Life History Patterns Emerge in Primate Study

Biologists expect to find connections between ecology and behavior in an evolutionary sense, but the links are often difficult to see; a new survey of primates reveals some

THE RUFFED LEMUR IS A PUZZLE. An inhabitant of Madagascan rain forest, this attractively marked species has—for its body size—the highest rate of potential population increase of all primates. The puzzle, as Caroline Ross of the University of Durham has recently shown, is that primates that live in rain forests tend to have relatively low rates of potential population increase. The ruffed lemur sticks out like a sore thumb. "Something strange is going on," says Ross, "or at least there is something going on that we've not yet been able to work out."

Ross has recently completed a survey of potential population increase in 58 primate species, from the largest (the gorilla) to the smallest (the mouse lemur), looking particularly at the effect of different environments. Environments range from rain forest, which is regarded as stable and predictable, to savannah, which is unstable and unpredictable, and Ross's research fits into classic ecological theory that seeks to link environmental predictability/unpredictability and potential population increase. This is not the first such survey on primates, but it is the first to yield a striking pattern.

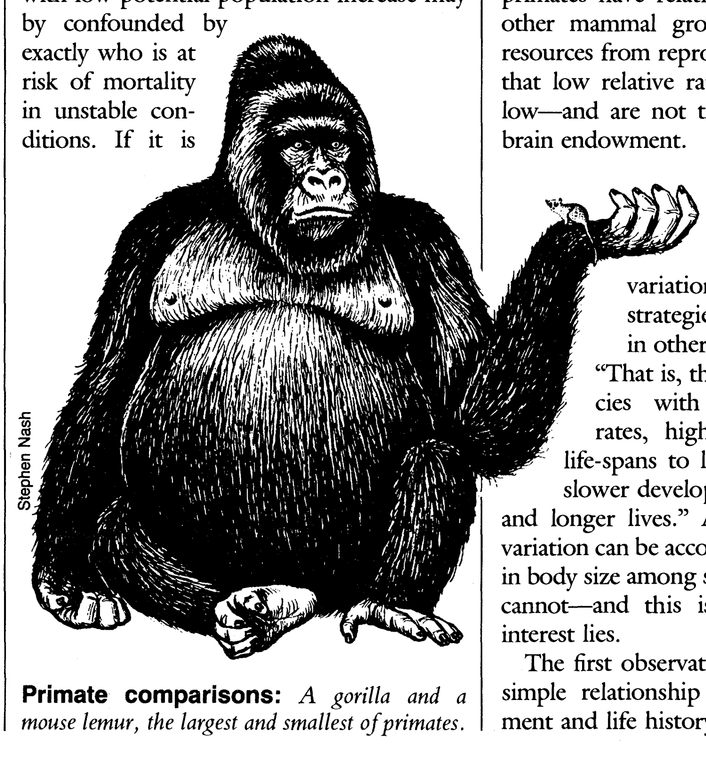
When body weight is taken into account, species that live in unstable environments have a higher than expected rate of potential population increase. The converse also holds, specifically that species in stable environments have a low relatively potential population increase. "This is an exciting finding," comments Paul Harvey, of Oxford University. "It gives you a pattern to try to interpret." Because the relationship between environment, body size, and various life history characteristics is incredibly complex, several interpretations are possible.

Ross's survey was done against the background of what ecologists call *r*- and K-selection theory, which was developed by Robert MacArthur and E. O. Wilson in the late 1960s. The theory addresses different reproductive strategies under different environmental conditions.

For instance, in unstable environments, in which resources fluctuate widely through seasonality or climatic catastrophe, species will be selected to breed rapidly. "In an unpredictable environment, there is uncertainty as to whether an organism will survive to reproduce next season," explains Ross. "Individuals that put a large amount of energy into reproducing immediately, rather than saving resources for a possible next season, will therefore be favored." A reproductive strategy that leads to high potential population increase is known as *r*-selection.

