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Some Unanswered Questions about Naked Mole-Rats

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Naked mole-rats are unusual for reasons beyond their eusociality. They share with only a few other species the combination of being almost completely subterranean, virtually blind, and depending for food mainly on large subterranean tubers that are located and approached from underground (Jarvis and Bennett, chap. 3; Brett, chap. 5). They are unique among rodents in being relatively hairless and ectothermic, and they may be the only social mammal that does not allogroom (Lacey et al., chap. 8). Although they are exceptionally uniform genetically (see Honeycutt et al., chap. 7; Reeve et al. 1990) and obviously cooperate extensively in their eusocial existence, surprisingly, they also continue to show frequent evidence of aggression (Reeve and Sherman, chap. 11) and even have special vocalizations associated with aggression (Pepper et al., chap. 9); sometimes colony mates fight to the death (this volume).

Some naked mole-rat characteristics that may not seem dramatic may nevertheless be of great importance in explaining why they have become so different, in particular ways, from their closest relatives. For example, they are smaller in body size than other mole-rats (Honeycutt et al., chap. 2; Jarvis and Bennett, chap. 3), and their burrows, which are typically excavated in heavy clay soil, are correspondingly smaller in diameter. These features seem to be most closely approached by *Cryptomys hottentotus hottentotus*, which lives in colonies of 2–14 animals in arid regions of South Africa, where the soil is hard, the food is not concentrated in large tubers, and, presumably, the predators differ from those in other areas. *Cryptomys damarensis*, which is endothermic and haired, lives in softer soils, has a larger body size (up to 220 g) and larger burrows, often feeds on large tubers, lives in colonies of 25 or more individuals, and has reproductive and work-related divisions of labor and overlapping generations (Jarvis and Bennett, chap. 3). The unique naked mole-rat combination of such features may actually have been crucial in allowing evolution of the more remarkable aspects of *Heterocephalus glaber* appearance and existence, because they greatly restrict the accessibility of naked mole-rat burrows to many predators. Presumably, this relative invulnerability, especially to homeothermic predators, surface predators that dig, and larger snakes, was instrumental in allowing naked mole-rats to become permanent inhabitants of burrows locatable to predators (but not accessible to them), which in turn allowed them to become more or less blind and to discard the expensive machin-

ery of homeothermy. Lowered mortality from predation is almost surely a correlate of still another naked mole-rat feature, their unusually long lives; lowered mortality tends to cause an incidental retardation of the onset of senescence (Williams 1957; Hamilton 1966; Alexander 1987; Alexander et al., chap. 1).

All in all, naked mole-rats may be said to have evolved to be dramatically different from other rodents in the combined features of their morphology, physiology, and behavior. It seems appropriate to view this change as having been facilitated by their having moved into an ecological niche rather dramatically different from that inhabited by any other mammal; that is, a niche involving almost completely subterranean life in relatively invulnerable burrow systems, with access to food items sometimes big enough to feed numerous individuals for days or weeks, a niche evidently accessible as well to certain kinds of predatory snakes (Jarvis and Bennett, chap. 3; Brett, chap. 4; Braude, chap. 6). Presumably, sociality on a scale of that shown by naked mole-rats would not be possible in regions outside the cyclically wet and dry tropics where it is perpetually warm, yet numerous plants have evolved the tendency to produce large tubers that enable them better to survive droughts.

The various special features of naked mole-rat life are not likely to be understood except as a result of understanding the *general* selective environment in which naked mole-rats evolved, in other words, through considering how all (or most) of their traits, collectively, may have evolved. It is also unlikely that reasonable explanations for the unusual attributes of naked mole-rats will be developed without greater understanding of their life-style and its evolutionary history. This volume is intended not only to answer questions but also to bring to the fore questions about special attributes as yet poorly understood and, if possible, to cast them in a light that may assist in their eventual analysis. The present essay is written in a hypothesis-generating spirit to bring a selectionist view to bear on the distinctive attributes of *H. glaber* mole-rats. It is attempted as a parallel to Darwin's search for a plausible explanation for sterility in helpers among eusocial forms (see Alexander et al., chap. 1) and under the supposition that it is sometimes easier to criticize or test an already generated idea than to dream up an idea and develop it. I presume that ideas about how events might possibly have happened represent necessary first steps in the scientific process and that there is often value in discussing hypotheses, especially sets of hypotheses generated around an unusual situation such as this one, even if one cannot yet achieve the stage of satisfying testability in each and every case.

Here I engage two general questions: (1) What can be said about the selective forces that have caused naked mole-rats to diverge so far from their closest relatives in the particular ways they have? (2) Why did naked mole-rats apparently fail to speciate during their rather dramatic divergence from their closest relatives? To accomplish this, I first examine some special features individu-

ally, in a comparative way, and then I attempt to discuss how all of the special features of naked mole-rats may fit together; that is, how considering them as a set may contribute to understanding their selective background.

Why Are Naked Mole-Rats Virtually Hairless?

VARIATIONS IN MAMMALIAN HAIRLESSNESS

Mammals are the organisms that have hair and produce milk. There are analogues for both traits in other organisms (pigeons produce a milklike food for their young, and many organisms have hairlike structures) but no homologues.

The amount and kind of hair varies extensively among different mammals. Relative hairlessness occurs in a variety of mammals, rarely for reasons that are entirely obvious (Lyne and Short 1965; W. J. Hamilton III 1973). For some aquatic mammals, both marine and freshwater (e.g., cetaceans, elephant seals, sirenids), a layer of fat beneath the skin seems to have proved a more appropriate correlate of homeothermy than a coat of hair; perhaps because hair causes drag in an aquatic environment, reducing the efficiency of locomotion, and also wet hair is not as efficient an insulation as fat. Although a variety of aquatic mammals have retained a hair coat (e.g., seals, walruses, otters, mink, muskrats, beaver), these species either live in cold climates or spend a significant amount of time out of the water (or both). Some mammals have replaced part or all of the hair coat with armor of one sort or another (e.g., armadillos, pangolins, anteaters; in some armadillos abundant ventral hair is retained); such forms live only in mild or tropical climates (Walker 1975). Several large, entirely (elephant, rhinoceros) or primarily (hippopotamus) terrestrial mammals have lost a hair coat in favor of a thick, leathery skin. It has been postulated that these tropical forms have a low body surface area in relation to their body mass and therefore have gained by increasing their ability to lose heat through the skin. As predicted from this hypothesis, temperate-zone, montane, and rain-forest-dwelling relatives of these forms (e.g., tapirs) have more hair (Walker 1975). As also predicted, juveniles of these forms have more hair than adults. A few mammal species (suids and some primates) are somewhat intermediate, having lost much of their hair (Lyne and Short 1965). Female mammals that bed down or nest in contact with their young, or carry infants on their venters, frequently have lost much of the hair on their venters and around the mammary glands (e.g., suids, rodents, some primates). In such cases, the youngest juveniles are also either virtually hairless (rodents), relatively so (suids), or only lightly haired on the particular parts of their anatomy that regularly contact the mother (primates).

