

Review article

A Hypothesis about the Significance of Symbionts as a Source of Protein in the Evolution of Eusociality in Naked Mole Rats

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Abstract

Eusociality in the naked mole rat *Heterocephalus glaber* (Bathyergidae) as well as in some termites may have evolved in part as a mechanism for maintaining cellulose digesting symbionts, as eusociality appears to have evolved in some termites. An extension of that hypothesis, proposed here, is that the symbionts themselves may be seen as important sources of protein and other nutrients in an otherwise severely protein restricted diet. The controlled consumption of symbionts in feces by individuals in the naked mole rat colony may have helped to establish and may maintain the eusocial structure of the colony by conserving protein and directing it to reproduction. Specific suggestions for laboratory experiments and field studies are made, along with predicted outcomes based on this hypothesis.

Keywords: *Heterocephalus*, naked mole rat, eusociality, symbiosis, nutrition, *Meiostoma*, *Castor*, *Erethizon*, *Cryptomys*

1. Introduction

Heterocephalus glaber, the naked mole rat of eastern Africa, is the "termite" of the mammalian world in that it dwells in subterranean colonies, consumes a cellulose-rich diet, and, most importantly, has a eusocial habit. Eusociality is

characterized by a colonial structure consisting of overlapping generations, with only one mating pair (or just a few individuals) that are reproductive. In the case of *Heterocephalus* the reproductives are one breeding female with 2–3 breeding males. The reproductives are supported by numerous physiologically and behaviorally immature and reproductively quiescent offspring serving in various capacities such as workers and soldiers (e.g. Alexander et al., 1991). The best known examples of eusociality are in the insect orders Hymenoptera (ants, bees, and wasps) and Isoptera (termites). The other genera of the mole rat family Bathyergidae have not been well studied yet. These include solitary mole rats, *Bathyergus*, *Georychus*, and *Heliophobius* as well as mole rat species ranging from social to eusocial in *Cryptomys* (Jarvis and Bennett, 1993; Jarvis et al., 1994). The one eusocial *Cryptomys*, *C. damarensis* seems to have evolved its habit convergently but under similar selection pressures to *Heterocephalus* (Jarvis et al., 1994).

The obligate requirement for cellulose-digesting microbial symbionts in some termites has been implicated in the evolution of eusociality in those termites (e.g. Cleveland et al., 1934). That is, transfer of symbionts by the feeding of feces from older termites to sterile, recently hatched or moulted young is facilitated by a social structure that includes proximity of several generations and care of offspring. The similarities between termites and the eusocial, cellulose-digesting naked mole rat *Heterocephalus glaber* (Bathyergidae) have been noted by many (e.g. Sherman et al., eds. 1991). In particular it has been hypothesized that eusociality in *Heterocephalus* may be an important part of the mechanism by which cellulose-digesting symbionts are transferred in feces to offspring born without symbionts (Lacey et al., 1991; Lacey and Sherman, 1991).

In this paper, it is proposed that microbial symbionts of *Heterocephalus* are an essential, albeit limited source of protein in the diet. Specific physiologies, morphologies and behaviors in *Heterocephalus* may have been established as a means of conserving protein and directing it to reproduction. Indeed the very phenotypes of cellulose-digesters, in general, may be products of their obligate symbiotic associations (Dyer, 1989). The necessity for passing symbionts throughout a colony may be an important factor in the evolution of eusociality in these and some other cellulose-digesters. The controlled consumption of scarce nutrients (symbionts in feces) may be part of the mechanism by which the eusocial structure of *Heterocephalus* colonies was established and is maintained. Nutrient scarcity may complement two other hypotheses concerning eusociality: that it arose in response to either the stress of predation (Alexander et al., 1991) or the challenge of burrowing in difficult substrates (Jarvis et al., 1994).

