

Behavioural Diversity in Chimpanzees and Bonobos

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Contents

List of contributors	page vii		
Preface	ix		
GOTTFRIED HOHMANN, CHRISTOPHE BOESCH & LINDA F. MARCHANT			
Behavioural Diversity in <i>Pan</i>	1		
CHRISTOPHE BOESCH			
PART I BEHAVIOURAL FLEXIBILITY			
INTRODUCTION BY TETSURO MATSUZAWA			
1 Multivariate and phylogenetic approaches to understanding chimpanzee and bonobo behavioral diversity	14		
DIANE M. DORAN, WILLIAM L. JUNGERS, YUKIMARU SUGIYAMA, JOHN G. FLEAGLE & CHRISTOPHER P. HEESY			
2 Chimpanzees in the dry habitats of Assirik, Senegal and Semliki Wildlife Reserve, Uganda	35		
KEVIN D. HUNT & WILLIAM C. MCGREW			
3 Behavioural adaptations to water scarcity in Tongo chimpanzees	52		
ANNETTE LANJOUW			
4 Bonobos of the Lukuru Wildlife Research Project	61		
JO A. MYERS THOMPSON			
5 Grooming-hand-clasp in Mahale M Group chimpanzees: implications for culture in social behaviours	71		
MICHIO NAKAMURA			
		PART II SOCIAL RELATIONS	
		INTRODUCTION BY VERNON REYNOLDS	
		6 Factors influencing fission–fusion grouping in chimpanzees in the Taï National Park, Côte d’Ivoire	90
		DEAN P. ANDERSON, ERIK V. NORDHEIM, CHRISTOPHE BOESCH & TIMOTHY C. MOERMOND	
		7 Ecological and social correlates of chimpanzee party size and composition	102
		JOHN C. MITANI, DAVID P. WATTS & JEREMIAH S. LWANGA	
		8 Agonistic relations among Kanyawara chimpanzees	112
		MARTIN N. MULLER	
		9 Relationships of male chimpanzees in the Budongo Forest, Uganda	124
		NICHOLAS E. NEWTON-FISHER	
		10 Dynamics in social organization of bonobos (<i>Pan paniscus</i>)	138
		GOTTFRIED HOHMANN & BARBARA FRUTH	
		PART III FEMALE STRATEGIES	
		INTRODUCTION BY MEREDITH F. SMALL	
		11 Why female bonobos have a lower copulation rate during estrus than chimpanzees	156
		TAKESHI FURUICHI & CHIE HASHIMOTO	
		12 Social relationships between cycling females and adult males in Mahale chimpanzees	168
		AKIKO MATSUMOTO-ODA	

vi CONTENTS

13 Seasonal aspects of reproduction and sexual behavior in two chimpanzee populations: a comparison of Gombe (Tanzania) and Budongo (Uganda)	181	17 How bonobos handle hunts and harvests: why share food?	231
JANETTE WALLIS		BARBARA FRUTH & GOTTFRIED HOHMANN	
14 Costs and benefits of grouping for female chimpanzees at Gombe	192	18 Hunting and meat sharing by chimpanzees at Ngogo, Kibale National Park, Uganda	244
JENNIFER M. WILLIAMS, HSIEN-YANG LIU & ANNE E. PUSEY		DAVID P. WATTS & JOHN C. MITANI	
15 The cost of sexual attraction: is there a trade-off in female <i>Pan</i> between sex appeal and received coercion?	204	PART V GENETIC DIVERSITY	
RICHARD WRANGHAM		19 The evolutionary genetics and molecular ecology of chimpanzees and bonobos	259
		BRENDA J. BRADLEY & LINDA VIGILANT	
PART IV HUNTING AND FOOD SHARING		Index	277
INTRODUCTION BY LINDA F. MARCHANT			
16 Variations in chimpanzee–red colobus interactions	221		
CHRISTOPHE BOESCH, SHIGEO UEHARA & HIROSHI IHOBE			

1 • Multivariate and phylogenetic approaches to understanding chimpanzee and bonobo behavioral diversity

DIANE M. DORAN, WILLIAM L. JUNGERS, YUKIMARU SUGIYAMA, JOHN G. FLEAGLE & CHRISTOPHER P. HEESY

INTRODUCTION

Primates exhibit considerable diversity in their social systems (Smuts *et al.* 1987), a phenomenon that is thought to have evolved through the interaction of many factors. These include: (1) ecological variables, particularly predation pressure and the abundance and distribution of food (Alexander 1974; Wrangham 1979, 1980, 1987; van Schaik 1983, 1989, 1996; Sterck *et al.* 1997); (2) social factors, primarily sexual selection and the potential risk of infanticide (Wrangham 1979; Watts 1989; van Schaik 1996); (3) demographic and life history variables (DeRousseau 1990; Ross 1998); and (4) phylogenetic constraints (Wilson 1975; DiFiore & Rendall 1994). Generally, tests of models of the effect of these variables on behavior have been made through broad comparisons of many taxa, usually across genera (Wrangham 1980; van Schaik 1989; DiFiore & Rendall 1994; Sterck *et al.* 1997). There have been fewer attempts to consider the influence of these factors on variability in social organization within and between closely related taxa, largely as a result of a dearth of species for which such data are available (but see Mitchell *et al.* 1991; Koenig *et al.* 1998; Boinski 1999; Barton 2000). In addition, most tests have focused intensively on a single class of traits, and their proposed influence on behavior (e.g. the influence of ecology on behavior, van Schaik 1989; but see Nunn & van Schaik 2000), rather than the role of all proposed factors. To date, no study has quantitatively examined the combined influence of ecology, habitat, demography, and phylogeny on behavior.

Chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*) provide a unique opportunity to address the variability of social behavior in relation to these factors within closely related taxa because they have been studied at several different sites for long (greater than 15 years) periods of time (e.g. chimpanzees: Goodall 1986; Nishida 1990b; Sugiyama 1999; Boesch & Boesch-Achermann 2000; bonobos: Malenky 1990; Kano 1992; White 1996b; Fruth & Hohmann 1999). Currently, authorities recognize one species of

bonobo, *Pan paniscus* (which is restricted in its distribution to the Democratic Republic of Congo) and three geographically distinct subspecies of chimpanzees, including *P. troglodytes verus* in West Africa, *P. t. troglodytes* in Central Africa, and *P. t. schweinfurthii* in East Africa (Fleagle 1999; but see Gonder *et al.* 1997 and Gagneux *et al.* 1999 for discussion of a potential fourth subspecies of chimpanzees, *P. t. vellerosus*, in Nigeria and Cameroon). Results from mitochondrial DNA studies have been used to estimate dates of divergence of chimpanzees from bonobos at approximately 2.5 million years ago (MYA), and between western (*P. t. verus* and *P. t. vellerosus*) and eastern/central chimpanzees (*P. t. schweinfurthii* and *P. t. troglodytes*) at 1.6 MYA (Morin *et al.* 1994; Gagneux *et al.* 1999).

There are currently eight habituated communities of chimpanzees (two communities each at Taï and Kibale, one each at Gombe, Mahale Mountains, Budongo, and Bossou), making chimpanzees the best studied of all nonhuman primates (Reynolds & Reynolds 1965; Sugiyama & Koman 1979; Goodall 1986; Nishida 1990a; Boesch 1996a; Wrangham *et al.* 1996; reviewed by McGrew 1992). Although chimpanzees have many features in common across sites, such as a primarily frugivorous diet and fluid fission–fusion, male-bonded social organization (but see Boesch 1996b), there is also considerable intersite diversity in chimpanzee behavior (reviewed in Wrangham *et al.* 1994). This intersite variation includes differences in both foraging strategies (including hunting, nut cracking, insect eating, and types of fallback resources) and social behavior (including party sizes, type and extent of association, the degree of seasonal influences on sociality, frequency of female transfer, and possibly male–female affiliation patterns). The most striking differences in behavior are between western (Taï and Bossou) and eastern (Gombe, Mahale, and Kibale) chimpanzees. Taï chimpanzees have been argued to be bisexually-bonded, rather than male-bonded (Boesch 1996b; but see Doran 1997), and to differ in their hunting strategies, relying on more cooperation than eastern chimpanzees (Boesch 1994).