Only two mammal species besides the above groups have virtually hairless adults and older juveniles: naked mole-rats and humans. Each of these species

appears to have evolved nudity independently of any other mammalian forms, since their close relatives are all relatively hairy. The exception to this statement is that most rodent newborns are naked; thus, only the older juveniles and adults of naked mole-rats have diverged in this regard from all other rodents. The hairlessness of non-newborns in naked mole-rats and humans is also similar in that in neither case is there either a dramatically thickened skin or armor (although a relatively thicker skin in naked mole-rats); it differs, of course, in that adult humans have retained abundant hair on the head, in the pelvic region, and in the armpits. The nudity of non-newborns in these two species, representing two of seven or more independent origins of relative hairlessness, seems more reminiscent of the kind of hairlessness of newborn altricial mammals; these two species may also be the only mammals in which nudity in newborns was followed by the evolution of nudity in older juveniles and adults.

Hairlessness in newborns is widespread in mammals, as is the absence or near absence of feathers in newly hatched birds (see discussion of altriciality below). This is probably the reason that hairlessness has been regarded as part of a neotenic trend, which may be a correct view in terms of developmental processes but does not provide an explanation in evolutionary or selective terms. Phenomena such as neoteny and allometry may represent inertial or constraining forces in the sense that natural selection must always operate on "last-year's model;" but in the same sense, all genetic, developmental, physiological, and morphological attributes of organisms represent inertial elements for selection. Unless one assumes that natural selection is helpless in the face of such inertias, the search for evolutionary (selective) explanations necessarily continues in approximately the same fashion as in the absence of information about such inertias. The general assumption of such searches is that selection is the *principal* (not the sole) guiding force of evolution.

HAIRLESSNESS AND ECTOTHERMY

Newborn mammals that are both naked and sometimes left by the mother in a nest also tend to be ectothermic, as are altricial vertebrates in general. This implies that there is merit in attempting to relate the evolution of hairlessness to that of altriciality.

An ectothermic organism is one that relies for its body temperature largely or entirely on external sources. Such organisms are often described as having "poor" or "inadequate" means of thermoregulation. This view is not productive of hypotheses as to the origin and basis of the trait, unless one imagines that selection has somehow been ineffective, and a trait that is disadvantageous has evolved. Such traits do evolve, as in senescence (Williams 1957), but only under conditions such as pleiotropy, with beneficial and deleterious gene effects continuing in concert whenever they derive from the same indivisible

chunk of genetic material. Such deleterious traits are saved only because their (currently) inevitable companion traits are sufficiently beneficial to overcome the deleterious effects, and no way of divorcing the two effects has yet appeared. In no organism, apparently, has a reason been generated for regarding ectothermy as a deleterious pleiotropic effect, and, contrary to the situation with senescence, no circumstances seem to exist that make such an explanation likely. Accordingly, it seems parsimonious to assume that ectothermy evolved in naked mole-rats because it is somehow advantageous.

One correlate of naked mole-rat ectothermy is a rather low metabolic rate, and it has sometimes been assumed that this is the source of the advantage, that a lowered metabolic rate simply allows naked mole-rats to subsist on fewer calories and therefore suggests a continuing problem in caloric intake that is greater or of a different nature than that encountered by the usual homeothermic mammal. The more appropriate correlate of problems in locating food in the tropics, however, would seem to be heterothermy, a capability that correlates with seasonal or cyclic food shortages. There are times when it is better to lower one's metabolic rate and enter some kind of resting stage, such as hibernation or estivation, so as to pass through the season of most severe food stress with the least metabolic expense. (Dormancy is probably most frequently regarded as a response to temperature stress, but one may wonder whether the most relevant temperature stress is that to which a species' food supply responds by becoming dormant or otherwise unavailable). Safety from predators must also be ensured (to an appropriate level) before vulnerable resting states can evolve. It seems evident that naked mole-rats must suffer sharply increased food problems during the droughts that are common in the arid tropical regions where they live. Because their predators (e.g., snakes that can move through their burrows) may or may not estivate during droughts, it is difficult to comment on whether naked mole-rats might have evolved ectothermy rather than heterothermy so as not to be entirely vulnerable to predators during seasons of low food availability.

A potentially profitable way to start thinking about the evolution of ectothermy in a previously homeothermic animal is to consider that it has evidently become more efficient, for whatever reason, for that animal to rely upon an external source of warmth. This situation would seem to prevail whenever such external sources are so reliable and effective that the expense of homeothermic machinery is superfluous. To understand when such conditions might exist, one must consider not only the external source of heat itself, but also the nature of threats, such as the inability to obtain food when it is crucial and the inability to escape from predators that are able to maintain a high rate of metabolism and predatory ability when external heat sources are minimal or absent. Naked mole-rats have apparently been largely relieved of homeothermic predators, and perhaps most of the predators that afflicted their less subterranean and larger ancestors; and their tropical burrow systems are relatively stable in both temperature and humidity.

