contention is supported indirectly by data from drug-discrimination studies in which attempts were made to delineate the neurochemical substrate of the amphetamine cue. Schechter and Cook (*11*) examined a number of specific biogenic amine depletors (for example, α-methyl-*p*-tyrosine and disulfiram) and selective receptor antagonists (for example, haloperidol, phenoxybenzamine) for their effects on the discriminative properties of amphetamine. Their data suggested that dopaminergic systems mediate the interoceptive cue produced by amphetamine. Others have reported similar findings (*12*).

Lead has been reported to affect many of the putative neurotransmitter systems. According to Shih and Hanin (*4*), studies in the rat have revealed either no change or decreases in dopamine levels. However, more recent reports show consistently that lead induces alterations in the dopaminergic system, and studies by Govani and colleagues (*13*) show that lead modifies dopamine synthesis in various directions according to the region examined. Moreover, no modification of the dopamine receptors (measured as either dopamine-sensitive adenylate cyclase or as [^{3}H]spiroperidol binding) was observed.

Theories abound regarding the neurochemical substrate involved in lead toxicity. The results of the present study suggest that with the appropriate manipulation of antagonists, depletors, and agonists, the drug-discrimination paradigm can provide insight into the nature of the increased drug thresholds observed in the lead-exposed animals in this study.

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Eusociality in a Mammal: Cooperative Breeding in Naked Mole-Rat Colonies

Abstract. *Laboratory observations on a field-collected colony of 40* Heterocephalus *have shown that only a single female breeds. The remaining individuals constitute two or three castes, each containing both sexes and distinguishable by size differences and the tasks they perform. These features, together with long life-spans, overlap of generations, cooperative brood care, and possible age polyethism provide parallels with the eusocial insects.*

Naked mole rats (*Heterocephalus glaber*: Rodentia, Bathyergidae) are found in the hot, arid regions of Kenya, Somalia, and Ethiopia. They live entirely underground in a system of extensive foraging tunnels running at root or tuber level and a deeper nest area (*1*). They feed largely on bulbs and tubers. Unlike other completely subterranean mammals, they live in large colonies (*2*).

Mixed colonies (*3*) of mole rats have been under laboratory observation for 6 years. In October 1977 an almost complete colony (*4*) of 40 individuals was collected at Mtito Andei, Kenya. There were 16 females and 24 males, of whom 4 males and 1 female were clearly juveniles and probably represented the most recent litter born in the colony. The breeding female was not caught (*5*). The mole rats were marked individually, established in an artificial burrow system (*6*), and given a year to adjust to captivity and for a new breeding female to establish herself. Then, after 100 hours of observation, the mole rats were rated according to their reproductive roles and the frequency with which they performed various tasks in the colony. In eusocial insects, a caste is any set of individuals of a particular morphological type or age group (or both) that performs specialized labor in the colony (*7*). By these criteria, *Heterocephalus* colonies appear to have a system of castes (Fig. 1).

"Frequent workers" are mole rats that frequently perform tasks associated with nest building and foraging. Included in the broad category of foraging are digging and transporting soil and the carrying of small items of food to the communal nest. During the latter activity, the frequent workers make repeated trips with food without pausing to eat. "Infrequent workers" show role overlap with the frequent workers, but perform tasks in the colony at less than half the rate of the frequent workers (25 percent of 616 observations). The mean weight of this group is significantly greater than that of the frequent workers. Further research is needed to determine whether this is a separate permanent caste. "Nonworkers" are usually the largest mole rats in the colony. They very rarely dig or transport materials. Their role is not easy to define, but appears to be partly reproductive in that males of this caste are the most likely to mate with the breeding female. Sleeping nonworkers are often joined by other individuals and their huddling significantly decreases the energy requirements of the colony (*8*). Nonworkers assist in the care of the young.