By contrast, in stable environments resources will be more reliable, and populations will eventually reach the carrying capacity of the environment, which will give an edge to those species that can compete most effectively for the finite resources. As a result, species in environments of this kind will be selected to be competitively successful, both as adults in daily foraging and as parents in producing viable offspring. Because such species may have to divert more of their energy budget to competition rather than reproduction, their potential rate of population increase may be lowered: they are K-selected.

This basic theoretical, dichotomous pattern of instability being associated with high potential population increase and stability with low potential population increase may by confounded by exactly who is at risk of mortality in unstable conditions. If it is the adults that are at risk, then the above arguments hold. But if it is the juveniles who suffer more, then the adults may opt (in a natural selection sense) to spread their reproduction over several years, and thus fall into the category of low potential population increase, in spite of existing in an unstable environment. This has been termed bet-hedging theory.



Primate comparisons: *A gorilla and a mouse lemur, the largest and smallest of primates.*

As always with this kind of comparative biology, body size is a major factor. For instance, for some fundamental engineering reasons, small species breed early, have a shorter time between litters, and several offspring per litter, all of which leads to a high potential population increase. The reverse is true for large species. Selection for high or low potential population increase can therefore work simply on body size, at least in theory. But it can also work directly on the reproductive components themselves. Comparisons between species must therefore be done with body size taken into account, thus giving *relative* values of life history factors, such as potential population increase.

By comparison with other mammalian groups, primates as a whole have low rates of potential population increase, for their body sizes. Several explanations have been advanced to account for this, none of which is entirely convincing. For instance, some researchers point to the fact that primates are essentially creatures of the tropics, and therefore experience more environmental stability than temperate species. But other tropical species are not noticeably *r*-selected as a group. Others point to the fact that primates have relatively larger brains than other mammal groups, which drains off resources from reproduction. But it may be that low relative rates of reproduction allow—and are not the result of—increased brain endowment.

In spite of this overall group characteristic, "Primates show a pattern of variation in their life history strategies similar to that found in other organisms," says Ross. "That is, they vary from small species with rapid developmental rates, high birthrates and short life-spans to larger species that have slower development, lower birthrates and longer lives." Although most of this variation can be accounted for by differences in body size among species, about 30% of it cannot—and this is where much of the interest lies.

The first observation is that "there is no simple relationship between the environment and life history strategies," says Ross.

In other words, you do not consistently find primate species with high potential population increase living in unstable environments, and vice versa. "The prediction of *r*- and K-selection theory (i.e., that unpredictable environments will be associated with small, 'fast' organisms and predictable environments with large, 'slow' organisms) is not realized," concludes Ross. Neither does bet-hedging seem to be important, because juvenile mortality is relatively more important than adult mortality in primates, and this would be expected to produce unusually low reproductive turnover in unstable environments.

There is a relationship, however, between high *relative* potential population increase and environmental instability. In other words, species that inhabit unpredictable environments have a higher potential population increase, for their body size. This means that, to some degree at least, selection has apparently worked on life history characteristics to boost reproductive turnover, without reducing body size.

Although Ross initially failed to find the converse relationship—low relative potential population increase in stable environments—finer analysis eventually showed this also to be true. Again, selection has to some extent apparently worked on life history parameters to decrease reproductive turnover, without increasing body size.

The result, then, is a nice symmetry, between high and low relative potential population increase and environmental circumstance. This can be taken as at least a nod in the direction of classic theory: "*r*- and K-selection fits better than we thought," notes Robert Martin of the Anthropological Institute, Zurich. But there are other interpretations. For instance, Harvey wonders whether mortality rates might underlie these patterns.

Specifically, says Harvey, mortality rates may be relatively higher in savannah environments compared with those in rain forests, for example. If this were the case, then fecundity rates inevitably would match them, boosting reproductive turnover in unstable environments and depressing them in stable environments. Currently there are insufficient data to test this idea conclusively.