HAIRLESSNESS AND ALTRICIALITY

Altricial juveniles that have come to depend on their parents for food and for virtually all protection from predators (as with naked, ectothermic forms) are in a position to dispense with homeothermy and use their parents as the (primary) external heat source. Such a juvenile might gain by refraining from use of nutrition provided by the parent to maintain a high metabolic rate when the parent is absent, and instead conserve ingested calories for later growth by maintaining a high metabolic rate *only* when external heat (e.g., from a parent or the sun) is available. Parents thus supply calories not only through food, but also through providing heat for metabolism. This set of attributes correlates with both nakedness in the juvenile and nakedness in at least the part of the anatomy of the parent that directly contacts the juvenile during brooding (e.g., brood patches of birds, naked bellies and mammary glands of mammals). It is probably significant that most naked juvenile birds and mammals occur in litters, and single offspring are rarely naked. Nakedness allows rapid absorption of heat from extrinsic sources such as the bodies of other individuals (parents or siblings in the case of altricial littermates, and other colony members and warmed soil on sunny days and into the night in the case of naked mole-rats). Coincidentally, it also causes or allows rapid heat loss to other individuals, which are always close relatives: siblings or offspring in most parental birds or mammals and colony members in naked mole rats.

Naked mole-rats live in the tropics, and they live underground. In laboratory colonies they bask under heat sources, even when the temperature in their tunnels is in the 25°–30°C range (Jarvis, Appendix). This basking often involves large numbers of bodies piled together, and a mole-rat that has been running through the tunnel system, or working, may dash to such a basking group and snuggle against the other bodies (Lacey et al., chap. 8). Similarly, a basking mole-rat may abruptly run off and feed or carry out some housekeeping task. In other words, their ectothermy does not mean that they simply tolerate lower metabolic rates; they obviously behave in ways that take advantage of external sources of heat, even when their surroundings are at a rather high temperature.

One aspect of ectothermy that seems not to have been discussed is that an ectothermic organism not only can survive a decided lowering of its body temperature, but it may also be able to function in a superior way at higher ambient temperatures than homeothermic species. Thus, some insects become so active at high temperatures (e.g., on warm sunny days) that they are virtually impossible to catch. Presumably this happens because their body temperatures are so high that they can move with unusual speed and their reaction times are very short. This effect may also occur in predators in tropical situations, perhaps even in the burrow systems of naked mole-rats. If so, then ectothermy in predators may make ectothermy in prey advantageous as well. Thus, perhaps only a prey animal with a very high temperature, not likely

under homeothermy, has the best chance of escaping a predator with a very high temperature. Perhaps some ectothermic juveniles are even able to increase their growth rates by using the sun as an external heat source that causes their body temperatures to rise above that of homeothermic species, enabling them to grow exceedingly fast. Good candidates are ground-nesting birds such as some arctic songbirds that grow and develop exceptionally fast and depart their predator-vulnerable nests within a week or so of hatching.

WHY DOES ALTRICIALITY EVOLVE?

The words “altricial” and “precocial” actually come from the ornithological literature and are still defined in most dictionaries in terms of their application to newly hatched birds. *Altricial* hatchlings, as with sparrows, starlings, and pigeons, are more or less naked and helpless; food is brought to the nest for them by their parents. In contrast, *precocial* hatchlings, as with chicks, ducklings, pheasants, and quail, are covered with down, agile, and ready to move out alongside their mother and pick up food themselves. There are degrees of intermediacy; for example, goslings (which typically have two or more adults attending them) are somewhat more helpless than ducklings (which are tended only by their mother). In all likelihood, the extreme differences between songbirds and gallinaceous birds and the rarity of intermediacy are the reasons why the terms altricial and precocial were applied so readily to birds and have retained their meaning there.

Other animals, of course, also display the kind of variation found in birds. Newborn rodents, including naked mole-rats, are naked, blind, and helpless, and they are born in a nest where they remain for some time. However, in other mammals such as ungulates, newborn often are able to stand alone within a few minutes and some, such as horses, can gallop alongside their mothers in less than an hour. Newborn ungulates may travel considerable distances with their mothers and may be required to follow a herd in its everyday activities. Again, there are intermediates: canine and feline babies are blind when born, but not naked, and not as helpless as newborn rodents; some ungulate newborns are physically less capable than others. Little attention has been paid to explaining the distribution of these variations in selective terms.

To develop an understanding of the concepts of altricial and precocial, it may be useful to apply them even more widely, for example, to insect juveniles. Maggots and the maggotlike larvae of some insects with complete metamorphosis (e.g., honey bees) can be regarded as altricial. In contrast, the nymphs of insects with incomplete metamorphosis, such as grasshoppers and crickets, are precocial in the same sense as some juvenile mammals and birds. Again, there are intermediates. For example, within the family Gryllidae, including all crickets, most juveniles would be seen as precocial. Their exoskeletons are hard, and they are agile, quick, and seek out their own food right

from hatching; there is no parent alive to assist them. But in genera such as *Anurogryllus* and *Gymnogryllus*, in which the female cricket prepares a closed burrow with a food cache before she lays her eggs and then tends her offspring until she dies (feeding them small, apparently unfertilized trophic eggs), the hatchlings are soft and fat, resembling termite juveniles (West and Alexander 1963; Alexander, unpubl. data). Many other examples could be given: thus, caterpillars may be soft and helpless or quick-moving and covered with urticaceous hairs or other defenses. Internal parasites, especially those living in the alimentary tracts of their hosts, tend to have the features of altricial juveniles.

Ricklefs (1974, 1975) began developing a theory to explain altricial and precocial juveniles when he showed that altricial nestlings of birds grow faster than the more precocial nestlings of related species. Faster growth may be the function of altriciality in a wide variety of species, but it is difficult to believe that others, such as human babies, have evolved to be as helpless as they are just so that they can grow faster, even if they do that. Because the special case of altriciality in the human baby is treated elsewhere (Alexander, in press), it is not considered here.

In general it is easy to understand why precocial organisms might gain from having the attributes that cause us to label them precocial. It is obvious why an ungulate would gain from being able to run alongside its mother soon after birth. Precocial birds are most often tended only by their mothers, are hatched in vulnerable nests on the ground, and eat the kind of food that can be captured by moving about on the ground or in the water. Juvenile insects in species with incomplete metamorphosis—that is, the precocial sort—live without parents in dangerous locations, and they are usually able either to run or leap, or else they produce various kinds of poisons or other deterrents to predators. Their abilities to do these things are what causes us to see them as precocial. The same is true of precocial larvae in forms with complete metamorphosis.

