



How does social behavior differ among sperm whale clans?

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ABSTRACT

When individuals primarily associate with and learn from those who behave similarly, society and culture become closely tied. Sperm whales (*Physeter macrocephalus*) exhibit multilevel social structure, the levels of which are differentiated in part by characteristic cultural behaviors. Sperm whales are organized into sympatric clans, with distinctive vocal repertoires that are socially learned. Other behaviors, such as movement patterns and foraging, also differ among clans. Here we ask whether the clan partition also includes divergences in social behavior. Off the Galápagos Islands, members of two clans differed consistently in diving synchrony, heterogeneity, and temporal stability of social relationships. While number of associates (indicated by social unit, group, and cluster sizes) were similar between clans, Regular clan members dived more synchronously and had more homogeneous relationships than the Plus-One clan members. Plus-One social units had generally longer associations than those of the Regular clan. Differences in surface-time coordination and quality of social relationships are likely byproducts of the clan segregation, which could affect alloparental care giving, therefore scaling up to differential calf survival rates between clans. This new dimension of behavioral divergence between sperm whale clans indicates that sympatric, socio-cultural entities of nonhumans can also display characteristic social behavior.

Key words: intraspecific variation, culture, sperm whale, *Physeter macrocephalus*, grouping, social structure.

Culture, defined as socially learned and group-specific behavior, is increasingly being recognized in primates, cetaceans, and some other nonhuman species (*e.g.*, Laland and Hoppitt 2003, Laland and Galef 2009). Culturally recognized behaviors in these species include food preferences, foraging techniques, migratory and movement behavior, vocalizations, play, and social conventions (Laland and Hoppitt 2003). Because cultural behavior is socially learned, social structure drives and molds cultural behavioral diversity, but it is important to consider that cultural diversity can in turn influence social structure (Cantor and Whitehead 2013).

Social learning of behavior among peers—the foundation of culture (*e.g.*, Boyd and Richerson 1985)—can affect the patterns of social relationships, thus shaping social structure. This could be direct, for instance, if individuals directly learn social norms from one another. It could also be indirect if socially learned behavior sets up conditions in which different social structures emerge. For instance the social structures of

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bottlenose dolphins (*Tursiops* spp.) may be structured by individually characteristic solitary or communal foraging methods, at least some of which are socially learned, as individuals preferentially associate with others using the same methods (*e.g.*, Ansmann *et al.* 2012, Daura-Jorge *et al.* 2012, Mann *et al.* 2012). Furthermore, cultural tendencies to engage in individual *vs.* communal foraging will affect attributes and measures of social structure. Even more indirectly, culturally learned foraging behavior may set up conditions, *e.g.*, a particular spatial or temporal distribution of the selected resources, in which different social structures are expected to be favored (*e.g.*, Krause and Ruxton 2002).

In some cases, social learning can promote the emergence of sympatric, behaviorally distinct groups (*e.g.*, Centola *et al.* 2007). Social behavior within such groups may tend to diverge over time due to behavioral innovations, founder effects, as well as transmission errors and biases (Koerper and Stickel 1980, Whitehead and Lusseau 2012). Alternatively, conformism and symbolic marking can homogenize behavior within social groups and accentuate differences between them (Cantor and Whitehead 2013). These processes could be operating on social behavior or in other kinds of socially learned behavior such as foraging that directly or indirectly impacts social structure, as in the case of the bottlenose dolphins mentioned above (Cantor and Whitehead 2013). Thus culture can augment and interact with the most-generally invoked factors driving interspecific and intraspecific variation in social organization: the spatiotemporal availability and predictability of resources, predation risk, and individual differences in social behavior (*e.g.*, Lott 1984, Kappeler *et al.* 2013, Sachser *et al.* 2013, Schradin 2013, Wolf and Krause 2014).

Here we investigate whether two sympatric clans of sperm whales in the eastern tropical Pacific that possess distinct foraging, movements, and vocalizations (Rendell and Whitehead 2003, Whitehead 2003, Whitehead and Rendell 2004) also show differences in their social behavior. While male sperm whales lead quasi-solitary lives, females and immatures live in nearly permanent social units (see Whitehead 2003), within which social relationships tend to be fairly homogenous. Social units form temporary groups, but only with other units from their own clan. These clans can overlap spatially and have minimal genetic differences between them, especially in the nuclear genome (Rendell *et al.* 2012, Whitehead *et al.* 2012). Thus differences in their social behavior are likely due directly or indirectly to culture. Individuals may be learning from each other ways of organizing social relationships, or, probably more likely, cultural behavior leads indirectly to differences in social structure between clans. In the latter, the candidate processes are different foraging behaviors, differences in microhabitat use, or simple stochasticity within socially isolated sets of animals.

