rats nutritionally deprived during their perinatal period and then afforded prolonged dietary rehabilitation demonstrate a significant decrease in the number of alpha and beta adrenergic receptors in the brain. No apparent change in the affinity for either ligand (DHK or DHA) was detected. Such an effect may be a consequence of permanent activation of central noradrenergic neurons inducing greater release of neurotransmitters in the recovered adults, and may be interpreted as the result of postsynaptic adaptations intended to balance the neuronal hyperactivity. The decrease in the number of adrenergic receptors as a consequence of perinatal undernutrition may induce changes in the reactivity to drugs whose mechanisms of action involve the central catecholaminergic system.

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The Regulation of Infanticide and Parental Behavior: Implications for Reproductive Success in Male Mice

Abstract. *Infanticide has been proposed to be a pathological response to overcrowding or other forms of environmental stress and thus a maladaptive behavior. However, in male house mice this behavior is predictable and is modulated by learning. Committing infanticide can increase a male's reproductive success and in some situations may therefore be an adaptive behavior.*

Infanticide, the killing of young, occurs in many species, including humans (*1*). Experiments with rodents on the effects of overcrowding on social behavior led to the hypothesis that infanticide is a response to a breakdown in social structure and, as such, is a pathological or nonadaptive behavior (*2*). Recently, it was suggested that in some circumstances an animal may benefit from committing infanticide (*3*). Infanticide is thus considered to have evolved in response to positive selective pressure and to be predictable and adaptive. Hrdy (*3*) classified infanticide in terms of the manner in which an animal might benefit from killing infants. Our experiments concern one category of infanticide—that relating to sexual competition between males.

It has been suggested that a male that commits infanticide can increase his reproductive success at the expense of competitors by killing a competitor's offspring and then mating with the mother. This sexual-competition hypothesis is based on Darwin's concept of sexual selection and involves three assumptions: (i) that there exist mechanisms to assess paternity so that males are unlikely to kill their own offspring, (ii) that the killing of a female's young results in her ovulating and mating with the infanticidal male sooner than she could have had her young not been killed (ovulation being inhibited in a lactating female), and (iii) that the behavior is mediated at least in part by genotype and thus heritable. If these criteria are met, then once the genotype for infanticide appears, it should rapidly increase in frequency in a population, since males with the infanticidal genotype should produce more offspring than males with the noninfanticidal genotype (*3*). Our experiments were designed to test the sexual-competition hypothesis.

There is evidence that only the one dominant male mouse in a breeding group mates and produces young (*4*). Since dominance status appears to be a major factor in determining the reproductive success of a male mouse, the relation of dominance status to the behavior of male mice toward newborn young was examined. Studies have revealed that mating experience reduces the proportion of male mice that commit infanticide (*5*). Thus, the possibility that mating experience per se might serve as a mechanism for parental recognition and inhibit male mice from committing infanticide only during the time that they would be in contact with their own young (3 to 8 weeks after mating) was also examined.

Male mice (CF1) that were sexually naïve were paired, and males that had mated with two females 2 weeks earlier were also paired (*6*). Members of a pair were placed together for 1 hour each day for 7 days. Dominance was assessed by observing males fighting during the last day of pairing and by examining each animal's rate of urine marking the next day. Dominant male mice deposit hundreds of urine marks, but subordinate males excrete urine in a few large pools (*7*). Only animals that could be clearly classified as dominant or submissive in terms of both aggressiveness and urine marking were examined for infanticide on the day after urine marking. For the test two newborn mice (sired by other males) were placed in the corner of a male's cage for 30 minutes. A preliminary study had demonstrated that neither the sex nor the age of the young influences the tendency of male mice to commit infanticide (*8*). Three behaviors were recorded when the young were removed from a male's cage: (i) infanticide—one or both of the young were severely wounded or killed; (ii) parental behavior—one or both of the young were found in the nest with the male hovering over them; and (iii) ignored—neither newborn mouse was wounded or in the nest, and both young were cold (*9*). Most sexually naïve dominant males committed infanticide, and most sexually experienced dominant males exhibited parental behavior. Subordinate males, regardless of mating experience, tended to behave parentally (Table 1).