The question that remains is, Why, when the selective pressures favoring precociality are removed, do juveniles become soft, helpless, and maggotlike? Is there a general answer, other than the dissatisfying or incomplete one that particular selective pressures are relieved or removed, or that there is some advantage to the parents (e.g., Eisenberg 1981) rather than to the juvenile itself? I think there is a general answer, and I would hypothesize as follows.

Juvenile life, in general, may be said to have two functions: first, to survive to the adult stage, and, second, to become the best possible adult; that is, to be maximally capable of doing whatever an adult has to do in order to reproduce as well or better than anyone else. That one function of the juvenile is to survive to the adult stage implies that it must get past certain dangers or causes of mortality. In general, the things that juveniles do to reduce risks from predators, parasites, food shortages, climate, and weather—to refer to Darwin's hostile forces of nature, or the causes of eventual reproductive failure—cause

the juvenile to become the type that we would call precocial. In other words, we usually apply the term precocial to physically capable juveniles that are able to protect themselves in some fashion from sources of mortality.

I propose the following hypothesis as a general explanation of altriciality (for a single exception, marsupials, see below). When relieved of the necessity or any importance of evolving to protect one's self from extrinsic hostile forces of nature, the juvenile organism is freed to devote a greater proportion of its calories to the task of becoming a better adult. This will be true, regardless of the means by which the relief is effected: by direct or continual parental solicitude, or by having been placed in a safe location by a now deceased or departed parent. Protected juveniles are free to evolve, earlier and earlier in their juvenile life, traits and tendencies—and to respond to events (e.g., growing, learning, practicing)—that are devoted solely to causing them to be better competitors as adults. Traits and tendencies that make one a better adult are not necessarily synonymous with traits that enable one to bypass or deal successfully with particular hazards along the pathway to adulthood. What we call precociality represents expensive ways of dealing with hazards that may terminate juvenile life.

One result of altriciality, as with the songbirds studied by Ricklefs, is to allow more calories to be devoted to growth. In songbirds this is possible because the nest is hidden and usually off the ground and because, in general, both parents provide food. Something parallel is true for subterranean rodents and crickets, as well as for species whose larvae are protected, for example, by being injected into wood.

It is possible for even the same activities to conflict with one another in quite different life stages. To choose a worst case—or one least likely to be grasped easily—I expect that even a newborn ungulate's ability to run alongside its mother within an hour after birth actually conflicts to some extent with its ability to run later in the ways and situations that an adult has to run. The reason for expecting this conflict is that expending calories and neurons on running ability as a newborn almost certainly subtracts from the ability of the juvenile to achieve most efficiently the best possible adult size and agility at the right time (e.g., as soon as possible). The fact that the newborn has evolved to run well so quickly compared with other prey species that hide offspring, moreover, implies that its ability is probably not profitable as practice for running well and fast as an adult many months or years later. Most precocial traits would more easily be seen as expenses that detract from the ability to generate optimal adult traits.

As suggested earlier, some special situations must be explained to be understood according to the idea being developed here. One such is the maggots that occur in dung, carrion, fungi, and other short-lived habitats. They are not necessarily protected from sources of mortality. Why, then, do they take on the aspect of being altricial? I hypothesize that because they cannot deter the seri-

ous threats in their habitat, their best bet is to get through the dangerous feeding stage and out of the larval habitat as fast as possible. As with internal parasites, which may also be protected, they have evolved to become mere sacks of efficient nutrition-grabbing ability. They load up their “grocery bags” as fast as possible and drop off or crawl out of the dangerous place where they have secured their food, to do nearly all of their development in the so-called pupal, or developmental, stage. They evolve a kind of apparent altriciality that enables them to grow as fast and as safely as possible. In fact, of course, they are highly “precocial” in terms of their ability to ingest their medium rapidly, and presumably many “altricial” juveniles are correspondingly precocial in respects that are not obvious but reflect preparation for assumption of some crucial adult activity or trait. Elsewhere (Alexander, in press), I argue that the human baby has evolved to become physically altricial because it thereby advanced the development (through both ontogeny and learning) of its complex brain, intellect, and social competence.

The single exception suggested to the hypothesis advanced here involves the extremely short gestation periods of marsupials. In some cases, gestation is even shorter than the estrous cycle. Thus, pregnancy does not interfere with the timing of estrus because the fetus is born before estrus recurs. In these cases, characteristic of species living under extremely unpredictable conditions that sometimes involve prolonged droughts, Low (1978) and others seem to have argued successfully that the mother gains by being able to discard a juvenile in the pouch in favor of another embryo in a diapause stage in the uterus, thereby initiating another offspring with minimal delay. Such females can repeatedly initiate embryos at a very high rate and low cost, discarding or saving them according to whether or not rain has been adequate to produce sufficient nutrition to make the effort of rearing an offspring worthwhile.

Why Did Naked Mole-Rats Begin to Live in Groups?

To understand group living in any species, one must eventually address two questions, (1) what selective forces initiated group living, and (2) what selective forces caused it to be maintained or elaborated? The two answers may be the same, but they need not be.

I have argued previously (Alexander 1974, 1977, 1979, 1989; see also Alexander et al., chap. 1) that the number of reasons for the onset of group living is small: (1) protection from predators as a selfish-herd effect (W. D. Hamilton 1971), or as a more efficient alarm system or deterrence; (2) group cooperation in securing some food item that is difficult to locate or capture; or (3) mere clustering on a scarce resource or habitat. I have rejected the notions that group living can evolve because the group serves as an information center (although groups may so serve when other reasons for group living are present) or that

group living can be initiated as a cooperative defense of food (e.g., Wrangham and Rubenstein 1986). I assume that such cooperation is unlikely unless groups have already formed for other reasons such as clustering on a scarce but relatively large or clumped food supply.

