

Clutton-Brock T H & Harvey P. Primate ecology and social organization.

J. Zool. 183:1-39, 1977.

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Using quantitative comparisons, the paper shows that species differences in group size, ranging behaviour, and sexual dimorphism among primates are consistently related to ecological variables, including diet type, timing of activity, and breeding system. By demonstrating these relationships, it indicated that much of the apparently bewildering variation in mammalian social behaviour might be explained by a few relatively simple generalisations. [The *SCI*® indicates that this paper has been cited in more than 255 publications, making it the most-cited paper published in this journal.]

Primate Rules OK

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In the 1960s, primate field studies proliferated as biological anthropologists sought to flesh out the bones of human evolution. Studies of chimps and baboons, gorillas and gibbons, spider monkeys and howlers provided evidence of a bewildering variety of social systems, yielding fascinating specifics but few generalisations. There was a widespread feeling that primates were so complex that we could only hope to describe their behaviour in increasing detail.

This was eventually challenged by John Crook. Fresh from showing that species differences in sociality among African weaver birds were related to differences in habitat type, Crook argued that differences in primate social behaviour and ranging patterns represented different evolutionary grades, corresponding to different habitat categories ranging from rain forest to desert.¹ This was a nice idea, but there was little evidence that differences in behaviour represented a series of evolutionary stages and plenty that social behaviour and ranging patterns varied widely between species allocated to the same grade.

To check this out, I spent much of my final undergraduate year at Cambridge carrying out a statistical analysis of interspecific differences in primate social behaviour and the next three years working out why two sympatric *Colobus* species that apparently shared the same diet and habitat type showed marked differences in group and range size. The answer proved to be a difference in the distribution of their food supplies.² This led me back to asking whether

differences in group size, ranging behaviour, and population density across other primate species might be systematically related to ecology, as they were in other groups of animals.^{3,4}

I had moved to a lectureship in animal behaviour at the University of Sussex and was examining the extent to which species differences in range size were related to group size when Paul Harvey, a lecturer in ecology, looked over my shoulder. "That's not behaviour," he said, "that's ecology." We agreed to work together and went on to show that species differences in group size, sex ratio and density, as well as patterns of ranging behaviour, were systematically related to ecological differences. Subsequently, we moved on to show that species differences in sexual dimorphism were systematically related to mating systems, though we failed to find a satisfactory explanation of the distribution of monogamy and polygyny. To minimize the problem that values for closely related species were not independent of each other, we calculated average values for each genus and used these to calculate probability values for the relationships that we found.

Initial reactions to the paper were mixed. As we had anticipated, a proportion of primatologists regarded it as a scandalous oversimplification, but others showed a more positive interest and began to use quantitative interspecific comparisons to test other evolutionary hypotheses. Since it offered a simple analysis of primate social systems, the paper was probably of most use to zoologists working on other animal groups, who not uncommonly regarded the primate literature as confusing, if not confused, and it was probably widely cited for this reason.

This paper proved to be the first of a series of joint papers by Paul Harvey and myself. Our subsequent work refined its conclusions and used similar comparisons to explore relationships between ecology and canine size, brain size and life history variables, while Harvey went on to play a leading role in the development of statistical techniques to control for the effects of phylogeny in quantitative comparisons.⁵ Interspecific comparisons are now widely used to test evolutionary hypotheses in related fields, while studies of primate behaviour have progressed a long way from the descriptive field studies of the 1960s. But plenty of biological puzzles remain—and I am interested to see that no one has yet produced a satisfactory explanation of the distribution of primate monogamy.

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2. Clutton-Brock T H. Primate social organization and ecology. *Nature* 250:539-42, 1974.

3. McNab B K. Bioenergetics and the determination of home range size. *Amer. Naturalist* 97:133-40, 1963. (Cited 245 times.)
[See also: McNab B K. The scaling of ecological phenomena. *Citation Classic. Current Contents®/Agriculture, Biology & Environmental Sciences* 20(39):12, 25 September 1989.]

4. Schoener T W. Sizes of feeding territories among birds. *Ecology* 49:123-41, 1968. (Cited 235 times.)

5. Harvey P H & Pagel M. *The comparative method in evolutionary biology*. Oxford, England: Oxford University Press, 1991.