## What Makes Bigger Brains?

Paul Harvey is interested in brains. In particular, he's interested in why some species are relatively brainier than others: monkeys are more generously endowed mentally than mice, for instance. The question is, how do such differences come about? "I've always leaned towards adaptive explanations," says Harvey, a theoretician at Oxford University, England. "I suspect that a species' ecology can play a large part in influencing the evolution of its brain size."

Harvey and his Oxford colleague Mark Pagel have now brought this ecological perspective to an age-old variant of the brain size problem: the so-called taxon level effect. "Most analyses have reported that if you look at closely related species—species within a genus, for instance—there is said to be very little variation in relative brain size," explains Harvey. "But distantly related species—species within and between different orders, for instance—usually are reported to show a wide variation in relative brain size."

In other words, it looks as if some kind of constraint is keeping relative brain size pretty steady; and it also looks as if the constraint is loosened only as species diverge further and further from each other.

Most explanations of this phenomenon invoke some kind of internal mechanism, particularly genetic constraint on changing brain size. In their report on page 1589 of this issue Harvey and Pagel suggest a shift away from the traditional genetic context and more towards an ecological, adaptationist context.

The taxon-level effect "has been recognized for a very long time," says William Atchley of North Carolina State University. "And there have been lots of different explanations." Atchley favors the idea that developmental timing might be key to the taxonlevel pattern. He does suggest, however, that "many different explanations may be acting together, linked in complex ways, and very difficult to tease apart."

Probably the most popular explanation is that the constraint is genetic, an idea most clearly stated a decade ago by Russ Lande, a population geneticist at the University of Chicago. "We know that body size can evolve rapidly in response to selection," says Lande, "and brain size follows on behind, but at a slower rate." It is no surprise that brain and body size evolution are genetically linked: it would be more surprising if body size were to change during evolution, with brain size remaining unchanged.

But the genetic constraint idea says that the link is more like a piece of elastic than a taut chain: body size sets off in a particular direction (under selection), and, after a lag, brain size sets in motion too. "This would explain why relative brain size in closely related species is so similar," says Harvey. "Only after the passage of considerable evolutionary time does brain size have a chance to catch up—at least, according to this model."

But about 3 years ago Harvey began to suspect that the traditional genetic model might be off track, at least to some degree. There were two points of attack: one was statistics and the other was ecology. "We used a better method of statistical analysis, and we took care to look for ecological influences," says Harvey. Gradually, after plowing through data on 927 species of mammal, a new pattern emerged: "The supposed gap between closely related and distantly related species began to narrow; and where large differences of relative brain size did occur across higher level taxa, it was often the result of one or two markedly different groups within the whole."

For instance, if you look at bats you see considerable variation of relative brain size across the order—this seems to fit in with the taxon-level effect. But, say Harvey and Pagel, this is because of a big difference in encephalization between fruit-eating and insect-eating species, the fruit-eaters being bigger brained. The Oxford researchers saw similar examples in several mammalian orders. And the take home message is that ecology can sometimes be important in influencing evolution of brain size; it is not just a question of evolutionary distance.

"Closely related species usually inhabit similar ecological conditions," says Harvey. "And as ecology is important in influencing brain size evolution, closely related species will usually have similar relative brain sizes. It is not that they are constrained by genetics. It is more that they usually don't have the ecological opportunity to shift. When closely related species do occupy different ecological conditions, then brain size can respond by rapid evolution to selection."

Harvey does not claim that ecology is all, and that genetic constraints are irrelevant. "I see our results as being something of a marriage between the two," he suggests.

Atchley, who, unlike Harvey, is a handson biologist, is currently putting some of these issues to experimental test. In the next year or so he will be completing a large breeding project with mice that is designed to show how readily brain size can change in response to selection, and at what point in an individual's development selection is most effective. "It's all very well to talk about genetic constraints and ecological constraints," says Atchley, "but you need some nitty gritty data." Harvey agrees: "Yes, the kind of genetic data that Bill can get will eventually help solve this one."

ROGER LEWIN



There is weather on Neptune. Voyager 2's view of Neptune in late May revealed these striking images from 134 million kilometers away as the spacecraft heads for a 24 August close encounter with the outermost of the giant gas planets. The dark spot, probably a swirling vortex, and the accompanying bright areas (seen here through five different filters) are particularly striking to planetary scientists because they had only the vaguest suggestions in telescopic views from Earth that there would be anything to see in Neptune's atmosphere. Uranus, Voyager 2's previous target, remained a nearly blemishless blue ball no matter how close the view. According to Reta Beebe of New Mexico State University, the haze that obscured Uranus is probably being cleared away by more vigorous convection on Neptune driven by an internal heat source.