clusters/year	0.01	0.85	−0.15	0.22
		Assoc.: 2 h/day	0.09	0.48	−0.08	0.52
Four-click codas	4	Mean rel.	0.14	0.89	–	–
		mtDNA	0.78	0.25	–	–
		Assoc.: clusters/2 h	0.48	0.37	–	–
		Assoc.: clusters/year	0.07	0.79	–	–
		Assoc.: 2 h/day	0.33	0.54	–	–
Clan	11	Mean rel.	−0.03	0.99	–	–
		mtDNA	0.58	0.18	–	–

Predictors included: mean pairwise relatedness (Mean rel.), mitochondrial DNA haplotype sharing (mtDNA) and three indices of social association (Assoc.: definition of association/sampling period). The whole repertoire relationship was also tested after omitting the only unit from the EC2 vocal clan: Unit P (No EC2). Note: P values were not corrected for multiple comparisons (such corrections would have increased P values).

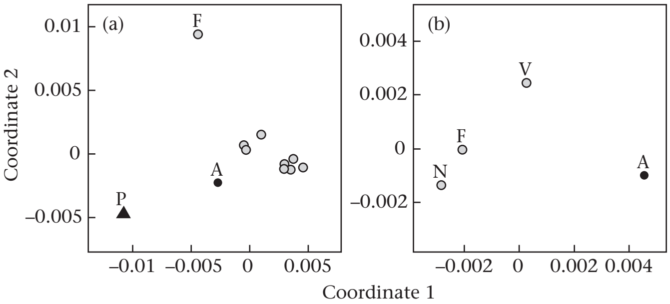

Figure 1. Multidimensional scaling plots of acoustic dissimilarity among social units. Acoustic dissimilarity was assessed for (a) whole repertoires (all codas $\leq$10 clicks in length) and (b) four-click codas. Point shading indicates mitochondrial DNA haplotype (black: BB; grey: A) and shape indicates acoustic clan (circles: EC1; triangle: EC2).

Across all individuals and within social units there were no statistically significant relationships between whole coda repertoire similarity or 5R1 coda similarity and any of the predictor variables that we examined (Table 3). These results were essentially unchanged when dependent calves were omitted (Table 3) or when stricter coda sample size requirements were used (Appendix 2).

Based on the power analysis, our ability to detect small effects of relatedness on acoustic similarity was relatively low. The acoustic similarity values for mother–offspring pairs had to be elevated by three times the mean value before the correlation was statistically significant at $P < 0.05$ (Table 4). If acoustic similarity values for additional close relatives (all individuals with $r \geq 0.2$) were also elevated, this level of statistical significance was reached when the mean acoustic similarity value was added to the values for these individuals (Table 4).

Relationships Between Vocal Clans

The data were consistent with some close kin relationships between members of different vocal clans and, thus, between individuals possessing fundamentally dissimilar coda repertoires. Each of the three genetically sampled individuals from the EC2 vocal clan had two potential second-degree relatives (half sibling or grandparent–grandoffspring) that were members of the EC1 vocal clan (Table 5). These were cases for which half sibling/grandparent–grandoffspring was the most likely option, based on likelihood ratios, and for which 'unrelated' was not a likely relationship at the 0.05 level of significance. The microsatellite data were also consistent with full siblings in three of these cases, but in each case either the mother of the proposed full sibling was known and not common to the EC2 vocal clan member, or the putative siblings differed in their mtDNA haplotype, excluding the possibility of full siblingship. In no case was parent–offspring a likely relationship. Three of the potential second-degree relatives had a different mtDNA haplotype than the EC2 vocal clan members, while the remaining three had their haplotype in common with the EC2 vocal clan members (Table 5). Thus, these instances of close kin in

Table 3
Correlation between acoustic similarity and genetic and social predictors across individual sperm whales

