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ORIGINAL PAPER

Indications of fitness differences among vocal clans of sperm whales

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Abstract Cultural variation can affect the genetic evolution of a species if there are consistent cultural differences that contribute to fitness variation between groups of individuals. In this study, measures of the reproductive success of groups of sperm whales from different cultural clans are used as proxies for fitness. We measure reproductive success using population length distributions from acoustic and photographic measurements and visual observations of the presence of calves. The results obtained are generally consistent between methods; there are large and significant differences between the clans in the measures of reproductive success. The results from this study strengthen the case for cultural hitchhiking in sperm whales by indicating that differences in culture between clans correlate with differences in fitness.

Keywords Culture · Fitness · *Physeter macrocephalus* · Reproductive success · Vocal clan

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Introduction

Although culture is a vital element of human lives, limited information is available on its significance for other animals. Rendell and Whitehead (2001) proposed a working definition of culture that will be used in this paper: “Culture is information or behaviour shared by a population or subpopulation—which is acquired from conspecifics through some form of social learning.” Using this definition, culture has been recognized in several species, such as chimpanzees (Whiten et al. 1999), birds (Lefebvre 2000) and some cetaceans (Rendell and Whitehead 2001).

Culture can be adaptively neutral (Slater 1983) or functionally important. A neutral culture, as is believed to exist for the songs of some songbirds (Slater 1983), does not have any direct effect on fitness. However, culturally transmitted traits can potentially influence fitness as much as genetically transmitted ones. For example, the advent of farming practices permitted farmers to be more efficient in food acquisition and, thus, reach higher densities and outcompete groups of hunter-gatherers (Aoki et al. 1996).

Cultural and genetic transmission can interact and result in gene-culture co-evolution (Aoki 2001). This interaction becomes observable when there are consistent cultural differences that contribute to fitness variation. Cultural traits that lead to higher fitness will be selected. Therefore, cultural differences can affect the genetic composition of a population if there is a correlation between genotypes and cultural trait values. Cultural hitchhiking (Whitehead 1998) is a form of gene-culture co-evolution (Feldman and Laland 1996). It is analogous to molecular hitchhiking in which the allelic diversity of a neutral locus is reduced by ongoing stabilizing selection due to persistent linkage disequilibrium. In cultural hitchhiking, the genetic diversity is reduced by the selection of a linked cultural trait (Whitehead 1998). Cultural traits driving hitchhiking should be stable across generations, affect fitness and be hard to assimilate (Whitehead 2005). Four species of toothed whales have outstandingly low mitochondrial DNA (mtDNA) diversity compared to what is expected given their population sizes (Whitehead 1998) and their geographic ranges (Whitehead 2003). All of these species have a matrilineal social structure, although with variations, and matrilineally transmitted cultural traits, such as vocal repertoire, habitat use, foraging and movement patterns, have been identified in two of them (Whitehead 2005). Cultural hitchhiking may be the cause of their low mtDNA diversity (Whitehead 1998).

The sperm whale (*Physeter macrocephalus*) is one these species. Global sperm whale abundance has recently been estimated at around 360,000 individuals, the majority of which inhabit the Pacific Ocean (Whitehead 2002), and they live at least 60–70 years (Rice 1989). Females have their first offspring around the age of ten (Rice 1989) and may give birth every 4–6 years until they reach their forties by which age the reproductive rate has fallen to very low levels (Best et al. 1984). Sperm whales are sexually segregated in adulthood; females stay with their young offspring in tropical or subtropical waters, whereas males quit their mother's social unit at about age six (Richard et al. 1996), gradually moving to colder waters (Rice 1989) and only return to the habitat of the females to mate in their late twenties (Best 1979).