Here I suggest (see also Alexander, *in press*) that group living that begins as one or both parents and a brood of offspring (as opposed to those that begin as a cluster of juveniles without parents or a collection of adults without offspring; see Alexander et al., chap. 1) may invariably evolve as a consequence of predator effects. We usually think of parental solicitude as involving primarily the feeding of offspring or perhaps even protection from climate or weather. It seems to me, however, that feeding and protection from the elements may always be secondary, and that what we call parental care may always begin as an effort to reduce the effects of predators on a brood. These efforts cannot take the form of placing offspring in a stationary nest or protected location until the parent has evolved a means of providing food for the juveniles. Once the ability of parents to feed offspring has become elaborate, it is easy to attribute the significance of parental care to feeding and forget that fed offspring typically are placed in hidden nests, and offspring that have the physical apparatus to secure their own food are also mobile. Thus, neither must they remain in a potentially vulnerable location, nor are they completely incapable of reacting to predators in ways that increase their likelihood of escape. It is unlikely that nests or juveniles can best be protected in regions that also have a maximal availability of food, or that areas of high food availability will also be maximally predator-free. In the second situation, parents are required to protect their offspring from predation in more or less direct and obvious fashions; in the first situation, the nature and location of nests (the initial acts of parental care) are determined by predation, even if parental feeding activities (necessitated by keeping the offspring in nests hidden or inaccessible to predators) are more obvious.

Perhaps our tendency to associate parental solicitude with feeding also returns to the significant amount of nutrition incorporated into the fertilized egg. Even here, however, one needs to know if the added nutrition — and sometimes increased time inside the mother's body — does not derive its adaptive significance solely from the decreased vulnerability of the larger (and later) juvenile to certain kinds of predators.

Alexander et al. (chap. 1) argued that parental behavior in termites, naked mole-rats, and some Hymenoptera turned into eusociality because these organisms moved into niches that were (1) food-rich in such ways that they need not be exited (or such that the risks of obtaining food were relatively small), (2) expansible (could accommodate expanding social groups), and (3) relatively predator-safe, yet in which it was also possible for individuals to carry out extremely risky or suicidal antipredator acts that would save enough partial relatives to make such heroism genetically profitable. In this scenario, predator

safety would be the driving force, both in naked mole-rats' becoming completely subterranean and in their evolving group living and eusociality (and also in their becoming small, thereby preventing large snakes and mammalian predators from entering the burrow systems).

A second argument regarding reasons for group living by naked mole-rats might be that group living was originally sustained as cooperation to compete against other families of naked mole-rats. This suggestion has been made repeatedly for the maintenance and elaboration of group living in humans (see discussions in Alexander 1979, 1987, 1989, in press), but not for its origin. For naked mole-rats, we must explain why broods of juveniles stayed at home, as they do in many of their relatives that are not eusocial (see Jarvis and Bennett, chap. 3). No one seems to have imagined that stay-at-home juveniles in other rodents are incipient soldiers that defend their parents and siblings against other families of conspecifics. Unless further investigation suggests such a scenario, there would seem to be little support for the hypothesis that naked mole-rats evolved eusociality as a cooperation to compete against conspecifics (note, however, that mole-rats in the laboratory do defend their colonies strongly against intrusions by conspecifics; Lacey and Sherman, chap. 10; Jarvis, chap. 13).

A third scenario (Jarvis and Bennett, chap. 3; Brett, chap. 5) is that naked mole-rats started living in groups because groups are needed to locate food (large subterranean tubers). This hypothesis does not seem to explain why *Heterocephalus glaber* initially began to live in groups. There is every reason to believe that naked mole-rat social groups arose out of parents' tending young juveniles, the juveniles subsequently tending increasingly to stay with the parents as they matured. Initially, these juveniles would not have contributed to parental care but would instead have represented a cost to the parent, not only as tiny nursing juveniles but as larger juveniles eating the same food as the parents. It seems unlikely that difficulty in finding food would cause juveniles to stay at home. Rather, parents would have gained if juveniles had left, allowing the parents sole access to their own food supply, which they would have already located since they were able to produce and raise juveniles. Juveniles may have stayed with parents initially because the parents had a safe burrow with food, and dispersal was risky because it had to take place aboveground. Or, because migrating aboveground was too risky, juveniles may simply have burrowed away from their parents' nest and thereby found food that the parents could also use (even if in this fashion they carried out the first helping behavior). In either case, predation would have been central to the continuing changes leading toward eusociality.

I suggest that food tended to be abundant for naked mole-rats early in the evolution of their social groups, even if it were also expensive (difficult to reach by burrowing) under the relatively predator-safe condition of remaining completely subterranean. I also suggest that the principal benefit realized from

group living was the increased possibility of escaping predators in the extensive burrow system. A pair of naked mole-rats with their offspring would surely be much more vulnerable to predation if they tended to stay in one location in a small burrow or chamber, such as near a single large tuber, which might otherwise provide sufficient food for a small family for a long time. Moreover, if the difficulty of locating food and getting to it were the sole explanation for group living, then colonies should be smallest in localities where tubers are most abundant. In such situations, additional colony members would be least valuable and most likely to interfere with reproduction. By far the largest naked mole-rat colony ($n > 295$ animals), however, was located in a garden of yams where food was more abundant than is typical (Brett, chap. 4). In a parallel fashion, I would expect social groups of wolves, hunting dogs, and other group-foraging organisms—groups that apparently do exist because of group-hunting—to be smallest when food is most abundant, whether the variation is geographic or seasonal. This may be the case, since wolf pairs sometimes den alone (presumably they produce young during times of food abundance), rejoining a pack after the young have left the den (Mech 1970).

If food is a problem of the nature or severity that would directly lead to ectothermy because of lowered metabolic rates (see Jarvis and Bennett, chap. 3), then it would seem that group living is even more difficult to explain in naked mole-rats. If naked mole-rats live in groups so as to locate food, for example, then (1) food sources would have to be located more effectively by group efforts (this is likely, since the subterranean life of naked mole-rats means that they must burrow to each new food source), and (2) food sources would have to be large enough to compensate for the losses suffered by having to share them with other group members. In other words, we would have to explain why naked mole-rats did not profit from locating large food sources and exploiting them as small nuclear families, even, perhaps, defending them against other naked mole-rats and forcing juveniles to disperse to different food sources. Some of the tubers on which naked mole-rats feed are indeed quite large and also quite separated from one another (Brett, chap. 5); this represents one set of criteria necessary for group living as a foraging benefit (Alexander 1974, 1977, 1989). As already noted, one reason this scenario was not played out may be that permanently locating near large tubers would cause small groups of naked mole-rats to be vulnerable to digging predators. In any case, most arguments make it seem that predators were either directly or indirectly involved in many aspects of the evolution of naked mole-rat eusociality.