The test for infanticide was conducted 3 weeks after some of the dominant males had mated because the length of pregnancy in house mice is 19 to 21 days. To determine whether the inhibition of infanticide, which had been observed 3 weeks after mating in the dominant, sexually experienced males, was temporary, the dominant males (N = 33) were retested 3 months after they had mated with two females (9 weeks after the initial test for infanticide). On the retest, 88 percent of the sexually experienced dominant males committed infanticide, and 12 percent exhibited parental behavior, whereas on the initial test, 15 percent of these males had committed infanticide, and 76 percent had exhibited parental behavior (Table 1). These findings demonstrate that infanticide is inhibited and parental behavior is facilitated 3 weeks after mating (when a female would deliver the male's offspring). But, between 3 weeks and 3 months after mating, this effect is lost. Since only about 45 percent of CF1 males without fighting or mating experience commit infanticide with this testing procedure (*8*, *10*), fighting and achieving dominance appear to facilitate the tendency of male mice to have a long-term facilitating effect on infanticide. Mating experience inhibits infanticide only during the time that a male would be likely to kill its own offspring.

Table 1. Behavior of 90-day-old dominant and subordinate male mice that had either mated with two females or were sexually naïve toward two newborn mice that were placed in the male's cage for 30 minutes. Significantly more sexually naïve than sexually experienced dominant males exhibited infanticide, while significantly more sexually experienced than sexually naïve dominant males exhibited parental behavior ($\chi^2 = 31.4$, d.f. = 2, $P < .001$). Significantly more dominant than subordinate sexually naïve males exhibited infanticide ($\chi^2 = 19.9$, d.f. = 2, $P < .001$). The sexually experienced dominant, sexually experienced subordinate, and sexually naïve subordinate males did not differ significantly in their behavior (χ^2, $P > .1$).

Behavior	Dominant				Subordinate			
	Sexually naïve		Sexually experienced		Sexually naïve		Sexually experienced	
	Number	Percent	Number	Percent	Number	Percent	Number	Percent
Infanticide	28	82	5	15	5	23	7	28
Parental	4	12	25	76	9	41	15	60
Ignored	2	6	3	9	8	36	3	12

Nonpregnant female mice ovulate every 4 to 5 days (*11*). With the exception of a period of postpartum estrus the night after parturition, lactation inhibits ovulation in mice (*12*). Also, implantation of the embryos is usually delayed by about a week in nursing CF1 females that are inseminated during postpartum estrus. [The length of the delay and thus the duration of pregnancy is influenced by the number of nursing young (*13*).] Thus, males that commit infanticide and mate with a nursing female should produce their young at a faster rate than noninfanticidal males. This possibility was examined by placing a sexually naïve male mouse ($N = 40$) in a cage with a female that had delivered a litter within the previous 15 hours (*14*). There was a statistically significant difference in the length of time before the female delivered the intruder male's offspring depending on whether the male killed all of the female's young [mean ± standard error of the mean: infanticidal males ($N = 22$), 22.1 ± 0.9 days; noninfanticidal males ($N = 10$), 29.8 ± 1.9 days, $t\,(30) = 6.3$, $P < .001$]. For cases ($N = 8$) in which one to three offspring of the first litter survived, the mean length of time for the next litter to be produced was 25.5 ± 2.8 days. None of the 40 males tested killed the offspring that they sired. A sexually naïve male mouse that kills a female's nursing young thus produces its own offspring sooner than does a noninfanticidal male.

This experiment was also conducted with 20 male mice that had mated with two females 3 weeks before being placed into a cage with a female that had delivered a litter within the previous 15 hours. The nursing females had all been inseminated by other colony males, and their litters had been reduced to eight young. None of the sexually experienced males appeared to kill any of the nursing young: only six of 160 young (4 percent) were not alive at weaning; this percentage of loss is observed even when a male is not present. The mean number of days before the birth of the offspring sired by these 20 males was 28.3 ± 2.0 days. Thus mating experience, rather than recognition of the female with which a male had mated, inhibits infanticide in male mice 3 weeks after mating.