"We have to pit different explanations against each other," says Harvey. "The pattern that Ross has uncovered is very interesting, and it must mean something."

■ ROGER LEWIN

ADDITIONAL READING

C. Ross, "The intrinsic rate of natural increase and reproductive effort in primates," *J. Zool. London* **214**, 199 (1988).

Costa Rican Biodiversity

A consortium of 14 Costa Rican organizations responsible for biodiversity will meet next month in San Jose to try to formalize nascent plans for a National Biodiversity Institute. One goal of the institute would initially be to create a collection and catalogue of all the plant and animal species throughout the country, an inventory that would effectively represent something like 5% of the world's biodiversity.

Costa Rican authorities have in recent years become enthusiastic about promoting conservation and ecological research efforts in their country, which measures something like the land area of the state of West Virginia. By the end of next year a little over 25% of the country will be designated as national park land, in half a dozen locations. The parks are significant in a global ecological sense because they preserve not only major rain forest habitat but also stands of tropical dry forest. By comparison with tropical rain forest, which is endangered enough by any standards, tropical dry forest is virtually extinct. Agriculture and ranching have virtually obliterated this unique habitat from Central America.

Costa Rican conservationists are therefore attempting to preserve what remains of the dry forest and restore presently denuded habitat in other park areas, the most ambitious restoration effort currently being in the northwest, the Guanacaste National Park. Initially the inspiration of Daniel Janzen of the University of Pennsylvania, the restoration project is run by Costa Rican organizations and includes economic exploitation of park land. "There is no other way for conservation projects in the tropics to be successful," says Janzen.

Speaking last week at the Smithsonian Institution in Washington, Janzen said there are three stages to conservation: "Save it; figure out what you've saved; and then put what you have saved to work for society." The currently tentative plans for a Costa Rican National Biodiversity Institute marks the second of these stages.

The traditional approach for creating an inventory of a biota—figuring out what you have saved—would involve calling on the time and expertise of international systematists in collecting, identifying, and classifying specimens, of about a million species in this case. "This would just bring more misery for everyone, because most systematists' resources are already grossly overextended," Janzen told *Science*. Instead, in Costa Rica, the collection and initial sorting is being done by farmers, other rural workers, and university students, many of whom previously worked in the park areas in more traditional jobs.

The biodiversity institute would be necessary in coordinating the countrywide collection effort and the analysis and storing of specimens. Researchers from other countries would be funded to visit the institute, where they would contribute to identifying and cataloging species; and they would be free to take specimens back to their own labs for work on taxonomic problems of their choice. Travel and other support funds often limit what researchers currently can do in systematics.

Janzen estimates that the necessary funds—for building an endowed institute, making the collections, and working them into thorough national field guides and identified reference collections—would amount to about $50 million over 10 years. "That's $50 a species," he notes, "and that's a bargain." The impetus from within Costa Rica for a biodiversity institute is an outgrowth of the indigenous involvement in conservation and biological science by many organizations there. As a result, Costa Rica has become something of a model for tropical conservation efforts. Crucial to the ultimate success of this internal impetus, says Janzen, is the parallel growth of interest in biodiversity that is currently blossoming in the upper echelons of government and industry in the Americas and in Europe.

"Biodiversity has gained a status at these levels," says Janzen, "but so far there is no real example of how to translate the interest into something tangible." What is necessary is some small, definable project, a group that knows what it wants to do, and how to do it. "Costa Rica could present that opportunity."

Once Costa Rica's proposal for a National Biodiversity Institute becomes formal, the search for financial support will begin. This will not be in the form of many small donations and grants, as has been the practice so far, says Janzen. Instead, the goal is that one or two major institutions will pick up the whole tab. High on the list of institutions to be approached are the U.S. Agency for International Development, its parallels in European countries, and large corporations. ■ ROGER LEWIN