I am led, then, to the following hypothesis: given the relative safety of their burrows, the ectothermy of their principal predators, the uncertainty and expense of maintaining adequate food supplies while also avoiding predators, and the reliability and inexpensiveness of the sun as a source of energy, naked

mole-rats have benefited from using the sun and one another (rather than food) as the principal sources of energy for keeping up body temperatures. As a result of this combination of factors, they have shed both the expensive machinery of homeothermy and their hair. Ectothermy and nudity together allow them both to increase and to decrease body temperatures swiftly (the latter, e.g., after digging in extremely warm sites), by movements between warm and cool (e.g., deeper) portions of the burrows and use of one another's body heat. Group living, food-getting, nakedness, ectothermy, and changes in predation thus may all be parts of a set of attributes that are unlikely to be understood unless they are considered *together* and as a response to a general selective situation, rather than individually as if their selective backgrounds consisted of individual and independent selective forces.

I am therefore suggesting that group living in naked mole-rats is essentially a response to predation. This particular response is possible because of the enormous food supply in the region (niche) they entered, and because the soil and habitat are conducive to the mole-rats' becoming almost completely subterranean. Food is essentially everywhere, and finding a big tuber represents nutritional insurance for a while. It is also possible that these tubers, which appear not to be eaten by many other animals, including humans, were not particularly fine food for species not evolved to use them. Moreover, a sacrifice of some sort may have been involved when *H. glaber* started to feed on them, but this sacrifice may have been more than offset by the benefits of predator avoidance in their new subterranean niche. The strategy of naked mole-rats, then, is to keep the burrow system so extensive that they simultaneously obtain access to an abundant food supply and remain prepared to escape whatever predators may still plague them, presumably snakes. This predator-prey relationship may now be rather specific, with certain snakes (from several genera; see Jarvis and Bennett, chap. 3; Brett, chap. 4; Braude, chap. 6) having become specialized at preying on naked mole-rats. The burrow systems may be designed largely to give the mole-rats the greatest relief from snake predators. If these things are all true, the structure of burrow systems should show it, in the form of specializations such as bolt holes (Brett, chap. 5) and rapid plugging capabilities (Brett, chap. 4; Jarvis, Appendix).

To summarize, I see naked mole-rats as "fugitive" eusocialists, essentially defenseless except through flight, and somewhat parallel to tropical wasps whose colonies are continually in jeopardy from army ants, whose queens are not physogastric, and whose queens and workers both flee. The link that is still missing is determining how and when naked mole-rats might carry out heroic acts that save enough relatives to make virtual suicide reproductive (see the appendix to this chapter). We still lack information on whether or not, as I predicted in 1976 at Northern Arizona University (see the Preface), reproductives in this eusocial form tend to senesce at later ages than workers (see Alexander et al., chap. 1; also Jarvis, chap. 13).

Why Do Naked Mole-Rats Remain Aggressive toward One Another?

The individual naked mole-rats within a colony are apparently extremely similar genetically (Honeycutt et al., chap. 7; Reeve et al. 1990), yet they show mild aggression almost continually (Reeve and Sherman, chap. 11) and sometimes fight to the death (Pepper et al., chap. 9; Lacey and Sherman, chap. 10; Jarvis, chap. 13; Faulkes et al., chap. 14). How can this be, given W. D. Hamilton's (1964) arguments with regard to maximizing inclusive fitness via close genetic relatives?

Alexander et al. (chap. 1) argued that much of the mild aggression shown in small-colony eusocial forms is actually part of a monitoring process that simultaneously tells the reproductive female whether or not any other females are beginning the morphological and physiological changes that will carry them toward queenship and tells the attacked individuals that their queen is still vigorous and healthy, able to present them with siblings to tend, and unlikely to weaken and die or be replaced as queen by one of their own sisters. This interpretation rests on the assumption that sisters, which are essentially genetically identical, continue to compete rather intensely for reproductive opportunities. As with the more severe aggression that occurs when, for example, two females simultaneously start developing toward reproductive dominance, or when an individual is ostracized and is killed or dies, such mild aggression may be evidence of severe competition between individuals that are essentially identical genetically.

Reeve and Sherman (chap. 11) analyzed "shoving" behavior (assumed to be a form of mild aggression) in captive *Heterocephalus glaber* colonies. They found that the breeding female did most of the shoving and that she shoved less-related larger individuals without regard to their sex. They concluded that, by shoving, a breeding female may incite colony mates to become more active and may also maintain her reproductive dominance. The kind of monitoring behavior postulated in chapter 1 would be expected to be directed preferentially toward larger and less closely related individuals but does not at first seem likely to be directed equally at males and females. However, males approaching breeding condition are a threat to the breeding female if their reproductive condition causes them to mate with other females or to affect the reproductive condition of other females (Jarvis [1981, chap. 13] reported that all males in a colony possess active sperm).

Why does aggression continue in *H. glaber* colonies when genetic differences are minimal or absent? Alexander (1979, p. 130; see also pp. 128–129) argued that "[to understand] why Hamilton (1964) was correct to focus his analysis upon relatedness in genes identical by immediate descent [as opposed to genes identical by nature but not necessarily by immediate descent], . . . one

needs only to consider the fates of mutants affecting nepotistic behavior. Such mutants represent the means by which the altruism of nepotism generates, increases, and becomes directed with precision. The successive waves of such mutants will always maximize their own spread by treating relatives as if their own likelihood of occurring in the relative depends upon the proportion of genes identical by immediate descent. This is because each new mutant will at first indeed tend to be present in just those proportions: for this reason better odds will not occur.”