2. The Symbionts of *Heterocephalus glaber*

The symbionts in the enlarged caecum of *Heterocephalus glaber* were first observed by Porter (1957) and Hill et al. (1957). These researchers recorded an abundance of *Balantidium* sp, and two strains of *Trichomonas muris*, as well as lesser numbers of *Trichomastix* sp, and various bacteria including two treponeme-like spirochetes. The feces were reported to contain both trophic and encysted balantidia. Porter (1957) was first to speculate on a possible digestive function for the caecal community of microbes.

It appears that the ciliate was misidentified in 1957 as *Balantidium* and in fact may be *Meiostoma*, a genus previously named from a solitary South African mole rat, *Georhynchis capensis* (Sandon, 1941). Identifications to species level for the caecal microorganisms from *Heterocephalus* (maintained at Roger Williams Park Zoo, RI) are in progress using electron microscopy and silver staining (Dyer and N. Grim, unpubl.).

The problem of a low protein diet has been long acknowledged in the field of termite research and is beginning to be acknowledged in research on naked mole rats. Sound wood has a protein content of less than 1%, therefore sufficient protein must enter the diets of cellulose-eaters by other means. It has been shown that in some termites, bacterial symbionts are able to fix nitrogen (Prestwich and Bently, 1980). The termite assimilates the nitrogen either by digesting the symbionts themselves or by taking up the fixed nitrogen directly. Nutrients including protein may be passed from termite to termite either stomodeally (from the mouth) or proctodeally (from the anus) (LaFage and Nutting 1978). Furthermore, Breznak (1984) has reported that some of the termite symbionts recycle waste uric acid internally, thus enabling the termites to excrete less nitrogen. Many of the nutritional adaptations of termites (LaFage and Nutting, 1978; Waller and LaFage, 1987) may have parallels in *Heterocephalus*.

Experiments by Buffenstein and Yahav' (1991) provided evidence that microbial fermentation in the caecum plays a role in *Heterocephalus* nutrition, as it does in many rodents. They showed that caecal bacteria synthesize short chain fatty acids (propionic and n-butyric acids, and especially acetic acid) and gasses (CO_2 , CH_4 , and H_2) in various proportions according to the amount of cellulose and starch in the diet.

Furthermore, Naumova (1974 and 1976) has shown by comparative anatomy and histochemistry that rodents with high cellulose diets such as *Heterocephalus* and *Castoridae* (beavers) use proteolytic enzymes to digest caecal symbionts and suggests that this may form the majority of the protein in the natural diet. This phenomenon was contrasted with more omnivorous rodents such as *sciuridae* (squirrels) which do not use proteolytic enzymes in this way. It is predicted that some members of the caecal community of *Heterocephalus* are nitrogen fixers and

that nitrogen fixation may provide the majority or even sole external source of nitrogen to both the microorganisms and their mammalian host.

3. The Consumption of Symbionts in Feces by *Heterocephalus*

The consumption of feces (and symbionts) by *Heterocephalus* has been well documented for laboratory colonies by Lacey et al (1991), Pepper et al. (1991), and Jarvis (1991a). Similar behaviors have yet to be seen in the field and in fact may be impossible to observe, as they occur in underground passages and chambers. These researchers have noted that captive adults tend to defecate and urinate in a specific toilet chamber. Two types of feces are produced: 1. Moist, soft, light colored primary feces, also called caecotrophs, which are immediately eaten (autocoprophagy) or fed to another individual usually to a juvenile or to the female reproductive (allocoprophagy); and 2. Dark, hard secondary feces, seldom eaten. The caecotrophs are the product of the first passage of food through the digestive system and contain cells of symbiotic microorganisms, while the dark, hard feces are the result of the passage of caecotrophs through the system. Thus, the caecotrophs are somewhat analogous to the cud regurgitated by ruminants and then further chewed and digested.

