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vious proposals (*10*) that vesiculation is facilitated by "contractile" properties of the coat elements. Comparative studies have documented the presence of similar membrane modifications (coats) on tubular and planar organelles which do not vesiculate, but which are active in the segregation and passage of fluid (*11*). These data implicate the coat in modulation of membrane permeability. Especially in models of membrane permeation which assume important roles for unstirred layers or vicinal water (*12*), the peg-shaped elements projecting into the unstirred layer are ideally situated to modulate its properties (*13*). Vesiculation, as well, could procede impelled by local changes in permeability and surface tension effected by the coat elements.

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Natural Selection of Parental Ability to Vary the Sex Ratio of Offspring

Abstract. *Theory and data suggest that a male in good condition at the end of the period of parental investment is expected to outreproduce a sister in similar condition, while she is expected to outreproduce him if both are in poor condition. Accordingly, natural selection should favor parental ability to adjust the sex ratio of offspring produced according to parental ability to invest. Data from mammals support the model: As maternal condition declines, the adult female tends to produce a lower ratio of males to females.*

Fisher (*1*) showed, and others (*2*) reformulated, that natural selection favors those parents who invest equally in both their sons and their daughters. When the parents invest the same in an average son as in an average daughter, natural selection favors a 50/50 sex ratio (ratio of males to females) at conception (*3, 4*). (For simplicity, we assume here that parents are investing equally in average offspring of either sex.) Individuals producing offspring in sex ratios that deviate from 50/50 are not selected again as long as these deviations exactly cancel out and result in a sex ratio at conception of 50/50 for the local breeding population. Such a situation is highly unstable, since random deviations from the 50/50 ratio in local populations rapidly favor those individuals producing their young in ratios of 50/50. We show here that under certain well-defined conditions, natural selection favors systematic deviations from a 50/50 sex ratio at conception, and that these deviations tend to cancel out in the local breeding population.

Imagine a population of animals (for instance, caribou) in which the condition of adult females varies from good to poor (as measured, for example, by weight). Assume that a female in good condition is better able to bear and nurse her calf than is a female in poor condition, so that at the end of the period of parental investment (PI), the healthiest, strongest, and heaviest calves will tend to be the offspring of the adult females who were in the best condition during the period of PI. Assume that there is some tendency for differences in the condition of calves at the end of the period of PI to be maintained into adulthood. Finally, assume that such adult differences in condition affect male reproductive success (RS) more strongly that they affect female RS. That is, assume that male caribou in good condition tend to exclude other males from breeding, thereby inseminating many

more females themselves, while females in good condition, through their greater ability to invest in their young, show only a moderate increase in RS. Under these assumptions, an adult female in good condition who produces a son will leave more surviving grandchildren that a similar female who produces a daughter, while an adult female in poor condition who produces a daughter will leave more surviving grandchildren than a similar female who produces a son.

In short, natural selection favors the following reproductive strategy. As females deviate from the mean adult female condition they should show an increasing tendency to bias the production of their young toward one sex or the other. Whenever variance around some mean condition is a predictable attribute of adults in a species, natural selection will arrange the deviations away from a 50/50 sex ratio at conception so that the deviations will tend to cancel out. Other things being equal, species showing especially high variance in male RS (compared to variance in female RS) should show, as a function of differences in maternal condition, especially high variance in sex ratios produced.

The model we are advancing depends on three assumptions, for which there are both supporting data and theoretical arguments.

1) The condition of the young at the end of PI will tend to be correlated with the condition of the mother during PI. This has been shown for many species (*5–7*) and is probably true of almost all animals with small brood sizes. It is sometimes true of species with large, highly variable brood sizes but need not be (*7*).

2) Differences in the condition of young at the end of the period of PI will tend to endure into adulthood. Although animals show some capacity for compensatory growth, we would be surprised if this claim were not often true. It has been demonstrated experi-

mentally for laboratory and farm animals (8). In rats, for example, differences in weanling size due to differences in litter size are maintained into adulthood (9). Throughout life, human twins lag behind their singleton counterparts in height and weight (10) and in RS (11).