In other words, nepotism spreads and is molded according to the likelihood that any new mutant will be present in any particular relative that is a candidate for nepotistic treatment, not according to the overall similarity of the two genotypes as a result of inbreeding or accidental similarity (see also Dawkins 1979; D. Krebs 1989). Early in the evolutionary trajectory of a mutant, it has approximately a 50% chance of being present in siblings, parents, and offspring of any individual that possesses it. Accordingly, the mutants affecting nepotistic behavior that will spread most rapidly are those that cause their bearer to treat relatives according to their likelihood of possessing it at the outset. Such mutants will tend to accumulate, and with inbreeding there will be a tendency toward genetic identity within populations in regard to all such genes. Contrary to intuition, however, this condition does not lead eventually to tendencies to ignore genetic differences and treat everyone alike. The reason is that no mutant leading to such behavior can invade the system just described. The existing mutations, which tend to cause their bearer to treat certain kinds of relatives as if each of their genes had the likelihood of being present that is given by immediate descent, cannot magically change their messages to the rest of the organism just because different individuals gradually become increasingly alike genetically. Even in populations of such genetically similar individuals, new mutants affecting nepotism will spread according to their tendency to cause treatment appropriate to their own initial likelihoods of presence in other individuals, not their eventual distribution. Accordingly, this argument predicts the condition found in naked mole-rats: regardless of their closeness of relationship as a result of inbreeding, in sexual organisms, relatives tend to treat each other as if they share only the proportion of genes that would be alike as a result of identity through immediate descent.

Why Don't Naked Mole-Rats Allogroom?

It may seem that naked mole-rats do not groom each other because of their hairlessness. Although hairlessness may be partly responsible for the paucity of ectoparasites in *Heterocephalus glaber*, it may not be sufficient to account for the absence of allogrooming. Humans are also hairless over much of the body, yet they groom and massage even the most naked parts of one another

a great deal. (Humans not only retain external parasites but also show tendencies toward skin infection, both apparently associated with hair follicles.) In naked mole-rats, the only observations suggesting allogrooming are those involving treatment of juveniles by elders, as with the rapid pushing of pups with the nose and the licking of pups by older colony mates (see Lacey et al., chap. 8; Lacey and Sherman, chap. 10). Naked mole-rats groom or clean themselves, primarily their feet, and they also scratch themselves, probably in response to the presence of subcutaneous mites. These mites may not be accessible through allogrooming, perhaps partly because naked mole-rats live in darkness and are essentially blind.

Naked mole-rats may fail to allogroom, then, because, first, their hairlessness has reduced ectoparasites to subcutaneous mites, and, second, because the locations of irritations by these mites are not readily available to individuals other than the infected one.

Why Have Naked Mole-Rats Not Speciated?

The question “why have naked mole-rats not speciated?” presumes that naked mole-rats all belong to a single species, and not enough is known to establish this as a fact (see Honeycutt et al., chap. 2). Species multiply when different populations diverge sufficiently that interbreeding is irreversibly prevented. Biologists recognize different species when they find distinctive populations living together and maintaining their differences, or when they decide on circumstantial evidence that two allopatric populations would not interbreed if the extrinsic isolation between them were to disappear. Naked mole-rats have a wide geographic range in Kenya, Sudan, and Somalia (Honeycutt et al., chap. 2). They vary considerably in body size and perhaps in other attributes (Brett, chap. 4; Jarvis et al., chap. 12). These differences may or may not be heritable, and they may or may not bear on the question of irreversible divergence. Even if allopatric populations of naked mole-rats were to prove genetically incompatible, the question of why they have not diverged more will remain, as will the question of why apparently only a single species lives in any region. All such questions, however, must remain unanswered until a great deal more information has been gathered.

Summary

The naked mole-rat is an unusually distinctive species, almost as distinctive among rodents as humans are among primates. A large number of the most interesting questions about its existence and how it evolved remain unanswered and will not be resolved until a great deal more information has been

gathered about the biology of *Heterocephalus glaber*. In view of the many decades that have been spent studying eusocial insects (in the case of the honey bee, centuries might be more accurate) and the number of significant questions still unanswered – and in view of the much longer lifetimes of naked mole-rats (and therefore cycling times for their colonies) and the greater difficulty and expense of keeping several colonies in the laboratory – we may expect many important questions about naked mole-rats to remain unanswered for a long time.

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Appendix

Lacey and Sherman (chap. 10) described interactions between naked mole-rats and a snake introduced into laboratory colonies, and Brett (chap. 4) and Braude (chap. 6) reported observations of snakes attacking *Heterocephalus glaber* colonies in the field (see also Jarvis and Bennett, chap. 3). Here I report an additional laboratory observation, which seems to me to support the suggestion, central to the above arguments about predation, that snakes within their burrow systems have long been a special jeopardy to naked mole-rats.

In September 1980, my assistant, S. Finger, and I gently introduced a small (ca. 25 cm in length) North American garter snake (*Thamnophis* sp.) into one of the naked mole-rat colonies at Michigan. No mole-rats were disturbed by the introduction, and the snake moved slowly down a straight tunnel about 3 m long (the tunnels at that time were yellow plastic tubes sold as Hamster Habit Trails).

Eventually the snake passed lightly over several basking mole-rats without disturbing them. One mole-rat raised its head slightly and seemed to sniff the air after the snake had passed. Near the corner at the end of this long tunnel, the

snake reversed itself and returned along the tunnel. By either touching them or passing near, the snake had by this time caused several basking mole-rats to stir and start to locomote, but none of them seemed oriented toward it. The snake continued back along the tunnel and eventually turned two left corners and entered another section of long tunnel paralleling the first section. After continuing down this tunnel for about 1.5 m, the snake reversed itself again. By this time, we had noticed that a single medium-sized mole-rat was walking slowly down the tunnel in the same direction that the snake had been taking before it reversed itself the second time, although it was about 50 cm behind the snake. This mole-rat walked in a peculiar way, as if it were stalking the snake. Within a few seconds, it became obvious to us that a second mole-rat, on the opposite side of the snake in the tunnel system and 30 cm or so distant from it, was also walking slowly toward the snake in the same fashion. When initially seen, both mole-rats were in regions recently vacated by the snake and presumably had picked up either its odor or the vibrations of its movements or both.

