

evidence that host-specific shifts in the composition of the community of mycorrhizal fungi⁵ and of the community of rhizosphere bacteria⁶ can also contribute to the observed negative feedbacks. It seems quite possible that these soil organisms are responding to differences in host secondary chemicals – both those within the root and those released into the soil – as suggested by Pellissier.

Pellissier also observes that we hadn't included direct interactions between the two plant species in our model. While such effects were not explicitly included in our simple model, in analyzing the influence of soil community changes we implicitly assumed that the plants directly compete and that their competitive ability was equivalent. As Pellissier points out, explicit inclusion of the wide range of potential direct effects between the plants may alter the outcome of our model. We are in the midst of evaluating these possibilities.

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Quantifying brain–behavior relations in cetaceans and primates

In their recent *TREE* review, Connor *et al.*¹ provide an excellent and thought-provoking comparison of behavioral ecological patterns between toothed whales (odontocetes) and terrestrial mammals, particularly primates. The authors end their review with a provocative call for efforts to quantify the relationship between behavioral ecology and brain size among odontocetes in a similar manner to Dunbar's analyses for primates^{2,3}. Nevertheless, in doing so they leave the reader with the impression that these quantitative studies have not yet been attempted. There are two studies that do exemplify the very approach Connor *et al.* advocate. These studies provide quantitative support for the 'combination of convergence and novelty'¹ suggested by observational and qualitative comparisons of brain and behavior between odontocetes and primates.

First, there is a significant positive correlation between pod size and encephalization quotient (a measure of relative brain size taking into account brain–body allometry) among 21 odontocete species from all six odontocete families⁴. Therefore, the relationship between one measure of sociality (i.e. social group size and brain size) appears to be similar in primates and odontocetes.

Second, although there is a positive correlation between encephalization level and gestation length among primates⁵, in an analysis using the same encephalization values for the 21 odontocete species already mentioned, there is no significant relationship between encephalization and gestation length among odontocetes⁶. Rather, body size accounts for more of the variation in gestation length than encephalization among odontocetes. Therefore, there is quantitative evidence for differences in brain and life history relationships across primates and odontocetes.

My point here is not to criticize Connor *et al.* but to strengthen and extend their emphasis on quantitative analyses of odontocete behavioral ecology by showing that these kinds of studies are already underway. It is, of course, important to continue to further these studies while moving towards formulating and testing hypotheses about the evolution of cetacean brain–behavioral relationships and its implications for general mammalian evolution.

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Reply from R.C. Connor *et al.*

Marino correctly points out that we overlooked her work relating brain and group size in odontocetes. This is an important subject, and worthy of study. However, there are problems with her analysis that prevent us from embracing her finding of a 'significant positive correlation between pod size and encephalization quotient among 21 odontocete species' as being equivalent to Dunbar's conclusions for primates¹.

The hypothesis in question holds that the size of the brain (or, more specifically, the neocortex) places a limit on the number of social

relationships that an individual can handle simultaneously¹. Individuals in Dunbar's primate 'groups' have their primary social relationships with each other and not individuals of other groups. Thus his 'group size' is very closely related to the mean number of social relationships of an individual. In contrast, the 'pod size' reported most often for odontocetes, and apparently used by Marino, is simply the number of individuals that are usually observed together at a given point in time. This may be very different from the number of social relationships of an individual for several reasons.

First, coastal bottlenose dolphins (*Tursiops* sp.), and probably many other cetaceans, live in fission–fusion societies in which the typical number of individuals found together (<10) does not reflect the size of the social network (>100) (Refs 2,3). If small-brained odontocetes such as *Inia*, *Platanista* and *Pontoporia* live in similar fission–fusion societies, then available 'pod size' data will significantly underestimate the number of social relationships individuals maintain.

Second, large groups of large-brained pelagic delphinids (e.g. *Lagenorhynchus*) might reflect nonsocial assemblages of smaller social units attracted to food sources or minimizing predation risk. Until these species are studied we simply do not know.

We conclude that while the number of social relationships maintained by individuals in a few large-brained, well studied odontocetes clearly rival or exceed nonhuman primates, a correlation between the number of social relationships individuals maintain and brain size among odontocetes has not been established.

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