MATERIAL AND METHODS

Photographic and Acoustic Sampling Effort

Groups of sperm whales were tracked visually and acoustically with a directional hydrophone, day and night (Whitehead 2003) during 2–4 wk research trips between 1985 and 2003 off the Galápagos Islands, Ecuador (Fig. 1). Recordings of sperm whale codas (stereotypical patterns of clicks used for communication) were made using a variety of hydrophones (frequency responses: 6 Hz–10 kHz, ± 3 dB; 1–10 kHz, ± 3 dB), recorders and amplifiers (details in Rendell and Whitehead 2003). Females and immature individuals were identified from photographs of

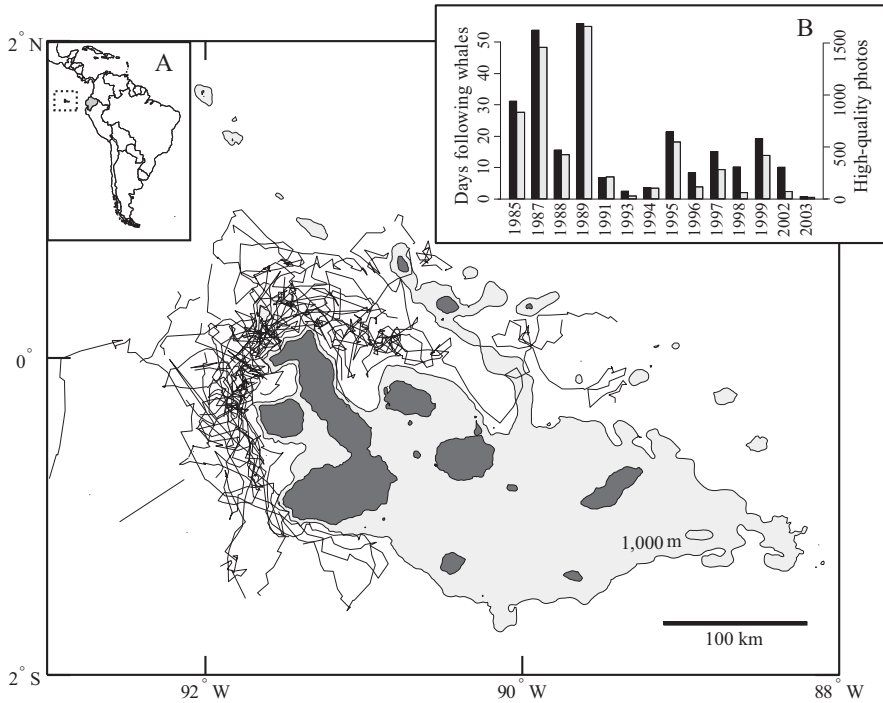


Figure 1. Spatio-temporal sampling effort off the Galápagos Islands, Ecuador, in the South Pacific Ocean. (A) The islands (dashed box) have darker shading, lighter shading represents waters less than 1,000 m deep (rarely used by sperm whales) and black lines represent the tracks of followed whales. (B) Black bars represent days following whales per year (of both clans); and gray bars represent the number of high-quality pictures ($Q \geq 3$) used for photo-identification.

natural markings on the trailing edge of tail flukes with the assistance of a computer program (Whitehead 2003). Black and white photographs were taken with 35 mm film SLR cameras until 2001, when we switched to equivalent digital equipment. The quality of each photograph was rated (from $Q = 1$, very poor, to $Q = 5$, very high quality) based on focus, exposure, orientation of the fluke in the frame, percent cover and tilt of the fluke in relation to the water surface (see Whitehead 2003). We excluded from the analyses photographs with $Q < 3$, calves (distinctively small individuals, likely < 2 yr old) and mature males (distinctively large animals). Our long-term data set comprised 3,943 coda recordings, 6,193 high-quality $Q \geq 3$ photographs, and social behavior data of photo-identified individuals collected during 12,550 d of group follows (that varied from hours to a maximum of 12 consecutive days and nights) over a period of 18 yr (Fig. 1).

Sperm Whale Clans

Vocal clans were defined as sets of social units of sperm whales (see Table 1) with high similarity in the repertoires of their coda vocalizations (Rendell and Whitehead

Table 1. Definition and estimation methods for the seven social metrics.

