

Big brains do matter in new environments

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Why are some species' brains so large despite the metabolic and developmental costs? Why would two species with the same body size have two different brain sizes? These have been central questions in the field of brain evolution for decades and are the driving questions behind the article by Sol *et al.* (1) in this issue of PNAS. Correlations among various measures of brain size, cognitive capacity, problem solving, and behavioral ecology have been recorded in many groups of animals. The conventional approach has been to interpret these correlations as proxies for "as-yet-unknown" causal relationships while relying on the assumption that large brains confer greater cognitive abilities. Such studies in recent years have benefited from enhanced methodological capacities to measure brain size (e.g., computed tomography), collect large behavioral databases, and apply powerful statistical tests to such data. Collectively, this body of work has brought to light some broad consistent patterns of association among brain size, cognition, and ecology across animal groups that can be summarized as follows.

Various measures of brain size (e.g., encephalization quotient, brain-body residuals, neocortex ratio) are positively correlated with

- feeding innovation, learning, and tool use in birds and primates (2–10);
- behavioral repertoire size in mammals (11);
- social complexity in birds, primates, carnivores, and some insectivores (8, 12–16);
- dietary complexity in primates (17–20); and
- unpredictability of the environment in hominids (21, 22).

Universal Principles

The significance of these findings is that, collectively, they suggest that there are some "universals" across animal groups in terms of which ecologies support, and perhaps encourage, large brains. Furthermore, these findings are consistent with a general "behavioral flexibility" hypothesis that says that large brains confer an advantage when responding to variable, unpredictable, and novel ecological demands through enhanced behavioral flexibility, learning, and innovation. According to this hypothesis,

brains have evolved to respond to environmental changes. Previous studies have shown that there is a correlation between brain size and environmental complexity (see examples above). Studies have also shown that measures of behavioral complexity or flexibility are positively correlated with success in responding to the environment (23, 24). However, up to now, we have not known whether these statistical associations represent a meaningful set of causal connections among these variables. A strong test of this hypothesis demands a demonstration that cognitive abilities mediate the connection between brain size and a species' ability to respond to environmental complexity. The work of Sol *et al.* (1) provides the strongest evidence to date that these causal

Birds with large brains and greater cognitive complexity are better able to cope with novel environments.

pathways exist. The authors demonstrate that powerful tests of hypotheses can be performed by using archived data that is quantifiable and ecologically relevant. The report by Sol *et al.* significantly advances our understanding of brain, behavior, and environment by providing empirical findings that bridge the gap between statistical associations and causation, thereby approaching the goal of being able to draw conclusions about the actual fitness outcomes of various hypotheses. This ability is, after all, the "bottom line" objective in these kinds of studies.

Sol *et al.* (1) were able to conduct a powerful study of brain size, innovation rate, and survival rate for several reasons. They were able to draw on a vast literature on introduction data, innovation reports, and brain size in birds. They controlled for several potentially confounding variables such as research effort. Also, they used residuals of a log-log least-squares regression of brain versus body mass to account for the allometric effects of body size on brain

size. In addition, the authors used path analysis to reveal the causal relationships among brain size, innovation rate, and invasion potential. This method allows for the testing of specific models that correspond to specific predictions about the causal connections among factors. Using a path analysis method, Sol *et al.* were able to interpret their findings in a causal, not simply correlational, context.

There are a number of compelling questions about brains, cognition, and ecology that are raised by Sol *et al.*'s (1) findings. Sol *et al.* found that birds with large brains and greater cognitive complexity (as measured by innovation rate) are better able to cope with novel environments (i.e., introduction into a new location). These findings are consistent with the general literature showing a positive relationship between large brains and environmental complexity and novelty. But what exactly is it about changing environments that requires cognitive complexity? Various hypotheses, e.g., extractive foraging (19, 25), social intelligence (26–28), and resource mapping (20) have focused on different aspects of complexity and change. But perhaps specific environmental domains *per se* are not critical in this matter. In the case of coping with a new location, as in Sol *et al.*'s study, there will be a myriad of aspects of the new environment that will be novel. Moreover, changes in one domain (for instance, resource distribution) often lead to adjustments in other (for instance, foraging group size) domains. It may be that, given the wide range of both social and technical environmental demands associated with large brains, a higher-order nonspecific ecological characteristic, such as unpredictability, is all that is necessary for large brains to be selected and maintained.

Cognitive Complexity

What do the findings of Sol *et al.* (1) and the previous literature imply about the nature of cognitive complexity? Does it involve specific factors? If so, are some factors correlated and others uncorrelated? If not specific factors, do these findings better support the concept of "g," or general intelligence? Sev-

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eral measures of cognitive complexity (e.g., tool making and use, number of social interactions) correlate positively with innovation rate in both birds and primates (6). This finding suggests that cognitive complexity is a general problem-solving ability or, less likely in my view, involves correlated evolution across various cognitive domains. The kinds of cognitive capacities that tie together in the literature we are discussing are those that involve behavioral flexibility and adaptive problem solving rather than highly specialized domains of memory or calculation such as seed caching (29, 30). Furthermore, the neuroanatomy is revealing. The parts of the brain in birds and primates that are correlated with complex ecologies and innovative behaviors serve similar high-level integrative and executive functions in both groups. In birds these structures are the nidopallium and the mesopallium (31). In primates the relevant area

is the neocortex (especially the frontal lobes). In both birds and primates these areas of the brain are the “on-line” executive processing regions allowing for opportunistic solutions to new problems. It makes sense, then, that an environment doling out uncertainty would encourage the enhancement of the very part of the brain that copes with uncertainty.

Finally, what factors determine whether a group of animals will maintain ecological stability by tracking the environment through migration, etc., and which will adapt by evolving mechanisms of cognitive and behavioral flexibility? Lefebvre and colleagues (6) suggest that less innovative birds might avoid environmental change by moving back and forth with the seasons. Larger-brained species might avoid moving and instead cope with environmental instability through innovation. This idea is reasonable. Perhaps one general pattern

is that if environmental changes tend to be regular within an individual's lifetime, e.g., seasonal, then species might be able to develop specific mechanisms for coping with those regular changes. However, if environmental changes tend to be unpredictable then a more general flexible cognitive strategy is required to survive.

To reiterate, Sol *et al.* (1) take us a step closer to causal explanations for the general patterns of relationship among brain size, cognition, and ecology across so many animal groups. Their approach offers us the potential to compare a wide range of different animal groups. So far, only birds and primates have been dealt with in this manner with any degree of depth. But there are other taxa, cetaceans, carnivores, perhaps even invertebrates, that are intriguing and critical comparison groups for gaining a handle on whether there are truly “universal” patterns of causation across brain, behavior, and ecology on Earth.

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