Allocoprophagy seems to occur mostly as a supplement to the diets of either juveniles or the female reproductive. As juveniles approach weaning (age one month) and for two months after weaning, they "beg" feces from adults (Lacey et al., 1991; Pepper et al., 1991; Jarvis, 1991a). This appears to be an essential aspect of their nutrition during development in that it is recommended that hand-reared juveniles be returned to the colony during this crucial time period after weaning to be fed feces (Jarvis, 1991b). The female reproductive is usually the largest individual in the colony and spends much of her time gravid. She cannot (or does not) perform autocoprophagy which involves bending over double to remove the feces directly from her anus. Other adults, often the reproductive males (perhaps simply due to proximity to her), feed her feces (Lacey et al., 1991).

4. A Hypothesis Concerning Feces Consumption

Feces consumption is apparently the mechanism by which symbionts of *Heterocephalus*, essential for the digestion of a cellulose diet, are passed on to juveniles as is the case with some termites. In addition, feces consumption is hypothesized here to be an important means for getting protein and perhaps other nutrients into the diets of *Heterocephalus*. Indeed, some minimum amount of protein (not yet determined for *Heterocephalus*) must be required for maturation and reproduction, as would be the case for any animal. For example,

Rogers (1979), recommends 12% protein for laboratory rats and Baker (1979) recommends 20% for gestation and lactation. Less than 5% can result in cessation of estrus (Smart, 1983). At the Philadelphia Zoo the diet of *Heterocephalus* contains about 9% protein (Toddes, personal communication). While 9% protein is notably low with respect to typical lab rodent diets, it may not be the true minimum for *Heterocephalus* survival, maturation, and gestation. Naumova (1974, 1976) has suggested that symbionts could serve as the sole source of protein in the diet of cellulose-eating rodents such as *Heterocephalus*.

For the sake of this argument, it will be assumed that the cellulose-rich tubers and roots in the natural diet of *Heterocephalus* are, like many similar plant structures, especially low in protein and B vitamins even if one includes the possibility of burrowing invertebrates. Of course, it will be necessary to collect and analyze all of the subterranean plant structures that form the natural diet of *Heterocephalus* in order to be able to state unequivocally that the diet is indeed low in proteins. The major question pertaining to this hypothesis is: What is the major source of protein at each stage of the *Heterocephalus* life cycle and is that source adequate for maturation or are symbionts in feces being used as a necessary supplement?

Nurslings (not yet cultivating caecal symbionts)

It is assumed that the nurslings, because they do in fact grow and develop, are getting sufficient protein from their sole food source, milk. The nutrient content of the milk has yet to be analyzed completely, however preliminary results of Kessler (1995) suggest it is about 7% protein. Milk consumption by nurslings should be seen as a potential drain on the limited protein reserves of the reproductive female and indirectly a drain on the protein reserves of the entire colony.

Weaned juveniles 1-3 months old

Specific begging behavior by juveniles elicits feeding of caecotrophs by attending older siblings. The caecotrophs consist of not only undigested cellulose but also numerous cells of the symbionts, representing what may be an important source of protein. Assuming that the reserves of protein are limited in the colony as a whole, this represents a net gain of protein and body weight for the developing juveniles. Jarvis (1991b) has noted that allocoprophagy seems essential to juvenile nutrition.

Workers 3 months-years old

These individuals cultivate symbiotic microorganisms in their caeca and

reingest and then digest some of those microbial cells when they perform autocoprophagy. Workers performing autocoprophagy and occasionally feeding others (weaned juveniles and female reproductive) with their own caecotrophs are hypothesized to be in a chronically protein-deprived state and as a result arrested in development. The reproduction of symbionts and the maintenance of a symbiotic caecal community will most likely also be limited by nutrients in the rodent diet. Thus, most *Heterocephalus* in the colony cannot mature to become reproductives unless some event such as the loss of the female reproductive alters the cycle of protein in the colony.