Social metric	Definition	Estimates based on	Method	Units of analysis
1. Social unit size ^{a,b,c}	Number of individuals in a social unit, which is a set of adult females and immature individuals that live and move together over periods of years, generally of one or more matriline.	Individuals associated with at least two other individuals during at least two 12 h identification periods spaced out by at least 30 d.	We considered the number of individuals assigned to the same social unit as in Christal <i>et al.</i> (1998).	Social unit
2. Mean group size ^{c,d,e}	Number of individuals in a group, which is a set of individuals moving together in a coordinated manner over periods of few hours to few days.	The number of photo-identified individuals for each day.	Two-occasion closed-population Lincoln-Petersen mark-recapture estimator: $g = \left[\frac{(x_1 + 1) \cdot (x_2 + 1)}{x_{12} = 1} \right] - 1,$ where x_1 are the number of individuals identified in the first half of the photo-identifications on that day, x_2 in the second half, and $x_{1,2}$ in both.	Days (estimated group size on day)
3. Cluster size ^{d,f,g}	Temporary subsets of a group, composed of the individuals at the surface swimming in the same direction and speed, side by side in a coordinated manner a few body lengths or less apart usually for a matter of minutes.	Observations of number of individuals in clusters within 500 m of boat only when whales were engaged in foraging. Clusters of socializing whales were not considered because they are very variable in size and can sometimes include all group members.	Mean cluster size for all records of cluster size for a social unit.	Social unit

(Continued)

Table 1. (Continued)

Social metric	Definition	Estimates based on	Method	Units of analysis
4. Dive synchrony ^{d,f,g}	Expression of behavioral coordination among group members when foraging.	The maximum interval (in minutes) between the starts of consecutive deep dives of grouped individuals during each hour, minus its expected value, as predicted by group size and the presence of calves, averaged first over hours of each day, and then over those days in which a particular clan was sampled with at least five of such hours.	Expected intervals for any hour are given by the regression model $d = const + \frac{b}{n} - \beta \cdot c,$ where d is the longest interval between consecutive dives for each hour, n is the number of dives made by the group during the hour, c is presence (1) or absence (0) of calves during the hour, and b and β are regression coefficients.	Days with groups of different clans
5. Social differentiation ^{d,h}	Variability in social relationships (homogeneous $S = 0$; heterogeneous $S \gg 0$), here used to estimate the variation in dyadic probabilities of association within social units.	The estimated coefficient of variation (CV) of the true association indices. Higher S -values indicate more heterogeneity within-social unit relationships.	S was estimated from the photo-identification data with association defined as for metric 6, using the maximum likelihood method described in the appendix of Whitehead (2008b), with standard errors estimated by bootstrap resampling technique.	Mean S -values within social units

(Continued)

Table 1. (Continued)

Social metric	Definition	Estimates based on	Method	Units of analysis
6. Strength of social relationships ^c	Proportion of time a pair of individuals was observed together in relation to the number of times that they were observed.	Associations among pairs of individuals diving within 10 min intervals. Within this period individuals are usually in well-synchronized diving cycles, at close spatial proximity (<600 m).	Half-weight association index: $HWI = \frac{x}{x + yab + \left(\frac{ya+yb}{2}\right)},$ where x is the number of 10 min sampling intervals that individuals a and b were observed together; yab is the number of intervals with a and b identified but not together; ya and yb are the number of intervals with only individual a , or b , were identified.	Mean HWI among pairs of members of a social unit
7. Temporal stability ^{d,i}	Temporal stability of association between two individuals is given by the average probability of re-association after a given time lag.	The rate of association over time, for instance if individuals A and B were identified as associates, then a randomly chosen associate of A after lag t was B .	Plotting of the Standardized lagged association rates (SLAR) over increasing time lags and fitting exponential decay models to the observed SLARs (Table 2).	SLAR for all members of each clan

^aChristal *et al.* 1998, ^bChristal and Whitehead 2001, ^cWhitehead 2003, ^dWhitehead 2008a, ^eOtis *et al.* 1978, ^fWhitehead 1996, ^gWhitehead 1999, ^hWhitehead 2008b, ⁱWhitehead 1995.

2003). In the South Pacific clans span ranges of several thousand kilometers and in all well-studied areas two or more clans are present. Social units were assigned to clans as in Rendell and Whitehead (2003), so we will summarize the methodology. The vocal repertoires of social units were identified based on interclick intervals of the codas. Codas were assigned to social units whose members were photo-identified within 2 h of the recording. We analyzed repertoires of social units that had at least 25 codas recorded. Coda repertoires were compared with an averaged multivariate similarity method and hierarchical cluster analyses were used to define the best partition of social units into vocal clans (see Rendell and Whitehead 2003). We examined social variation between the two principal clans found off the Galápagos Islands: “Plus-One clan” (predominantly codas with the final interclick interval extended), and “Regular clan” (predominantly codas with 4–8 regularly spaced clicks).