In many environments mice form small breeding groups called demes that typically consist of one dominant male, which may produce 95 percent of the offspring in a deme, a few subordinant males that do not reproduce, and a number of adult females with nursing young (*4*, *15*). The tendency to commit infanticide is inhibited in subordinate male mice, suggesting that they are not a threat to the offspring produced by the dominant male as long as the dominant male is alive. All subordinate males used in our studies mated when placed with sexually receptive females. Subordinate males thus provide a reserve of reproductively competent males. When the dominant male in a deme dies, the subordinate males will fight until one becomes dominant (*15*). Since the new dominant male will probably not have mated, achieving dominance will increase the likelihood that this male will kill the nursing offspring of the previous dominant male. When a female's nursing young are killed, the length of time for the female to produce young sired by the new dominant male will be reduced. This satisfies the requirement of the sexual-competition hypothesis for an infanticidal male to produce his own offspring at a faster rate than a noninfanticidal male.

Once a new dominant male begins mating its tendency to commit infanticide is inhibited and parental behavior is facilitated during the time that a female would be nursing this male's offspring. The sexual-competition hypothesis states that for infanticide to be an adaptive trait there must be a mechanism for assessing paternity to ensure that a male will not kill his own offspring. Since only one dominant male mouse in a deme produces offspring, it appears that having mated 3 weeks before coming in contact with newborn young is sufficient to ensure that the dominant male will not kill its own offspring.

The third assumption of the sexual-competition hypothesis is that infanticide is a heritable trait. It is presumed, therefore, that variation in the tendency of male mice to exhibit infanticide or parental behavior toward nursing young reflects variation in genotype. However, infanticide is just one of a host of traits (for example, aggression, urine marking, and sexual behavior) that require the presence of circulating gonadal steroids to be exhibited in adulthood and that are modulated by gonadal steroid concentrations during early life; these behaviors are also modified by experience (*10*, *16*). The process by which selection operates on behaviors that are modulated by both gonadal hormones and experience, and are therefore thought to be polygenic (*17*), is unclear. But our findings are consistent with the hypothesis that infanticide is a predictable and adaptive behavior in male mice, since in some situations, infanticide can increase a male's reproductive success.

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6. All CF1 male mice used in the studies were housed separately in plastic mouse cages when 35 days old and tested when 70 to 90 days old.
7. Males that had been paired were placed on either side of a wiremesh partition in a box (30 by 30 by 15 cm) for 1 hour. Whatman 2 filter paper was used as the substrate, and when it is placed under a black light fluorescent bulb (GE F15T8-BLB), the individual urine marks can be counted [C. Desjardins, J. A. Maruniak, F. H. Bronson, *Science* **182**, 939 (1973)].
8. Two newborn male or female mice were placed in a cage with a sexually naïve male ($N = 15$ males per group). The results were (i) female pups: infanticide, 44 percent; parental toward, 19 percent; and ignored, 37 percent; (ii) male pups: infanticide, 44 percent; parental toward, 25 percent; and ignored, 31 percent (χ^2 test, $P > .1$). Other sexually naïve males ($N = 30$ per group) were tested for their response to newborn or 7-day-old mice by the same procedure. The results were (i) newborn mice: infanticide, 50 percent; parental toward, 23 percent; and ignored, 27 percent; (ii) 7-day-old mice: infanticide, 43 percent; parental toward, 50 percent; and ignored, 7 percent ($P > .1$).
9. A male mouse virtually never exhibits infanticide toward one newborn mouse and parental behavior toward the other when two young are placed into the male's cage.
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14. Each pregnant female was housed in a cage (30 by 30 by 15 cm) divided in two by a wooden partition. Three hours after a litter was delivered, a male was placed into the empty area for 30 minutes, after which the barrier was removed. Males were thus placed with females before the time of postpartum estrus. The number of days from the introduction of the male to the delivery of the next litter was recorded, and the original young that survived were weaned at this time or when they were 30 days old. The number of young in the new litter that survived to 5 days of age was counted to assess the possibility that some young had been killed.
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Malnutrition and Fertility