Indeed the very neoteny of naked mole rats in general, manifested in part by their striking hairlessness, might conserve some protein, in that hair production requires the synthesis of the protein, keratin. Furthermore, the high mortality rate of workers observed in natural populations (although not in lab populations raised on nutritious diets) (Jarvis et al., 1994) may be in part a result of protein deficiency. However, protein deprivation is unlikely to be the only reason that a given worker does not live to become reproductive. There are extensive observations on aggression in the colony that must be considered a major factor as well (e.g. Jarvis 1991a).

The female reproductive

One strategy for compensating for a general state of protein deprivation is to direct some of the total protein resources of the colony to one pair of reproductives. Thus the colony as a whole remains protein deprived and unable to reproduce, with the exception of the mating pair. The female reproductive perhaps by means of her aggressive behavior, demands and receives extra caecotrophs from workers and reproductive males in her vicinity. She alone can attain a greater size, can support repeated pregnancies, and can provide sufficient milk to allow growth and development of offspring.

Faulkes and Abbott (1993) showed that the reproductive female maintains dominance not through any pheromonal signal but by direct aggressive contact with others in the colony. Loss of the female reproductive, may leave an opportunity for another female to acquire (perhaps through aggression) the extra caecotrophs needed for full reproductive activity. Margulis et al. (1995) demonstrated that the removal of a breeding pair from a colony, allowed some of the larger female workers to become aggressive (including fights to death) and in some cases reproductive. Faulkes et al. (1994) removed non-reproductive males from a colony and noted that they quickly gained weight, increased the size of the testes, and increased production of spermatozoa. It should be noted that in these experiments, the usual protein-rich lab diet was provided; less protein

might have resulted in even more aggression and a slower gain of weight and reproductive functions in fewer individuals.

The male reproductives

Two observations about male reproductives support the hypothesis that protein deprivation is an essential factor in regulating the interactions of the colony. It has been observed that reproductive males often provide caecotrophs to the reproductive female, perhaps due to their proximity to the female (Lacey et al., 1991). Also it has been noted that males, upon becoming reproductive, often experience a drop in body weight and have even been described as "emaciated" (Jarvis et al., 1991). This may be due in part to the aggression of the queen in stealing food from those in her vicinity. A net loss of caecotrophs from the male to the female also may contribute to the weight loss.

Summary of the hypothesis

Protein is a limiting factor for the growth and reproduction of the *Heterocephalus* colony. In a natural population, there may be enough protein for the reproductive success of only one mating pair. The numerous non-reproductive, cooperative offspring are maintained in a state of neoteny (non-reproduction) because they are obliged to cultivate their own meager source of protein, caecal symbionts, and a part of this protein must be directed to the developing offspring and female reproductive. The "cooperation" observed seems to be more like acquiescence to aggression. The larger, more aggressive female reproductive tends to acquire more caecotrophs. Theoretically, any non-reproductive female in the colony has the potential to become reproductive if there are none more aggressive than she. In *Heterocephalus*, protein deprivation may have been one factor selecting for eusociality and may help to maintain the eusocial condition. Thus the social structure is held together by a forced rationing of protein and a coerced directing of protein to the reproductives. As with any complex trait, there are very likely to be multiple factors contributing (or permissive) to the eusocial condition. Thus in addition to protein deprivation and the necessity of directing limited protein (in caecotrophs) to reproductives (described in this paper) and the passage of symbionts to offspring in caecotrophs (Lacey et al., 1991; Lacey and Sherman, 1991; Cleveland et al., 1934), the other published hypotheses for the origin of eusociality of Alexander et al. and Jarvis et al. must be included here: maintaining safety from predation (Alexander et al., 1991) and cooperation for the extremely challenging task of burrowing through hard substrate (Jarvis et al., 1994) or in the case of *Cryptomys damarensis*, the challenge of burrowing through very soft substrate (Jarvis et al., 1994).

