PRIMATES

Comparative Primate Socioecology

Edited by P. C. Lee

CSBEA

CAMBRIDGE

CAMBRIDGE

more information - www.cambridge.org/0521593360

This page intentionally left blank

Comparative Primate Socioecology

Comparative studies have become both more frequent and more important as a means for understanding the biology, behaviour and evolution of mammals. Primates have complex social relationships and diverse ecologies, and represent a large species radiation. This book draws together a wide range of experts from fields as diverse as reproductive biology and foraging energetics to place recent field research into a synthetic perspective. The chapters tackle controversial issues in primate biology and behaviour, including the role of brain expansion and infanticide in the evolution of primate behavioural strategies. The book also presents an overview of comparative methodologies as applied to recent primate research that will provide new approaches to comparative research. It will be of particular interest to primatologists, behavioural ecologists and those interested in the evolution of human social behaviour.

P.C. Lee is a lecturer in Biological Anthropology at the University of Cambridge and Fellow of Downing College. She began field work on baboons in 1975 and has maintained an interest in the socioecology and behaviour of primates and other large mammals ever since. She has written numerous papers and has co-edited three previous volumes on primates – *Primate Evolution*, *Primate Ecology and Conservation* and *Primate Ontogeny, Cognition and Behaviour* (all 1986) – and has co-authored *The Threatened Primates of Africa* (1988).

Cambridge Studies in Biological Anthropology

Series Editors

Selected titles also in the series

11 Kenneth M. Weiss *Genetic Variation and Human Disease* 0 521 33660 0 (paperback)

12 Duane Quiatt & Vernon Reynolds *Primate Behaviour* 0 521 49832 5 (paperback)

13 Gabriel W. Lasker & C. G. N. Mascie-Taylor (eds) *Research Strategies in Biological Anthropology* 0 521 43188 3

14 Stanley J. Ulijaszek and C. G. N. Mascie-Taylor (eds) *Anthropometry* 0 521 41798 8

15 C. G. N. Mascie-Taylor and Barry Bogin (eds) *Human Variability and Plasticity* 0 521 45399 2

16 Stanley J. Ulijaszek *Human Energetics in Biological Anthropology* 0 521 43295 2

17 Roy J. Shephard and Anders Rode *Health Consequences of 'Modernisation'* 0 521 47401 9

18 Marta M. Lahr *The Evolution of Modern Human Diversity* 0 521 47393 4

19 Lyliane Rosetta and C. G. N. Mascie-Taylor (eds) *Variability in Human Fertility* 0 521 49569 5

20 G. Richard Scott and Christy G. Turner II *Anthropology of Modern Human Teeth* 0 521 45508 1

21 Clark S. Larsen *Bioarchaeology* 0 521 4964 1 (hardback), 0 521 65834 9 (paperback)

22 P. C. Lee (ed) *Comparative Primate Sociology* 0 521 59336 0

Comparative Primate Socioecology

EDITED BY P.C. LEE

CAMBRIDGE
UNIVERSITY PRESS

PUBLISHED BY THE PRESS SYNDICATE OF THE UNIVERSITY OF CAMBRIDGE
The Pitt Building, Trumpington Street, Cambridge, United Kingdom

CAMBRIDGE UNIVERSITY PRESS
The Edinburgh Building, Cambridge CB2 2RU, UK
40 West 20th Street, New York, NY 10011-4211, USA
477 Williamstown Road, Port Melbourne, VIC 3207, Australia
Ruiz de Alarcón 13, 28014 Madrid, Spain
Dock House, The Waterfront, Cape Town 8001, South Africa

http://www.cambridge.org

First published in printed format 1999

ISBN 0-511-02013-9 eBook (netLibrary)
ISBN 0-521-59336-0 hardback
ISBN 0-521-00424-1 paperback

Contents

Contributors

ROBERT BARTON
Department of Anthropology, University of Durham, Old Elvet, Durham DH1 3HN, UK

ALLISON BEAN
Department of Biological Anthropology , University of Cambridge, Downing Street, Cambridge CB2 3DZ, UK

NICHOLAS BLURTON JONES
Graduate School of Education and Department of Anthropology, Moore Hall, University of California at Los Angeles, Los Angeles, CA 90024, USA

ROBIN DUNBAR
Population Biology Research Group, School of Biological Sciences, Nicholson Building, University of Liverpool, Liverpool L69 3BX, UK

ROBERT A. FOLEY
Department of Biological Anthropology , University of Cambridge, Downing Street, Cambridge CB2 3DZ, UK

KRISTEN HAWKES
Department of Anthropology, University of Utah, Salt Lake City, UT 84112, USA

CLARE HOLDEN
Department of Anthropology, University College London, Gower Street, London WC1E 6BT, UK