Acoustic measure	Unit	*N*	Predictor	Matrix corr.	*P*	No calves		
						N	Matrix corr.	*P*
Whole repertoire	All	20	Relatedness	−0.06	0.56	16	−0.10	0.43
			mtDNA	0.10	0.52		0.11	0.50
			MO	−0.03	0.79		0.00	0.77
			Assoc.: clusters/2 h	0.06	0.30		0.11	0.21
			Assoc.: 2 h/day	0.05	0.42		0.04	0.56
			Unit	0.05	0.36		0.06	0.42
	A	3	Relatedness	0.01	0.83		–	–
			Assoc.: clusters/2 h	−0.03	0.83		–	–
	F	6	Relatedness	0.29	0.31	5	0.18	0.77
			Assoc.: clusters/2 h	−0.34	0.19		−0.28	0.49
	J	4	Relatedness	−0.42	0.38	3	0.92	0.51
			Assoc.: clusters/2 h	0.13	0.61		−0.86	0.16
	S	3	Relatedness	−0.59	0.49		–	–
			Assoc.: clusters/2 h	−0.60	0.50		–	–
	U	4	Relatedness	−0.70	0.20	3	−0.82	0.51
			Assoc.: clusters/2 h	0.28	0.46		0.99	0.16
5R1	All	13	Relatedness	0.01	0.95	11	0.09	0.54
			mtDNA	0.18	0.30		0.15	0.50
			MO	0.03	0.70		0.00	0.98
			Assoc.: clusters/2 h	0.04	0.64		0.00	0.95
			Assoc.: 2 h/day	0.04	0.60		0.03	0.65
			Unit	0.05	0.51		0.10	0.29
	A	3	Relatedness	0.56	0.16		–	–
			Assoc.: clusters/2 h	0.60	0.17		–	–
	S	3	Relatedness	−0.86	0.16		–	–
			Assoc.: clusters/2 h	−0.85	0.16		–	–
	U	3	Relatedness	0.11	0.84		–	–
			Assoc.: clusters/2 h	−0.52	0.50		–	–

Predictors included: pairwise relatedness (Relatedness), mother–offspring relationships (MO), mitochondrial DNA haplotype sharing (mtDNA), fine social association (Assoc.: cluster in 2 h sampling period), coarse association (Assoc.: identified in the same 2 h in a daily sampling period), and social unit membership (Unit). These relationships were also tested after omitting dependent calves. Only individuals with at least 25 codas analysed were included in this whole repertoire analysis, and only those with at least five 5R1 codas analysed were included in this 5R1 analysis.

Table 4
Power analysis for individual-level Mantel tests

Add (% of mean)	Mother–Offspring		Relatedness ≥0.2	
	Matrix corr.	*P*	Matrix corr.	*P*
Unmodified	−0.06	0.56	−0.06	0.56
10	−0.05	0.63	−0.03	0.74
50	0.00	0.99	0.07	0.47
100	0.05	0.57	0.19	0.05
200	0.15	0.10	0.38	<0.001
300	0.24	0.01	–	–
400	0.31	<0.001	–	–

Matrix correlations between pairwise genetic relatedness and whole repertoire acoustic similarity were tested after modification of acoustic similarity values to either (1) known mother–offspring pairs or (2) all those with pairwise relatedness ≥0.2. Values were modified by adding a percentage of the mean acoustic similarity value.

different clans do include paternal relatives but may also include maternal relatives.

DISCUSSION

We did not find evidence of individual and social unit acoustic repertoires being much influenced by either close kinship or social association (matrix correlation coefficients <0.12 for all tests using whole repertoires and data from all units). Considering that coda repertoires in the study area differ substantially between clans (Gero, Bøttcher et al., 2016), and more subtly between units (Gero, Whitehead et al., 2016), these results are consistent with convergence at the unit and clan levels having a large role in homogenizing coda repertoires.

Table 5
Putative second-degree relatives across vocal clans

EC2 ind	Sex	mtDNA	EC1 ind	Unit	Mother	Sex	mtDNA	Relatedness
P4	M	BB	Scar	F	Pinchy	M	A	0.40
			TBB	S	–	F	A	0.13
Prego/Pasta	F	BB	Tooth	T	–	F	A	0.21
			Fruit salad	A	–	F	BB	0.24
P9/calf	M	BB	Oryx	A	–	F	BB	0.22
			Snowman	A	Oryx	F	BB	0.28

Potential Functions of Coda Repertoires

Such convergences of vocal repertoires within social groups, found in numerous species (e.g. Boughman, 1998; Sewall, 2009), may or may not be functional. Primarily, they can serve to signal group membership or to strengthen social bonds and promote group cohesion (Tyack, 2008). In addition to within-unit dyadic bonding (Schulz et al., 2008), sperm whale coda repertoires may function to socially delineate vocal clans (Gero, Bøttcher et al., 2016; Rendell & Whitehead, 2003), as well as perhaps to signal unit membership (Gero, Whitehead et al., 2016). However, we did not find that acoustic repertoires reflected social relationships among social unit members or among social units within clans. Thus, while the four-click coda types used by certain social units could function as unit identity signals, as suggested by Gero, Whitehead, et al. (2016), they appear not to carry any additional information about kinship or social bonds.