Bonobos are less well-studied than chimpanzees, with

only two long-term study sites, Wamba and Lomako. Like chimpanzees, bonobos are highly frugivorous and are characterized by a fission–fusion society with female dispersal. However, they are reported to differ from chimpanzees in the nature of social relations within and between the sexes (with more frequent male–female and female–female association), in their reduced levels of aggression within and between communities, and in their more frequent and varied sexuality (e.g. de Waal 1989; Wrangham & Peterson 1996; Nishida 1997). Intersite differences in bonobo behavior have also been reported (White 1992; White 1996b).

Until recently, chimpanzees and bonobos have been viewed as morphologically (e.g. Susman 1984), genetically (e.g. Ruvolo *et al.* 1994), and behaviorally (e.g. de Waal 1989; Wrangham & Peterson 1996; Nishida 1997) distinct species. During the last decade, the number of long-term chimpanzee studies has increased, and researchers have emphasized the diversity in chimpanzee behavior across sites. One result of this is that the dichotomy between chimpanzee and bonobo behavior has been challenged (Boesch 1996b; Fruth 1998; McGrew 1998; Stanford 1998). Stanford (1998) suggested that ‘the dichotomy currently drawn between the social systems of chimpanzees and bonobos may not accord well with field data’ (p. 406). In a commentary following his article, several authors support his position that many of the previously perceived distinctions between the two species were a result of unequal sampling (Fruth 1998; McGrew 1998); others disagree and see clear behavioral differences (de Waal 1998; Kano 1998; Parish 1998).

One reason for these disparate opinions is that comparative studies have not assessed overall similarity and dissimilarity between species, but rather have focused on one or, at most, a few aspect(s) of behavior (e.g. reproductive behavior: Takahata *et al.* 1996; hunting: Boesch 1991; Stanford *et al.* 1994; Mitani & Watts 1999; grouping patterns: Chapman *et al.* 1994; Sakura 1994; Boesch, 1996b; Doran, 1997; cultural diversity: McGrew 1992; Whiten *et al.* 1999). To date, no study has quantified the behavioral variation in chimpanzees and bonobos based on a wide range of traits from many sites. Furthermore, although several hypotheses have been offered to explain the evolution of specific behavioral traits, such as increased male–female affiliation as a female counter strategy to reduce the risk of infanticide (van Schaik 1996), or the role of herb consumption in bonobo sociality (Wrangham 1986a), few studies have specifically examined whether proposed behaviors and causal factors vary in a predictable manner across taxa.

The overall objectives of this study are to examine the

range of variation in behavior within and between chimpanzees and bonobos, and to identify the factors associated with this variability. We did this through four steps. First, we constructed a data matrix of 82 characters, chosen specifically to represent the key components of *Pan* social structure and behavior and the factors (ecological, habitat, and demography) considered potentially important in the evolution of sociality. Second, we used multivariate analyses (Sneath & Sokal 1973; Flury & Riedwyl 1988) to examine overall behavioral similarity within and between species of *Pan*, and to identify which behavioral characters are important in distinguishing taxa. Third, we used multivariate analyses to consider the extent to which differences in habitat, ecology, demography, and phylogeny were associated with the observed patterns of behavior in African apes. Finally, we used phylogenetic analyses (Nunn & van Schaik 2000; Borgerhoff *et al.* 2001) to place the similarities and differences among the study populations in an explicitly evolutionary context, by reconstructing the evolution of behavioral, ecological, and demographic characters onto the accepted phylogeny of *Pan*. We tested whether changes in specific factors, argued to be important in the evolutionary history of *Pan*, such as (1) increased herbivory or (2) seasonality of rainfall, are associated with predictable behavioral differences, such as (1) more stable groups or (2) altered patterns of association. This combination of multivariate and phylogenetic analysis enabled us to formulate new hypotheses based on the identification of novel patterns of association of traits.

METHODS

Data matrix

A data matrix of 90 variables for six distinct chimpanzee and bonobo studies, referred to here as taxa (*sensu stricto* ‘operational taxonomic unit’) was compiled primarily from the published literature, with additional original data contributed by one coauthor (YS). Characters were chosen to describe key components of social structure and behavior as well as those factors considered potentially important in the evolution of *Pan*. Invariant traits were culled, resulting in a reduced data set of 82 variables (data and complete list of references are available in an electronic appendix¹).

Variables

The 82 variables, which include both continuous and coded data, can be divided into the following four data subsets:

I. Behavior Subset (n = 57)

This describes *Pan* social structure and behavior and includes the following five subsets. *A. Social Behavior Within Communities* documents male–female, female–female and male–male social relationships. *B. Social Behavior Between Communities* documents territoriality, the nature of interactions between communities, and the patterns of dispersal between them. *C. Reproductive Strategies* documents mating strategies and behavior, sexual selection, and infanticidal behavior. *D. Social Structure* assesses fission–fusion nature of the community by describing party size and composition, the extent of male–female association, and time spent as solitary individual. *E. Cultural Behavior* is limited to cultural behaviors that were well studied at several sites (so that absence of a behavior cannot be ascribed to differences between observers, or in the lengths of studies) and, when present, are common among the majority of individuals in a community (or some clear and predictable subset). Since data describing the frequencies of occurrence (both within and between communities) of many recently described behaviors (Whiten *et al.* 1999) are not currently available, these characters were not included in this study.

A. Social Behavior Within Communities (n = 20)

Adult patterns of grooming: Who grooms most frequently?

1. Grooming dyads (0 = male/male; 1 = male/female; 2 = female/female)

Adult patterns of association (0 = absent; 1 = rare; 2 = common): What is the degree of

2. Male–male association
3. Male–anestrous female association
4. Female–female association

Dominance hierarchies (0 = none; 1 = linear; 2 = high, middle and low rank detectable):

5. Female dominance hierarchy
6. Male dominance hierarchy
7. Male–female dominance? (0 = no dominance; 1 = males dominant to females; 2 = females dominant to males)

Cooperation (0 = never; 1 = rare; 2 = common):

8. Male–male coalitions for home range defense
9. Male–male coalitions for rank acquisition
10. Male–male coalitions in committing infanticide

Food sharing:

11. Food most commonly shared among adults (0 = meat; 1 = fruit)

Percentage of sharing among adults when:

12. Females share food with males
13. Females share food with females
14. Males share food with males
15. Males share food with females

Miscellaneous

16. Presence of genital–genital (G–G) rubbing (0 = absent; 1 = rare; 2 = common)
17. Presence of rump contact (0 = absent; 1 = rare; 2 = common)
18. Female response to immigrants (0 = welcome; 1 = neutral; 2 = aggressive)
19. Immigrants associate with (0 = males; 1 = females)
20. Percentage of infanticide victims who are cannibalized

B. Social Behavior Between Communities (n = 8)

21. Territorial (0 = no; 1 = yes)
22. Observed extra-group mating (0 = never; 1 = rare; 2 = common)
23. Degree of female transfer from natal community (0 = absent; 1 = <25%; 2 = 25–50%; 3 = 50–75%; 4 = >75%)
24. Degree of male transfer from natal community (0 = absent; 1 = <25%; 2 = 25–50%; 3 = 50–75%; 4 = >75%)

During inter-group encounters, there is:

25. Peaceful intermingling (0 = absent; 1 = rare; 2 = common)
26. Mating between members of adjacent communities (0 = absent; 1 = rare; 2 = common)
27. Female G–G rubbing (0 = absent; 1 = rare; 2 = common)
28. Most common interaction during inter-group encounters (0 = very aggressive; 1 = somewhat aggressive; 2 = aggressive leading into peaceful; 3 = nonaggressive)

C. Reproductive Strategies (n = 14)

29. Percentage of copulations that occur in maximal swelling
30. Mean length of postpartum amenorrhea (in months)

Percentage of matings that:

31. Are opportunistic
32. Occur in consortship
33. Are possessive
34. Have a dorsal–ventral mating position
35. Have a ventral–ventral mating position
36. Are interrupted by other males
37. Are initiated by males
38. Are obtained by the alpha male

Infanticide:

39. Occurs (0 = absent; 1 = present)
40. Percentage of infanticides committed by males
41. Percentage of infanticidal events occurring within a community
42. Percentage of infanticide victims who are male

D. Social structure (n = 9)

Percentage of parties that are:

43. Mixed sex and age classes
44. All-male
45. Mothers and dependent offspring only
46. Adult males and females with no offspring present
47. Solitary individuals
48. Mean party size
49. What percentage of time do adult females (with dependent offspring) spend alone
50. Size of female core area relative to that of males (in percent of male home range)
51. Is there a sex difference in day range? (0 = no; 1 = males travel farther)

E. Cultural Behavior (n = 6)

Tool use:

52. Occurrence of nut cracking (0 = absent; 1 = present)
53. Occurrence of ant or termite fishing (0 = absent; 1 = present)
54. Use of tools for food acquisition (0 = absent; 1 = present).
55. Occurrence of hunting or mammal eating (0 = absent or very rare (less than 1 per year); 1 = occasional; 2 = common)
56. Percentage of mammalian prey that are red colobus monkeys (0 = >50% ; 1 = 25–50%; 2 = <25%)
57. Individuals who obtain prey most frequently (0 = lone individuals; 1 = group of males).

II. Ecology Subset (n = 8)

Resource density and distribution are hypothesized as influencing female competitive regimes and resultant social behavior (e.g. van Schaik 1989). Increased reliance on herbs (with resulting decreased competition) has been argued to be a key factor in the evolution of sociality of bonobos (Wrangham 1986a). Differences in ripe fruit availability have been suggested as playing an important role in the relative sociality of female chimpanzees across sites (reviewed in Doran 1997). Since measures of resource availability and seasonal variation in diet (including fallback resources use) are not available from all sites, we use diet as a proxy. Ecological variables represent diet, ranging behavior, and home range overlap, and include:

Percentage of time spent feeding on:

58. Fruits
59. Herbs and leaves
60. Insects
61. Nuts
62. The average percentage of time spent feeding per day
63. Home range size (km²)
64. Amount of home range overlap (0 = absent; 1 = <25%; 2 = 25–50%; 3 = 50–75%)
65. Average day range (m).

III. Habitat Subset (n = 9)

These variables represent the physical characteristics of the environment, as well as relative predation and competition risk at the study site.

66. Elevation (m)
67. Average annual rainfall (mm)
68. Seasonal variation in rainfall (average number of months per year in which rainfall is less than 50 mm)
69. Mean minimum temperature (degrees Celsius)
70. Mean maximum temperature (degrees Celsius)
71. Degree of variation in mean monthly temperature (variation in monthly mean maximum or minimum temperature in 1 year)
72. Latitude (absolute number of degrees north or south of equator)
73. Number of sympatric anthropoid species present at site
74. Number of potential predators present at site.

IV. Demography Subset (n = 8)

These variables represent the demographic and life history variables at a study site.

75. Total community (unit-group) size
76. Adult sex ratio (female/males) in the community
77. Sex ratio (females/males) at birth
78. Mean length of maximum swelling (in months)
79. Percentage of estrus cycle spent in maximum swelling
80. Age at first pregnancy (years)
81. Average interbirth interval (months)
82. Number of adult males in community (unit-group).

Taxa

The taxa include two samples each of *P. t. schweinfurthii* (Gombe and Mahale), *P. t. verus* (Bossou and Taï), and *P. paniscus* (Lomako and Wamba), and are referred to by study-site name. Sites were selected because they provided the only existing studies from which data were available for a minimum of 20% of the 82 variables. We are not suggesting that these six sites represent the entire potential range of chimpanzee and/or bonobo behavior. Regrettably, no long-term study of habituated *P. t. troglodytes* is available for comparison.

At a few study sites, more than one community has been studied, although none had complete data for more than one community. Therefore, all variables were based on a single community when possible (Gombe, Kasakela; Mahale, M; Taï, North; Lomako, Eyengo; and Wamba, E 1). Since many of these studies have been ongoing for 20 years or more, and since behavior and demographic variables can alter through time, demographic data used in each study were taken, when possible, from the same time period as the behavioral data. For example, the demographic data from Bossou were taken from the same time period as Sakura's (1994) behavioral data.

The Bossou chimpanzee community is considered 'unique' by many ape researchers because it is a small isolated community (with one to two adult males), which has been relatively stable in size and composition for over 20 years. Although the presence of so few males at Bossou is unique for data presented here, this demographic makeup is not unique among all currently known communities (e.g. only one to two adult males have been present in the Taï (North) community since 1995; Boesch & Boesch-Achermann 2000). Although data from Taï, Gombe, and Mahale are based on the presence of neighboring contigu-

ous communities, the relative isolation of the Bossou community is also no longer unique to Bossou. The chimpanzees at Gombe have become increasingly isolated from other chimpanzee communities through time. Thus, Bossou provides an important case for evaluating how changing ecological, demographic, and environmental factors influence behavior in *Pan*.

Broad genetic sampling of chimpanzee mitochondrial DNA haplotypes across Africa has provided an understanding of the phylogenetic relationships of *Pan* subspecies included in this study (Bradley & Vigilant, Chapter 19). While there is no clear subdivision within chimpanzee subspecies, the two subspecies considered here (*P. t. verus* and *P. t. schweinfurthii*) form clear monophyletic clades, which cluster together to the exclusion of the bonobos. Therefore, all chimpanzees are more closely related to each other than they are to bonobos, and genetic similarity is greater among individuals within a chimpanzee subspecies than across subspecies.

Multivariate analysis

We use multivariate analysis to assess overall phenetic similarity, or overall similarity without any consideration of phylogeny. This method does not distinguish between features shared through inheritance from a common ancestor versus those that are acquired uniquely in a particular set of related taxa.

Distance statistics are used to summarize chimpanzee and bonobo affinities based on each of the four data sets (behavior, demography, ecology, and habitat). More specifically, average Euclidean distances (or average taxonomic distances, or ATDs) are calculated among taxa within each data set using data standardized to Z-scores for each of the 82 variables (Sneath & Sokal 1973; Reyment *et al.* 1984). This approach makes no parametric assumptions about homogeneity of dispersion matrices, normality, and so on, and some missing data can be accommodated without bias. Because raw variables are in very different scales and dimensionality, conversion of variables to Z-scores serves to weight them equally and render them commensurate and dimensionless (e.g. virtually all will take on values between -2.0 and +2.0). Tabular results of ATD matrices discussed in text are available in electronic appendices.

The information in the ATD matrices is then summarized and presented graphically via clustering and ordination. We used the UPGMA algorithm (unweighted pair group method with arithmetic mean) for clustering (Sneath

& Sokal 1973), and principal coordinates for ordination to reduce the information into two or three orthogonal axes of variation (Gower 1966; Rohlf 1972). Minimum spanning trees are superimposed on the ordination to help identify the group(s) most similar overall to another group(s); this also helps to disclose any distortion of the total ATD in the reduced dimensional space. We also examine the correlations between the original standardized data and their principal coordinates scores. This helps to identify especially influential variables associated with each axis of variation, and can thereby reveal 'contrast vectors' among groups in many cases (Corruccini 1978; Jungers 1988).