The female mole rats in all these castes are nonbreeding, and probably most will never breed. Histology of the ovaries of nonbreeding females shows them to have many primordial and primary follicles, but few secondary and tertiary follicles (*9*). The females are probably not sterile, but the ovaries appear to be quiescent. Spermatogenesis was evident in males from all the castes, suggesting that all are potentially able to inseminate the breeding female. Small males, however, have difficulty in copulating with the larger breeding female.

The breeding female resembles the nonworkers in size and does not perform tasks in the colony. She is the only female in the colony to breed and, in the laboratory, produces one to four litters of up to 12 young a year. Prominent teats and a perforate vagina are characteristic of the breeding female. Histology of the

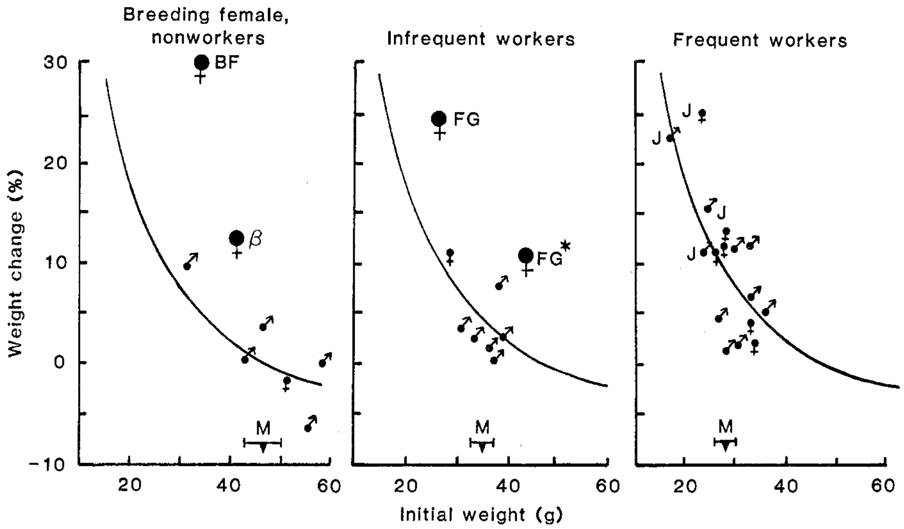

Fig. 1. Percentage weight change in the colony from August 1978 to May 1979, the time during which the breeding female established herself. The weight changes of the breeding female (*BF*), the β female (β), and the two fast-growing females (*FG*) are greater than expected. *FG** is the fast-growing female that later replaced the breeding female, and *J*'s are juveniles weighing under 12 g on capture. In all castes, some individuals show little weight change. The power curve $Y = (1224.96X^{-1.25}) - 10$ is calculated from the percent weight change for all of the colony except the breeding female, the β female, and the two fast-growing females. Mean weights (*M*) and standard errors shown for each caste (except *BF*) are for August 1978. The mean weight differences between castes are significant ($P < .005$). One male infrequent worker and one female frequent worker died during this period and are not included in the results.

ovary of an estrous female revealed, in addition to the expected range of follicles, larger accumulations of interstitial gland tissue than those found in the ovaries of nonbreeding females (*9*). Within the nonworker class of the captured colony there was what I termed a "β female," who resembled the breeding female in periodically becoming perforate and showing well-developed teats, but did not breed. She also exhibited a higher level of aggression than the breeding female. Her role in the colony had not been fully determined when she accidentally escaped from the artificial burrow system and died; she was not replaced by another β female.

Young born to the colony are kept warm in the communal nest by sleeping mole rats of all castes, but suckled only by the breeding female. The breeding female does not isolate herself at parturition time, and in the laboratory the young are born both in the nest and in the burrow system. If the colony is alarmed, young are carried out of the nest by both sexes of the two working castes; when the danger is past, the young are carried back by members of all the castes. Because of the difficulties associated with observing mole rats within the nest and the high mortality of the young when the colony is disturbed, I have not been able to see if both sexes and all castes treat the young similarly. During weaning, the young feed on food brought to the nest by the workers and beg feces from members of all castes, but not from the breeding female. When fully weaned (1 to 2 months) they join the frequent worker caste. They grow very slowly and attain the mean size for a frequent worker when they are more than 1 year old. The genetic relatedness among colony members is not known, but the fact that the young join the worker caste suggests that the colony may be an extended family.