In other cases, learned vocalizations can function as signals of individual identity, in which case selection should favour that they be unique, rather than shared, as among bottlenose dolphins, which have individually distinctive signature whistles (Tyack, 1997). Antunes et al. (2011) and Gero, Whitehead, et al. (2016) suggested that signalling individual identity may be a function of the 5R1 coda type, which is a coda type with widespread use that shows individual variation. This coda type, however, does not appear to carry direct information about kinship or social bonds.

Evidence for Vocal Transmission Among Broad Matrilines

Previous evidence strongly suggests that codas are socially learned, given that they are not accounted for by geography, or, to the extent that it has been examined, by genetic similarity (Rendell et al., 2012; Rendell & Whitehead, 2003). Additionally, differences between repertoires of adults and younger individuals (Gero, Whitehead et al., 2016; Schulz et al., 2011) were consistent with expectations of social learning (see, for example, McCowan & Reiss, 1997). That coda repertoires did not correlate with genetic relatedness in the present study adds to this evidence that social learning is a major factor in the development of coda repertoires. The current study also goes beyond its predecessors in presenting several lines of evidence that show how this social learning operates over the sperm whale social networks that we studied.

Vocal clans in the Pacific are not matrilineally monophyletic; they contain individuals with multiple mtDNA haplotypes, some of which are shared between clans (Rendell et al., 2012; Rendell & Whitehead, 2003), and the transfer of an individual between clans has been documented (Rendell & Whitehead, 2003). Likewise, in our data, two haplotypes were detected in the EC1 vocal clan, one of which was shared with the EC2 vocal clan (Table 1). However, transfer of individuals, or units, between vocal clans appears to be rare, and correlations between mtDNA haplotype sharing and acoustic similarity, including clan membership, have been demonstrated in the Pacific Ocean (Rendell et al., 2012; Whitehead, Dillon, Dufault, Weilgart, & Wright, 1998) and in the present study (Table 2).

Although not statistically significant, at the unit level the correlations between mtDNA haplotype and all measures of repertoire similarity were large and positive (Table 2). At the individual level, the correlations between mtDNA haplotype and acoustic similarity measures were not as strong, but mtDNA haplotype sharing was still the factor with the largest effect size (Table 3). This suggests an element of maternal descent in both vocal repertoires and clan membership.

Mitogenomic diversity is low among sperm whales (Alexander et al., 2013), such that haplotype sharing does not necessitate close maternal kinship, but we can still confidently designate individuals with different haplotypes as being from different matrilines. Thus, the unit from the EC2 vocal clan is not maternally related to most of the social units from the EC1 vocal clan. However, with only one social unit from the EC2 clan included in this analysis, we cannot draw robust conclusions about the degree of mtDNA haplotype sharing and maternal kinship among vocal clans in the Atlantic Ocean.

That pairwise relatedness does not much correlate with acoustic similarity suggests that vocal learning is not constrained to be from close family members. Rather, the correlation with mtDNA haplotype sharing suggests that the coda repertoires of social units are a product of vocal learning occurring more broadly, within large groups that contain distant maternal relatives, as has been found in killer whales (Deecke et al., 2010). Presumably, these groups would be vocal clans. However, we are hesitant to conclude that finer kinship plays no role in acquiring vocal repertoires. We determined pairwise relatedness based on biparentally inherited markers and thus cannot distinguish maternal relatedness from paternal relatedness, which we would not expect to correlate with vocal learning based on sperm whale social structure. Thus, in our analysis, paternal relatedness would impede our ability to detect links between close maternal kinship and acoustic similarity. Additionally, as demonstrated by the power analysis, very strong effects, or moderate effects that affected a greater proportion of pairs of individuals, should have been detected, but our ability to detect subtler effects at the individual level was limited (Table 4).