3) Adult males will be differentially helped in RS (compared to adult females) by slight advantages in condition. In all species showing negligible PI by males, male RS is expected to vary more than female RS, and considerable evidence supports this claim (4, 12). In theory, slight advantages in condition should (because of male competition to inseminate females) have disproportionate effects on male RS compared to the effects on female RS.

We assume that sex ratio at birth in mammals is a measure of tendency to invest in one sex more than in the other. With this assumption, available data from several species support the prediction that females in better condition tend to invest in males (13–15). Adverse environmental conditions for the mother during pregnancy are correlated with a reduced sex ratio at birth in deer and humans. Experimentally induced stress of piglets in utero apparently reduces the sex ratio at birth. In dogs, deer, and humans, two variables that correlate with decreased maternal investment per offspring (maternal parity and litter size) correlate with reduced sex ratios at birth. Likewise, increasing litter size in mink and sheep correlates inversely with sex ratio at birth. Naturally occurring variations in sex ratio at birth can be large; in two seal species (16), females pupping early in the season produce sex ratios larger than 120/100, while females pupping late produce a complementary ratio (less than 80/100).

Since females in good condition are assumed to outreproduce females in poor condition, it is not possible for genes producng one sex ratio to accumulate among females in poor condition and genes for the complementary sex ratio to accumulate among females in good condition. Instead, natural selection must favor one or more genes that adjust the sex ratio produced by an adult female to her own condition at the time of PI. In species such as mammals, in which males determine sex of offspring, female control of the sex ratio must involve differential mortality by sex, either of sperm cells (17) or of the growing young during PI. If, as in

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caribou, maternal PI extends over a period of time in which maternal condition may unpredictably deteriorate, then the female who can make adjustments during that period should outcompete the female who adjusts the sex ratio only at the very beginning of PI. In general, of course, the earlier the adjustment, the better. Differential male mortality during the period of parental investment ought to be part of the mechanism by which a female adjusts the sex ratio of her young in such a way as to maximize her eventual reproductive success. Differential male mortality in utero has been demonstrated for deer, cows, and humans; and most of the differential mortality takes place early in pregnancy (18).

As it applies to mammals, the model amounts in part to an adaptive interpretation of early differential male mortality. We know of no alternate functional model for such differential mortality. The usual nonfunctional argument (that the unguarded X chromosome of the male predisposes him to differential mortality) not only fails as a general explanation of differential mortality by sex (19), it also fails to account for the influence of maternal condition on differential mortality in utero and for species differences in the degree of early differential mortality. Careful attempts to measure the contribution of the unguarded X chromosome of the human male to his differential mortality in utero have concluded that the contribution must be negligible (20). That variations in sex ratio as large as those observed in nature should be a matter of indifference to the individuals producing them seems most unlikely.

The application of the model to humans is complicated by the tendency for males to invest parental effort in their young (which reduces variance in male RS), and by the importance of kin interactions among adults (21). Despite these complications, the model can be applied to humans differentiated on a socioeconomic scale, as long as the RS of a male at the upper end of the scale exceeds his sister's, while that of a female at the lower end of the scale exceeds her brother's. A tendency for the female to marry a male whose socioeconomic status is higher than hers will, other things being equal, tend to bring about such a correlation, and there is evidence of such a bias in female choice in the United States (22). The corresponding prediction is satis-

fied: Sex ratio at birth correlates with socioeconomic status (14).

If the model is correct, natural selection favors deviations away from 50/50 investment in the sexes, rather than deviations in sex ratios per se. In species with a long period of PI after birth of young, one might expect biases in parental behavior toward offspring of different sex, according to parental condition; parents in better condition would be expected to show a bias toward male offspring.

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23. R.L.T. and D.E.W. independently conceived the basic theory. The collection of data and writing of the paper were performed by R.L.T. alone. We thank I. DeVore, B. J. LeBouef, and T. Schoener for detailed comments. We thank H. Hare for help finding references. R.L.T. thanks I. DeVore for advice and unfailing support throughout. The work was completed under an NIH postdoctoral fellowship to R.L.T. and partly supported by NIMH grant 13156 to I. DeVore.

