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Paternity in humpback whales, *Megaptera novaeangliae*: assessing polygyny and skew in male reproductive success

SALVATORE CERCHIO*†, JEFF K. JACOBSEN‡, DANIELLE M. CHOLEWIAK†§, ERIN A. FALCONE** & D. ANDREW MERRIWETHER††

*Museum of Zoology and Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI, U.S.A.
†Cornell Laboratory of Ornithology, Ithaca, NY, U.S.A.
‡Department of Biological Sciences, Humboldt State University, Arcata, CA, U.S.A.
§Department of Neurobiology and Behavior, Cornell University, Ithaca, NY, U.S.A.
**Cascadia Research, Olympia, WA, U.S.A.
††Department of Anthropology, University of Michigan, Ann Arbor, MI, U.S.A.

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Mating system theory predicts that differences between the sexes in potential reproductive rate and an operational sex ratio skewed strongly towards males should result in intense male competition, polygynous mating and high variance in male reproductive success. Accordingly, humpback whales are thought to be polygynous with differences in reproduction among males related to alternative mating tactics. However, there is currently a lack of data on male reproductive success. We tested predictions regarding male reproductive success in humpback whales using molecular assessment of paternity in a population in the Mexican Pacific. Parentage analysis was conducted for 125 mother–calf pairs and a sample of 297 males using 13 microsatellite loci. Two separate analyses were conducted, based upon conservative and relaxed criteria for the assignment of paternity. In the conservative analysis, 40 paternities (32.5% of tested calves) were assigned among 33 males, whereas in the relaxed analysis, 62 paternities (49.6% of calves) were assigned among 51 males. Regardless of analysis, the distribution of male reproductive success deviated from a random mating model, with significantly larger than expected variance (conservative, $P = 0.011$; relaxed, $P = 0.022$), and significantly more than expected males siring three calves (conservative, $P = 0.021$; relaxed, $P = 0.011$). However, most successful males sired only one calf and no male was assigned more than three calves, so reproductive skew was not severe. Therefore we conclude that this population has a polygynous mating system, but without the large variation in male reproductive success expected by apparent skew in the operational sex ratio and degree of male competition for mates.

Polygyny is the most common mating system found in mammalian species (Clutton-Brock 1988, 1989). The degree of reproductive skew among polygynous males is in part a function of potential reproductive rates of males and females, and the operational sex ratio, OSR (Kvarnemo & Ahnesjo 1996; Shuster & Wade 2003). A difference in the potential reproductive rates of males and females leads to a skew in OSR, which can be further exaggerated by behavioural differences between the sexes and demographic characteristics of the population. With greater skew in OSR towards males, the intensity of male competition for females increases, as does variance in reproductive success (RS) among males. When the OSR is severely skewed and variance in male RS high, there is strong sexual selection on males and alternative mating tactics should evolve (Gross 1996).

Little is known about mating systems of most baleen whales, due to their typically large and dispersed populations and the difficulty of observing them. Currently, there are no published measures of male mating success, or realized RS for any species of baleen whale. The reproductive behaviour of humpback whales is the best understood (Clapham 1996, 2000), however lack of

Correspondence and present address: S. Cerchio, Wildlife Conservation Society, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024, U.S.A. (email: scerchio@wcs.org).

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information on male RS has made it impossible to do more than speculate on the details of the mating system. Humpback whales migrate seasonally in all ocean basins and breeding takes place primarily in low-latitude waters in winter months. Whales fast during this period, at a time when there are no ecological resources critical to reproductive success or survival, and little if any predation pressure on breeding adults (Clapham 1996). Thus, in the absence of selection from feeding or predation pressure, sexual selection is the primary force shaping breeding behaviour of the species, a situation that is rare among vertebrates.

Gestation in humpback whales is approximately 1 year and females give birth to a single calf on average every 2–3 years (Chittleborough 1958; Clapham & Mayo 1990; Glockner-Ferrari & Ferrari 1990). Therefore the potential reproductive rate of males is at least two to three times greater than that of females due simply to the female reproductive cycle. Female residency on the breeding grounds is shorter than that of males and is temporally staggered among females (Gabriele 1992; Craig & Herman 1997; Jacobsen et al. 2002). Most females ovulate once during their 5-month breeding season, although the minority that fail to conceive the first time ovulate two or three times (Chittleborough 1954, 1965). Therefore, oestrus is short relative to residence time and is likely to be broadly asynchronous among females. This asynchrony in the timing of migration and oestrus serves to skew the OSR severely towards males (Clapham 1996). Because of these factors, we would predict intense competition among males for mates, strong male reproductive skew, strong sexual selection on males, and the evolution of alternative mating tactics (Andersson 1994; Gross 1996; Kvarnemo & Ahnesjo 1996; Shuster & Wade 2003). Observations of male behaviour partially support these predictions, with the documentation of several alternative mating tactics, including a phylogenetically derived and male-limited acoustic display, song (Payne & McVay 1971; Darling 1983), and intense physical competition for single females (Tyack & Whitehead 1983).