Our results are consistent with the scenario suggested by Rendell et al. (2012) in which coda repertoires are preferentially learned from mothers, other close maternal kin or close associates, but are then horizontally transmitted more broadly among less closely related members of social units or among social units in the same vocal clan. These patterns would also be expected if learning is from a particular member of the social unit, say the oldest female. Both these scenarios are consistent with models that indicate that the emergence and maintenance of clan structures requires some level of biased social learning (Cantor et al., 2015). Rendell et al. (2012) also hypothesized that horizontal transmission between vocal clans may occur through females occasionally transferring between clans, which, as discussed below, is consistent with our data.

Genetic Flow Between Vocal Clans

Prior to the present study, genetic similarity based on biparentally inherited markers had been examined in relation to vocal clan membership in only a single preliminary analysis based on five microsatellite markers (Whitehead, 2003, p. 300). As in the present study, Whitehead (2003) found no difference in nuclear genotypes between clans. Based on the contrast of significant differentiation in mtDNA sequences between oceans versus relative homogeny of microsatellite alleles, it appears that males disperse and mate between ocean basins more than females (Lyrholm, Leimar, Johanneson, & Gyllensten, 1999). Contrasting patterns between mtDNA and microsatellite-based relatedness suggest the same may be true between clans – that males mate between clans while females more typically remain within their natal clan (see Rendell, Whitehead, & Coakes, 2005). We detected paternal relatives between vocal clans, further supporting the idea that males mate across clans. For three of the potential second-degree relatives between clans, relatedness must be paternal, because these individuals have a different mtDNA haplotype than the EC2 vocal clan members (Table 5).

Coda Repertoire Variation and Kin Discrimination

Sperm whales in the Dominica population preferentially associate with kin (Konrad et al., 2018a) and care for the calves of kin (Konrad et al., 2018b) within their social units. The lack of correlation between mean pairwise relatedness and coda repertoire similarity (Table 2) suggests that these kin-biased patterns of association and alloparental care do not operate using vocal signals carrying kinship information. Sharing of mtDNA haplotype was better correlated with coda repertoire similarity (Table 2), but there were only two haplotypes in our study population, so mtDNA haplotype sharing conveys little information for kin recognition. It is possible that while the coda types that we examined in detail (four-click codas and 5R1 codas) seemed to be likely candidates as identity signals (based on Gero, Whitehead, et al., 2016), they may not be the codas used for kin recognition. Among killer whales, for example, patterns of call type similarity among matrilines differ among call types (Filatova, Burdin, & Hoyt, 2013), and, in a study of northern resident killer whales, variation in only one out of three call types assessed correlated with kinship (Deecke et al., 2010).

However, our evidence suggests that coda repertoire similarity is not a direct indicator of kinship. Nevertheless, there are other ways that kin selection could be mediated by vocal identity signals. For example, sperm whales may be able to recognize each other by differences in these vocalizations and have knowledge of their actual maternal relationships to close relatives, such as half siblings, either directly, or using familiarity as a proxy (see Pfefferle et al., 2016). Alternatively, kin discrimination could operate using nonvocal cues (such as visual cues), or information synthesized from multiple vocal and nonvocal cues.

Conclusion

Beyond potentially encoding vocal clan and social unit membership (Gero, Whitehead et al., 2016), individual and social unit variation in coda repertoires does not discernibly relate to close kinship or social bonds. The combination of these results supports a scenario in which coda repertoire may be initially learned preferentially from mothers and other close associates. Following this, mother and kin influences appear to then be diffused by horizontal learning at the unit level or clan level, as well as individual peculiarities in vocal repertoire. It is possible that kin discrimination among sperm whales could be driven by familiarity with distinct vocal signals of individuals or social units, but the potential identity signals do not appear to intrinsically encode kinship information. Vocal learning has been demonstrated in several mammal species (Tyack, 2008), but research projects with sufficient data to assess function and transmission of learned vocalizations are rare among wild mammals. Through this study, we increase understanding of cultural transmission among mammals and how variation in learned vocalizations relates to patterns of genetic relatedness. In particular, our data are not consistent with an individual's coda repertoire being very largely identical to its mother's, or that an individual's coda repertoire is learned mainly from close social associates. Instead, the learning seems broader, from both the unit as a whole, and from other units in the clan, potentially homogenized by conformism. Moving forward, we hope that techniques such as playbacks will soon give insight into whether and how sperm whales use the information on individual, social unit and clan identity contained in their coda repertoires.