The ATD matrices, produced from each data subset, are then compared directly to each other via matrix correlations (or the standardized Mantel statistic) in order to discover predictable patterns of covariation (or the lack thereof). Significant correlations among such matrices were determined using a permutation approach (e.g. 5000 random permutations of one of the matrices in a pair-wise comparison; one-tailed probabilities are reported). The magnitude of the matrix correlation is less important than its level of significance. All calculations were performed using NTSYS-pc, version 1.80 (Rohlf 1993).

Phylogenetic analysis

The evolution of behavioral, ecological, and demographic characters was reconstructed onto the accepted phylogeny of the study populations *sensu stricto* Brooks & McLennan (1991; see also Wrangham 1986b; Ghiglieri 1987; Kappeler 1999), using MacClade 4.0 (Maddison & Maddison 2000), with the mountain gorilla as an outgroup. The theoretical and practical applicability of phylogenetic methods to the study of individual populations within a species is an intensively debated issue (see discussion in Borgerhoff *et al.* 2001). It is worth emphasizing that we did not use these data to generate a phylogeny for African apes, but rather mapped individual features onto an accepted molecular phylogeny. As noted below, this phylogeny is not, in fact, the most parsimonious resolution of this data set. However, our goal was not to generate a phylogeny of African apes based on behavioral characters. Rather it was to use phylogenetic methods to reconstruct the probable history of character evolution among a group of variously related populations of apes.

For this aspect of the study, continuous characters were recoded into a discontinuous format using visual gap coding. All characters were entered as unordered and unpolarized, that is we placed no limitation on how a character can change

through time. We did not examine the habitat characteristics of the study sites for this part of the study. In addition, two characters from the behavior subset were eliminated because of extensive missing data (frequency of possessive mating and frequency of interrupted mating) and a third character (frequency of ventral-ventral mating) was eliminated because it was the reciprocal of another character and therefore contained no additional information. Using this tree with the data set mapped onto the accepted phylogeny of the populations studied, we calculated consistency indices (CI) and retention indices (RI) for the entire tree, for individual characters, and for subsets (or ensembles) of characters. These are two widely used measures of the extent to which the data indicate that there has been parallel evolution in the characters. The CI indicates how many changes in a character take place in a tree, although it does not indicate where changes occur in the tree. The RI indicates to what extent characters define nodes (for examples, see discussion in Kitching *et al.* 1998). We also examined the distribution of features throughout the tree, reconstructed ancestral states and character evolution using maximum parsimony and tabulated the changes reconstructed along each branch, using the 'almost all changes' options of MacClade 4 (Maddison & Maddison 2000).

RESULTS

Multivariate analysis

BEHAVIORAL AFFINITIES

Overall behavioral affinities

The average taxonomic distance for all taxa, based on the 57 behavioral variables, and summarized by UPGMA clustering (Figure 1.1(a)), indicates that chimpanzee and bonobo behavioral affinities are similar to those reflective of phylogeny. The phenogram displays two clusters, (1) bonobos (Wamba and Lomako) and (2) chimpanzees. However, within the chimpanzee cluster, the *P. t. schweinfurthii* taxa (Gombe and Mahale) cluster together, as would be expected on the basis of phylogeny, unlike the *P. t. verus* taxa (Taï and Bossou). Bossou is distant from all other common chimpanzees, and does not show special affinity to the other *P. t. verus* taxon (Taï), as would be predicted on the basis of phylogeny alone.

This distinction is even more apparent in the principal coordinates ordination of the same behavior distance matrix (Figure 1.1(b)). The first two principal coordinates axes

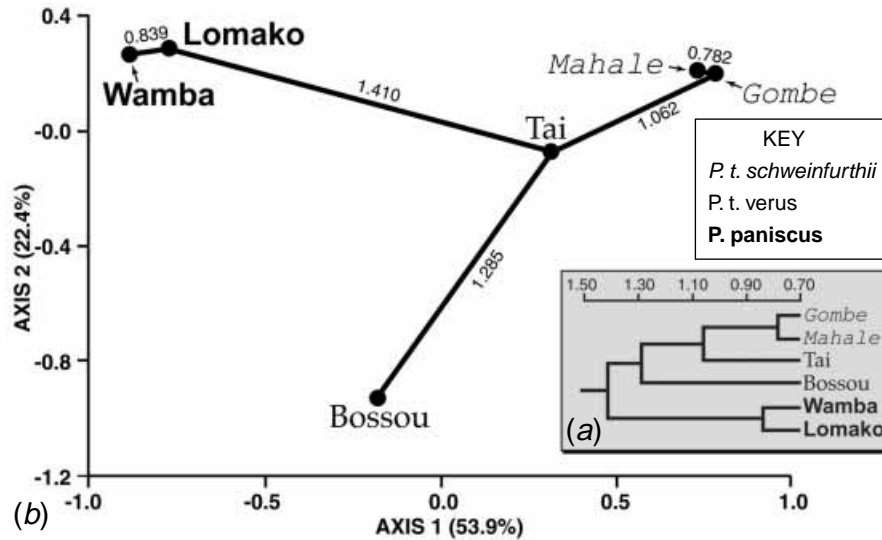


Fig. 1.1. Summary of average taxonomic distances generated from BEHAVIOR data subset ($n = 6$ taxa, 57 variables) using (a) UPGMA clustering and (b) principal coordinate analysis. In principal coordinate summary, taxa are joined to nearest neighbor by minimum spanning trees; average taxonomic distances between taxa are indicated. Contrast vector is itemized separately in Table 1.1.

account for 76% of the variation in the data, with the first axis alone accounting for more than half of total variation. Along the first axis there is a tight clustering of the two bonobo taxa (Wamba and Lomako), and an even tighter clustering of the two *P. t. schweinfurthii* taxa (Mahale and Gombe), with the *P. t. verus* taxa intermediate between them. Tai groups most closely with Mahale and Gombe; Bossou falls mid-way along the axis, although closest to Tai in overall behavioral similarity. Along the second axis, Bossou (and Tai to a much lesser extent) is the major outlier.

What variables are influential in driving the behavioral affinities?

Thirty-three of the original 57 behavioral variables are significantly correlated with the first axis, and are thus influential in distinguishing taxa along it, primarily serving to separate bonobos from chimpanzees (Table 1.1(a)). Twenty-nine of these 33 (significant) variables have complete or nearly complete data (data missing from 0–1 sites). The 29 variables include ‘bonobo’ traits, which occur commonly in bonobos, and are absent or rare in chimpanzees (strong male–female and female–female bonds, less disparity in

male and female ranging behavior, less violent and more varied inter-group encounters), and ‘chimpanzee’ traits, which are common in chimpanzees and absent, or greatly reduced, in bonobos (strong male bonds, infanticide, territoriality, frequent hunting of monkeys, and tool use) (Table 1.1(a)).

Of these significant variables for which data is complete for *all* sites ($n = 21$), Bossou chimpanzees share (1) 38% with all chimpanzees to the exclusion of bonobos (including tool use, mating style, male dominance to females and longer postpartum amenorrhea), (2) 38% with bonobos to the exclusion of all other chimpanzees (including the absence of (a) hunting, (b) territoriality and (c) differentiated male–male relationships), and (3) 24% with Tai chimpanzees and bonobos, to the exclusion of *P. t. schweinfurthii* (including the absence of infanticide and more frequent association between males and females) (Table 1.1(a)).

Five variables are influential in distinguishing taxa along the second axis, and thus Bossou and, to a lesser extent, Tai, from all other taxa. These include nut cracking, a behavior shared exclusively by Tai and Bossou, as well as behaviors that are unique or exaggerated in frequency at Bossou compared to every other site, including male transfer and heightened male–female and female–female social relations (Table 1.1(b)).