The mating system of humpback whales is generally considered polygynous or promiscuous (Herman & Tavolga 1980; Darling 1983; Clapham 1996), however this assumption has never been tested due to a lack of data on individual male RS. Copulation has never been observed in approximately 30 years of research on the species globally, thus there are no behavioural estimates of mating success. Several authors have suggested a lek mating system (Herman & Tavolga 1980; Clapham 1996; Cerchio 1999), involving extended 'choruses' of singing males, and as-yet-undocumented female choice. Implicit in the lek model is large variance in male RS, the primacy of singing as an intersexual signal to attract females, and lower RS associated with secondary tactics. Alternatively, it has been suggested that song is used primarily as an intrasexual signal to establish dominance among males (Darling 1983; Darling & Bérubé 2001), implying variance in male RS by rank. Conversely, it has been suggested that skew in male RS may not be severe due to the dispersed nature of breeding females and the consequent inability of males to monopolize multiple females (Clapham 1996). Molecular analysis indicates that females are serially promiscuous across seasons (Clapham & Palsbøll 1997), and certain males may have higher RS than others relative to dominance in competitive interactions (Nielsen et al. 2001).

Here we present the first detailed data on paternity and individual male reproductive success for a baleen whale. We tested the hypothesis of polygyny and show that the mating system of humpback whales may not conform entirely to prior predictions based solely upon the apparent OSR and observations of male behaviour.

METHODS

Study Site, Sample Collection and Molecular Analysis

The Revillagigedo Archipelago is one of four or five major breeding areas for humpback whales in the North Pacific, located 700 km off the Mexican Pacific coast at 18°N. Photographic mark–recapture and genetic data indicate that this subpopulation is small and distinct relative to other North Pacific subpopulations (Medrano-Gonzalez et al. 1995; Urbán et al. 1999, 2000). During 1996–2001, we photographed 917 individuals on 3655 occasions. Point estimates of population abundance ranged from 1240 to 1515 individuals with 95% confidence intervals spanning 1080 to 1750 (Jacobsen et al. 2002).

We collected 923 skin samples of humpback whales by standard biopsy techniques (Lambertsen 1987; Clapham & Mattila 1993) and sloughed skin collection (Clapham et al. 1993; Valsecchi et al. 1998) from 1997 to 2001 off Socorro and Clarion Islands, Revillagigedo Archipelago, Mexico. Similar to the findings of Clapham & Mattila (1993), reaction to biopsy darting was low, with approximately 44% of biopsy events resulting in no noticeable reaction (Cerchio 2003). We attempted to photographically identify all sampled whales, resulting in 584 samples with a tail identification, and 257 samples with a dorsal fin identification (entirely mothers and calves), representing 91.1% of all samples. Consequently, it was determined prior to molecular analysis that 248 individuals were sampled on multiple occasions from two to five times, for 528 samples.

DNA was extracted using QIAgen DNeasy extraction kits. All samples were genetically sexed by multiplex PCR of the ZFX/ZFY fragment (Bérubé & Palsbøll 1996) and genotyped at 13 microsatellite loci (EV001, EV014, EV021, EV037, EV094, EV096 and EV104: Valsecchi & Amos 1996; GATA098, GATA028, TAA031, GGAA520, GATA417 and GATA053: Palsbøll et al. 1997b). Published PCR conditions and/or primers were altered for certain problematic loci to reduce allelic dropout and equalize amplification of heterozygous alleles, or to reduce double peaks associated with adenylation (final conditions in Cerchio 2003, and available on request). PCR products were sized on an ABI 377 automated sequencer using GENESCAN and GENOTYPER software (Applied Biosystems, Foster City, California, U.S.A.). Samples that did not amplify, amplified weakly, or had ambiguous results were

reamplified at the given locus up to five times. Any remaining ambiguous results were entered into the final database as missing data for the given locus, resulting in 97.7% of loci typed among all individuals.

Paternity Analysis

Results of two parentage analysis programs, CERVUS 2.0 and NEWPAT XL, were compared and combined to create 'conservative' and 'relaxed' data sets of putative fathers. CERVUS (Marshall et al. 1998) uses a maximum likelihood approach to assign paternity, and determines confidence based upon the difference in LOD scores (i.e. the logarithm of the likelihood ratio) between the most likely candidate and the second most likely candidate using a simulation that incorporates characteristics of the sample. NEWPAT (Worthington Wilmer et al. 1999) searches for candidate males that are genotypically compatible with the mother and calf, and evaluates confidence using a randomization approach to determine the chance of obtaining a compatible match at random.