Social Metrics

We compared clans using seven social metrics, all direct measures of the extent to which individuals were photo-identified together: three estimates of the number of individuals in different social levels: (1) social unit size, (2) group size, and (3) cluster size, and four measures of interindividual association: (4) dive synchrony within groups; (5) social differentiation, S , among all pairs of individuals within social units; (6) half-weight association indices, HWI, among all pairs of individuals within social units; (7) standardized lagged association rates, SLAR, among all pairs of individuals within clans). We chose the first three because they indicate the number of associates that individuals experience with different definitions of association; the remainder are good proxies for, and inform different aspects of, the quality of relationships: (4) behavioral coordination within groups, (5) heterogeneity of relationships within social units, (6) strength of relationships within social units, and (7) temporal stability of relationships among members of different units within the same clan. Definitions of social metrics and methods of estimation are presented in Table 1.

Clan Comparison

We primarily asked whether there are differences in the social metrics between the social units from the two main vocal clans. As a cross-validation, we further asked the reversed question: how can we best separate the two clans using these metrics? To answer the former, we used Student’s t -tests (two-sample unequal variance) to test the null hypothesis of no mean difference between the Regular and Plus-One clan, for all social metrics other than SLAR (see below). We also measured the magnitude of the differences with Cohen’s d effect size (difference in means divided by combined standard deviation, SD), which informs how many SDs difference there is between the means of the two groups on a given social metric. In these tests, the unit of analysis was the mean value of the social metric for each available social unit. However, group size data typically involved individuals from two or more social units at the same time, so we used days spent following sperm whale groups as the units of analyses (Table 1).

To answer the latter, we applied a linear discriminant analysis (LDA). We aimed to express how different were the two clans as a linear function, evaluating which of the social metrics were important in quantifying their differences. We further aimed to predict the classification of a new unknown social unit into a clan, given the descriptors of its social behavior. Here, the mean value of a metric for each social unit

was also used as the unit of analysis, thus standardized lagged association rates (SLAR) and group sizes were not considered. We started by building the saturated LDA model with all five remaining social metrics; then used forward and backward stepwise leave one out cross-validation to test whether models with fewer variables would have higher prediction accuracy. At each step, a new LDA model was created—by including variables not in the model (forward) or excluding those already in the model (backward)—and its prediction accuracy was estimated. The processes stopped when the accuracy did not improve, indicating that the resultant model was more efficient than other formulations.

Finally, we compared how social relationships changed over time in each clan by fitting four exponential decay models (SLAR1-4) with different possibilities for the decay of relationships over time to the lagged association rate data within clans (Table 2). Because members of a social unit are, by definition, permanent associates, in this context the lagged association rate primarily summarizes the dynamics of the associations among social units as they form groups. The first model, SLAR1, is constant, with no decay, representing permanent associations; in SLAR2, the association rate decays down to zero, representing associations that occurred for a given time lag and then never again; in SLAR3 the rate decays down to a lower level after a given time lag and then levels off, representing a mix of long-lasting and more temporary associations; the last model, SLAR4, is a sum of two exponential decay processes down to zero, representing two levels of disassociation, at a shorter and a longer time lag (the full description of the models and their parameter interpretation are available elsewhere: Whitehead 1995, 2008a). The SLAR models were fitted by iterative convergence to the original association data. We selected the most parsimonious model for each clan with the lowest quasi-Akaike Information Criterion (QAIC) (Burnham and Anderson 2002), to account for the overdispersion of the association data. The degree of support for the models was given by differences in the QAIC with the best fit model (ΔQAIC) and standardized relative QAIC weights ($e^{(-0.5 \cdot \Delta\text{QAIC})}$) (Burnham and Anderson 2002). We obtained standard errors for the model parameters using the temporal jackknife procedure (omitting 30 d periods of data each time) (Whitehead 2008a). SLAR and related analyses were performed in SOCPROG (Whitehead 2009a), while the remaining analyses were done in R environment (R Development Core Team 2014).

RESULTS

There was generally greater variation in the social level sizes between units in the same clan than between the clans (Fig. 2A–C, Table S1). The Plus-One clan appeared to contain smaller social units (mean unit size: Regular 13.6, Plus-One 10.7 individuals), that formed larger groups (mean group size: Regular 16.7, Plus-One 22.9 individuals), and larger clusters (mean cluster size: Regular 1.6, Plus-One 1.8 individuals) but such differences were not statistically significant at the 5% level (Table 3).