KATE E. JONES
Roehampton Institute, School of Life Sciences, West Hill, London SW15 3SN, UK

PETER M. KAPPELER
AG Verhaltensforschung/Okologie, Deutsche Primatenzentrum, Kellnerweg 4, 37007 Gottingen, Germany

PHYLLIS C. LEE
Department of Biological Anthropology, University of Cambridge, Downing Street, Cambridge CB2 3DZ, UK

RUTH MACE
Department of Anthropology, University College London, Gower Street, London WC1E 6BT, UK

ANN MACLARNON
Roehampton Institute, School of Life Sciences, West Hill, London SW15 3SN, UK

MARIA A. VAN NOORDWIJK
Department of Biological Anthropology and Anatomy, Duke University, P.O. Box 90383, Durham, NC 27708-0383, USA

CHARLES L. NUNN
3323 Ridge Road, Durham, NC 27705-5535, USA

JAMES F. O'CONNELL
Department of Anthropology, University of Utah, Salt Lake City, UT 84112, USA

J. MICHAEL PLAVCAN
Department of Anatomy, New York College of Osteopathic Medicine, Old Westbury, NY 11568, USA

ANDREW PURVIS
Department of Biology, Imperial College at Silwood Park, Ascot, Berkshire SL5 7PY, UK

KATE ROBSON-BROWN
Centre for Human Evolutionary Research, Department of Archaeology, University of Bristol, Clifton, Bristol, UK, and Department of Biological Anthropology, University of Cambridge, Downing Street, Cambridge CB2 3DZ, UK

CAROLINE ROSS
Roehampton Institute, School of Life Sciences, West Hill, London SW15 3SN, UK

CAREL P. VAN SCHAIK
Department of Biological Anthropology and Anatomy, Duke University, P.O. Box 90383, Durham, NC 27708-0383, USA

KAREN B. STRIER
Department of Anthropology, University of Wisconsin, 5240 Social Science Building, 1180 Observatory Drive, Madison, WI 53706-1393, USA

ANDREA J. WEBSTER
Department of Biology, Imperial College at Silwood Park, Ascot, Berkshire SL5 7PY, UK

DAISY K. WILLIAMSON
Hominid Palaeontology Research Group, Department of Human Anatomy and Cell Biology, University of Liverpool, Ashton Street, Liverpool L69 3GE, UK

Preface

Comparative studies have become both more frequent and more important as a means for understanding the biology, behaviour and evolution of mammals. Historically, studies of primate socioecology have been in the forefront of the field and many interesting methodological developments in comparative socioecology have emerged from earlier work. This is not to say that other animals have not been examined – for example, there are excellent studies of seals, carnivores and ungulates, not to mention extensive work on birds.

But primates are particularly interesting in that they have complex social relationships and diverse ecologies, as well as representing a large radiation of morphologies. Socioecology, as used here, is taken to represent the interactions between characteristics of the resource base, its mode of exploitation, reproductive biology and life history, and the observed social system. In this sense, primates can be considered as a test case for hypotheses that the solutions to ecological problems have a social root. Thus, the chapters in this book seek to explore the diverse relations between sociality and resources, mating systems, energetics and reproduction. Questions of biological or physiological constraints on sociality are also examined.

Since the 1987 publication of *Primate Societies* by Smuts *et al.*, field researchers have added greatly to our knowledge of primate social systems and ecological variation, and this book attempts to synthesise some recent work. It is perhaps notable that the socioecology of the primates is not approached with a taxonomic structure here. Rather, this book tries to cover less well-known species that have been the focus of recent field studies, and specific issues that are of current theoretical interest for primates as diverse as lemurs and humans.

Part 1
Comparative methods

Editor's introduction

Our ability to analyse variation within and between taxonomic groups has been enhanced by the development of techniques for the statistical manipulation of comparative data, but we have yet to reach a consensus on which techniques are appropriate for specific analyses. Thus, several possible approaches are presented. A comprehensive overview of the pros and cons, as well as how to carry out different comparative techniques can be found in Harvey and Pagel (1991).

It should be noted that there are two separate issues involved in phylogenetic analyses. The first of these is fundamentally *statistical*. Although it has long been recognised that the use of 'species' data in comparative analyses on closely related taxa may violate statistical assumptions of independence of data points (e.g. Crook, 1965), this was elaborated in relation to phylogenetic similarity in allometry by Felsenstein (1985). Stated simply, closely related taxa may share traits derived through that genealogical relationship rather than as a result of selection, and species as such are not independent within lineages. This issue had been at least partially explored in earlier socioecological and life history research on primates through data reduction techniques – the use of mean values for different taxonomic levels – the 'higher node' approach (e.g. genera: Clutton-Brock and Harvey, 1977; subfamily: Harvey, Martin and Clutton-Brock, 1987).