Are the results from each subset of behavior similar?

A comparison of the ATD matrices from each of the five subsets of behavior (within-group, between-group, social

Table 1.1. Contrast vector among variables for behavior subset
(a) Contrast vector among variables (Axis 1) for behavior subset

Character: 'Bonobo' Traits	Load	Bossou	Character: 'Chimpanzee' Traits	Load	Bossou
<i>I. No missing data</i>			<i>I. No missing data</i>		
Lack of preference for red colobus	^a -0.917	2	Degree of male-male association	^a 0.917	2
Fruit (versus meat) is most commonly shared food item	^a -0.917	2	Frequency of hunting or mammal meat-eating	^a 0.917	2
Intergroup encounter – G-G rubbing common	^a -0.880	1	Tendency for groups of males to hunt more frequently than solitary males	^a 0.917	2
Immigrants associate with females (versus males)	^a -0.880	1	Territorial	^a 0.917	2
Intergroup encounter – mating common	^a -0.872	1	Male-male coalition: home range defense	^a 0.917	2
Frequency of ventral-ventral mating	^b -0.789	1	Tool use: ant or termite fish	^a 0.880	1
Degree of male-female association	^b -0.806	3	Tool use: for food acquisition	^a 0.880	1
Degree of female-female association	^b -0.806	3	Males dominant to females	^a 0.880	1
			Frequency of dorso-ventral mating	^b 0.789	1
			Occurrence of infanticide	^b 0.806	3
			Percentage of infanticides that are within group	^b 0.784	3
			Male-male coalition: for rank	^b 0.775	2
			Time spent alone by females	^b 0.762	3
<i>II. Data missing from one site</i>			<i>II. Data missing from one site</i>		
Nonaggressive intergroup encounters	^a -0.973		Males share food with males	^a 0.876	
Male-male rump contact	^a -0.833		Mean length of postpartum amenorrhoea	^a 0.893	
Female core area size relative to male's	^a -0.847		Percentage lone individual	^a 0.853	
Females share food with males	^b 0.765	1	Male-male cooperation for infanticide	^b 0.791	1

(b) Contrast vector among variables (Axis 2) for behavior subset

Character	Load	Bossou
<i>I. No data missing</i>		
Percentage of parties-mothers	^a -0.890	Unique
Degree of male transfer	^a -0.830	Unique
Tool use – nut crack	^a -0.812	Shares with Tai
<i>II. Data Missing From one Site</i>		
Males share food with females	^a -0.904	
Adult grooming – who grooms who most?	^b -0.804	

Notes:

Load is the correlation between original variable and the summary variable; $n = 6$ taxa; 4 degrees of freedom; ^a data significant at $p < 0.05$ (i.e. $r = \pm 0.81$); ^b marginally significant ($0.05 < p < 0.1$). Similarity of Bossou to other sites is indicated by: 1, similar to all other chimpanzee sites; 2, similar to bonobos and distinct from all other chimpanzee sites; and 3, similar to Tai chimpanzees and bonobos and distinct from *P. t. schweinfurthii*.

structure, sex, and culture) indicates that all matrices are highly correlated with each other, except the sex matrix, which is not significantly correlated with any matrix, and the social structure matrix, which is only significantly correlated with within-group and cultural matrices (data in the electronic appendix). UPGMA clustering (of ATD data) from each behavioral data subset (except sex) indicates a clear segregation of chimpanzees and bonobos. Results from the different data subsets vary primarily in the relationship of Bossou to other taxa.

Affinities based on reproductive strategies (sex) indicate a clustering of taxa that is independent of phylogeny, with Lomako, Bossou, Taï and to a lesser extent, Wamba, clustering together versus Gombe and Mahale chimpanzees. As a result of greater than average missing data (20%), these results should be viewed with caution. The presence or absence of infanticide drives clustering patterns in this subset.

DEMOGRAPHIC AFFINITIES

The average taxonomic distances for all taxa, summarized by UPGMA clustering (Figure 1.2(a)), indicate that chimpanzee and bonobo demographic affinities show little similarity to either the known phylogenetic relationship or behavioral affinities of the taxa. Mahale and Taï cluster together versus all other taxa. Bonobos cluster together, but they are also similar to Gombe chimpanzees. Demographically, Bossou does not show strong overall similarity to any other taxa.

Principal coordinate analysis illustrates this more clearly: there are three distinct clusters on the basis of demographic variables (Figure 1.2(b)). The first two principal coordinate axes account for 86.2% of the variation in the data, with the first axis accounting for 59.4%. Traits that distinguish taxa along the first axis and, thus, Mahale and Taï from other taxa, include larger community size, higher adult female/male sex ratio, and longer interbirth interval. Traits that are correlated with the second axis and distinguish Bossou from other taxa include fewer adult males in the community and a decreased age of first pregnancy.

BEHAVIORAL ECOLOGY AFFINITIES

The average taxonomic distances for all taxa, summarized by UPGMA clustering (Figure 1.3(a)), indicate that chimpanzee and bonobo affinities based on diet and ranging behavior (ecology) show almost no similarity to the known phylogenetic relationships of the taxa. Neither the bonobo taxa nor any chimpanzee subspecies cluster together. There is much less variance in ATDs between taxa in this data

subset than in any other. In the principal coordinate ordination, taxa space themselves evenly, with 61.1% of the total variation explained nearly equally by the first two axes (Figure 1.3(b)). The percentage of fruit in the diet is a significant variable in the separation of taxa along the first axis; bonobos and Taï chimpanzees have a tendency towards greater frugivory than the other taxa. The amount of herbs and leaves in the diet does not distinguish taxa.

HABITAT AFFINITIES

The average taxonomic distances for all taxa, summarized by UPGMA clustering (Figure 1.4(a)), indicate that chimpanzee and bonobo affinities based solely on physical characteristics of the environment (habitat) show a pattern suggestive of phylogeny, but with two obvious exceptions. Contrary to phylogenetic predictions, (1) Taï clusters with the bonobos and (2) Bossou is distant from all other taxa. The first two principal coordinate axes account for 77.4% of the variation in the data. Bossou separates from the other taxa on the basis of its greater rainfall and higher average maximum temperature; bonobos and Taï, to a lesser extent, are distinguished from (other) chimpanzees primarily by reduced seasonality of rainfall in their habitats (Figure 1.4(b)).

COMPARISONS OF RESULTS FROM THE FOUR DATA SETS

Having considered chimpanzee and bonobo affinities based on four independent data sets, we next ask which, if any, data sets give similar results. The behavior and habitat ATD matrices are highly correlated (electronic appendix). This indicates that patterns of association determined from 57 variables that summarize social behavior and nine variables describing the physical habitat are similar.