Genotyping errors of microsatellite markers can lead to the false exclusion of true fathers (Vigilant et al. 2001). Both CERVUS and NEWPAT support criteria to allow genotyping errors and assign paternity despite mismatching loci when confidence is otherwise high. It can be argued that only the most confident data should be used in paternity analysis, and thus only stringent criteria allowing no mismatches should be used to avoid false paternity assignments (as in Worthington Wilmer et al. 1999). However, falsely excluding a real father is equally problematic particularly when evaluating the distribution of RS among all males. False exclusion will reduce the number of paternity assignments, resulting in inflated numbers of males with no or few offspring and negatively biased estimates of RS. For this reason we evaluated error in our genotypic database and tested our hypothesis using two data sets of putative fathers bracketing stringent and relaxed criteria for paternity assignment. We recommend that this approach be routinely applied when false exclusion of real fathers can bias conclusions. Conversely, when evaluating individual RS, such as when testing behavioural correlates of RS, only stringent criteria assignments should be used because random false exclusions will reduce sample size but not bias results (Cerchio 2003; Cerchio et al. 2003).

Test of Polygynous Mating

We explicitly defined polygynous mating as an unequal set of reproduction probabilities among sexually mature males (i.e. a deviation from a random mating system). To test this hypothesis of polygyny, we employed a randomization simulation to determine whether the observed distributions of male reproductive success differed from what would be expected if all males had an equal probability of fathering a calf (i.e. a Poisson distribution). Parameters included (1) the number of males in the population (initially estimated at 600, half of our lower population estimate), (2) the number of calves born in each year of the study (estimated from mark–recapture of mothers), and (3) the proportion of males in the population that were sexually mature (estimated at 0.82, using an age at sexual maturity of 5 years: Chittleborough 1965; a survival rate for calves of 0.818: Gabriele et al. 2001; and a survival rate for adults of 0.963: Mizroch et al. 2004). The simulation generated simulated paternities for each of the 5 years of the study. Within a year, the estimated number of calves born was assigned a father from among the sexually mature male candidates, with equal likelihood of paternity among males. The simulated calves and candidate males were then randomly subsampled to match the actual numbers that were genetically sampled. If both a calf and its assigned father were sampled, it represented a simulated paternity assignment. These were summed across the 5 years to produce the simulated number of paternity assignments each year, the number of males assigned zero, one, two, three, or more offspring, and the mean and variance of RS among all fathers (used as expected values of test statistics). After 1000 simulations, the observed values were compared to the expected distributions for each test statistic to determine the probability of the observed data in a randomly mating population (statistical significance evaluated at an $\alpha = 0.05$). The mean reproductive success distributions output by the random model fit a Poisson distribution well ($\chi^2_2 = 0.314$, $P = 0.86$), as expected.

Note that the variables output by this procedure are not parameter estimates for the population, but rather specific properties of the sample dependent on the proportions of males and offspring that were sampled (e.g. the '0 offspring' category of reproductive success is a prediction of how many males will not be assigned a calf in this sample, either because they had no RS, or because their calves were not sampled). An extension of this approach is presented in Cerchio (2003), which extrapolates a best-fit model of RS to the entire population and estimates the output statistics as population parameters, but those results are beyond the scope of this paper.

RESULTS

Molecular Analysis

Microsatellite analysis of the 923 samples yielded 619 unique multilocus genotypes. Summary statistics for the 13 microsatellite loci are presented in Table 1, compiled for 619 individuals after removal of identical genotypes. The number of alleles per locus ranged from 4 to 19 with a mean of 10.1, and expected heterozygosity ranged from 0.330 to 0.898 with a mean of 0.707 (Table 1). No locus deviated significantly from Hardy–Weinberg expectations in a chi-square goodness-of-fit test, as implemented by CERVUS 2.0; however, permutation analysis of FSTAT v2.9.3 (Goudet 1995, 2001) yielded a significant deviation at $P = 0.032$ for locus TAA031. This result is probably related to the relatively high failure rate and consequent large proportion of missing data for this locus (76% individuals typed). This deviation was not significant following a Bonferroni correction for table-wide error

Table 1. Descriptive statistics of 13 microsatellite loci used in parentage analysis

Locus	Rep	*k*	*N*	H_O	H_E	F_{IS}	HW	Excl	Null freq
GATA098	4	9	619	0.821	0.818	−0.000	0.455	0.644	−0.0035
GATA028	4	6	619	0.355	0.351	−0.013	0.384	0.199	−0.0037
TAA031	3	15	472	0.807	0.835	0.033	0.032	0.676	0.0157
GGAA520	4	19	601	0.882	0.898	0.019	0.156	0.792	0.0084
GATA417	4	19	617	0.870	0.861	−0.008	0.392	0.726	−0.0051
GATA053	4	10	619	0.829	0.822	−0.009	0.532	0.647	−0.0039
EV001	2	4	619	0.549	0.550	−0.001	0.265	0.273	0.0001
EV014	2	7	619	0.672	0.643	−0.045	0.942	0.413	−0.0271
EV021	2	6	618	0.709	0.698	−0.017	0.592	0.470	−0.0088
EV037	2	15	619	0.889	0.885	−0.005	0.666	0.768	−0.0022
EV094	2	7	619	0.672	0.693	0.029	0.421	0.452	0.0192
EV096	2	13	607	0.834	0.810	−0.028	0.838	0.635	−0.0147
EV104	2	4	619	0.338	0.330	−0.022	0.861	0.179	−0.0124
Mean/overall		10.3	605.2	0.710	0.707	−0.003	0.423	0.99998	