In contrast, between-clan variation was clearer for interindividual association measures (Fig. 2 D–F). Average association indices were not statistically different between clans (mean HWI: Regular 0.15, Plus-One 0.20). Social units that were members of the Plus-One clan dived less synchronously (mean residual no-dive gap: Regular 6.3, Plus-One 0.7 min). They were also more homogeneously associated, with less variable association indices (mean S : Regular 0.4, Plus-One 0.0) (Table 3).

Table 2. Models fit to Standardized Lagged Association Rates (SLAR) ranked by the lowest quasi-Akaike Information Criteria (QAIC) for each of the two clans of sperm whales off the Galápagos (Plus-One, Regular). Δ QAIC, QAIC weights and likelihood indicates the relative support for each model. Details on the interpretation of the model parameters are available elsewhere (Whitehead 1995, 2008a).

SLAR model		QAIC	Δ QAIC	QAIC weight	Likelihood
	Plus-One clan				
SLAR3	$s(t) = 0.015 + 0.027 \cdot e^{(-0.491 \cdot t)}$	1,232.06	0	0.68	1
SLAR4	$s(t) = 0.069 \cdot e^{(-1.038 \cdot t)} + 0.088 \cdot e^{(-0.454 \cdot t)}$	1,233.98	1.92	0.26	0.38
SLAR2	$s(t) = 0.025 \cdot e^{(-0.0002 \cdot t)}$	1,237.44	5.38	0.05	0.07
SLAR1	$s(t) = 0.023$	1,240.95	8.89	0.01	0.01
	Regular clan				
SLAR4	$s(t) = 0.043 \cdot e^{(-0.0002 \cdot t)} + 0.028 \cdot e^{(-1.005 \cdot t)}$	8,011.47	0.00	0.65	1
SLAR2	$s(t) = 0.046 \cdot e^{(-0.0002 \cdot t)}$	8,012.73	1.26	0.35	0.53
SLAR3	$s(t) = 0.038 + 0.061 \cdot e^{(-1.218 \cdot t)}$	8,036.69	25.22	0.00	0
SLAR1	$s(t) = 0.041$	8,052.07	40.6	0	0

Moreover, the SLAR plots (Fig. 3) and the most parsimonious models for temporal stability of within-clan relationships (Table 2) suggest that the Regular clan units were engaged in briefer associations: mean of 1.0 d (1/1.00) for the Regular clan *vs.* 2.0 d (1/0.491) for the Plus-One clan. The higher SLAR rates for the Regular compared with the Plus-One clan can be explained by the greater degree of social differentiation (individuals keep associating preferentially with the same small set of preferred companions).

In the linear discriminant analysis, the prior probability (*i.e.*, the observed proportion) of social units being from the Plus-One clan was 0.27, and 0.73 from the Regular clan. The saturated LDA model ($Clan = 0.12 \cdot Unit\ size - 1.12 \cdot Cluster\ size + 0.35 \cdot dive\ synchrony + 0.36 \cdot S - 1.64 \cdot HWI$) had only moderate prediction accuracy: 63% of correctly *a posteriori* assignment of social units to clans. By removing variables from the saturated model, the resultant reduced models were more efficient. Both forward and backward stepwise procedures yielded predictive models (forward: $Clan = 0.15 \cdot Unit\ size + 0.38 \cdot dive\ synchrony$; backward: $Clan = 0.14 \cdot Unit\ size + 0.38 \cdot dive\ synchrony + 0.28 \cdot S$) that were equally accurate (correctness rates of 91% for both). Along the linear discriminant, the Plus-One social units clustered towards the negative, and the Regular's clustered towards the positive values. The reduced models endorsed *t*-test results, which indicated that dive synchrony and *S* were significantly different between clans. Dive synchrony seemed to be the most divergent social metric between the two clans (see also Cohen's *d* in Table 3).

In summary, the two clans principally differed in behavioral coordination (dive synchrony), heterogeneity of relationships within units (*S*) and the temporal stability of social relationships among units (SLAR). We should, however, bear in mind a few caveats regarding the nature of our comparison. We reported social differences between two, out of five, known vocal clans (Rendell and Whitehead 2003). There are substantial logistical challenges in collecting long-term data on deep-diving

cetaceans in offshore waters over large spatial scales. Thus at the moment we can only speculate whether the social contrasts would extend to other clans.

DISCUSSION

In addition to vocal, movement and foraging behaviors (Rendell and Whitehead 2003, Whitehead and Rendell 2004, Marcoux *et al.* 2007a), our long-term study adds social behavior to the distinctions among the sperm whale clans inhabiting the Pacific waters. While clan partitioning is likely driven by cultural processes at a broad scale (Rendell and Whitehead 2003, Whitehead *et al.* 2012), we suggest that fine-scale social variation was shaped by a predefined clan partition, and therefore is a by-product—rather than a cause—of cultural segregation.

