

Eusocial Coprophagous Diploids—Who is Reproducing?

JOHN HARTUNG

*Department of Anesthesiology, State University of New York,
Downstate Medical Center, 450 Clarkson Avenue, Brooklyn,
NY 11203, U.S.A.*

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Troyer (1984) has put forth the insightful hypothesis that sociality among herbivores who digest plant structural tissue has been given impetus by the close contact required to exchange obligate gut symbionts.

For most such animals, one or a few coprophagous exchanges is enough for a lifetime. In exception are at least two conspicuously eusocial diploids, primitive termites and mole rats, who go out of their way on a daily basis to assure that all members of the social group (family) have homogenous symbiont pools.

Given the intensity of the mutual dependence between mole rats and termites and their respective symbiont pools, it is fair to ask who is reproducing when a termite or mole rat gives birth to or nurtures offspring. For example, from the symbiont's point of view, a primitive termite is a casing that limits its reproductive success—the more casings the better. The symbiont homogenate pool is related to the pool in a new casing by $r = 1$. The casing is related to a new casing by $r = \frac{1}{2}$. The combined interest in offspring $= (1 + \frac{1}{2}) \times \frac{1}{2} = \frac{3}{4}$ —a conspicuous figure in the evolution of eusociality (Williams & Williams, 1957; Hamilton, 1964).

Eusociality is an evolutionarily stable strategy (Maynard Smith, 1974) for hymenoptera, but is it really an ESS for primitive termites and mole rats? Could an individual take advantage of the system? If not, then the symbionts are pure subjugates. This seems unlikely given the amount of time, cross-pool competition and coordinated within-pool evolution that has gone on between gut symbionts (see Troyer, 1984, for review). When a mole rat interacts with its sibs and parents ($r = \frac{1}{2}$ for all), is its behavior a compromise between the mole rat and its gut symbionts ($r = 1$ between symbiont pools)? That is, do individual termites and mole rats behave above and beyond the call of kin selection while their symbionts moderate their effect on their casing's behavior in a manner that is less than optimal for their own self interest?

Perhaps this could be tested experimentally. If all the symbionts in a mole rat's gut were killed and replaced with functional but relatively non-related symbionts from a non-related mole rat, would the mole rat's family treat him/her non-eusocially? Would the whole nest's intestinal fortitude fall apart until the resident microbes defeated the intruders? Might non-related termites interact with more "kin recognition" if their gut symbionts were caused to be identical?

Perhaps recognition in general is affected by gut symbiont effects on odors. If so, the amount of time it takes for a newly formed social group to become cohesive could be shortened by accelerating their rate of symbiont pool homogenization. Indeed, sociality may be influenced by extracellular symbionts in much the same manner that intracellular microorganisms manipulate the reproductive compatibility of some Diptera and Cleoptera (see Wade & Stevens, 1985, and references therein).

Implications for the effect of symbiont homogenization on the time-course of romantic relationships are intriguing. A little chemical/olfactory recognition can go a long way. Too much familiarity might cause behavior more appropriate to sibs. If that leads to physical intimacy outside the relationship, the symbiont pool would find new hosts.

REFERENCES

- HAMILTON, W. D. (1964). *J. theor. Biol.* **7**, 1.
MAYNARD SMITH, J. (1974). *J. theor. Biol.* **47**, 209.
TROYER, K. (1984). *J. theor. Biol.* **106**, 157.
WADE, M. J. & STEVENS, L. (1985). *Science* **227**, 527.
WILLIAMS, G. C. & WILLIAMS, D. C. (1957). *Evolution* **11**, 32.