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Appendix 1

Acoustic Recording System

Vocalizations were recorded using one of several recording set-ups: In 2005, we used a Fostex VF-160 multitrack recorder (44.1 kHz sampling rate) and a custom-built towed hydrophone (Benthos AQ-4 elements, frequency response: 0.1–30 kHz) with a filter box with high-pass filters up to 1 kHz, resulting in a recording chain with a flat frequency response across a minimum of 2–20 kHz. In the 2007, 2009 and 2011 seasons, we used a Zoom H4 portable field recorder (48 kHz sampling rate) and a Cetacean Research Technology C55 hydrophone (frequency response: 0.02–44 kHz) and no filters. During the 2008, 2010 and 2012, we used the custom-built towed hydrophone (Benthos AQ-4 elements, frequency response: 0.1–30 kHz) with a filter box with high-pass filters up to 1 kHz, resulting in a recording chain with a flat frequency response across a minimum of 2–20 kHz. This was connected to a computer-based recording system as a part of the International Fund for Animal Welfare's (IFAW) LOGGER software package (48 kHz sampling rate) or PAMGUARD (minimum 48 kHz sampling rate). In 2014–2016, recordings were made through the deployment of animal-borne sound and movement Dtags (Johnson & Tyack, 2003). Dtags record two-channel audio at 120 kHz with a 16-bit resolution, providing a flat (±2 dB) frequency response between 0.4 and 45 kHz.

Table A1
Number of codas recorded across years and the recording type used in each case

Year	*N* codas	Recording type
2005	420 (356)	Towed hydrophone
2007	40 (40)	Towed hydrophone
2008	1050 (245)	Towed hydrophone
2009	304 (190)	Towed hydrophone
2010	2574 (716)	Towed hydrophone
2011	116 (0)	Towed hydrophone
2014	397 (225)	Dtag
2015	1489 (552)	Dtag
2016	137 (48)	Dtag

Numbers in parentheses denote the numbers of codas assigned to individuals in the present study.

Appendix 2

Correlation between Acoustic Similarity and Genetic and Social Predictors Using Stricter Inclusion Criteria

Table A2
Correlation between acoustic similarity and genetic and social predictors across individual sperm whales, using stricter inclusion criteria than in Table 3 (main text)

Acoustic measure	Unit	*N*	Predictor	Matrix corr.	*P*	No calves		
						N	Matrix corr.	*P*
Whole repertoire	All	13	Relatedness	−0.11	0.50	11	−0.10	0.63
			mtDNA	−0.02	0.92		0.00	0.96
			MO	−0.08	0.49		−0.05	0.84
			Assoc.: clusters/2 h	−0.05	0.75		−0.16	0.21
			Assoc.: 2 h/day	−0.07	0.58		−0.16	0.27
			Unit	−0.04	0.76		−0.16	0.20
	F	4	Relatedness	0.87	0.29		–	–
			Assoc.: clusters/2 h	0.82	0.05		–	–
	J	4	Relatedness	−0.42	0.38	3	0.92	0.51
			Assoc.: clusters/2 h	0.13	0.61		−0.86	0.16
	U	3	Relatedness	−0.72	0.17		–	–
			Assoc.: clusters/2 h	−0.67	0.16		–	–
5R1	All	8	Relatedness	0.25	0.13			
			mtDNA	0.13	0.58			
			Asso (fine)	−0.17	0.33			
			Asso (coarse)	−0.12	0.37			
			Unit	−0.03	0.95			

These relationships were also tested after omitting dependent calves. Predictors included: pairwise relatedness (Relatedness), mother–offspring relationships (MO), mitochondrial DNA haplotype sharing (mtDNA), fine social association (Assoc.: cluster in 2 h sampling period), coarse association (Assoc.: identified in the same 2 h in a daily sampling period) and social unit membership (Unit). Only individuals with at least 75 codas analysed were included in this whole repertoire analysis, and only those with at least 25 codas analysed of the 5R1 type included in this 5R1 analysis.