AFFINITIES BASED ON TOTAL DATA SET

When the entire data set of 82 variables is combined, results are similar to those produced from the behavior data set (Figure 1.5(a) and (b)). This is hardly surprising given that variables are weighted equally and behavioral variables make up the vast majority of the total data set. Figure 1.5(b) lists the variables that are significant, in addition to behavior variables discussed previously (Table 1.1), and those that are significantly correlated with the first axis, and thus serve to distinguish chimpanzees and bonobos. The variable most highly correlated to the first axis (including all behavioral variables), is the average number of months with less than 50 mm of rainfall, with the bonobo locations showing

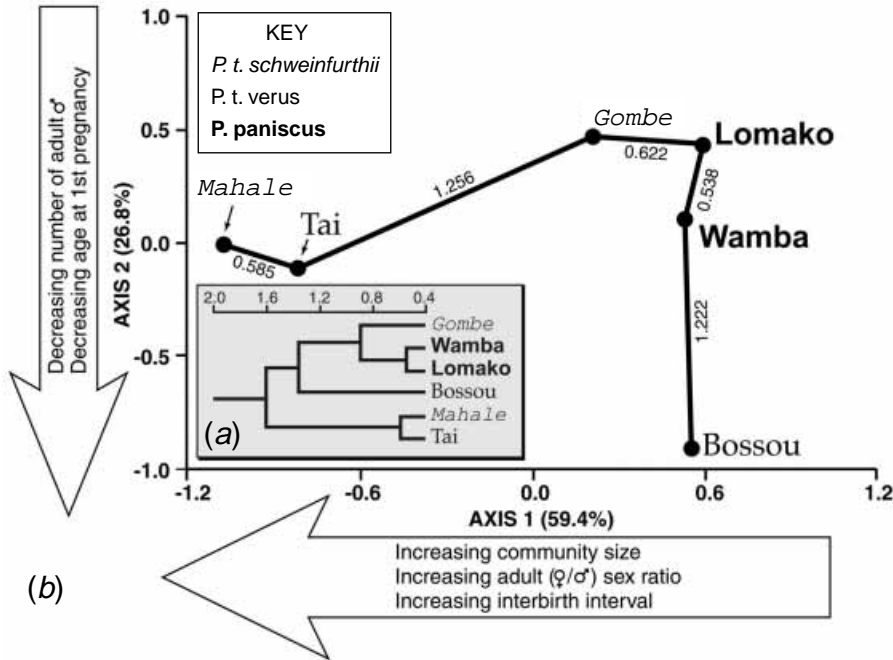


Fig. 1.2. Summary of average taxonomic distances generated from DEMOGRAPHY/LIFE HISTORY data subset ($n=6$ taxa, 8 variables) using (a) UPGMA clustering and (b) principal coordi-

nate analysis. In principal coordinate summary, taxa are joined to nearest neighbor by minimum spanning trees; average taxonomic distances between taxa are indicated.

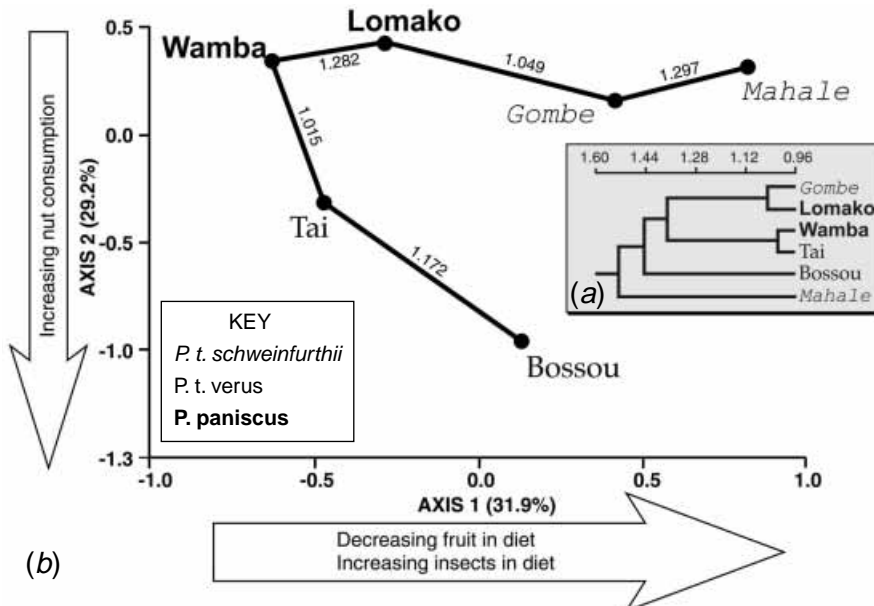


Fig. 1.3. Summary of average taxonomic distances generated from ECOLOGY (diet and ranging behavior) data subset ($n=6$ taxa, 8 variables) using (a) UPGMA clustering and (b) principal coordi-

nate analysis. In principal coordinate summary, taxa are joined to nearest neighbor by minimum spanning trees; average taxonomic distances between taxa are indicated.

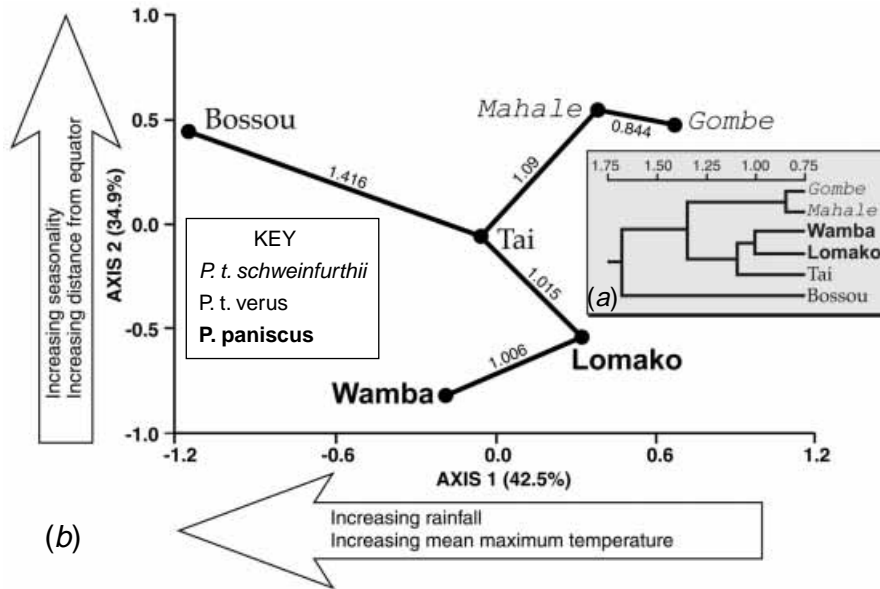


Fig. 1.4. Summary of average taxonomic distances generated from HABILAT data subset ($n = 6$ taxa, 9 variables) using (a) UPGMA clustering and (b) principal coordinate analysis. In principal coordinate

summary, taxa are joined to nearest neighbor by minimum spanning trees; average taxonomic distances between taxa are indicated.

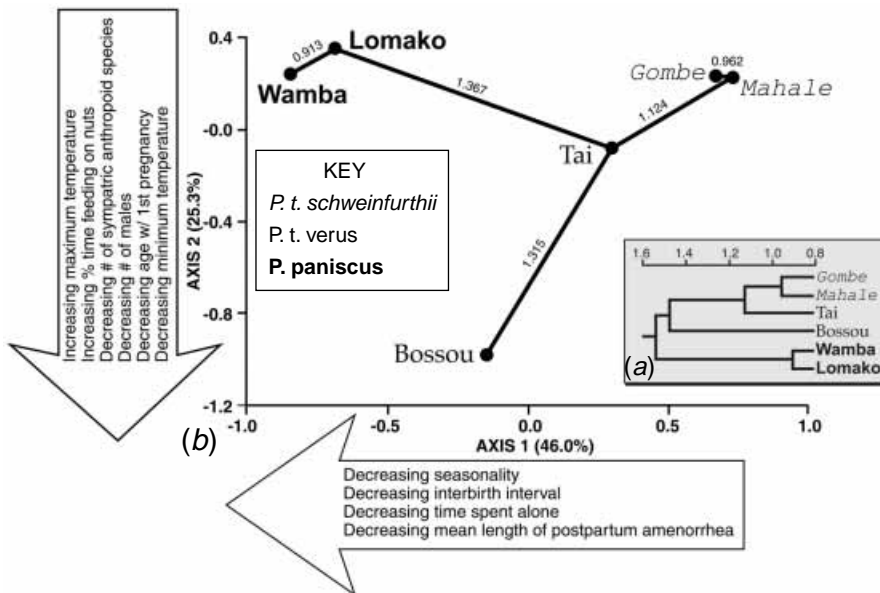


Fig. 1.5. Summary of average taxonomic distances generated from ENTIRE chimpanzee and bonobo data subset ($n = 6$ taxa, 82 variables) using (a) UPGMA clustering and (b) principal coordinate analysis. In principal coordinate summary, taxa are joined to nearest neighbor by minimum spanning trees; average taxonomic

distances between taxa are indicated. Note that the contrast vectors show only significant nonbehavioral variables; the behavioral variable loadings are essentially the same as those seen in Table 1.1.