Evidence from young born in captivity and from the growth rates of the colony suggests that within the colony and even within a single litter some individuals grow faster than others (Fig. 1). These mole rats may become nonworkers and replacements for breeding females, while the slower-growing individuals may stay permanently in the worker castes. This suggests that some workers show age polyethism (a progressive change of roles), while others permanently remain in these castes and never have the opportunity to breed. Established female members of the nonworking caste also appear to remain nonbreeding; they do not replace the breeding female if she dies, suggesting that there is a limited period of time during which fast-growing females retain the ability to breed.

Additional supportive evidence follows. Even on an unrestricted diet, some mole rats remain significantly smaller than others. In the colony of 40, some worker mole rats showed little weight change during the 3 years of captivity; in the older laboratory colonies, worker mole rats, at least 7 years old, remained small. Nonworkers are thus not simply the oldest members of the colony. The female that assumed the breeding role in the colony after capture was not the largest; the two nonworking females were larger. The breeding female and five other mole rats were removed from the main colony in mid-July 1979 and established in an adjoining burrow system in olfactory (but not physical) contact with the parent colony. Within 6 weeks, two other females had perforate vaginas and well-developed teats; after 12 weeks, one was obviously pregnant and the second had reverted to the imperforate nonreproductive condition. Both of these mole rats were fast-growing infrequent workers (Fig. 1). The only nonworking female remaining in the colony showed no sign of reproductive activity. In one of the mixed colonies (*3*), in the absence of a fast-growing replacement female, a nonworking female assumed a dominant but nonbreeding role—again suggesting that the assumption of breeding is age-linked.

Suppression of reproduction in other females by the breeding female necessitates physical contact between her and the colony, perhaps through tactually transmitted substances, possibly pheromones in her urine. The colony has communal toilet areas, and after urination the mole rats frequently groom their bodies with their hind feet, perhaps transferring substances left by the breeding female onto the bodies of the rest of the colony (*10*).

Evidence that a colony normally has only one breeding female is provided by the finding of only one breeding female in each of three field-collected colonies (183 mole rats). Soon after four mixed colonies (*3*) were established, two females in each colony came into estrus simultaneously and fought violently until one of the pair died; this has never been observed in established colonies.

While *H. glaber* colonies are similar in many respects to cooperatively breeding birds and mammals, they differ in including many litters as helpers, in separating nonbreeding individuals into (at least incipient) castes, and in having some females that apparently remain nonreproductive throughout their lives. *Heterocephalus* differs from the eusocial insects in not having a clearly defined reproductive male, but similarities are numerous. The difficulty in capturing the breeding female (*5*) suggests that she is rarely exposed to situations of danger and is the individual least likely to be killed by predators or accident; this is typical also of eusocial insects. *Heterocephalus* resembles the termites more closely than it resembles the Hymenoptera in that the mole rats are diploid (*11*), have male and female members of the working castes, the young contribute to colony labor, some working individuals are able to become fully reproductive when the breeding female is removed, pheromones may be involved in caste determination, and the young obtain food from the adults by coprophagy. These features, together with the overlap of generations that allows several generations of offspring to assist the parent in the care of the young and the finding of food, parallel the eusociality of insects and seem to qualify *Heterocephalus* as a eusocial animal—the only vertebrate for which this can be suggested at present. Furthermore, as with the termites, these findings demonstrate that, despite its importance in the Hymenoptera (*12*) haplodiploidy is not a necessary prerequisite for the evolution of eusociality.