Overall, our findings indicate variation in the social behavior of sperm whales from different clans. Most obviously, clan memberships imply differences in diving synchrony, heterogeneity and temporal stability of social relationships, with members from Regular clan diving more synchronously but with associations that are relatively more heterogeneous and briefer than the Plus-One clan. However, the clans showed no statistically significant variation in the sizes of lower social level, such as social units, groups, clusters. Taken together, our results suggest that social life is more unit-oriented for members of the Regular clan. Compared with a member of the Plus-One clan, a Regular-clan sperm whale has relatively more equivalent relationships with its co-members. Grouping with other units is less frequent and less prolonged for these Regular units. In the Plus-One clan the emphasis seems more on dyadic individual relationships, expressed by larger social differentiation, as well as associating with other units in the clan, rather than the unit itself.

Such fine-scale social variation may ultimately propagate into fitness differences between members of different clans (see also Marcoux *et al.* 2007b). Dive synchrony is an expression of social affiliation and behavioral coordination among group members. Primarily, it is an inverse measure of the quality of calf-protection at the surface: the more synchronous their characteristic 40 min dives are, the less reliably there will be babysitters at the surface for calves (Whitehead 1996). Because the provision of alloparental care seems to be a key function of the social units (Gero *et al.* 2013), differences in diving and surface-time synchrony, along with variation in quality and duration of social relationships among females, could lead to different rates of calf survival between clans. Additionally, diving synchrony serves as a proxy for foraging coordination and perhaps cooperation at depths, where more echolocating individuals might be more likely to find a food patch and could potentially assist one another in prey capture. Thus, differences in diving coordination could lead to differences in feeding success between clans (see also Marcoux *et al.* 2007a). Fitness differences between clans could also arise indirectly, through learning of other behavioral patterns exclusively within a clan. Social patterns affect the flow of behaviors through social learning (*e.g.*, Voelkl and Nöe 2010, Cantor and Whitehead 2013), thus the between-clan variation in social relationships could indicate different paths by which innovations and predominant behaviors are transmitted within the clans over time. For instance, as is the case for some other species in which variation in fine-scale social interactions can affect foraging strategies (*e.g.*, Aplin *et al.* 2012, Atton *et al.* 2014), movement patterns and micro-habitat use of sperm whales can be socially learned within the clan (Whitehead and Rendell 2004) and determine diet composition (see Marcoux *et al.* 2007a) as well as potentially feeding success of clan members.