Rep = repeat motif length in base pairs, *k* = number of alleles, *N* = number of individuals genotyped, H_O = observed heterozygosity, H_E = expected heterozygosity, F_{IS} = population-wide F_{IS} values for each locus and overall (calculated by FSTAT v2.9.3), HW = probability test of deviation from Hardy–Weinberg equilibrium (permutation over all samples, FSTAT v2.9.3), Excl = exclusion probability of second parent (in parentage test when one parent is known), and overall exclusionary power of all loci (calculated by CERVUS 2.0), Null Freq = estimated frequency of null alleles or nonamplifying alleles (calculated by CERVUS 2.0).

(Rice 1989). Total exclusionary probability of the multilocus genotypes in a paternity analysis, as calculated by CERVUS 2.0 when one parent is known, was high at 0.99998, and estimated null allele frequencies were negative or low (<0.02) for all loci (Table 1). All but two of 125 mother–calf pairs shared at least one allele at all genotyped loci; the two exceptions involved the same single locus, GGAA520, one of the previously identified loci that showed occasional allelic dropout. Since the mother–calf mismatches were rare, the locus did not deviate from Hardy–Weinberg equilibrium, and in both cases one individual was a homozygote, these mismatches were most likely due to allelic dropout as opposed to a true null allele or mutation (the latter would typically result in mismatching heterozygotes, with mother and calf alleles one step apart). Definitive evidence of germ-line mutation was consequently undetected and presumably very low; conservatively, if the two mother–calf mismatches at GGAA520 were in fact due to mutation, the estimated mutation rate would be roughly 0.001 per genotype. Population-wide F_{IS} values (FSTAT, Goudet 2001) were low for all loci, well below 0.05, indicating a low incidence of inbreeding. When partitioning the sample into adult males and females, an analysis of molecular variance (AMOVA, Excoffier et al. 1992) yielded no significant difference in allele frequencies ($V_{sex} = 0.00913$, $P = 0.332$), indicating that males and females came from the same population.

Paternity Analysis

The 619 genotyped individuals included 141 calves (70 male and 71 female; 125 of which were associated with a sample of the mother), eight yearlings (four of which were matched by genotype to a previous year calf), 297 males and 177 females presumed to be adults (based upon size, behaviour, and/or reproductive status in the case of females known to have calved). Given our point estimates of population size (1200–1500) and assuming sexual parity, we sampled 40–50% of the males and 32–40% of adults in the population. Using dorsal fin and tail identification photographs, we identified 231 different mother–calf pairs between 1997 and 2001 (Table 2) and consequently sampled 54% for paternity analysis.

We estimated error in our genotypic data using 528 samples of 248 individuals that were determined from identifications photographs to be sampled multiple times. Additionally, 13% of singly sampled individuals ($N = 50$) were regenotyped. All detected errors were due to inconsistencies in PCR or mistakes in scoring, since compared genotypes were from the same individuals. Average error among all loci was 0.006 per locus, or 0.082 per genotype. However, average error rate among the three most problematic loci was high at 0.020 per locus, whereas among the remaining 10 loci only 0.002 per locus (or 0.020 per 10-loci genotype). The three problematic loci were among the most polymorphic and therefore highly informative for paternity inference. Therefore rather than exclude them we incorporated the error estimates into the paternity analysis and generated two data sets of putative

Table 2. The sample of humpback whale mother–calf pairs (MC) used in the genetic paternity analysis and results of paternity assessment by year

	1997	1998	1999	2000	2001	Total
MC sighted*	24	30	45	80	52	231
MC sampled†	6	15	31	57	16	125
% MC sampled	25	50	69	71	31	54
Conservative paternity assignments	2	6	9	17	6	40
Relaxed paternity assignments	3	9	16	27	7	62

*Number of different pairs sighted during each year.
†Total number of sighted mother–calf pairs that were genetically sampled (both individuals) for each year.

fathers to evaluate the effect of allowing mismatches on the ultimate conclusions.

First, stringent parameter analyses were conducted assuming no errors in the genotypes (a strict exclusion analysis: '0.0 error rate' in CERVUS, '0 mismatches allowed' in NEWPAT). This analysis was likely to exclude some real fathers due to genotypic errors. Additional parameters in CERVUS included 600 candidate males in the population, with 0.5 sampled (given a population estimate of ca. 1200 and 297 male genotypes in the final sample). Second, relaxed parameter analyses were run in CERVUS with a 0.006 per locus genotyping error rate, and in NEWPAT that allowed one mismatched locus of any allelic size difference (to account for all types of scoring mistakes and PCR artefacts) and a low threshold for null alleles (< 0.001). Analyses allowed two ungenotyped loci per comparison, so all comparisons were done with a minimum of 11 loci.

