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.
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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

0036-8075/80/0208-0665$00.50/0

lacked stable social structure; if they are excluded, the average rate of female recruitment from within the natal colony increases from 0.48 to 0.61. The recruits that were not from known colonies rarely were known satellite animals; most frequently recruits were from unknown satellite or colony sites outside our study population.

The first and second conditions promote heterogeneity among colonies, but the high rate of gene flow into colonies (condition 3) should reduce its magnitude. However, male gene flow into a colony with small effective population size, as in marmots, produces a founder effect, thus increasing heterogeneity. The resulting balance of forces yielded the observed degree of heterogeneity.

We calculated Wright's (*10*) inbreeding coefficients, F_{ST}, F_{IS}, and F_{IT}, for the variable loci found in East River Valley marmots (Table 1). F_{ST} is a genetic variance and also an index of cumulative inbreeding relative to the gene frequency of the foundation period of the population (*11*). Its magnitude in marmots was comparable to that of blood variants in Papago and Yanomama Indians (*13, 17*), a magnitude greater than that reported for blood types for the population of modern Japan (*18*), and a magnitude less than that reported for allozyme loci of the facultatively inbreeding plant *Phlox cuspidata* (*19*). The value of F_{ST} reflects the structure of a population, but it also may reflect genetic bottlenecks in a population. In 1970, our study population was one-third its present (1977) size, and only four females produced litters. Perhaps such a genetic bottleneck contributed to the high value of F_{ST} calculated for marmots.

F_{IS} and F_{IT} are inbreeding coefficients that give the probability of two identical alleles at a locus being derived by descent from a common ancestor within the subpopulation (F_{IS}) or from a common ancestor in the total population (F_{IT}) (*20*). Positive values of F_{IS} and F_{IT} occur when there is an abundance of conditions that increase homozygosity in a population; conversely, negative values occur when conditions create excesses of heterozygotes. On the assumption of no overdominant selection, negative values for these coefficients occur when there is a systematic avoidance of consanguineous matings (*10*). The values of F_{IS} and F_{IT} in marmots were negative for seven variable loci, and the averages over all loci were negative (Table 1). Close inbreeding in marmots is unknown to us. There is nearly total dispersal of male offspring from their natal colony, and hence there is little possibility of either mother-son or sib matings. The dominant male is typically dead or deposed from the colony before his daughters are sexually mature at 2 or 3 years of age. Litters produced in our study included only two first-cousin matings and one aunt-nephew mating. Both F_{IS} and F_{IT} are fixation indices of individuals relative to colonies or to the East River Valley population. The negative values of these indices indicate a low probability of fixation of genetic variants.

In conclusion, the patchiness of suitable marmot habitat in the Rocky Mountains and the degree of temporal stability of colonies are conditions that favor genetic drift. However, the high rate of gene flow into colonies, the dispersal of most young, and the de facto avoidance of inbreeding indicate that this system actively retards the fixation of genetic variants. Hence the social structure of marmot populations does not provide a suitable model for the acceleration of evolution by the fixation of genetic variants. The presence of genetic heterogeneity among colonies indicates that in this population system drift is active, allele frequencies are widely divergent in

Table 1. The range of gene frequencies (p) and the weighted mean of gene frequencies ($\bar{p}$) found in nine colonies of marmots. G_H is a statistical measure of genotypic heterogeneity among colonies, and χ^2 is a statistical measure of the heterogeneity of gene frequencies among colonies. F_{ST}, F_{IS}, and F_{IT} are the inbreeding coefficients described by Wright (*10*).

Expressed gene	Range p	$\bar{p}$	G_H (d.f. = 16)	χ^2 (d.f. = 8)	F_{ST}	F_{IS}	F_{IT}
Esterase-2	0.33 to 0.77	0.61	30.25*	15.89*	0.07	−0.29	−0.22
Esterase-1	0.64 to 1.00	0.77	26.31*	15.30	0.07	−0.25	−0.22
Transferrin	0.75 to 1.00	0.89	12.19	8.60	0.04	−0.13	−0.12
Phosphoglucomutase	0.78 to 1.00	0.92	33.47**	28.70**	0.13	0.01	0.13
Leucine aminopeptidase	0.86 to 1.00	0.97	14.35	13.91	0.06	−0.03	−0.04
Phosphoglucoisomerase	0.89 to 1.00	0.99	10.53	23.10*	0.10	−0.01	−0.00
Esterase-3	0.93 to 1.00	0.99	5.77	8.15	0.04	−0.01	−0.00
Esterase-4	0.94 to 1.00	0.99	4.73	9.16	0.05	−0.01	−0.12
				$\Sigma\chi^2$ = 122.81*** d.f. = 64			
				Mean	0.07	−0.09	−0.07

*P < .05. **P < .01. ***P < .001.