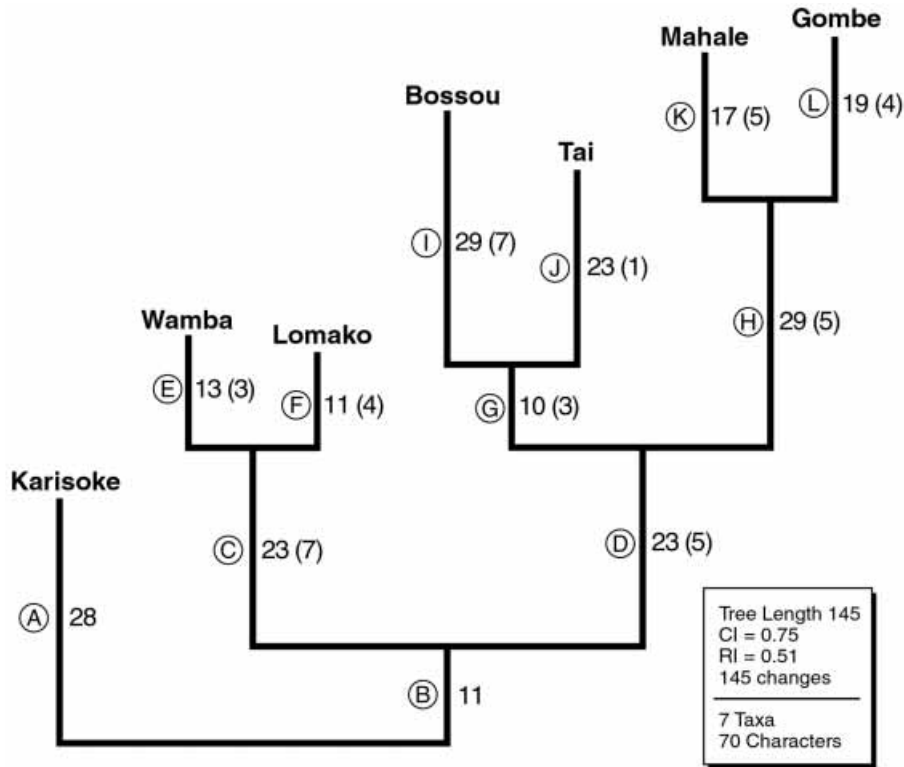


Fig. 1.6. Molecular phylogeny of study populations used in this study with the number of character changes along each branch indicated. The higher number indicates total changes (both ambiguous and unambiguous); the number in parentheses is the number of unambiguous changes (discussed in the text). The character changes along each of the lettered branches are listed in the electronic appendix.

reduced seasonality of rainfall. Additional variables that are significantly correlated include infanticidal behavior (absent in bonobos) and interbirth intervals (shorter in bonobos).

Phylogenetic analysis

The reconstruction of trait evolution accords well with and complements the results of the multivariate analyses by placing the similarities and differences among the study populations in an explicitly evolutionary perspective. Overall, these data (excluding the habitat features) mapped onto the chimpanzee phylogeny have a consistency index of 0.75 and a retention index of 0.51. The lower retention index reflects the fact that many of the features included in

this analysis are characteristic of individual study populations and hence do not contribute to resolution of nodes.

Among the different subsets of the data, the large behavior subset has a consistency index of 0.76, similar to that for the overall tree, and a retention index of 0.58. The smaller number of ecological features has a slightly higher consistency index (0.82) but a substantially lower retention index (0.40), reflecting the fact that the ecological changes tend to be characteristic of individual sites or studies rather than groups of sites. The demographic and life history characters have a lower consistency index (0.62) and a very low retention index (0.11), reflecting the fact that the data on life history and demography largely record site-specific differences, and these features are rarely shared by related populations.

Figure 1.6 shows the number of character state changes occurring along each of the branches in the accepted phylogeny of the study populations. Because of the homoplasy (parallel evolution of similar features) in the data and the lack of additional outgroups, there were several equally parsimonious reconstructions of character change for many traits on this tree and, hence, many changes that cannot be

reconstructed precisely using parsimony. The reconstructed changes are referred to as ambiguous changes when there are several possible reconstructions and thus the beginning and/or ending character states are impossible to reconstruct precisely, and as unambiguous changes when the character change along the branch node can be reconstructed precisely. In our tabulations, we have shown both the total number of (ambiguous + unambiguous) changes and the number of unambiguous changes along each branch. The overall pattern is the same for both sets of changes (for individual characters changing along each branch, see the electronic appendix).

The node uniting bonobos and chimpanzees is characterized by 11 character changes (Figure 1.6). These are, by necessity, all ambiguous as we did not root the tree or have any additional outgroup except the mountain gorillas. If the condition in the mountain gorillas is taken as the appropriate outgroup (for lack of any comparable data on any other gorilla taxon), then the ancestral chimpanzee lineage was characterized by several differences in ecology, demography, and behavior. These include a decrease in folivory, an increased day range, an increase in both the time and the percentage of the cycle of maximum sexual swelling, an increase in the age of first pregnancy, an increase in the frequency of female transfer, a decrease in the frequency of male transfer, an increase in the amount of mating initiated by males, changes in group cohesion, including an increase in time spent as lone individuals (rather than in a party), particularly for females, as well as an increase in the frequency of nursery parties (mothers and offspring to the exclusion of males). Greater knowledge of the ecological and behavioral features of lowland gorillas, a more concerted effort at identifying features distinguishing chimpanzees from other apes, and a consideration of the likely ancestral conditions for African apes would undoubtedly modify this list.

The individual branch leading to the bonobo populations and that uniting all of the chimpanzee groups are each well-supported. The lineage leading to bonobos (Wamba and Lomako; *Pan paniscus*) as a species is characterized by 23 ambiguous and seven unambiguous features. The unambiguous features are mostly related to intergroup encounters and reproduction, including decreased aggression, more frequent intergroup mating, occurrence of ventral-ventral mating and G-G rubbing, lack of male dominance to females, and by the tendency of immigrant females to associate with females rather than males. Each of the bonobo populations is characterized by a much smaller number of site-specific features.

The common node uniting western (Taï and Bossou; *Pan troglodytes verus*) and eastern populations (Gombe and Mahale; *Pan troglodytes schweinfurthii*) is supported by a total of 23 changes, 5 of which are unequivocal. The unambiguous changes uniting the different populations of *Pan troglodytes* include using tools to acquire food, termite fishing with tools, longer interbirth interval, decreased frequency of mixed-sex parties, and increased frequency of male-male coalitions.

The patterns of character evolution in the two subspecies of *Pan troglodytes* are strikingly different. The eastern chimpanzees, *Pan troglodytes schweinfurthii*, have many more shared features than site-specific characteristics, while the western chimpanzees, *Pan troglodytes verus*, have few shared features and many site-specific features. Thus, the common branch leading to the Gombe and Mahale populations is characterized by a total of 29 changes of which 5 are unambiguous. In contrast, the number of characters that are unique to each of these sites is much smaller – 17 for Mahale and 19 for Gombe. These findings accord well with the multivariate results that found that these two populations clustered tightly in all analyses, but were usually well-separated from the (western) chimpanzees. The unambiguous changes on the Mahale-Gombe branch include increased number of male parties, lone individuals and lone females, increased cooperative male infanticide and post-infanticidal cannibalism, and reduced female sharing.