The use of CERVUS and maximum likelihood in parentage analysis is powerful and now common, however, it is important to consider the effect that confidence level in paternity has on the power to assign true fathers, particularly when considering population-wide reproductive success. Choosing a high confidence level (i.e. 95%) decreases type I error, but may increase type II error unacceptably. For example, in the simulation reported by Marshall et al. (1998, Figure 2a), approximately 44% of true fathers in the sample were excluded when using a confidence level of 95%, and 14% were excluded at 80% confidence (not reported by Marshall et al. 1998, but estimated from their Figure 2a). Conversely, when increasing power by choosing a lower confidence of 80%, fully 20% of accepted paternity assignments were incorrect by definition. Therefore, to minimize type I error while maximizing power, we evaluated CERVUS assignments in the relaxed analysis on a case-by-case basis by considering mismatched loci between candidate and offspring and the effect of locus-specific error rates.

In our relaxed parameter analyses CERVUS sometimes assigned a father at 80% to 95% confidence with two or three mismatches between calf and putative father (assumed genotype errors), which we found highly suspect due to the multiple mismatching loci. This most likely occurred because CERVUS assigns confidence based upon the critical value of the Delta statistic, Δ, the difference in LOD scores between the most likely father and the second most likely father (Marshall et al. 1998), irrespective of the value of the formers LOD score or number of genotype mismatches. In addition, CERVUS at times assigned a father that mismatched at a locus with a low estimated error (i.e. an unlikely error, and therefore most likely a true exclusion), over a putative father that mismatched at a particularly error-prone locus. Similarly, confidence in a most likely father was sometimes low ($< 80\%$), due to a second most likely male that had errors at one or more low-error loci (resulting in a low Δ). The result in these cases was the exclusion of a male that appeared to be a good candidate, due to the program not distinguishing among the probabilities of error at different loci. Worthington Wilmer et al. (1999) reported similar issues in their comparison of CERVUS and NEWPAT in a study of paternity in grey seals, *Halichoerus grypus*. Consequently, our relaxed data set of putative fathers was constructed by comparing the results of both programs and applying two criteria: (1) only one error per genotype was allowed at any locus, compensating for the tendency of CERVUS to assign fathers with multiple errors, and (2) confidence in paternity had to exceed 80% in NEWPAT, allowing for fathers excluded by CERVUS ($< 80\%$ confidence) that had a high confidence in NEWPAT (no assignments were accepted if they had $> 80\%$ confidence in CERVUS only).

Conservative parameter paternity analyses yielded 35 paternity assignments with both programs in full agreement at a confidence level of greater than 95% (confidence level was in fact $> 99\%$ for 34 assignments in CERVUS and 31 in NEWPAT). For the final conservative set of putative fathers, an additional five assignments were added that contained one error among the three most error-prone loci, and had greater than 90% confidence for both CERVUS and NEWPAT in the relaxed analyses. This resulted in a total of 40 paternities assigned among 33 males (Tables 1, 2). The relaxed set consisted of 62 putative fathers among 51 males (Tables 1, 2), at a confidence level greater than 80% (confidence level was in fact $> 90\%$ for 58 assignments in NEWPAT and 38 assignments in CERVUS). There were four cases in which the two programs conflicted in assignment in the relaxed analysis. In all cases of disagreement the male assigned by NEWPAT was the second most likely candidate in CERVUS. Furthermore, the most likely candidate of CERVUS had either multiple mismatched loci or a single mismatch at a locus with a low estimated error rate, and therefore most likely represented a legitimate exclusion. In all cases the male assigned by NEWPAT was chosen.

Test of Polygynous Mating

The random mating model was first run assuming 600 males in the population, 82% of which were sexually mature, generating distributions of all test statistics with equal probability of paternity among mature males. In the relaxed data set, the observed 62 paternity assignments were a good fit with the 61.8 assignments predicted on average by the model (Table 3). However, the 40 assignments of the conservative set were far fewer than expected ($P < 0.001$). Two explanations are (1) true fathers were excluded in the conservative set due to errors, and thus the relaxed set was more accurate, or (2) the actual population of males contributing to paternity was larger than that estimated with our mark–recapture data, suggesting that the relaxed set included false assignments, and thus the conservative set was more accurate. We tested for polygynous mating based on both explanations to bracket the range of genotype error and population size estimates, providing a robust test of the hypothesis. We therefore ran a second set of simulations under the assumptions of (2), using 900 males as an estimate of males in the population (half of the upper 95% confidence limit of our abundance estimates). The average expected number of assignments, 41.3, was a good fit to that observed in the conservative data set (Table 3).