Direct measurements of plasma prolactin concentrations in lactating women on both supplemented and nonsupplemented diets in Gambia (*1*) do not support Bongaarts' (*2*) view that the length of lactational amenorrhea is mainly dependent on the suckling stimulus. Plasma prolactin concentrations fell more rapidly among mothers on supplemented diets although the frequency of breastfeeding remained the same (*1*). Also, seasonal variations in plasma prolactin and milk yield were associated with significant differences in maternal nutrition and physical labor and were not explained by the frequency of infant feeding (*1, 3, 4*). The prolonged high prolactin concentrations found in undernourished mothers may ensure milk synthesis when food intake is limited. "The lower hormonal levels associated with improved maternal nutrition may shorten the period of post-partum infertility despite prolonged breast feeding" (*1*).

Lactational amenorrhea can range from a median of 5.3 months in Boston to 17.7 months in Zaire (*5*). In a prospective study in Bangladesh, Chen *et al.* (*6*) found that the median duration of lactational amenorrhea with a surviving child was 17 months. This long period was related both to child feeding practices and to the poor nutritional status of the mother and child. These authors noted that "while fertility was high by Western standards, it was well below the biological maximum, particularly in the 20–24 age group," and was not explained by use of contraceptives or induced abortion. A seasonal variation in number of births was observed, as well as a seasonal effect on termination of lactational amenorrhea; the frequency of termination rose at the peak of the major rice harvest. Chen *et al.* concluded that the interaction of maternal nutrition and child feeding practices "suggests that a nutritional programme could possibly shorten the duration of lactational amenorrhea by 50 percent or more. If this were to occur, it would shorten the average birth interval by about 20 percent, producing a corresponding rise in the birth rate, unless some other means of fertility control were introduced and accepted."

The lactation data cited by Bongaarts from Kippley and Kippley (*7*) are atypical and incomplete. The data are reported as "number of experiences," which is not defined, and these differ markedly from the number of mothers. There are no data on age, parity, or nutrition of the mothers.

An important omission in the Bongaarts discussion of the interaction of nutritional status and the frequency of suckling is the fact that after 6 months of age, and sometimes earlier, as was found in the Gambia (*4*), breast milk alone is not sufficient for the proper growth and health of the infant (*8*). Continued nursing, however, is important because breast milk is often the only source of high-quality protein.

Bongaarts' evaluation of the significance of the delaying effect of undernutrition on age of menarche (*9*) is based on the assumption that menarche is an independent event in the reproductive span. Data on both historical and contemporary populations, however, show that the age of menarche is integrated with rates of physical growth and reproductive potential; the age of menarche of a population is thus part of a consistent biological history (*10, 11*). For example, among the seasonally, marginally nourished Bush people of the Kalahari (*12*), the average age of menarche is 15.5 to 16.0 years (*13*). A young woman who marries at age 16 has a low probability of having a child the first year because of the long period of adolescent subfecundity, which lasts until physical growth is completed. In fact, the average maternal age at the birth of a first child among the Bush people is 20 to 21 years (*13*). In the United States, however, where the mean age of menarche is now 12.8 years, girls have completed their growth and the period of adolescent subfecundity by age 16 (*11*); a 16-year-old bride, therefore, would be at high risk of pregnancy the first year of marriage.

Although Bongaarts doubts a secular trend in age of menopause, recent data, which classified women under the most conservative definition of the menopause—12 consecutive months without a cycle—show that the menopause takes place now on average at 51 years of age in a well-nourished society (*14*), whereas historically it was 47 to 48 years (*10*). These data, therefore, indicate a secular trend of age of menopause similar to the secular trend in age of menarche of 3 or 4 months per decade (*9, 15*). It has also been reported that fat women have a later age of menopause than do slender women (*16*), and plump girls have an earlier age of menarche (*10, 16*). Therefore, the reproductive span of well-nourished, noncontraceptive women on average is longer than that of undernourished women (*10, 16, 17*). Of course, in most well-nourished societies reproduction