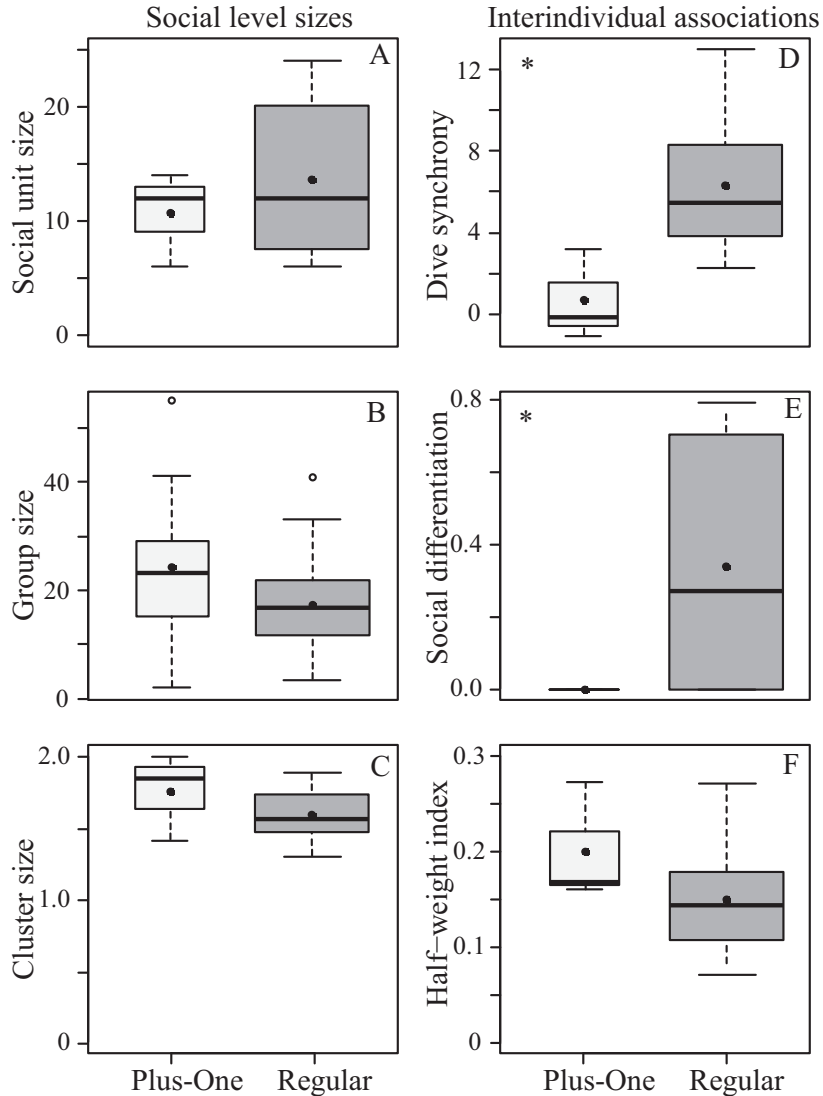


Figure 2. Social behavior variation among sperm whale vocal clans (Plus-One, Regular): (A) Social unit size (number of photo-identified individuals); (B) Group size (number of individuals in temporary association); (C) Mean cluster size while foraging (number of individuals seen together at the surface); (D) Dive synchrony (residuals of no-dive gap in minutes, from the dive synchrony regression model); (E) Social differentiation (S , estimated CV of the actual rate of association); (F) Half-weight association indices (mean HWI within units, estimated proportion of times pairs of individuals were seen together). Boxplots show mean values (black dots), median (horizontal bar), 1st and 3rd quartiles (box, which widths are proportional to sample sizes), minimum and maximum values (whiskers). Asterisks represent Student's t -test statistical significance at $P < 0.05$ (Table 3).

Table 3. Mean values of social metrics for units of the Regular and Plus-One clans off the Galápagos Islands. Only social units to which we have data for all social metrics (except group sizes; see text) were included in the tests.

Social metric	Regular clan ($\bar{x} \pm \text{SD}$)	Plus-One clan ($\bar{x} \pm \text{SD}$)	<i>t</i>	df	<i>P</i>	Cohen's <i>d</i> (95% CI)
Social unit size (individuals)	13.6 ± 7.0	10.7 ± 4.2	-0.9	6.41	0.42	0.46 (-0.89, 1.79)
Group size (individuals)	16.7 ± 6.6	22.9 ± 14.6	-1.4	12.74	0.18	0.66 (-0.03, 1.33)
Cluster size (individuals)	1.6 ± 0.2	1.8 ± 0.3	0.9	2.62	0.45	0.74 (-0.65, 2.08)
Dive synchrony (residual no-dive gap in minutes)	6.3 ± 3.5	0.7 ± 2.3	-3.2	5.84	0.02 ^a	1.74 (0.16, 3.25)
Social differentiation <i>S</i>	0.35 ± 0.34	0.00 ± 0.00	-2.8	7.00	0.03 ^a	1.13 (-0.032, 2.52)
Dyadic relationships (mean within-unit HWI)	0.15 ± 0.06	0.20 ± 0.06	1.2	3.64	0.31	0.80 (-0.60, 2.16)

Note: Cohen's *d*: effect size and 95% confidence intervals (CI). HWI: half-weight association index; *S*: social differentiation (estimated coefficient of variation of the true HWIs).

^aSignificant at $P < 0.05$.

There are a few explanatory mechanisms for the emergence of behaviorally-distinct clusters in a population, such as the sperm whale vocal clans. Intrapopulation variations in social behavior are usually assigned to genetic, ontogenetic, ecological, and/or cultural factors (*e.g.*, Schradin 2013, Cantor and Whitehead 2013, Cronin *et al.* 2014). Pinning down the principal mechanism can be challenging (*e.g.*, Whitehead 2009b, Allen *et al.* 2013, Mace 2014). In our case, sperm whale vocal clans are sympatric, span large areas (Whitehead *et al.* 1998, Rendell and Whitehead 2003), are not genetically distinguishable (Whitehead *et al.* 1998, Rendell *et al.* 2012), and contain individuals from all age classes (Rendell and Whitehead 2003). Therefore behavioral differences between clans are unlikely to be environmental, genetic, or ontogenetically driven; they are more parsimoniously ascribed to social learning (Rendell and Whitehead 2003, Whitehead *et al.* 2012, Whitehead and Rendell 2014). More specifically, behavioral distinctions between clans can emerge when (1) individuals with similar behavior preferentially associate (also called assortment, homophily) and (2) associations reinforce behavioral similarity (social influence) through social learning (see Centola *et al.* 2007, Cantor and Whitehead 2013). In this way, the population would segregate into clans if sperm whales with similar social behavior tend to associate more often—either actively by preferential association among like-minded individuals; or passively by differences in habitat use strategies (see Croft *et al.* 2009, Farine 2014). However, it is much more likely that matching of acoustic behavior structures the associations among sperm whales (see Rendell and Whitehead 2003, Schulz *et al.* 2008): coda types are used for communication, are learned socially and only individuals with highly similar vocal repertoires tend to associate. Indeed vocal similarity is how the clans were initially recognized (Rendell and Whitehead 2003).