5. Predictions Based on the Hypothesis that Protein Conservation has Led to Eusocial Behavior in *Heterocephalus*

Milk

Preliminary results of Kessler (1995) suggest that *Heterocephalus* milk is about 7% protein. How much milk is consumed by offspring remains unknown. In any case, the extra protein in the form of caecotrophs consumed by the female reproductive and not fed by the female to others is predicted to be sufficient for the quantity of protein supplied to the offspring. That is, the protein is part of a balanced equation. What goes into the female reproductive and whatever nitrogen the symbionts fix, must come out in the form of her own body weight as well as the body weights of her numerous offspring at weaning and in the mass of her symbiotic community.

Caecotrophs

The primary (caecotroph) and secondary feces of both natural and lab-reared *Heterocephalus* have not been analyzed for nutrient content. However, Kenagy and Hoyt (1980) analyzed the feces of *Dipodomys microps* (Heteromyidae), a kangaroo rat for nitrogen content (presumably correlated with amino acid content). Feces consumed by *Dipodomys* (and retrieved by sacrificing animals) had a nitrogen content of about 5%, while rejected feces had about 3% nitrogen. The rodents appeared to be choosing a higher protein supplement.

Kenagy and Hoyt (1980) also observed coprophagy in twelve other rodent species (none of them *Heterocephalus*) and found that rodents could distinguish between primary and secondary feces and tended to reject the latter. Coprophagy occurred most frequently in rodents with diets high in cellulose. *Microtus californicus* (Cricetidae) a herbivorous vole and *Dipodomys microps* (Heteromyidae) a kangaroo rat both reinjected more than 25% of feces produced. In contrast *Dipodomys merriami*, a granivore ingested almost no feces. The authors conclude that coprophagy is more related to diet than phylogeny. Cellulose-eaters perform coprophagy more often.

The difference in protein content between primary and secondary feces in *Heterocephalus* is likely to be an approximation of the amount of protein taken in by the animal as it digests the primary feces. Actual counts of number of caecotrophs consumed by individuals at various stages multiplied by the protein content would indicate the amount of protein consumed through caecotrophs.

It is predicted that the workers will be found to be consuming less protein per body weight than developing offspring or the female reproductive. The total amount of protein (and other nutrients) consumed by the female reproductive

(whatever protein is in the root diet plus the caecotrophs) will provide her sufficient surplus for gestation and lactation. In fact this quantity of protein may be at or near the 20% of diet, needed for growth and reproduction for most well-studied captive rodents (e.g. lab rats and mice).

One of the few experiments on coprophagy has involved preventing the consumption of feces by laboratory rats. This was accomplished by using "restraint collars" and resulted in decreased growth rate, perhaps due to a lack of B vitamins or amino acids (Barnes et al., 1963 as reviewed by Kenagy and Hoyt, 1980). It is predicted that reproductive females of *Heterocephalus* denied access to feces will stop reproducing and lactating or will have considerably fewer and weaker offspring. Growth of juvenile *Heterocephalus* will be slowed or stopped. Body weights of workers will decrease. Similar results might occur with the administration of antibiotics (which will kill the caecal symbionts) producing a dramatic, negative effect on the well-being of the colony. However this experiment should be done only with extreme caution or not at all as it may result in complete loss of the colony. Jarvis (1991b) warns against use of oral antibiotics for bacterial infection because of the effects on the caecal microorganisms.

Root structures

The root structures that comprise the natural diet of *Heterocephalus* have not been analyzed yet. It is predicted that these roots are sub-optimal in respect to content of protein and other nutrients needed for growth and reproduction of rodents of this size and fecundity. Most zoo and laboratory diets for *Heterocephalus* are likely to be overly rich in protein and vitamins, because these diets tend to be based upon optima established for typical lab rats and mice. Zoos and labs are understandably conservative with dietary experiments on rare and valuable animals. Nevertheless, the diet of an omnivorous or granivorous rodent which might include protein-rich nuts and seeds may be quite inappropriate for *Heterocephalus*. Furthermore a diet overly rich in protein may obscure some of the normal aggressive, dispersive, reproductive, and feeding behaviors in a captive colony.