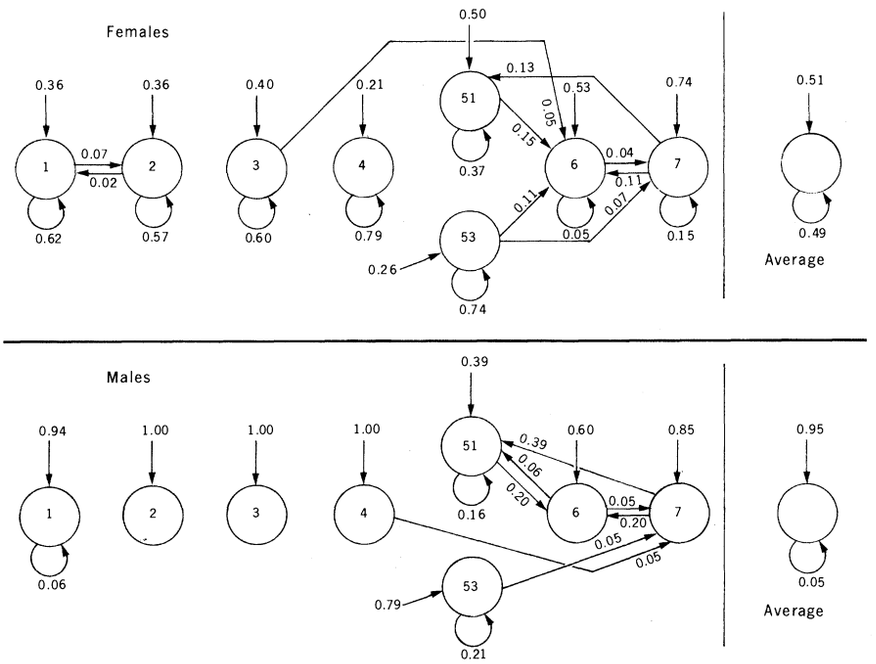

Fig. 1. Sources of male and female colony residents as observed from 1962 to 1977. Rates of intercolony moves are shown; straight arrows to each circle represent recruits from unknown sources, and curved arrows at the bottom of circles represent recruitment from within the natal colony.

colonies, and the genetic variance of the population is enhanced. Thus, these data best support a model of gradual evolution. The similarity between the social substructure of marmot populations and that of many other mammals suggests the generality of our conclusions (*14, 21*).

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Visual Effects of Auditory Deprivation: Common Intermodal and Intramodal Factors

Abstract. *Visual temporal acuity, as measured by the critical flicker frequency decreased and then increased during 24 hours of auditory deprivation. This intermodal effect is similar to intramodal changes in the critical flicker frequency of the nonoccluded eye during monocular deprivation; a single mechanism appears to underlie both phenomena.*

Until recently it has been assumed that different patterns of change in sensory sensitivity are generated for inter- and intramodal, nondeprived perceptual channels in response to sensory deprivation of a single modality. Unimodal deprivation results in a progressive, negatively accelerated improvement in the sensory sensitivity of nondeprived modalities for a variety of measures and modalities (*1*). These intermodality changes are predicted by and support ascending reticular activating system (ARAS) theories of sensory threshold regulation (*2*). Intramodal changes, on the other hand, are characterized by an initial depression in sensitivity followed by an enhancement phase. Thus, sensory deprivation of one eye results at first in a decrease in visual temporal acuity and then is followed by a progressive improvement of sensitivity in the nonoccluded eye (*3*). These intramodal changes have been explained on the basis of the law of denervation supersensitivity (*4*) as interpreted by Sharpless' (*5*) concept of disuse of neural pathways.

In a recent review of these areas (*6*), we have suggested that conceptual and empirical similarities between the two situations may make it fruitful to look for a common mechanism. In both cases, a compensatory change occurs in nondeprived sensory channels, the major difference being that the intramodal changes exhibit the depression-enhancement effect not observed in intermodal studies. As the short-term (less than 24 hours) intermodal effects of unimodal deprivation have not previously been investigated, an observation of the depression-enhancement component under these conditions would implicate a single rather than two separate mechanisms and open the way for a unified model to account for both intra- and intermodal effects. We now report for what we believe to be the first time that performance declines and then improves on an intermodal measure during unimodal sensory deprivation.

Twenty-two male university students were recruited and randomly divided into two groups of 11 subjects each. The experimental subjects were required to live, one at a time, for a 24-hour period at the University of Manitoba Sensory Isolation Laboratory. Auditory deprivation was achieved by confining these subjects to a sound attenuation chamber (mean reduction, 80 dB), by having them wear sound reducing (30-dB) earplugs, and by cautioning subjects against generating unnecessary noise (*7*). All living and experimental activities, including visual testing, took place in the chamber. Care was taken to ensure a patterned sensory environment for all modalities but the auditory. The deprivation setting and procedure has been discussed elsewhere (*6*). All members of both groups were instructed to have a normal night prior to the beginning of the experiment and to avoid all medications and alcohol. Since there are no outcome differences between a "confined-to-laboratory" and a nonconfined control group in auditory deprivation studies (*1, 6*), the 11 control subjects were required to report to the laboratory for testing at the same time intervals as the testing times for the experimental subjects. For comparison purposes the visual testing for critical flicker frequency (CFF) closely followed the procedure employed in previous interocular (*3*) and intersensory studies (*1*). The monocular CFF of the right eye was determined at 0, 3, 6, 9, 12, and 24 hours of deprivation for the experimental subjects and at the equivalent time for control subjects. Visual testing was preceded by a meal or a snack and by 15 minutes of dark adaptation. The CFF threshold for each subject consisted of the mean of eight trials, separated by 5-second intervals, obtained by the descending method of limits.

The stimulus consisted of a white light, at an initial frequency at a random value between 60 and 150 cycles per second. The light was presented by a cold cathode modulating lamp (Sylvania type R1131c) mounted at the rear of a standard viewing chamber (Lafayette model 1202C). The subject was required to centrally fixate the stimulus as it was presented through a Plexiglas diffuser 1.25 mm in diameter. The distance from the stimulus to the eye was 36.25 cm, and

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