Once the sperm whale population is structured into vocal clans, other behavioral variations, which may be functionally neutral (*e.g.*, Hahn and Bentley 2003) such as

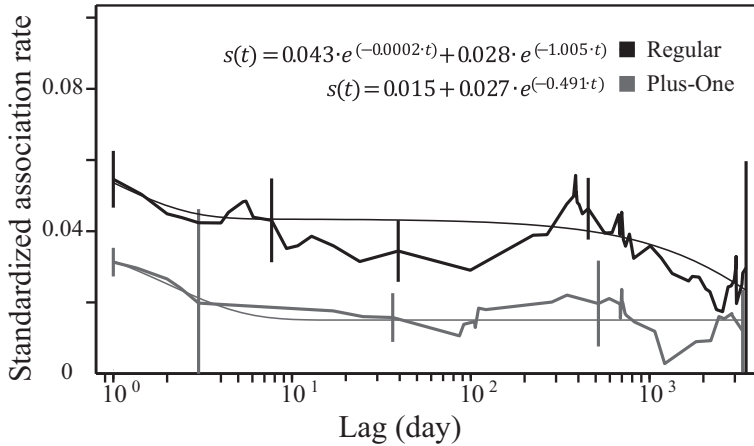


Figure 3. Standardized lagged association rates (thicker lines) and best fit models (thinner lines; Table 2) among whales within each vocal clan (black: Regular; gray: Plus-One). Low overlapping of the standard errors (vertical bars, from a jackknife procedure) suggest significant differences.

the social behavior we report here, may emerge and disappear through drift over time (Cavalli-Sforza and Feldman 1981). Analogously to phylogenetic processes (Koerper and Stickel 1980, Boyd and Richerson 1985), such changes in frequencies of socially learned behaviors occurring by neutral processes involving no selection or preference would amplify the differences between the behavioral repertoires of the segregated clans. Therefore, it may be parsimonious to view the social variation between clans as a consequence of a predefined partition in the whales' social network, with individuals and social units replicating the patterns in dive synchrony and social behavior of their clan members, and drift leading to distinctive variation among clans in either the social behavior itself or other behavior that directly or indirectly affects social structure (e.g., Whitehead and Lusseau 2012).

Behavioral segregation within populations adds another layer of complexity to intraspecific variation in social structure (Kappeler *et al.* 2013). We showed that some elements of the sociality of sperm whales are mapped onto the upper level divisions of their society. These findings are among the few showing that culturally marked groups of nonhumans living in the same area have characteristic social behavior (see also Cronin *et al.* 2014). In perhaps the closest known parallel, sympatric killer whale (*Orcinus orca*) ecotypes in the eastern North Pacific have distinctive social structures (Baird 2000), and the evolution of these ecotypes may have been driven by cultural differences (Riesch *et al.* 2012). However the ecotypes are now so different that there have been calls to recognize them as distinct species (Morin *et al.* 2010). Social variation between sperm whale clans further shows that their behavioral segregation is not limited to communicative signals. The presence of sympatric clans with rich, divergent, culturally initiated behavioral norms suggest that sperm whale populations could carry multiple traditions. Multiple traditions within populations are considered a rare trait for nonhuman societies (e.g., Whiten *et al.* 1999, Allen *et al.* 2013), but they might remain unrecognized either because behavioral ecologists have failed to look for them, or because intrapopulation behavioral variation is fully, but incorrectly, attributed to ecological or genetic differences. Sorting out the contribu-

tion of culture from other factors in driving intraspecific variation remains a timely challenge (Kappeler *et al.* 2013, Mace 2014).

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SUPPORTING INFORMATION

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Table S1. Summary of the social metrics among social units of two vocal clans of sperm whales off the Galápagos Islands (Plus-One and Regular): unit size (number of photo-identified individuals), mean cluster size while foraging (number of individuals), dive synchrony (residuals of no-dive gap in minutes, from the dive synchrony regression model), social differentiation (S), association indices (HWI).