Schieffelin and Sherman (1995) starved a *Heterocephalus* colony for 18 hours and then offered food. The mole rats tugged food from each other and in general larger individuals prevailed. The diet of this colony was not reported to be especially low in protein nor was behavior concerning caecotrophs observed. It is predicted that reproductive females and juveniles will become even more aggressive in acquiring both food and caecotrophs, if they are starved or if their dietary protein is brought down to levels found typically in roots. It is predicted

that digging and foraging behavior will become more pronounced in workers on a lower protein diet and the reproductive female may have fewer offspring and/or fewer litters per year. There may be fewer attempted dispersions and fewer attempted splinter colonies as well. All of these changes in behavior might well be considered somewhat negative or undesirable and too great a risk to the perceived well being of animals on display in zoos. However, an experiment in further reducing dietary protein could be started with caution if an extra splinter group not on display were available.

Termites – Vade ad termitem, o piger, et considera vias eius, et disce sapientiam!
(paraphrased from Proverbs 6)

Strategies for coping with low nitrogen diets are already well known in the termite literature. These include recycling of uric acid, scavenging dead termites (Breznak, 1984) and most importantly, nitrogen fixation (Prestwich and Bentley, 1980) It is predicted that *Heterocephalus* and its symbionts may have similar mechanisms for the acquisition and conservation of nitrogen.

6. Coprophagy in other Cellulose-Rich Diets of Rodents

Relevant to this hypothesis about eusociality in *Heterocephalus* are the habits of other rodents, truly reliant on high cellulose, low protein diets. Unfortunately, these can be as difficult to study *in situ* as *Heterocephalus*. The social structures of cellulose-eaters range from solitary (as in *Erethizon* and most bathyergid mole rats) to convergent eusociality (as in *Heterocephalus*, *Cryptomys* and perhaps *Castor*). This suggests that a cellulose diet supplemented by symbionts may be permissive to eusociality but is certainly not a guarantee of it. More observations of the other bathyergids are needed. Meanwhile, studies of the North American porcupine, *Erethizon dorsatum* (Erethizontidae) and the North American beaver, *Castor canadensis* (Castoroidea) provide a few tantalizing clues about how a diet of woody plant parts might have influenced reproduction and growth in those species.

The North American porcupine (*Erethizon dorsatum*), a solitary wood-eating rodent, has a greatly lengthened gestation (210 days) resulting in just one offspring and extended lactation (127 days), during which very small quantities of milk are produced. Offspring mature in two years (Roze, 1989). This extremely slow reproductive rate may be a consequence of the lack of protein and vitamins in a diet of wood. Females have been observed to eat feces of the young, presumably to clean the nest site. It is hypothesized but not yet observed that coprophagy may be a regular habit of porcupines at all stages in the life cycle (Roze, personal communication). Furthermore, porcupines appear to be

"hyperparasitized", that is naturally loaded with a variety of nematodes, protists and other parasites, and yet the animals do not appear diseased (Roze, 1989). Roze (personal communication) speculated that porcupines may be digesting some of these parasites and that they provide an important dietary supplement. Thus, the problem of protein deprivation in this rodent may have been solved in a solitary manner by slowing reproduction and maintaining a large number of digestible parasites, accessible either directly or via coprophagy. More experiments and observations are needed.

North American Beavers (*Castor canadensis*), prodigious consumers of wood, are very likely candidates for rodent eusociality for several reasons. The reproductive arrangement is harem-like in that one male mates with about four females. Non-reproductive offspring remain with the parents in the lodge for three years, during which time they have been observed "babysitting" younger siblings outside of the lodge, and cooperating in the building and repair of the dam and lodge (Ryden, 1989). What exactly occurs within the lodge has been difficult to determine. Thus it is not known how cooperative siblings might be or what role coprophagy (which is known to occur) might have in behavior and nutrition. Naumova (1974, 1976) has suggested that caecal symbionts in *Castor* and other cellulose digesting rodents might be the sole protein source in the diet.