But there is a second, more interesting, question raised by comparative analyses, that of the *evolutionary* similarity within and between related taxa (Purvis and Harvey, 1995), and it is in this context that the value of phylogenetically controlled comparisons is most apparent. One of the most common and accessible techniques, Comparative Analysis by Independent Contrasts (CAIC), is presented by Purvis and Webster in Chapter 3. The value of CAIC lies in its simplicity and in the detailed primate phylogeny derived by Purvis. Some problems with the method are also considered.

The fundamental question, however, remains whether the comparative study seeks to determine if evolutionary change in traits has occurred, or whether it seeks to identify variation between species or groups of species in an attempt to determine causality in this observed variation. Often, a comparison of the results obtained from several different analytical techniques may allow for more robust interpretations. This procedure is used in a number of the chapters in subsequent parts of the book. Another technique for exploring evolutionary variation is that of nested analysis of variance. Originally devised to determine which taxonomic level explained the observed variance in a trait, and thus to limit comparisons to that 'independent' level, it has a further utility in partitioning variance between these taxonomic levels and thus provoking evolutionary explanations. Methods such as correcting for degrees of freedom in nested ANOVAs also address the problem of statistical dependence (see Smith, 1994). Interestingly, there may be times when different taxonomic levels explain variation for distinct variables, suggesting that it would be difficult, if not impossible, to 'control' for phylogeny by selecting a single independent higher taxonomic node for analysis. For example, among primates, variance in adult body weight is greatest at the level of the subfamily, whereas that of density is greatest at the population level (Vella, 1995).

If two species share traits, is this the result of evolutionary convergence or simply due to sharing ancestral traits between closely related descendants? If we are exploring evolution within and between lineages, then obviously the lineages themselves are part of the data we are examining. It becomes critical to know both the phylogenetic relationships and to tease apart the ancestor–descendant traits, as noted by Purvis and Webster. The potential to determine separate evolutionary events by cladistic analysis is outlined by Robson-Brown (Chapter 2). Such techniques are far more accessible with current programs, but users need to be aware of the debates about homology and analogy explored by Robson-Brown.

Other techniques, which rely on 'species' data but allow for an assessment of the effects of phylogeny on the observed patterns, are potentially available; for example the use of maximum likelihood estimators for co-evolution in discrete traits (e.g. Pagel, 1994; Mace and Holden, Chapter 15), or multidimensional scaling of traits which can produce visible clusters among close phylogenetic relatives (e.g. Bean, Chapter 13). MacLarnon, Chivers and Martin (1986) produced evidence for phylogenetic similarity in gut areas among primates using multidimensional scaling, with a consistent cluster of colobines in analytical space, despite observed differences in diets from fruits, through seeds to mature leaf (Davies and Oates, 1996). The power of such analyses lies in their ability to explore patterns explicitly due to shared descent. Other possible means for incorporating phylogeny that do not rely on phylogenetic subtraction, and thus the assumption that the mean of nodes reconstructs a single ancestral state (e.g. Pagel and Harvey, 1988; Stearns, 1992), could lie in non-linear modelling, in nested analysis of covariance, or in principle components data reduction techniques. Consensus on the 'most' appropriate technique is still to be found.

The point of providing several different techniques and perspectives in this book is to focus researchers on making explicit the hypothesis being tested. Is it an evolutionary explanation, a mechanical or physiological one, or a functional relationship? These issues are presented by MacLarnon in a general overview of methodology (Chapter 1). When and why should species be expected to vary? How do rates of evolution within lineages vary? What are the effects on traits? Are predictive trends the aims of the analysis or are we seeking mechanisms in evolution? The technique used, or combinations of methods, needs to be tailored to suit the questions. Even after 30 years of debate, no single method can yet be considered sufficient or even the most appropriate, and it is the question not the methodology that should drive the exploration.

References

Clutton-Brock, T.H. and Harvey, P.H. (1977). Primate ecology and social organisation. *Journal of Zoology, London* **183**, 1–39.

Crook, J.H. (1965). The adaptive significance of avian social behaviour. *Symposium of the Zoological Society of London* **14**, 181–218.

Davies, A.G. and Oates, J.F. (1996). *Colobine Monkeys*. Cambridge: Cambridge University Press.

Felsenstein, J. (1985). Phylogenies and the comparative method. *American Naturalist* **125**, 1–15.

Harvey, P.H., Martin, R.D. and Clutton-Brock, T.H. (1987). Life histories in comparative perspective. In *Primate Societies*, ed. B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham and T.T. Struhsaker, pp. 181–96. Chicago: University of Chicago Press.