As the two mole-rats approached the snake from either side, it became obvious that the snake was aware of the presence of both mole rats. It moved first one way and then the other, stopping each time when it was near or, in one case, had actually touched one of the stalking mole-rats. As the two mole-rats came nearer to it, the snake increased the speed of its locomotion until it was literally thrashing its way back and forth between the two mole-rats. When the mole-rats were about 30 cm apart, one of them seized the snake's body with its incisors and immediately and very rapidly bit its way down the body for several centimeters (several bites per second). It then released the snake, which writhed as if fatally wounded. The other mole-rat then seized and bit the thrashing snake in a similar fashion, and the snake appeared dead. The biting occupied only a few seconds, and then the two attacking mole-rats moved away from the snake, apparently giving it no further attention. The attack occurred so swiftly that we had no time to interfere.

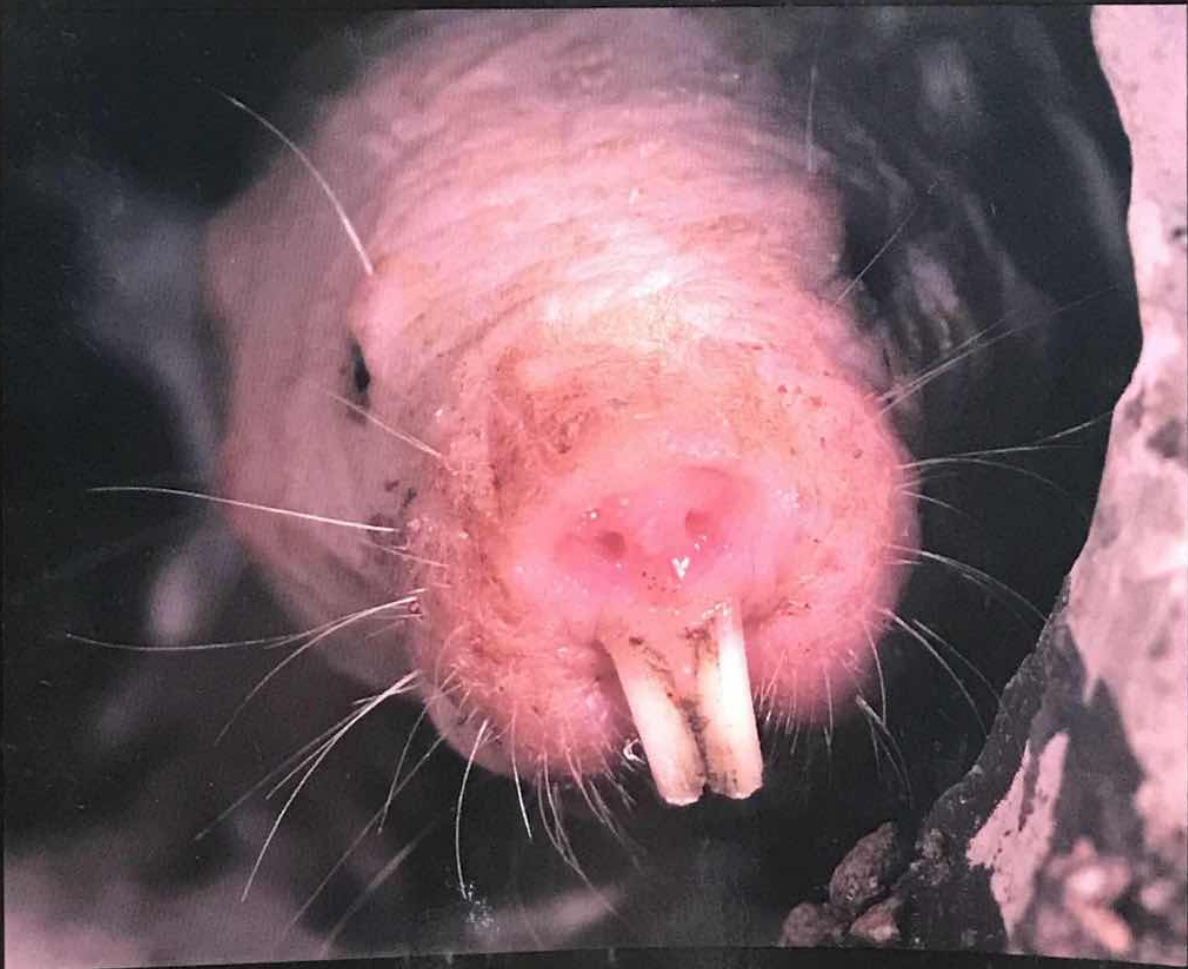
The dead snake lay for several hours where it had been killed; during intermittent observations, no mole-rats were seen to pay attention to it. At the end of this time, I watched a small colony member pick the snake up with its incisors and carry and drag it to the refuse chamber, about 2 m away. The snake was not examined to count the bites inflicted on it or to discover why they were so quickly fatal.

Although this particular kind of snake was a novelty for the mole-rats, the peculiar rapid bites inflicted by the mole-rats, not observed in any other context, and the almost immediate termination of interest in the snake that had been so attractive to the mole-rats only a few seconds before suggest that *H. glaber* has special responses to potential predators in the burrows. Lacey and Sherman (chap. 10) did not report any fatal attacks on the milk snake they introduced to *H. glaber* tunnel systems. The difference between the outcome

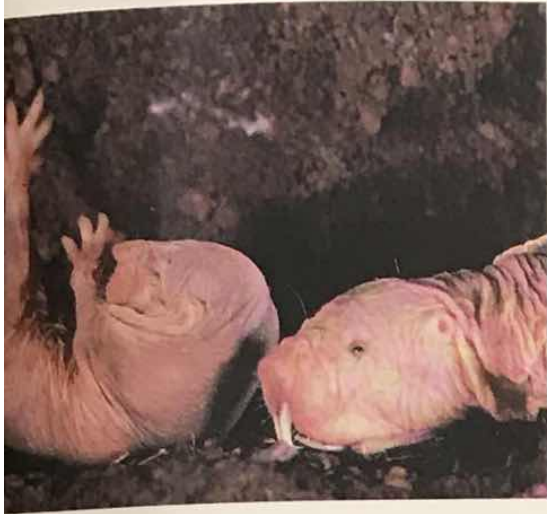
that I observed and those reported by Lacey and Sherman may have been caused by the difference in the size or species of the snake (theirs was considerably larger), or the rapid and continual locomotion (or thrashing about) of the snake in this case, which evidently incited the naked mole-rats to seize and bite it.

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