synchrony between rhythms might disrupt the timing or function of circadian systems involved in long-term memory processes (for example, protein synthesis). Alternatively, disturbed circadian organization might act as a nonspecific stress to produce memory changes. Recent evidence suggests that many treatments which alter memory act by producing or mimicking stress responses (*19*). Regardless of the mechanism, circadian organization appears to be an important factor in memory processes, and disturbing circadian organization can produce retrograde amnesia. Psychometric tests to detect memory disturbances in travelers suffering from jet lag would be enlightening.

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7. The activity of all the rats was recorded during the initial experiments. However, since training and testing did not affect the activity of the control rats, they were housed in the main animal quarters during later experiments. There were no differences between the performance of controls housed in the activity-monitoring cages and that of controls housed in the main animal quarters.
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Sex-Biased Litter Reduction in Food-Restricted Wood Rats (*Neotoma floridana*)

Abstract. *Mothers of eastern wood rats (*Neotoma floridana*) normally invest their lactation energy equally in male and female offspring, but alter that investment when their food is severely restricted during lactation. The effect of the altered investment is a significant bias against males in both mortality and growth.*

A sexual bias in growth and mortality of nestling wood rats, *Neotoma floridana*, is induced by severely restricting the diet of their mothers. These observations bear on ideas about the effect of mating systems and maternal condition on litter or brood reduction.

Brood reduction by selective starvation of nestlings has been reported in many species of birds (*1, 2*), but there are few reports of litter reduction in mammals (*3*). It has been argued that food-stressed parents would be expected to alter the sex ratio of their offspring to favor the less costly sex (*4*), or females, in polygynous species (*5*). Most studies of brood reduction, however, have not explicitly considered the sex of the starved nestlings. My results may be the first to demonstrate experimentally induced sex-biased litter reduction in mammals.

Laboratory-raised *Neotoma* were housed in 23 by 45 by 20 cm wire-topped plastic cages equipped with wood shavings and drain-tile shelters. The animals were given free access to food and water. Each female was mated to a compatible male, and they were caged together until the young were born. Cages were examined daily. When a birth occurred, mother and young were placed in a clean cage and were assigned either to control or food-restricted groups. Controls continued to have free access to food. Food-restricted rats had a measured daily ration calculated from the formula $F = 5.35 + 0.02\,M$, where F is the daily food ration (in grams) and M is the body mass of the rat (in grams) on the day of the measurement; this fairly severe restriction amounted to about 70 to 90 percent of the maintenance requirement of a nonreproductive female of equivalent body mass. As a measure of their condition the body mass of all individuals was determined daily. The length of the experiments was 20 days from the birth of the young unless the mother's body mass fell below 75 percent of her mass on the first day of the experiment; free access to food was then given for the rest of the experiment. Under normal conditions, young wood rats are thermally and nutritionally weaned by about 20 days of age

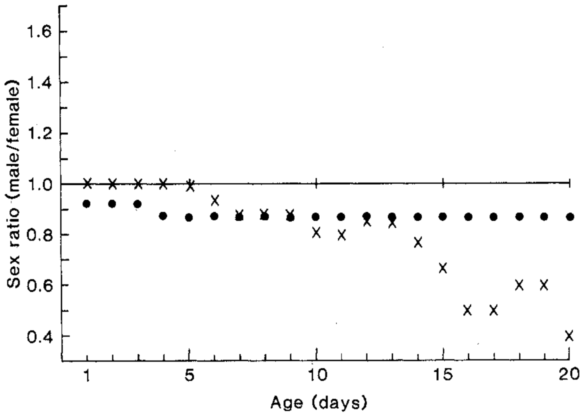

Fig. 1. Changing ratio of males to females in (●) control litters ($N = 29$) and (X) litters in which the mother's food was restricted during lactation ($N = 32$). N is the total number of young at birth.

(*6*). A total of 22 litters was studied.

Brood reduction is an active process in which one (or more) young is selectively eliminated to benefit those remaining. Whether it is practiced in a particular case would depend on the relation between the loss in fitness due to the death and the expected gain in fitness due to enhanced survival of the remaining young. The mortality differential for the reduction of experimental litters from three to two young exceeds the theoretical one described by O'Connor (*2*). The average fitness gain to the parents is therefore sufficient to warrant the loss of one, but not of two, offspring.

Some investigators (*7, 8*) concluded that parents ought to bias the sex ratio of their offspring in response to a number of demographic and environmental conditions whenever they gain more in fitness by producing more of one sex than they lose by producing fewer of the other. For example, parasitic wasps alter the sex ratio of their offspring on the basis of the relative availability of hosts of different sizes or in response to subtle differences in local mate competition (*8*). Trivers and Willard (*5*) argued that maternal starvation would shift the balance to favor females in a polygynous breeding system if (i) starvation of the parents during the period of parental care influences the condition of the young at the end of parental care, (ii) the condition of a weanling at the end of parental care influences its condition as an adult, and (iii) the condition of adults influences their reproductive success. Under these conditions, only by producing high-quality young could parents achieve any reproductive success through sons, whereas mediocre daughters might reproduce.