Table 3. Paternity assignments and observed reproductive success (RS) distributions of male humpback whales during 1997–2001, for the conservative analysis (CA) and the relaxed analysis (RA), and results of tests of random mating for both analyses

		900 male simulation*			600 male simulation†	
	CA	Expected value	*P*	RA	Expected value	*P*
Number of calves tested	125			125		
Total paternities assigned	40	41.3	0.448	62	61.8	0.529
Mean RS among fathers	1.21	1.09	**0.015**	1.22	1.14	0.067
Variance in RS among fathers	0.297	0.100	**0.011**	0.293	0.142	**0.022**
RS distribution across 5 years for males with						
0 paternities	264	258.9	0.170	246	242.1	0.260
1 paternity	28	34.8	0.101	43	48.0	0.194
2 paternities	3	2.9	0.581	5	6.2	0.403
3 paternities	2	0.2	**0.021**	3	0.5	**0.011**
RS distribution within years for males with						
1 paternity	34	39.2	0.171	54	57.6	0.299
2 paternities	3	1.0	0.075	4	2.1	0.175

Significant values are given in bold.
*Expected values assuming 900 males in the population and given a random mating model where all sexually mature males have equal probability of paternity, and the *P* value of the conservative observed data in the expected distribution.
†Expected values as for 900 male simulation, but assuming 600 males in the population, and *P* values of the relaxed observed data in the expected distribution.

Regardless of our estimate of the male population and our assumptions of genotyping error, the results indicated a deviation from random mating and provided support for a mating system that is mildly polygynous (Table 3). We expected that mean RS and variance in RS among successful males would be larger in a polygynous mating system than predicted by the random mating model. In terms of RS distribution, we specifically expected to observe more males siring no offspring, fewer males siring one offspring, and more males siring multiple offspring than predicted by the model. The observed variance in RS among fathers was significantly greater in both sets than predicted by the models (Table 3, $P = 0.011$ for conservative, and $P = 0.022$ for relaxed). Mean RS among fathers was significantly greater in the conservative set than the mean predicted by the model (Table 3, $P = 0.015$), and marginally greater than that in the relaxed set (Table 3, $P = 0.067$).

The distribution of RS among the assigned fathers was assessed by summing all paternities across the five seasons, and also by considering multiple paternities only within seasons. Considering RS across all seasons, the number of males with no calf assignments was larger than expected on average and the number with one calf was less than expected on average, however not significantly so, for both conservative and relaxed sets (Table 3). Also the number of males with two calves fit the predictions well for both sets (Table 3). However, there were significantly more males than expected siring three calves in both sets (Table 3, $P = 0.021$ for conservative, and $P = 0.011$ for relaxed). No male sired more than three calves in our sample. Therefore, we conclude that deviations in mean and variance in RS from the random model are due primarily to the two males (conservative analysis) or three males (relaxed analysis) observed to sire three calves across the five study seasons.

Considering RS distribution within seasons, only males with two calves in the same year were tallied in the '2 paternities' RS category (no male was assigned three calves within a year). In the conservative set, three males sired two calves in a single season, and four males did so in the relaxed set. These observed values were greater than the average in the random models, however not significantly so (Table 3, $P = 0.075$ for conservative, and $P = 0.175$ for relaxed). In both data sets, if one more male sired two calves within a season, the distribution of paternities would deviate significantly from a random distribution.

Sampling of mother–calf pairs varied among years, with 1997 being poorly sampled because it was a pilot season without dedicated effort towards calves (Table 2). As a result, the inclusion of 1997 in the random mating analysis potentially reduced the power of the test because the proportion of sampled calves was reduced relative to 1998–2001 data. Therefore the procedure was repeated excluding the 1997 sample for the four remaining years. The results strengthened the findings of the 5-year test, with significantly larger mean RS among fathers ($P = 0.007$ for conservative, and $P = 0.028$ for relaxed), significantly larger variance in RS among fathers ($P = 0.005$ for conservative, and $P = 0.006$ for relaxed), and significantly more males siring three calves across the four years ($P = 0.011$ for conservative, and $P = 0.007$ for relaxed). Considering within-season RS distribution, the number of males siring two calves was greater than random, but again was not significantly different ($P = 0.063$ for conservative, and $P = 0.173$ for relaxed).

DISCUSSION

The data presented here on the reproductive success of male humpback whales are the most extensive to date for

any baleen whale. We have used molecular analysis to provide the first information on individual paternity and male RS, and a novel test of random mating to provide the first evidence of polygyny in humpback whales. Our observations suggest a deviation from random mating and that certain males have slightly greater RS on average. However, mating skew was not severe among fathers, and many males in the population may contribute to subsequent generations. There were no highly successful males in the sample, and the reproductive skew was only obvious across several seasons. An extension of the simulation model (used here only to test against a null prediction) estimated that the best-fit distribution of male RS was an approximation of a gamma distribution skewed only slightly beyond Poisson expectations (Cerchio 2003).

Few previous studies have addressed reproductive skew in baleen whales. Nielsen et al. (2001) used an indirect Bayesian approach to estimate the number of breeding males in the North Atlantic population of humpback whales. Their point estimate of 6540 was larger than the 5000 males estimated in the population (by genetic mark–recapture: Palsbøll et al. 1997a; by photographic mark–recapture: Smith et al. 1999), and had a large 95% confidence interval of 3800–16 760. Nielsen et al. (2001) concluded there was a large effective population size of breeding males, and that variance in RS was low, congruent with the findings of our more direct assessment of reproductive skew. However, they sampled only 7% of males in the population and assigned paternity to approximately 6% of 146 calves (the exact number of assignments was not reported). Given the low assignment rate and large confidence interval of their estimate, it is unclear whether these conclusions were due to a lack of statistical power to detect reproductive skew. Furthermore, Nielsen et al. also concluded (tentatively) that dominant males were likely to sire three times more offspring than subdominant males, which is somewhat in contradiction with their and our conclusion of low variance in RS.

