Sound Playback Experiments with Southern Right Whales (*Eubalaena australis*)

Abstract. *A variety of sound recordings were played to southern right whales. Whales approached the loudspeaker and made frequent sounds in response to recordings of other southern right whales, but swam away and made relatively few sounds in response to playbacks of water noise, 200-hertz tones, and humpback whale sounds. Thus it appears that southern right whales can differentiate between conspecific sounds and other sounds.*

Playback of sounds to mysticetes has rarely been attempted (*1*). We present here the results of playback experiments which demonstrate that southern right whales (*Eubalaena australis*) can differentiate between sounds made by other southern right whales and a variety of other sounds. The experiments were conducted off the southern coast of Argentina (42°23′S, 64°03′W), where right whales were observed from mid-May through mid-December 1977. The whales spent most of their time swimming or resting at the surface.

The head of each southern right whale is adorned with a distinct pattern of dermal eruptions (callosities) that are colonized by cyamids (whale lice). By photographing these callosity patterns, we could identify individual whales on any given day (*2*). From more than 1000 photographs taken throughout the 15 playback experiments (a total of 19.8 hours), we identified 18 individual whales, some of which were present during more than one experiment.

An array of hydrophones was fixed 124 m in front of our observation hut, and the sounds made by the whales were tape-recorded during all periods of observation (*3*). To determine which whale made a particular sound, the array was linked to a real-time, underwater sound-direction finder (*4*), which indicated in less than 1 second the bearing to any sound between 30 and 500 Hz that was 3 dB (re 0.0002 μbar) louder than the ambient noise.

Five types of sounds were selected for playback to the whales: (i) water noise, (ii) 200-Hz tones, (iii) humpback whale sounds, (iv) southern right whale sounds, and (v) imitation southern right whale sounds (*5*). In the first three experiments, sounds were broadcast from an underwater loudspeaker suspended 3 m beneath a rubber boat. During all subsequent playbacks, the loudspeaker was fixed on the bottom of the gulf, 128 m north of the observation hut (*6*).

The general procedure for a playback experiment was as follows. We identified each whale, tracked its movements with a theodolite (*7*), and recorded its sounds for at least 16 minutes (mean, 31 ± 15 minutes) prior to the experiment. We began a playback when the whales had passed and were swimming away from the loudspeaker (*8*). Two selections were played for equal amounts of time (mean, 11 ± 6 minutes) and were separated by a period of silence (mean, 2 ± 1 minutes) (*9*). This sequence is referred to as a trial. In each of 12 experiments, a single trial was run. In the three experiments with

Table 1. Sound scores (A columns) and swimming scores (B columns) for each whale for all the playbacks (first trial data only). The sound score for the selection is the whale's rate of sound production in sounds per minute. In experiments 2, 4, and 6, we could not accurately determine which whale in the group made the sounds. In these cases, the group's sound rate was divided by the number of whales in the group and the result entered once as the sound score (bracketed). The swimming score is the sum of the distances the whale swam toward the loudspeaker, minus the sum of the distances it swam away, divided by the total distance it swam (a negative swimming score signifies that during the playback the whale swam away from the loudspeaker more than it swam toward it).

Experiment	Date	Whale	Pre-playback A	Playback selection									
				Water noise		200-hz tones		Humpback whale sounds		Right whale		Imitation	
				A	B	A	B	A	B	A	B	A	B
1	18 July	A	0.00									0.17*	+0.92*
2	18 August	B	[0.00]			[0.00*]	−0.40*			[0.15]	+0.40		
		C					−0.86*				+0.66		
		D					−0.81*				+0.20		
		E					−0.91*				+0.08		
3	24 September	F	0.05			0.00*	−0.35*			1.95	+0.42		
4	4 November	G	[0.00]									[0.35*]	+0.75*
		H											+0.75*
5	6 November	I	0.00					0.00	−0.28	0.80*	+0.79*		
6	8 November	H	0.18					1.22*	−0.12*	1.83	+0.68		
		J	[0.00]					[0.05]	−0.37	[0.07*]	+0.87*		
		K							−0.37		+0.87*		
7	8 November	L	0.18					0.78	−0.49	0.85*	+0.45*		
8	10 November	M	0.08	0.10*	+0.09*					0.25	+0.16		
9	11 November	N	0.00	0.00*	−0.41*					0.83	+0.68		
		I	0.00	0.00*	+0.02*					0.58	−0.18		
10	15 November	P	0.00	0.00	−0.21			0.00*	−0.82*	0.09	−0.09		
		Q	0.00	0.00	−0.21			0.00*	−0.82*	0.18	+0.96*		
11	27 November	N	0.00	0.00	−0.94					0.00*	+0.67*		
12	29 November	R	0.00					0.00*	−0.41*	0.00	−0.39		
13	30 November	R	0.00	0.00*	−0.24*					0.00	−0.11		
14	30 November	N	0.00							0.00*	−0.94*		
15	2 December	S	0.61							2.36*	−0.40*		

*Score is for first selection played in experiment.