However, sperm whale society is apparently not strictly matrilineal. Female sperm whales form nearly permanent social units containing about 12 animals, some matrilineally related, some not (Mesnick 2001). In the South Pacific, sperm whale social units can be assigned to one of five vocal clans (Rendell and Whitehead 2003). Units belonging to a clan share the same repertoire of codas (a stereotyped rhythmic series of clicks) and preferentially associate with other units (to form a "group") of the same clan. Groups from different clans seem to have distinctive diets (Marcoux et al. 2007), movement patterns and feeding success (Whitehead and Rendell 2004), and clans show differences in their distributions of maternally inherited mtDNA haplotypes (Rendell and Whitehead 2003). Thus, the sperm whale's cultural variation seems to possess some of the prerequisites for cultural hitchhiking. The variation also has some temporal stability; the vocal output of a clan is stable over periods of up to 6 years (Rendell and Whitehead 2005). Although this is shorter than the reproductive life-span of one generation (Rice 1989), there are currently no data over longer intervals (Rendell and Whitehead 2005). Fitness differences between clans are necessary for cultural hitchhiking to operate (Whitehead and Rendell 2004). The differences should be consistent and should occur over a long period of time to have a real effect on population biology and, perhaps, on genetic diversity.

In this study, we investigate proxies of the reproductive success of sperm whale clans over a period of 15 years. We use population length distributions from acoustic and photographic measurements and visual observations of the presence of calves to assess the reproductive success of groups from different clans as integrated over several years.

Materials and methods

For this study, acoustic and observational data were collected from 10- to 13-m auxiliary sailing vessels in the South Pacific Ocean between 1985 and 2000. Groups of female sperm whales with their juveniles were followed visually and acoustically (see "Appendix" in Whitehead 2003). Groups were defined as animals identified in association on the same day. If n_A whales were photo identified (Arnbom 1987; Christal et al. 1998; Whitehead 1990) during 1 day and n_B during another day, then we considered that we followed the same group during the 2 days if: $m_{AB} > 0.25 \times \text{minimum}\ \{n_A, n_B\}$, where m_{AB} is the number of whales identified on both days (Weilgart and Whitehead 1997). We did not have enough information to identify individual social units within these groups, but we could assign groups to vocal clans if codas were recorded during an encounter (Rendell and Whitehead 2003). Only groups that could be assigned to clans in this way were included in the analysis. We used photo-identification methods (Arnbom 1987; Christal et al. 1998; Whitehead 1990) to ensure that groups only entered the analysis once. We estimated the number of immature animals in these groups in three ways: acoustic size measurement, photogrammetric size measurement and direct observation of calf presence.

Codas were recorded using omni-directional hydrophones. A total of 7,888 codas from 59 groups of four clans (called "Regular", "Plus-one", "Short" and "Four-plus"; see Rendell and Whitehead 2003) were included in the analysis (Table 1). We measured the inter-pulse interval (IPI) of each click within a coda using cross-correlation and cepstrum methods developed by Goold (1996) (see Rendell and Whitehead 2004; Marcoux et al. 2006). We then estimated the body length of the animal producing the codas using the equation developed by Gordon (1991):

$$\text{Total length} = 4.833 + 1.453\text{IPI} - 0.001\text{IPI}^2 (R = 0.99)$$

Because the IPI measuring routine encountered problems when estimating low IPI values, a lower limit of 2 ms (corresponding to a body length of 7.7 m) was set. Therefore, the acoustic method could not have measured codas from animals younger than about 4 years old

Table 1 Data set used for the acoustic and the photographic measurements

Method	Years	Location	Clan	Number of groups	Number of measurements
Acoustic	1985	Galápagos	Regular	23	1,664
	1987	Galápagos	Plus-one	5	360
			Regular	23	1,664
			Short	6	691
	1989	Galápagos	Four-plus	2	79
			Plus-one	5	360
			Regular	23	1,664
	1991	Galápagos	Regular	23	1,664
			Short	6	691
	1992	West Pacific	Short	1	4
	1995	Galápagos	Regular	23	1,664
	2000	Chile	Four-plus	3	211
			Plus-one	9	2,569
			Regular	10	2,310
Photographic	1985	Galápagos	Plus-one	1	22
			Regular	10	261
	1987	Galápagos	Plus-one	2	155
			Regular	4	279

(estimated from Rice's (1989) growth curve, see Marcoux et al. 2006). For each group, we calculated the proportion of recorded codas made by whales smaller than 9.2 m, the size at which most of the females become sexually mature (Rice 1989). We used an analysis of variance with categorical factors "clan" and "location", and post-hoc pairwise *t*-tests on factor "clan", after data were arcsine transformed and weighted by the number of codas recorded from each group.