The finding of low variance in male RS differs from what might be expected for this mating system based upon observations of male behaviour and sexual selection theory. Several investigators have suggested a lek or lek-like model for the humpback whale mating system (Herman & Tavolga 1980; Clapham 1996; Cerchio 1999). There are distinct differences from 'classical' leks, particularly the lack of rigid male territories and the tendency for displaying males to move around. This has raised questions regarding the appropriateness of the classical lek model (Clapham 1996), however, these observations are not unique among lekking species, having also been noted for some frogs (Arak 1983; Shimoyama 1993). The mild skew in male RS is contrary to the expectation of lek mating systems in terrestrial species, typically involving large variance in male RS (Payne 1984; Höglund & Alatalo 1995; Mackenzie et al. 1995). However, mating skew is negatively correlated with lek size (Höglund & Alatalo 1995; Widemo & Owens 1995). Breeding population sizes of humpback whales are large (>4000 for Hawaii: Cerchio 1998; >2000 for the Mexican Pacific: Urbán et al. 1999; >10 000 for the West Indies: Smith et al. 1999) and individuals move throughout the breeding regions with apparent fluidity (Baker & Herman 1981; Darling & McSweeney 1985; Cerchio et al. 1998). Consequently, congregations of displaying and competing males in breeding habitat tend to be relatively large. It is not surprising that in such aggregations the success rate of high-ranking males would be limited. Therefore, the finding of low skew does not in itself refute a lek model. Female assessment of singing males and mate choice by display characteristics await further investigation.

The existence of a mild skew as opposed to a strong skew in RS has implications for classification of the mating system, and the significance, relative payoffs, and origin and maintenance of alternative mating tactics. We suggest and evaluate five nonexclusive alternative explanations for mild polygyny in this population: (1) dispersion of females, (2) evenness of reproductive payoffs among alternative tactics, (3) female preference according to compatibility at the major histocompatibility complex, MHC, (4) a population age structure biased towards young males, and (5) sampling bias.

Dispersion of Females

Low variation in male RS is consistent with the conjecture that females are widely dispersed and therefore difficult to monopolize (Clapham 1996). When evaluating the dispersion of individuals on humpback whale breeding grounds, it is necessary to consider geographic scale and individual mobility. Relative to the oceanic range of populations and annual migration, humpback whales aggregate in dense concentrations for purposes of breeding. This is in stark contrast to the widely dispersed open-ocean distribution of fin whales, *Balaenoptera physalus*, and blue whales, *B. musculus*, during their breeding seasons (Payne & Webb 1971; Mizroch et al. 1984; Watkins et al. 1984, 1987). Therefore, in the context of baleen whale population distribution and individual mobility, female humpback whales may not be as highly dispersed as might seem from the perspective of terrestrial mammalian populations.

Furthermore, although little is known about oestrus in humpback whales, it is most certainly short relative to the residence of males on the breeding ground and highly asynchronous among females (Chittleborough 1954, 1965; Clapham 1996). This would allow mobile males to encounter many oestrous females during the extended breeding season. In such a system, highly successful males should be able to serially monopolize reproduction of many females without necessarily sequestering groups of females (Emlen & Oring 1977; Shuster & Wade 2003). In this way, the dispersed nature of the temporal distribution of receptive females can at least partially counteract the effect of geographical distribution. Therefore, although a dispersed geographical distribution may contribute to limiting RS, we do not believe that low variation in male RS can be entirely attributed to the dispersion of females. Shuster & Wade (2003) showed that the temporal distribution of female receptivity can be an indicator of sexual selection intensity, but only under certain conditions.

Specifically, if individual male RS covaries across the entire season, then a 'dominant' or highly successful male would be able to obtain matings across the season with many females, and we would expect high variance in RS among males. Conversely, if there is not high covariance in male RS across the season, then the skew in OSR and degree of male competition at any one time may exaggerate the potential for RS skew and sexual selection. This occurs when males that are unsuccessful at one point are successful at some other point in the season. Apparently, there are other factors in our population prohibiting successful males from maintaining consistent competitive superiority across the season, and we suggest three possible explanations below.