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more than one trial, the same two selections were played in the same sequence for approximately equal amounts of time in each trial; trials were separated by periods of silence (mean, 20 ± 18 minutes) that were longer than the periods separating the selections.

For each experiment, we determined the movement of each whale, its distance from the loudspeaker, and the number of sounds it made (see Fig. 1). We scored the whale's response to a playback selection on the basis of the number of sounds it made (sound score) and its swimming pattern (swimming score). Table 1 lists the sound and swimming scores for all the whales during the experiments (data given are for first trials only).

The distribution in the swimming scores shows a significant difference ($P < .01$, Kruskal-Wallis test) from what would be expected if the playback had no effect on the whales' behavior. However, there were no significant differences ($P > .40$, Wilcoxon's signed-rank test) between sound and swimming scores for the first and second selections in a trial, meaning that the whales were not responding preferentially to the first selection (*10*). When right whale sounds were played, the sound scores were significantly different ($P < .01$) from the preplayback sound scores and the sound scores for the playback of water noise. The swimming scores when right whale sounds were played were significantly different ($.01 < P < .05$, Mann-Whitney U test) from the swimming scores when water noise, 200-Hz tones, and humpback whale sounds were played.

Behaviorally, this means that during playbacks of right whale sounds, the whales responded by making more sounds and swimming toward the loudspeaker. In response to the three other sound selections, the whales swam away and did not make more sounds. When a whale was exposed to a series of trials on the same day, its responses decreased with increasing exposure to the playback sounds (see Fig. 1) (*11*).

These results strongly indicate that southern right whales can differentiate between conspecific sounds and a variety of other sounds. To the best of our knowledge, this represents the first instance in which such evidence has been gathered for any species of whale in the wild. We believe that the playback technique presented here would be useful in determining the biological function of the sounds in a whale's acoustic repertoire.