This causal chain can be applied to *Neotoma*. (i) Food restriction during lactation as used here significantly affects the condition of the young at weaning age (33.1 ± 3.3 grams was the average mass in experimental litters versus 53.3 ± 2.1 grams in controls). (ii) A direct correlation between mass at weaning and adult body size has been documented in mice (*9*). When all adults in the colony that had been part of this experiment as nestlings were pair-matched on the basis of age and sex, adults from the control litters were significantly heavier than those from the food-restricted litters ($t = 2.52$, d.f. = 4). (iii) There was only a weak correlation between maternal body mass and litter size ($r^2 = .20$). Field studies show that larger males are more successful in securing and holding territories and attracting mates (*10, 11*).

The genus *Neotoma* is reported to have a polygynous mating system in nature (*11, 12*). Presumably, *N. floridana* is polygynous also. Since there is no difference in cost to the parents of producing male or female offspring (*6*), an increased investment in females at the expense of males should occur under conditions of restricted food for the mother.

Food-restricted females do alter their energetic investment in sons as opposed to daughters. As one estimate of investment, I calculated the energy value of the increase in the mass of male versus that of female nestlings by multiplying their average mass each day by the estimated energy equivalent of tissue (*6*). The sum of the daily increments represents the maternal investment in the mass of the young (*13*). Control females invest 49 percent of the total in males, whereas food-restricted females invest only 32 percent in males.

This altered investment produces higher mortality and reduced growth in male nestlings. The ratio of male to female offspring in both control and food-restricted litters is near 1.0 at birth. It remains at that level in control litters, but declines progressively to 0.40 in food-restricted litters by day 20 (Fig. 1). The decline begins on day 5 and is strikingly consistent in the bias against males. In all litters except one, every male in the litter died before there were any deaths among females (in the exceptional litter, consisting of one female and one male, both young died within 12 hours, the female first). A χ^2 value of 4.57 ($P < .05$) indicates a significant association between sex and mortality from birth to 20 days in food-restricted litters. In the ten control litters, only one young (a male) died; there were four young in this litter, but because of a previous injury the mother had only three nipples. The average body mass of nestlings of both sexes from food-restricted litters was reduced below that of controls (Fig. 2). Males were slightly heavier than females in control litters, but the reverse occurred in food-restricted litters. At 20 days, the surviving food-restricted males had a significantly smaller body mass than their female littermates and were much smaller than control males.

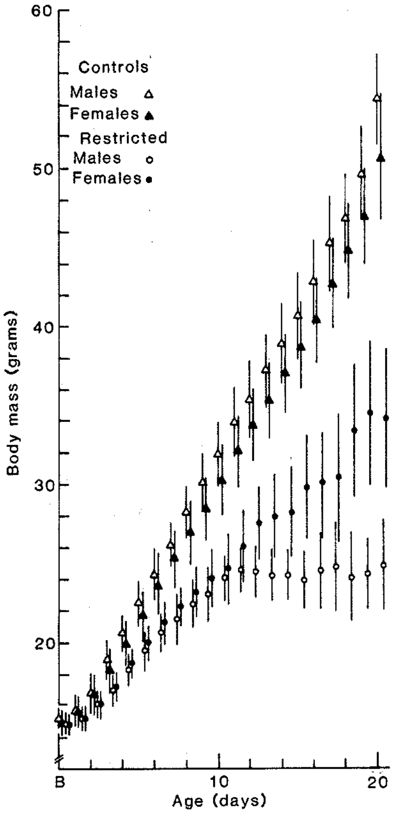

Fig. 2. Average body mass of male and female nestlings in control litters and litters in which the mother's food was restricted during lactation. Vertical bars indicate 95 percent confidence intervals.

Discrimination against males took the form of active rejection by the mother. After daily measurements were made on each litter, the young and their mother were replaced together in their cage. Control mothers usually quickly retrieved all young in a corner of the cage, and the young reattached themselves to her nipples. Food-restricted mothers ignored or physically removed the young that subsequently died. Several days before they died, these young became progressively lighter in mass and were often found outside the nursing group, alone and cold. Active rejection seems to be based on some direct assessment of sex, since males and females did not differ in size at the time that the rejection first occurred. The mechanism by which the mother determines sex is unknown, but the genitals of neonates are visually distinct to humans from birth onward, and males probably excrete androgen metabolites in urine, which the mother ingests. Lactating laboratory *Rattus* (Long-Evans) have been shown to interact differently with male and female pups; among other differences, they direct significantly greater amounts of anogenital licking toward males (*14*).

An alternative strategy for a food-restricted female might be the investment of all her resources in production of one large son rather than several small daughters. The average total investment of food-restricted females is 167.8 kilojoules through day 20, whereas the investment required for one male that is the size of the average control male is 214.2 kilojoules (*13*). At this level of restriction, production of one large male does not seem to be possible even if it were advantageous.