Can this behavior in beavers be called eusociality? The term and its definition have been firmly established in the literature for eusocial insects and as such is quite restrictive. The myriad workers of most colonies of eusocial hymenopterans and isopterans live their brief lives with no possibility of ever reproducing. The longer-lived reproductives often are quite morphologically distinct and attained their role in the colony through specific behavioral pathways such as seasonal dispersions. Rodents in general seem unlikely candidates for eusociality. However I am in agreement with Sherman et al. (1994) that an expanded definition for eusociality is appropriate. Certainly it should be acknowledged that eusociality is a continuum. Overlapping generations and cooperation between siblings can be a consequence of greatly lengthened cycles of reproduction and maturation. This can result in spans of time in which a particular family group fits all of the criteria for eusociality. That is, a particular breeding pair of animals may be surrounded by 2-3 generations of cooperating (non-reproductive) offspring. The fact that maturation and dispersal of the offspring are inevitable (or facultative), should not detract from the fact that a eusocial structure was maintained for a significant period of time. Indeed lack of or delayed maturation and dispersal set up some of the conditions required for temporary eusociality. As Alexander et al. (1991) stated it, "Why tarry in the nest?" A diet restricted in certain nutrients may be one factor contributing to such postponements. Therefore, I would argue that North American Beavers are during any particular three year period eusocial and that many other rodents on restricted (high cellulose) diets should be examined carefully for social and

eusocial behaviors. Unfortunately, so many of these rodents tend to burrow (or build lodges) that observations of natural behavior will always be challenging.

7. Conclusion

This paper has presented the hypothesis that a diet high in cellulose and restricted in protein has been an important factor in the evolution of eusociality in *Heterocephalus* and perhaps some version of eusociality in other rodents such as *Castor*. This particular strategy for a low protein diet seems to have entailed culturing protein-rich symbionts in the caecum and practicing aggressive behaviors that ration those symbionts, in the form of caecotrophs, to those members of the community most involved with either reproduction or growth. Other members of the community, the "workers", may be maintained in a non-reproductive state, in part, by a lack of protein. Furthermore the proximity and the nurturing behavior of workers toward juveniles in this social structure, seem to be essential for passing the symbionts to the young. Thus, may have evolved a eusocial structure consisting of a small number of breeders surrounded and supported by non-breeding offspring, suspended in neoteny. However, by no means, can this be the complete story for two good reasons:

Firstly, the extensive work in both field and lab of Alexander and Jarvis et al. (1994) has resulted in their hypotheses that eusociality evolved in response to predation (Alexander et al., 1991) and/or to the challenge of digging through a hard (or extremely soft) substrate (Jarvis et al., 1994). Furthermore, Lacey (Lacey et al., 1991; Lacey and Sherman, 1991) has acknowledged the importance of eusociality in transfer of symbionts (as first suggested by Cleveland et al. for termites in 1934). The hypothesis of this paper that protein deprivation and rationing are factors in the evolution of eusociality should be seen as complementary to an overall understanding of what is likely to be a complex set of selection pressures for eusociality in rodents.

Secondly, this paper has been mainly a review and synthesis of the literature, resulting in a new conclusion about how eusociality in *Heterocephalus* may have occurred. Several ambitious experiments and field projects have been proposed and this from an author who does not have her own laboratory colony of *Heterocephalus* and who has never been to Africa. Nevertheless, it is hoped that those who can make regular forays into the field and who keep lab colonies might be inspired. The existing experimental literature on the diets and coprophagic habits of other rodents as well as termites can be and should be extended to *Heterocephalus* in hopes of elucidating their importance and hypothesized connection to eusociality.

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