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3. Individuals in five mixed colonies came from several burrow systems. In time, each established a caste system similar to that described in this report.
4. Blocked portions of the burrows left open by us were evidence that not all the colony had been caught. Two females of the 40 individuals captured were injured and destroyed, and three others (two males and one female) died during the first year.
5. Few breeding females have ever been caught in the field, suggesting that these are the individuals least likely to be caught by predators.
6. The artificial burrow system, consisting of small Perspex chambers linked by 10 m of transparent tubing, was maintained in a heated room (27°C) with a high humidity. Lamps placed against portions of the burrow system provided additional warmth. Damp soil and food (a variety of root crops, greens, and fruit) were placed in some chambers. Dried grass was provided for nesting.
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Male Vole Urine Changes Luteinizing Hormone–Releasing Hormone and Norepinephrine in Female Olfactory Bulb

Abstract. *Female prairie voles (*Microtus ochrogaster*) exposed to a single drop of male urine on the upper lip showed changes in concentrations of luteinizing hormone–releasing hormone (LHRH) and norepinephrine in olfactory bulb tissue; no such changes occurred in dopamine concentration. The changes were measured in the posterior but not the anterior olfactory bulb tissue of females within 1 hour after they were exposed to urine. These females also showed rapid increases in serum concentrations of luteinizing hormone. Females exposed to water on the upper lip showed none of these changes. These results suggest that in this species LHRH and norepinephrine in the olfactory bulb may mediate luteinizing hormone release in response to external (pheromonal) chemical cues.*

In many mammalian species estrous cycles and ovulation are viewed as "spontaneous"; that is, females of reproductive age continuously exhibit reproductive cycles (*1*). In some species, however, external stimuli play a prominent role in the control of reproduction. For example, in the prairie vole *Microtus ochrogaster*, both estrus and ovulation depend on stimuli provided by the male. In the vole, female reproductive processes, as measured by behavioral estrus and increases in uterine weight, are activated within 24 to 48 hours by either brief physical contact with the male or with male urine (*2*). The capacity of stimuli from the male, including chemical cues in his urine, to induce estrus in the female requires an intact olfactory system (*3*) and direct physical contact with the urine (*2*). This information as well as evidence from other species (*4*), indicate that the vomeronasal organ–accessory olfactory bulb system may mediate the effects of male urine on female reproductive activation.

A critical component in the timing of events leading to mammalian reproduction is the secretion of luteinizing hormone–releasing hormone (LHRH) (*5*), which regulates pituitary luteinizing hormone (LH) release. Studies of the functional role of LHRH have focused on the preoptic-hypothalamic areas; however, nerve terminals containing LHRH are also found in the olfactory bulb (*6*). Moreover, LHRH positive cell bodies and fibers are localized in the posterior half of the olfactory bulb (*7*).

The catecholamines norepinephrine (NE) and dopamine provide an additional level of regulation over female reproduction (*8*). These neurotransmitters have been found in the olfactory bulb (*9*) and studies have related NE to stimulation and dopamine to inhibition of reproductive processes under olfactory control (*10*). In the experiments described here we examined the relationships among localized (anterior or posterior) olfactory bulb LHRH and catecholamine concentrations as well as serum LH levels in female prairie voles exposed to male prairie vole urine.

Intact, reproductively inactive females (*11*) were exposed to either urine or distilled water. Urine was collected from sexually experienced males, and urine or water was applied to the females by placing a single drop (approximately 200 μl) on the upper lip. Females (seven per group) were decapitated at 1, 15, 30, or 60 minutes after they were stimulated. Blood was collected for LH assay (*12*) and olfactory bulbs were removed and prepared for LHRH (*13*) and NE and dopamine (*14*) assays. Each olfactory bulb was dissected into anterior and posterior tissue samples (*15*).

At all the time intervals after stimulation we found a significantly greater concentration of LHRH in the posterior (Fig. 1A) compared to anterior (Fig. 1B) olfactory bulb extracts in both urine-treated [F (1,48) = 31.8, $P < .001$] and water-treated [F (1,48) = 31.3, $P < .001$] females (*16*). Sixty minutes after urine application, concentrations of LHRH in the posterior olfactory bulb increased 185 percent and were significantly higher