Harvey, P.H. and Pagel, M. (1991). *The Comparative Method in Evolutionary Biology*. Oxford: Oxford University Press.

MacLarnon, A.M., Chivers, D.J. and Martin, R.D. (1986). Gastrointestinal allometry in primates and other mammals, including new species. In *Primate Ecology and Conservation*, ed. J.G. Else and P.C. Lee, pp. 75–85. Cambridge: Cambridge University Press.

Pagel, M. (1994). Detecting correlated evolution on phylogenies: a new method for analysis of discrete categorical data. *Proceedings of the Royal Society, Series B* **255**, 37–45.

Pagel, M. and Harvey, P.H. (1988). Recent developments in the analysis of comparative data. *Quarterly Review of Biology* **63**, 413–40.

Purvis, A. and Harvey, P.H. (1995). Mammal life history evolution: a comparative test of Charnov's model. *Journal of Zoology, London* **237**, 259–83.

Smith, R.J. (1994). Degrees of freedom in interspecific allometry: an adjustment for the effects of phylogenetic constraint. *American Journal of Physical Anthropology* **93**, 95–107.

Stearns, S. (1992). *The Evolution of Life Histories*. Oxford: Oxford University Press.

Vella, A. (1995). Primate Population Biology and Conservation. PhD thesis, University of Cambridge.

1 *The comparative method: principles and illustrations from primate socioecology*

ANN MACLARNON

Introduction

There are two major means of investigation across a wide range of sciences, both natural and social. These are the experimental method and the comparative method. In the so-called hard sciences – physics and chemistry – and also the 'harder' end of biology, investigation is more commonly by experimental manipulation. Other biological questions, notably those concerning evolutionary history and adaptation, are more or less inaccessible to experimentation, as are other aspects of the natural world, such as astronomical phemonena. Exploration of these areas and the development of explanations are undertaken largely by the comparative method, whereby common patterns and principles of variability are sought out, providing the basis for possible interpretation in terms of causes and effects. Similarly, in the social sciences, comparisons can be made across space and time of different societies, divisions or aspects of societies, with the aim of uncovering the origins and explanations of present features and past changes.

The comparative method has its origins in the realisation of the Enlightenment that the natural world can be understood and explained in terms of common principles and predictable variation. It involves testing the generality of suggested explanations for characteristics or phenomena, in contrast to *ad hoc*, one-off explanations that may merely reflect coincidence rather than causal connection. Predictions can be made from proposed general principles, and tested on further species, societies, stars or galaxies, and if borne out, they provide increased support for the validity of a principle.

The fundamentals of the comparative method were first expounded in the mid-nineteenth century by John Stuart Mill in his book *A System of Logic* (1872, 1967) in the chapter 'Of four methods of experimental inquiry'. These four methods essentially describe the basic principles of logical deduction used in scientific inquiry today, including the comparative method. Despite the fact that Stuart Mill's examples mostly come from the physical rather than the living world, the applications of the methods as outlined, their difficulties and limitations, are entirely pertinent to the comparative method in biology, including socioecology. The four methods are as follows:

1. Method of Agreement. 'If two or more instances of the phenomenon under investigation have only one circumstance in common, the circumstance in which alone all the instances agree is the cause (or effect) of the given phenomenon.' (1967, p. 255).
2. Method of Disagreement. 'If an instance in which the phenomenon under investigation occurs, and an instance in which it does not occur, have every circumstance in common save one, that one occurring only in the former; the circumstance in which alone the two instances differ is the effect, or the cause, or an indispensable part of the cause, of the phenomenon.' (1967, p. 256).

   These two methods can be combined in the Joint Method of Agreement and Difference:

   'If two or more instances in which the phenomenon occurs have only one circumstance in common, while two or more instances in which it does not occur have nothing in common save the absence of that circumstance, the circumstance in which alone the two sets of instances differ is the effect, or the cause, or an indispensable part of the cause, of the phenomenon.' (1967, p. 259).
3. Method of Residues. 'Subduct from any phenomenon such part as is known by previous inductions to be the effect of certain antecedents, and the residue of the phenomenon is the effect of the remaining antecedents.' (1967, p. 260).

   (Note: By 'antecedent' Stuart Mill is referring to conditions rather than ancestors.)
4. Method of Concomitant Variation. 'Whatever phenomenon varies in any manner whenever another phenomenon varies in some particular manner, is either a cause or an effect of that phenomenon, or is connected with it through some fact of causation.' (1967, p. 263).

The main principles of scientific inquiry are established in the first two Methods, while the third and fourth can be seen as special cases of the Method of Difference. The Method of Difference describes a basic principle of good experimental design whereby all factors bar one are the same for all samples, and thus any difference in findings between the samples is related