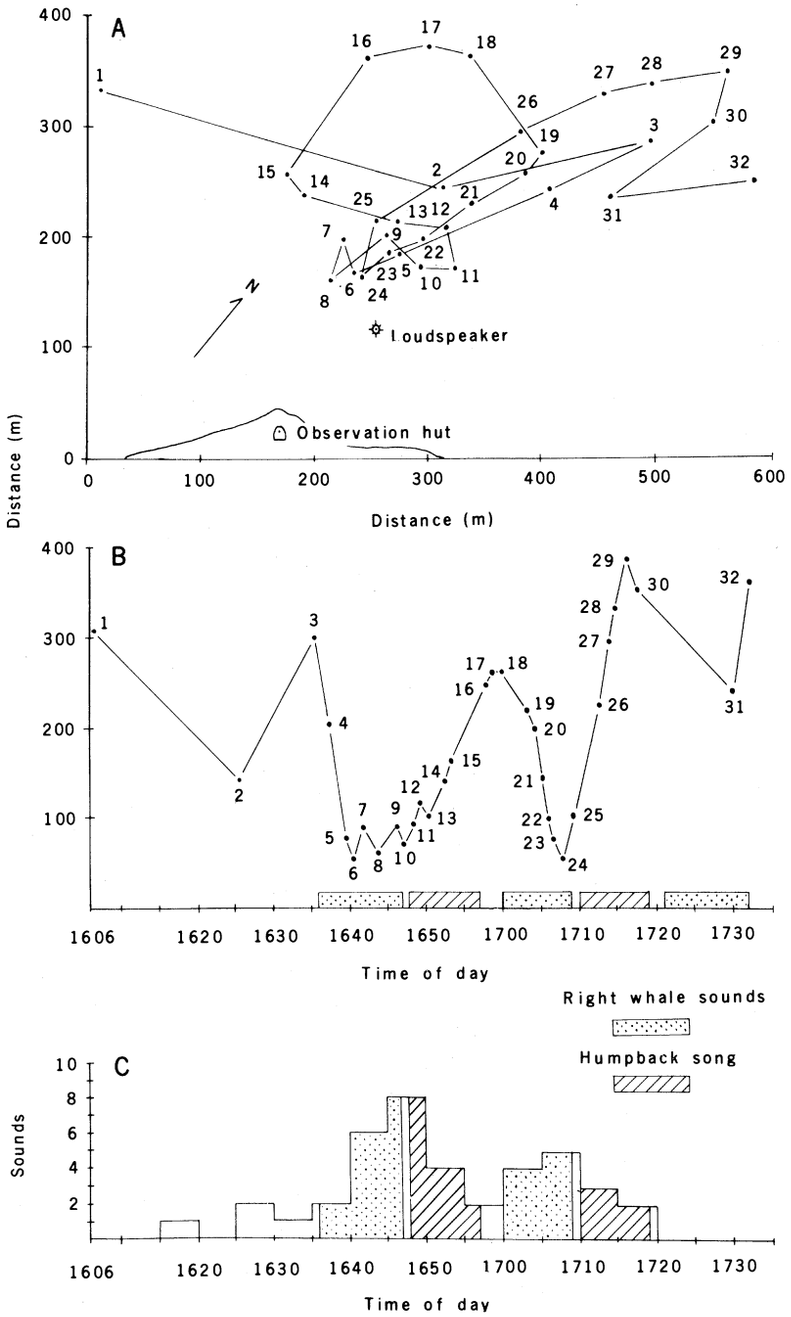

Fig. 1. Response of Whale L (experiment 7) to right and humpback whale sounds (*5*). (A) The path of the whale in the area of the loudspeaker (numbered points represent position of whale ± 0.5 m). (B) The distance of the whale from the loudspeaker. (C) The number of sounds made by the whale per 5-minute interval.

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References and Notes

1. W. C. Cummings and P. O. Thompson, *U.S. Fish Wildl. Serv. Fish. Bull.* **69** (No. 3), 525 (1971); ——, J. F. Fish, *Antarct. J. U.S.* **9** (No. 2), 33 (1974).
2. R. S. Payne *et al.*, in preparation.
3. The receiving system consisted of three AQ-17 hydrophones (with amplifiers) and a Nagra IV-S tape recorder or Sony TC-520CS cassette recorder. The system was flat ± 3 dB (re 0.0002 μbar) from 50 to 3000 Hz.
4. This device was designed and built by C.W.C. It utilized the phase-time information from a stationary, two-dimensional hydrophone array to compute the direction to the sound. Tests conducted in situ indicate that the system was accurate to within ± 12° (C. W. Clark, in preparation).
5. The first four selections were tape recordings, whereas the imitation was spontaneous. The 200-Hz recording consisted of a 200-Hz tone lasting 2 seconds and repeated every 10 seconds; 200 Hz is in the midfrequency range of sounds made by southern right whales [(*1*); R. S. Payne and K. Payne, *Zoologica (N.Y.)* **56** (No. 4), 159 (1971); C. W. Clark, personal observation]. A phonograph record [R. S. Payne, *Songs of the Humpback Whale* (CRM Records, Del Mar, Calif., 1970)] provided the humpback whale sounds. Two tapes of southern right whale sounds were used. In experiments 2 and 3, the playback consisted of three low, frequency-modulated sounds lasting a total of 3.4 seconds and repeated every 10 seconds. In all the other experiments, we used a tape of sounds recorded in 1977 from a group of four whales, none of

which were resighted during any of the experiments.

6. Sound broadcasting equipment included a Sony TC-800B tape recorder, a crystal microphone, a Realistic MPA-20 amplifier, and a University 30 underwater loudspeaker. Sensitivity curves for the loudspeaker and microphone are not available. However, comparison between the spectral characteristics of the original playback sounds and the rerecorded sounds were made and the rerecorded sounds were judged to be good reproductions of the originals. The tape recorder and amplifier were flat ± 5 dB (re 0.0002 μbar) from 50 to 3000 Hz. Signal intensities 1 m from the loudspeaker were estimated as 95 ± 10 dB (re 0.0002 μbar).
7. This technique, pioneered by R. S. Payne, was accurate to ± 0.5 m at 1 km. During the first playback experiment, the theodolite was not used. Distances were calculated from photographs in which the whale, boat, and nearby landmarks appeared in the same frame. We estimate an accuracy of ± 5 m.
8. Water depth at the loudspeaker and hydrophones during the experiments averaged 5.8 ± 2.0 m. Water depth for the whales averaged 7.8 ± 4.5 m.
9. There were five exceptions. In experiments 1, 4, 14, and 15, we played one selection only. In experiment 10, we played 10 minutes of humpback whale sounds, 5 minutes of water noise, and 10 minutes of right whale sounds.
10. The results indicate that the responses to the second selection were independent of the responses to the first selection.
11. Whale N (see Table 1) was seen during three experiments when we played the tape of southern right whale sounds. On its first exposure, its response was typical: it swam toward the loudspeaker and increased its rate of sound production. Sixteen days later, it swam toward the loudspeaker but remained silent. Three days after this, it remained silent and swam away, never once turning toward the loudspeaker.
12. We thank C. Walcott and R. S. Payne for help and encouragement during the study, and C. Walcott and D. G. Smith for reading the manuscript. We also thank G. Blaylock, A. Macfarlane, J. Crawford III, and T. W. Clark for field assistance, and S. J. Clark for darkroom assistance. Supported in part by a grant from the National Geographic Society and by facilities and equipment from the New York Zoological Society and the State University of New York at Stony Brook.