Photographs taken alongside individuals from 17 groups of whales from two clans (Regular and Plus-one) off the Galápagos Islands in 1985 and 1987 (Table 1) allowed the photogrammetric estimation of the body length using the equation developed by Gordon (1990). Analytical methods and a summary of the data are given in Waters and Whitehead (1990). We again calculated the proportion of individuals smaller than 9.2 m in the sampled groups and used the same analysis procedure as for the acoustic data, excluding the "location" factor, as all the photogrammetric data were obtained off the Galápagos Islands.

The presence/absence of calves for each group encountered was recorded during encounters with each group. A calf was defined as an infant in the 1st year of life (about 4–5.5 m in length; Whitehead 1996). Calves are easy to recognize, as they usually suckle (descend next to mature female for short dives; Gordon 1987), and they have restricted diving abilities (they frequently stay at the surface or dive for shorter periods than adults; Whitehead 1996; Best et al. 1984). For this analysis, we had data from 53 groups from four clans in Galápagos during 1987 and 1989 and Chile during 2000 (Table 2). We fitted log-linear models to these data incorporating combinations: the binary variable "presence/absence of calf", the categorical variables "clan" and "study" (a combination of the year and the location) and their interaction terms. We calculated second-order Akaike information criterion ($\mathrm{AIC_c}$), $\mathrm{AIC_c}$ differences ($\Delta\mathrm{AIC_c}$) and Akaike weights (w_i) for each model (Burnham and Anderson 2002). We also summed Akaike weights across models to assess the relative importance of each variable and interaction term (Burnham and Anderson 2002). Finally, we used chi-square contingency tables to investigate the single-factor effects of year (using data from the same clan off the Galápagos), location and study (Table 3). The statistical analyses were carried out using Systat 11. In all cases, the units of statistical analysis was the group, and this was considered independent, as the sperm whales encountered are usually members of only one group.

Results

Acoustic data were available for 60 groups. There was an overall significant difference among the clans for the proportions of codas made by whales smaller than 9.2 m in each group ($F_{(3,54)}=4.421$, $p=0.007$; Fig. 1a). The proportion of small whales for the Short clan was significantly lower than that among the Regular clan ($p=0.004$ Bonferroni corrected $\alpha=0.008$). There was no significant difference between the three locations ($F_{(2,54)}=0.513$, $df=2$, $p=0.601$).

Table 2 Data set used for the log-linear model of visual observation of calves

Study			Calf		Total
			Presence	Absence	
Chile 2000	Clan	Four-plus	0	4	4
		Plus-one	0	0	0
		Regular	5	9	14
		Short	2	7	9
	Total		7	20	27
Galápagos 1987	Clan	Four-plus	0	0	0
		Plus-one	7	0	7
		Regular	4	4	8
		Short	0	0	0
	Total		11	4	15
Galápagos 1989	Clan	Four-plus	0	2	2
		Plus-one	3	0	3
		Regular	5	1	6
		Short	0	0	0
	Total		8	3	11

The counts are the number of groups

Table 3 Data used in chi-square contingency tables to test the effect of "year", "location" and "study"

Table	Effect	Clan	Study
1	Year	Regular	Galápagos 1987 Galápagos 1989
2	Year	Short	Galápagos 1987 Galápagos 1989
3	Location	Regular	Chile 2000; Galápagos 1987 Galápagos 1989
4	Study	Four-plus	Chile 2000 Galápagos 1989

For the photogrammetric method, data were available from 17 groups. The difference between the two clans off the Galápagos in the proportion of whales measuring less than 9.2 m within each group was near significant ($F_{(1,\ 15)}=4.464$, $p=0.052$), with groups of the Plus-one and Regular clans containing 40 and 34% of individuals less than 9.2 m, respectively (Fig. 1b).

The three log-linear models with the lowest $\mathrm{AIC_c}$ all included the interaction term between the variables clan and presence of calf (Table 4). This interaction term received the largest summed Akaike weight (0.814 compared to 0.808 for the term study×clan and 0.774 for the term calf×study). The single-factor contingency tables indicated that there was no interaction between presence of calf and year, presence of calf and location and presence of calf and study (likelihood ratio chi-square and Fisher exact test, all p value>0.10). All the groups of the Plus-one clan had calves, as opposed to half the Regular clan groups and around one fifth of the Short clan groups, whereas no Four-plus groups were observed with calves (Fig. 1c). We are confident that these results are not confounded by group size, as a logistic regression of the probability of detecting a calf on the number of individuals identified in the group showed no significant relationship (univariate logistic regression, $p=0.359$).

