CORRESPONDENCE

Eusociality in a microtine rodent

Naked mole-rats (*Heterocephalus glaber*) were thought to be the only eusocial mammal, but recent data show that Damaraland mole-rats (*Cryptomys damarensis*) are also eusocial[1,2]. Jarvis and Bennett[2] conclude that eusociality evolved twice in the Bathyergidae but in no other subterranean rodents. Furthermore, Jarvis *et al.*[3] state in their recent *TREE* article that herbivory and living in an expandable underground burrow – two factors associated with the evolution of eusociality – are seen in the eusocial mole-rats but in no other cooperatively breeding vertebrate.

There is another herbivorous rodent that inhabits burrows and fulfills the criteria for eusociality (overlap of generations, reproductive division of labor, and cooperative care of young[4,5]). The pine vole (*Microtus pinetorum*) is a fossorial cooperatively breeding rodent[6,7]. In apple orchards in the eastern United States, social groups consisting of two to nine adults plus young[8] live in underground burrows that extend under two to four trees. Offspring remain at the nest beyond the age of sexual maturity while breeders produce successive litters[8]. It has been assumed that social groups are composed of parents and offspring but DNA fingerprinting is needed to verify this. Only one female reproduces in most groups[8]; the number of breeding males is unknown. Non-breeders engage in parental behaviors including huddling over and grooming pups; they also engage in nest building and food caching[9]. However, the social organization of pine voles has not been examined in habitats other than orchards; the density of pine voles is lower in natural settings[10], which may result in smaller groups, fewer groups or lack of group formation.

I agree with Sherman *et al.*[11] that eusociality is best viewed as a continuum that includes the cooperative breeders, although pine voles and naked mole-rats would fall at different points along the continuum. Even though pine voles live in expandable underground burrows like mole-rats, ecological and other differences between voles and African mole-rats may yield important insights into the evolutionary basis for variation in eusocial systems. For example, in the pine voles' orchard habitat, rainfall is abundant and the apple trees are evenly distributed; however, the distribution of food resources is not known.

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Energetic or biomass equivalence rule?

Cotgreave's stimulating article[1] published recently in *TREE* discusses why the relationship between species abundance and body size in animals often appears to be quite dissimilar in different studies. To consider this, one needs a good starting point – that is, the general relationship between body size and population abundance to which some particular relationships might be compared. Cotgreave takes the relationship suggested in Damuth's[2] seminal work to be such a point. However, this choice is open to argument.

Because of the differences in spatial and taxonomic scales of the species collections used in the original studies, it is not surprising that various numerical estimates for the slope of the regression of the log-transformed population abundance on log-transformed body mass have been obtained (see Cotgreave's Table 1). Among them, two studies, one performed by Damuth[2,3] and another by Peters[4], stand out as involving the largest number of species from many taxonomic groups and from all over the world.

However, these workers come to alternative conclusions. Damuth has found that the population abundance (*N*) is proportional to the mean body mass (*W*) raised to the power of –0.75, whereas Peters found the power to be –1. These conclusions may imply a quite different pattern of population metabolism and biomass through body size. If *N* scales as $W^{-0.75}$, then the population metabolism will be independent of body size, that is, a large-bodied species will require the same amount of energy as a small-bodied one. This is known as the energetic equivalence rule (see Ref. 1). Mathematically it follows from the fact that the individual metabolism scales as $W^{+0.75}$, and $W^{-0.75} \times W^{+0.75} = 1$. On the other hand, if *N* scales as W^{-1}, large species will require less energy than small ones. Then 'the biomass equivalance rule'[4] instead of the energetic rule should be accepted, since the biomass of populations rather than the metabolism does not depend on body size.

In order to estimate which of the above rules is to be valid, I would like to call attention to another empirical generalization discovered by Sheldon *et al.*[5] and repeatedly supported afterwards (e.g. Refs 6 and 7). This rule came from biological oceanography, where the invention of the Coulter Counter in the mid-1960s made it possible to count all particles suspended in the water, and ATP determination enabled the distinction between live and dead matter. It can be stated in a way that, irrespective of organisms' taxonomic status, the total number of organisms available within body mass interval, *dw*, is equal to $n_0 \times w^{-2} \times dw$, where n_0 is a proportionality constant. Let us apply this rule to body mass pattern within a species. Then the species abundance is:

$$N = \int_{W_0}^{W_{max}} n_0 w^{-2} dw = n_0 (W_0^{-1} - W_{max}^{-1})$$

where W_0 is the body mass of newborn animals, and W_{max} is that of the oldest animals in the population. Because $W_{max} \gg W_0$, this can be simplified to $N = n_0 \times W_0$. Finally, since the body mass of newborns is proportional to the animals' mean body mass[4], it follows that *N* is proportional to W^{-1}, which is exactly the same as Peters[4] has suggested. It seems that two empirically justified and mutually consistent general relationships – one of Peters[4] and the other of Sheldon *et al.*[5] – would provide a good basis for a discussion on how and why particular forms of those relationships depart from the general models.

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