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Genetic Variation in Social Mammals: The Marmot Model

Abstract. *The social substructure and the distribution of genetic variation among colonies of yellow-bellied marmots, when analyzed as an evolutionary system, suggests that this substructure enhances the intercolony variance and retards the fixation of genetic variation. This result supports a traditional theory of gradual evolution rather than recent theories suggesting accelerated evolution in social mammals.*

Recent theory suggests that the population substructure and demographic processes of social mammals may significantly accelerate evolutionary change. In particular, genetic drift due to small effective population size and inbreeding in social groups would lead to heterogeneity among groups. This heterogeneity coupled with the chance isolation of groups was proposed as a mechanism for the fixation of chromosomal variants in populations, and hence the rapid evolution of mammals compared to other vertebrate classes (*1*). Such accelerated evolution contrasts with the more traditional view of gradual evolution by gene substitution (*2*). In the traditional model the rate of evolution is proportional to the genetic variance of the population (*3*). This paper reports a 2-year study of the distribution of allozyme variation in colonies of a social mammal, the yellow-bellied marmot (*Marmota flaviventris*), and considers the maintenance, fixation, and variance of genetic variation in social groups.

The population biology of the yellow-bellied marmot, a large ground squirrel inhabiting the mountainous regions of western North America, has been studied since 1962 (*4*). Detailed data are available on the life histories, demography, and social substructure of marmots residing in the upper East River Valley of Gunnison County, Colorado. Throughout the study marmots were trapped, marked for individual recognition, and then released at the site of capture. Social relations within colonies were observed for more than 250 hours each summer. In the East River Valley marmots occupy rock outcrops in or near meadows; such habitat is patchy in its distribution (*5*). Smaller satellite sites are occupied by one or a few marmots, and marmots at these sites are characterized by high turnover, poor reproductive success, and lack of a social structure (*5, 6*). Larger habitat patches contain colonies of one or more polygynous groups each consisting of a territorial male, a harem of two or three females, yearlings, and young of the year (*7*).

Blood was sampled from the femoral vein from all members of nine colonies, a total of 112 animals, during the summers of 1976 and 1977. Eight variable allozyme systems with two alleles at each locus were identified (Table 1) by starch gel electrophoresis (*8*). We examined potential selective forces that might affect the dispersion of this genetic variation (*9*). There was a significant positive association of transferrin genotype and aggressive arena behavior, a correlation (P = .06) between leucine aminopeptidase gene frequency and population density, and gametic disequilibrium between transferrin and esterase-2 and between esterase-1 and esterase-2. We found no association between any gene frequency, genotype, or individual heterozygosity and altitude, age, sex, habitat, survivorship, litter size, and other behavioral variables. Although we cannot rigorously exclude the action of selection on these loci, its magnitude was not sufficient to prevent significant genetic heterogeneity due to drift from acting within the spatial and temporal structure of marmot colonies.

Heterogeneity among colonies (Table 1) is indexed by Wright's F_{ST}, which is the actual variance of gene frequencies of subdivision relative to the maximum possible variance (*10*); it may also be interpreted as an inbreeding coefficient (*11*) (see below). This measure is not directly testable for significance but permits comparisons with other studies. Genotypic frequencies for three loci were heterogeneous (*12*). Gene frequencies for three loci were heterogeneous according to a χ^2 test (*13*) related to F_{ST} by the formula $\chi^2 = F_{ST}2N_t$ where N_t is the total number in the population. The χ^2 summed for all loci as a test of overall heterogeneity was highly significant (Table 1).

There are three conditions that promote heterogeneity among social groups (*14*), and these conditions are consistent with the observed structure of the East River Valley marmot population.

1) *Restriction of mate selection to those in the social group*. There was no evidence of "cheating" (*15*) in mate selection among colony members. The allozyme phenotypes of 66 young from 26 litters supported the hypothesis that the young were without exception produced by colony residents. The probability of matings by transient marmots is lowered because marmots mate within 2 weeks after emergence from hibernation (*16*), males actively defend their territories and marmot vagility is virtually zero during this period when the ground is snow-covered (*5*).

2) *Low exchange rate of individuals between groups*. Intercolony movement was limited. Only 40 of 790 marmots studied since 1962 made moves between our study populations, and only 15 of those moves may have resulted in gene flow as indicated by subsequent reproductive activity of these dispersers.

3) *Preferential recruitment of juveniles from their natal colony*. Females are preferentially recruited into their natal colony (*5*) (Fig. 1). The rate of male recruitment from sources outside our study populations was high, hence the rate of gene flow into colonies was high. Colonies 6 and 7 (Fig. 1) frequently

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