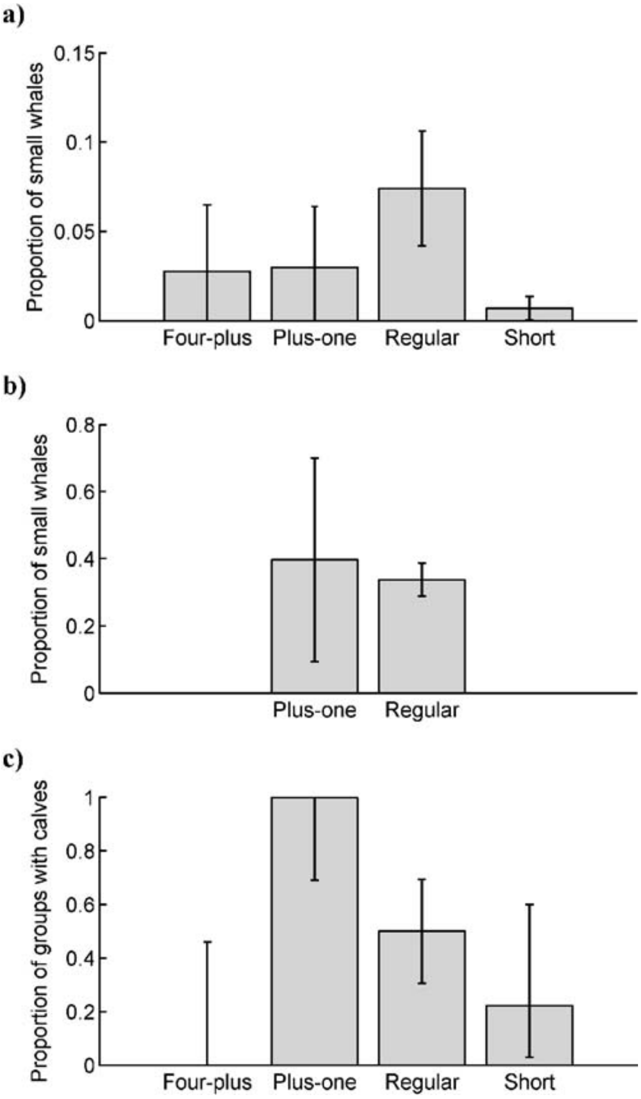

Fig. 1 Measures of reproductive success of sperm whale clans estimated using the three different methods: **a** the proportion of sperm whales smaller than 9.2 m measured acoustically and **b** photographically (note that there were no data available for the Four-plus and Short clans), and **c** the proportion of groups observed with a calf. *Error bars* represent 95% confidence intervals on the means (**a** and **b**) and on binomial maximum likelihood estimates (**c**)

Discussion

Differences in measures of reproductive success between clans were large and consistent between two of the three methods used (Fig. 1). The Plus-one clan seems to have the highest proportion of smaller whales and calves followed by the Regular clan, according to the photogrammetric and visual methods, but the acoustic measurement method gives a different direction in the difference between these clans. Both the acoustic measurement and visual detection of calves indicate that the Short and Four-plus clans appear to have lower reproductive success.

The methods integrated over several years in different ways. The presence of calves was noted for three different years and appeared consistent between years, but this method would only have recorded calves born within a year of observation, and thus, reflects reproductive success over the year previous to observation. In contrast, by setting the limit for young whales at 9.2 m for photographic and acoustic measurements, calves from several different years are included in the analysis; thus, the differences detected are cumulative effects over several years. Data were collected from the same clans in areas thousands of kilometres apart, so within-clan variance in ecological conditions is likely to be much higher than between-clan variance. The lack of variation in the proportion of small whales among areas argues that the

Table 4 Second-order Akaike information criterion for small sample size (AIC_c) for the set of converging models to estimate the presence of calf in a group, and their number of estimable parameters (*K*), AIC_c differences (ΔAIC) and Akaike weight (w_i; Burnham and Anderson 2002)