The original explanation for the evolution of sex ratio (*5*) included the idea that females in better than average condition would invest preferentially in male offspring. The mothers in our colony seemed to be in excellent condition, yet control litters show sex ratios of 1.0. A proximate explanation for this is that all of the offspring born to control mothers could be weaned in excellent condition; under unrestricted circumstances, there is no reason to sacrifice any young. Behavioral sex-biased litter reduction, then, should only work in one direction, in this case against males. Brood reduction strategies seem to be a way of responding adaptively to food levels that fluctuate unpredictably over the time interval of a reproductive event.

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Ascending Endorphin Inhibition of Distress Vocalization

Abstract. *Distress vocalizations were produced in adult guinea pigs by electrical stimulation of the dorsomedial thalamus or the septum-preoptic area. Both of these forebrain-derived vocalizations were increased by systemic administration of naloxone and were inhibited by analgesic periventricular gray stimulation. Naloxone blocked the inhibitory effects of the analgesic stimulation on thalamic vocalizations. Stimulation of nonanalgesic mesencephalic sites in close proximity to the periventricular gray increased the anterior-elicited vocalizations. These data provide evidence for ascending endorphin-mediated inhibition of excitatory forebrain sites for distress vocalizations.*

Numerous studies have confirmed that electrical stimulation of the periventricular gray (PVG) produces analgesia in a variety of species (*1*). This effect seems to be related to activation of endorphin-mediated systems, since such analgesia is at least partially antagonized by naloxone (*2, 3*). Indeed, analgesic PVG stimulation increases the concentration of endorphins in human cerebrospinal fluid (*3, 4*). We now provide evidence that endorphins inhibit brain-stimulated distress vocalizations as well as pain.

We have previously determined that distress vocalizations elicited by social isolation are under endorphin inhibition (*5*). For example, naloxone increases the frequency of such vocalizations in both young guinea pigs and chicks tested in social isolation. It seemed reasonable that the vocalizations (once localized in the brain) would also be responsive to more direct types of endorphin stimulation. In an earlier study (*6*) we used electrical stimulation of the brain to map the adult guinea pig brain for distress vocalization loci. The most reliable areas for obtaining the vocalizations included the ventral septum-preoptic area and the dorsomedial thalamus. Less reliable sites included the dorsomedial hypothalamus, medial forebrain bundle, and certain amygdaloid nuclei. No loci were detected in the cortex or cerebellum. These vocalization sites correspond to those yielding emotional vocalizations in other species (*7*), and correspond to brain areas containing a moderate to high density of opiate receptors (*8*).

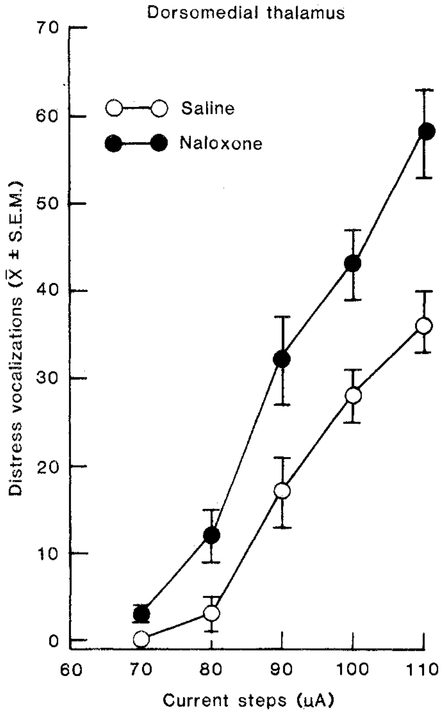

Fig. 1. Effects of saline and naloxone HCl (1 mg per kilogram of body weight) on the frequency of distress vocalizations in adult guinea pigs receiving electrical stimulation of the dorsomedial thalamus. Data were obtained from screening 13 electrode sites in seven animals.

On the basis of these preliminary findings, we analyzed the effects of naloxone and PVG stimulation on distress vocalizations elicited from the septum-preoptic area and the dorsomedial thalamus in adult albino guinea pigs. Animals were surgically prepared with indwelling monopolar electrodes (1-mm tip exposure, skull ground) aimed for the septum-preoptic area or dorsomedial thalamus, and an additional set in the PVG (*9*). One week after surgery, animals were screened for forebrain vocalizations through the use of 60-Hz sine-wave current administered in an ascending 10-μA current series. During each trial, current was applied during a 30-second period in which six 0.5-second stimulations were administered every 5 seconds. Animals distress vocalized immediately after the end of forebrain stimulation during the 4.5-second intertrial intervals. By comparison, "painlike" screams induced by stimulating mesencephalic sites immediately surrounding the PVG occurred in concert with the stimulation. The pitch of these painlike screams seemed to be higher than that of the distress vocalizations, and resembled vocalizations that accompany the application of an acute nociceptive stimulus such as a clip to the limbs of a guinea pig. Distress vocalizations were also recorded during a 30-second period after stimulation, reflecting the long decay of the response. These poststimulation distress