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Memory and Hibernation in Citellus lateralis

Abstract. *Squirrels learned to escape from a water bath by making a visual discrimination. Twenty-four hours after reaching criterion for learned behavior, the animals were exposed to the first of two 11-day cold exposures. The animals that hibernated had better retention of the learned behavior.*

Hibernation provides an opportunity to study the effects of low body temperature on memory under natural physiological conditions. We found that hibernation improved retention of learned behavior, a result that could have been predicted because (i) low temperature reduces turnover of protein and other macromolecules likely to be involved in memory, and (ii) external stimuli, which may alter established memory, are reduced in number during hibernation.

Many treatments applied soon after learning impair memory, apparently most effectively by interfering with consolidation of learned material (*1*). New input into an established memory trace may result in disruption of neural processes associated with the original learning. Consolidation theorists suggest that this physical disruption of the memory trace may account for observed amnesic effects (*2*). Electroconvulsive shock and drugs administered to rats have been reported to cause amnesia, possibly by blocking storage and retrieval of new information (*3*).

Facilitation of memory by hibernation raises questions regarding the extent to which memory is dependent upon quiesence in storage area. Most experiments concerned with the effects

of lowered body temperature on behavior have involved artificial hypothermia administered to nonhibernators (*4*). Unfortunately there has been little work on the learning ability of hibernators, although a few species have been trained to respond in operant situations (*5*). Others have not investigated the effects of hibernation on retention of learned behavior.

In this study of memory retention in the hibernator *Citellus lateralis* (the golden mantled ground squirrel), we (i) determined the feasibility of train-
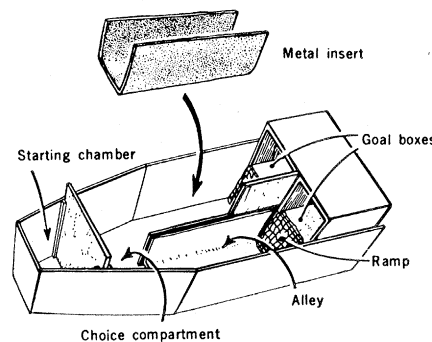

Fig. 1. The training apparatus. Each alley was 45 cm long. The distance from the starting chamber to an escape ramp was 80 cm. The water depth was 27.4 cm. The apparatus had a capacity of 80 liters. The water temperature was 34° ± 1 °C.

ing ground squirrels to make visual discriminations in an escape paradigm, (ii) observed the effect of reversal training on performance, and (iii) measured the effect of hibernation on the retention of a learned task. Twenty squirrels were captured in the area of Costilla, New Mexico, and housed in individual cages. The laboratory temperature was 24° ± 3 °C. Diet consisted of five pieces of Wayne lab chow (20 ± 2 g) daily and was supplemented weekly with vegetables and peanuts. Animals had free access to water.

The water-filled discrimination apparatus consisted of a starting chamber and two parallel alleys (Fig. 1). The entire apparatus with the exception of the goal boxes was painted gray. The two alleys had removable metal inserts, one black and the other white. When these were in position, the walls and floors were covered. By exchanging these inserts the color of the alleys could be changed, which ruled out a position effect. The goal box for the incorrect color choice was obstructed by a piece of glass covering the ramp. Liquid detergent (65 ml) was added to the 80 liters of water to decrease the amount of air trapped in the fur; this treatment prevented passive floating and made it necessary for the animals to actively swim.

The animals' level of drive during training was estimated to be high. The animals never adapted to the water, and escape was always rewarding.

The "correction" method was applied throughout discrimination and training. If a squirrel made an incorrect choice, it was allowed to correct its error. If the squirrel did not attempt to swim back within 5 minutes, the trial was terminated. This method was preferred to the noncorrection method because pilot data demonstrated that *C. lateralis* learn with fewer trials by correction methods.

During the acquisition stage each animal was introduced into the apparatus. Behavior was shaped such that each subject would orient itself with respect to the goal boxes. Eventually all the animals learned to swim down either alley and to climb the wire ramps into the goal box. The colored metal inserts were not employed during these training sessions. If any side preferences appeared, they were shaped out during the training by forcing the animal to swim down the unpreferred alley. Criterion was an uninterrupted approach without a place preference. A trial period started at the time the sliding door