Model	*K*	AIC_c	ΔAIC	w_i
Clan × calf + study × clan + study × calf + calf	13	73.99	0.00	0.32
Clan × calf + study × clan + study × calf	12	74.57	0.58	0.24
Clan × + study × clan	10	75.19	1.20	0.17
Calf × study	3	76.00	2.01	0.12
Clan × calf + study × + study × calf + study	14	77.70	3.71	0.05
Clan × calf	4	78.48	4.49	0.03
Calf × study + study × clan	9	79.11	5.12	0.02
Calf × study + clan × calf	6	79.13	5.14	0.02
Clan × calf + study × clan + calf × study + clan	15	81.62	7.63	0.01
Study + clan	6	82.17	8.18	0.01
Study	3	82.56	8.57	0.00
Clan	4	82.58	8.59	0.00
Calf + study + clan	7	84.81	10.82	0.00
Calf + study	4	84.89	10.90	0.00
Calf + clan	5	85.01	11.02	0.00
Calf	2	87.56	13.57	0.00

variation in this proportion between clans is not driven by environmental differences.

Due to limitations of the automated routine for the calculation the IPIs of the codas, only whales larger than 7.7 m (which corresponds to a female of 6 years of age and a male of 4 years of age; from Rice's (1989) growth curve) could be measured. Estimates for the proportion of small animals by this method were much lower than for the photogrammetric method (Fig. 1), which reflects the observation that immature sperm whales do not usually produce codas (Marcoux et al. 2006). Therefore, the IPI analysis probably only detected a fraction of the small whales present during the recordings, and it should be noted that the validity of comparing these data between clans depends critically on the assumption that there is no heterogeneity among clans in the tendency for young whales to produce codas.

Body size estimates from photographs are also biased against calves because they are unstable at the surface, which makes it harder to obtain a good photograph for body length estimates (Waters and Whitehead 1990). Consequently, our calculation of the ratio of whales smaller than 9.2 m in each group based on photographs (Fig. 1b) is probably an underestimate. Visual observations might also be biased against calves that are sometimes hard to see, although they also spend more time at the surface than adults. However, there is no reason to believe that these biases would not be consistent between clans. Finally, it should be noted our interpretation of the varying size structures among clans depends on growth rates being comparable between clans. If for some reason clans were to grow at different rates, then they could have the same age structure (and so the same proportion of immature animals) but have different size structures as we have found. Although we are not aware of any data suggesting growth rate variation among groups from whaling data, specific data on growth rates from each clan would be necessary to firmly discount this possibility.

For gene-culture co-evolution to occur in sperm whales at the level of clans, differences in culture that translate into fitness divergence between clans are needed. Behavioural and dietary differences among the clans have been documented (Rendell and Whitehead 2003; Whitehead and Rendell 2004; Marcoux et al. 2007). In this study, we used the proportion of young whales within groups and the presence of a calf in a group from each clan as a proxy to measure the fitness of clans, as fitness is the relative contribution of a phenotype to subsequent generations (Purves et al. 1998). The survival of the calves for their first few years of life is included in the acoustic and the photogrammetric proportion data, as we included whales up to 9.2 m of length. These measures suggest strong and consistent differences in fecundity and recruitment between groups of different clans over a 15-year period and 4,000-km distance span.

Although this study uses measurements of reproductive success as a proxy for fitness, some other components of fitness, such as viability, fecundity, mating ability and adult survival, are missing and, currently, unmeasurable at anything like the necessary precision for sperm whales (Whitehead 2003). Lack of knowledge of these components lowers the power of the present analysis, but it seems unlikely that they could balance the pronounced differences in reproductive success that we have demonstrated.

We have shown that the prerequisites for cultural hitchhiking to affect genetic evolution appear to be in place in sperm whales and, specifically, that cultural variation correlates with fitness differences among clans. Although genetic differences can also affect fitness, available evidence shows no sign of heterogeneity in nuclear genes among the clans (Whitehead 2003) but much evidence for strong behavioural variation that could affect fitness and that correlates with culturally transmitted vocal traits. We, therefore, suggest that gene-culture co-evolution is a feasible cause of the low mtDNA diversity in this species. Such phenomena have been considered very rare outside humans.

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