Payoff of Alternative Tactics

The distribution of male RS may be dependent on the relative effectiveness of different male tactics. Reproductive males engage in a variety of well-documented behaviours while on the breeding grounds, including singing, physically competing for single females, and consorting with both nonlactating and postpartum females. Behavioural analysis of fathers in this study indicated that successful males used a variety of these alternative mating tactics, no one tactic predominated among males, and some males may favour specific tactics (Cerchio 2003; Cerchio et al. 2003). This suggests that males may successfully use several tactics and that payoffs may be relatively even among different tactics. This type of mating system would be more complex and flexible than a strict lek, and reminiscent of lekking ungulates, such as the fallow deer, *Dama dama* (Thirgood et al. 1999). Such evenness among alternative tactics would explain the existence of only mild polygyny. The existence of female mating tactics, and variation in preferred tactics among females, would reinforce and promote evenness in success among male tactics. For instance, some females may preferentially incite competitive groups of males (as suggested for right whales, *Eubalaena* sp.: Kraus & Hatch 2001; Parks 2003), whereas others may preferentially associate with singers and consorting males in pairs. Such associations between male and female tactics have been documented in genetically based alternative strategies of side-blotched lizards, *Uta stansburiana* (Zamudio & Sinervo 2000; Sinervo & Zamudio 2001), but we are unaware of examples involving behavioural polyphenotypes as found in humpback whales.

Mate Choice for MHC Compatibility/ Heterozygosity

The major histocompatibility complex (MHC) is a multigene complex associated with critical functioning of the immune system and disease resistance. MHC-disassortative mating preferences resulting in progeny with high heterozygosity, and thus enhanced disease resistance, have been documented in humans, mice and some fish (Penn 2002; Bernatchez & Landry 2003). If females choose only those males with dissimilar allelic complements at their MHC, also referred to as mate choice for compatibility or heterozygosity (Tregenza & Wedell 2000; Penn 2002), the result in terms of male reproductive skew would be mild polygyny because no class of male could dominate reproduction. Furthermore, song complexity in avian systems has been implicated as an indicator trait of MHC diversity and resultant disease resistance (Møller et al. 2000; Garamszegi et al. 2003). Humpback whale song is highly derived in a phylogenetic context, being more complex and acoustically diverse than song in other mysticetes (e.g. blue, fin and bowhead whales). Therefore, complexity in humpback whale song may advertise immunocompetence and disease resistance, and thus allow females to choose males indirectly based upon the MHC.

Skewed Population Age Structure

Populations of humpback whales in the North Pacific were severely depleted by whaling in the 19th and 20th centuries, until protected in 1966 (Rice 1974). Population estimates have steadily increased from the mid-1970s to recent estimates in the 1990s (Cerchio 1998; Urbán et al. 1999; Calambokidis et al. 2001), indicating continuing recovery of populations; however, current estimates are below prewhaling estimates, which themselves are likely negatively biased. Therefore, it is safe to assume that the population is not at equilibrium and the age structure is probably biased towards young animals. If competitive ability is correlated with age so that experience beyond the age of physical maturity is important to RS (age-based indicator mechanisms: Brooks & Kemp 2001), we might expect less skew in RS among males than at equilibrium, because there are fewer competitively superior animals in the population and many males of similar ability competing for females. This trend might be expected if mate choice focused more on song cues and singing ability, which is potentially dependent on experience, than on physical competition, which would probably favour younger, more vigorous males.

Sampling Bias

Lastly, we must consider the potential for bias in our sample and analysis. Because we sampled a relatively large proportion of the male population, it is unlikely that we would not have sampled at least some highly successful males if they existed. Several studies in avian systems have correlated male RS with attendance and participation in breeding activities (Payne & Payne 1977; Pruett-Jones & Pruett-Jones 1991); therefore, if a sampling bias existed, we might expect it to be a positive bias towards successful males. The random mating model assumed all males had an equal probability of fathering calves, a necessary simplification of residency patterns of males common among indexes of skew (Nonacs 2000). This is likely to be violated since some males may spend less time on the breeding grounds or be entirely absent in some years. Again, it seems most probable that underrepresented males are those with lower success, introducing a positive

bias in detecting skew. Therefore, we believe our study would have detected a strong skew if one existed; however, it is impossible to rule out bias entirely. There remains the possibility that some sampled males have higher RS in other unsampled areas; this is an unavoidable limitation of studying a large mobile mammal with a potentially large range. A related issue regards how representative our study population is; the Revillagigedo population is relatively small with a high resighting rate as compared to, for example, the Hawaii (Cerchio 1998) or West Indies (Smith et al 1999) populations. In a larger, less resident population, variance in RS among males could be even lower than that documented here due to the sheer numbers of males competing and a more dispersed distribution of females. Our data are currently the best available for this species, however, these reservations should be acknowledged.

A final important consideration is the short length of this study relative to the life expectancy of the species, which is probably in excess of 50 years (Chittleborough 1965). A long-lived male's reproduction over 5 years is unlikely to reflect his lifetime RS. If a male is able to maintain a slight advantage in reproduction, as we have documented here, over his extended lifetime, then it could result in a much greater advantage in lifetime RS relative to the population at large. Conversely, if success is age dependent, then the slight variation detected in this study may entirely disappear when considering lifetime RS. Only very long-term studies evaluating the change in RS of individual males over their lifetime (and the lifetimes of potentially multiple investigators) will be able to address this question.

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