Compared with the eastern (Mahale and Gombe) populations, the western chimpanzees from Bossou and Taï are striking for their lack of similarity. The node linking them is characterized by a total of only ten changes of which three are unambiguous (nuts in their diet, nut-related tool use, and higher degree of association between males and anestrus females).

In contrast, the Taï chimpanzees show 23 site-specific characteristics (one unambiguous) and the Bossou chimps have diverged more from their last common ancestor (with the Taï chimpanzees) than any population in the study, with 29 changes, of which 7 are unambiguous. The unambiguous change unique to the Taï population is a dramatic increase in the frequency of male parties. The Bossou population is characterized by a smaller home range, decreased age at first pregnancy, increased frequency of parties including mothers and offspring, and several features related to the presence of only one male, including greater frequency of alpha male mating, decreased number of male-male coalitions, increased male transfer, and increased male sharing with females.

The phylogenetic differences in the patterning of changes in eastern and western chimpanzees accords well with the results of the multivariate analyses, in which the geographically close Mahale and Gombe always clustered together and are distinct from the western chimpanzees, whereas the two western sites – Taï and Bossou – were as distant from one another as they were from the eastern chimpanzees. Indeed, the Bossou population was the most widely separated chimpanzee population in all of the multivariate analyses, and also has the greatest number of site-specific changes in the analysis of trait (character) evolution.

DISCUSSION

Distinctive features of African apes

CHIMPANZEE–BONOBO DICHOTOMY

A major goal of this study was to examine the extent of similarities and differences between bonobos and chimpanzees, an issue that has recently been brought to the forefront by Stanford's (1998) stimulating review of this topic. In the multivariate analyses, bonobos and chimpanzees segregate on the basis of overall behavior (based on 57 variables), as well as in nearly every subset of behavioral data, including social relationships and social structure within the community, intercommunity relationships and in culture related to tool use and hunting. Traits that distinguish bonobos from chimpanzees in this study include: (1) greater female sociality, as indicated by greater male–female and female–female association, reduced tendency for females to be found alone, and less disparity in male and female ranging behavior; (2) absence of male dominance and a greater tendency for females to possess and be responsible for distribution of resources; (3) more varied intergroup encounters, as indicated by G–G rubbing and mating between communities during intergroup encounters; and (4) different mechanisms by which female immigrants transfer into and become established in a new community, as indicated by their associating with other females versus males. Traits that are common in chimpanzees and absent, or greatly reduced, in bonobos include: (1) strong male–male bonds, as indicated by a high degree of male–male association and the frequent formation of male–male coalitions to establish and maintain rank, defend territories, and while engaging in infanticidal activities; (2) male dominance to females; (3) decreased female sociality; (4) territoriality and aggressive defense of home range; (5) frequent hunting of monkeys; and (6) tool use for food acquisition.

The large number of character changes that are reconstructed along both the branch leading to bonobos and that leading to chimpanzees in the phylogenetic analysis are in accord with the results of the multivariate analyses. These two species are each distinguished by numerous character changes; moreover, the unique evolutionary changes reconstructed in the evolution of the bonobo ancestor and in the chimpanzee ancestor accord with those identified in other studies (Wrangham 1986b; Ghiglieri 1987; White 1996a).

These results are noteworthy in reinforcing the distinction between the two species, at least on the basis of currently available data. In and of itself, this is a not insignificant point given Stanford's (1998) recent claim. Yet in addition, this study provides the first quantitative analysis of similarities and differences between the two species based on a wide range of variables.

CHIMPANZES: DICHOTOMY BETWEEN EASTERN AND WESTERN POPULATIONS

Results from multivariate analysis indicate similarity in behavior within the eastern chimpanzees (*Pan troglodytes schweinfurthii*) at Mahale and Gombe. However, the western (*Pan troglodytes verus*) chimpanzees at Taï and Bossou are widely separated from one another. Ecologically, behaviorally, and in terms of demography and habitat, the two sites are often more similar to another ape population (chimpanzee, bonobo, or gorilla) than to each other (Figure 1.7). This same pattern is evident in the phylogenetic analyses. The branch leading to the eastern chimpanzees is one of the longest in the tree, reflecting the fact that Mahale and Gombe share many unique features relative to other chimpanzees. In contrast, the two western populations are linked by a very short branch and show many more changes characteristic of the individual sites.

Geographic distances between Mahale and Gombe (200 km) and Taï and Bossou (300 km) are similar (Boesch & Boesch-Achermann 2000), and therefore are unlikely to explain the behavioral differences, particularly since dispersal (as evidenced by maternally transmitted genotypes) has been detected over distances of 900 km in *P. t. verus* (Morin *et al.* 1994). Results of wider variation in western versus eastern chimpanzee behavior are interesting, in part, because they coincide with greater genetic (mtDNA) variability. However, whether this indicates a true difference in the variation in behavior of western versus eastern chimpanzees is unclear, since this finding is based on a very small sample size, with only two communities of each subspecies, one of which (Bossou, discussed below) is characterized by

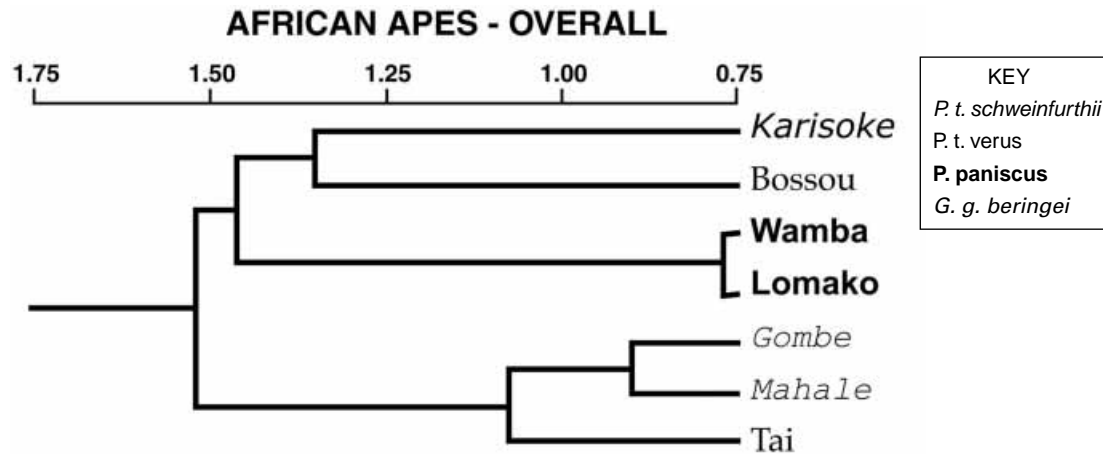


Fig. 1.7. A phenogram of the UPGMA clustering of African apes, including mountain gorillas in addition to bonobos and chimpanzees, based on average taxonomic distances computed from overall data set ($n = 7$ taxa, 81 variables).

unusual demographic and environmental conditions. Additional study of chimpanzees from a wider range of their geographic distribution should clarify the issue. Currently, there are three additional ongoing studies of habituated eastern chimpanzees (Kanyawara, Ngogo, and Budongo). As more data on chimpanzee behavior become available from these and other sites, it will be interesting to test whether there remains a behavioral distinction between eastern and western chimpanzees.

Two key traits distinguish western from eastern chimpanzees (considered in this study). First, the presence of nut eating and associated tool use occurs in western (but not eastern) chimpanzees, a trait that has been noted previously (McGrew 1992), and which does not typify all known western chimpanzees (Boesch 1994). Second, western chimpanzees show greater male-(anestrus) female association and affiliation than eastern chimpanzees, where females are less social and spend more time alone with their offspring. This decreased female sociality is coupled with the absence or reduction in frequency of infanticide in western chimpanzees. The prevalence of infanticide has been documented at every eastern site studied to date, including sites not included in this study, such as Kanyawara, Ngogo, and Budongo (Clark-Arcadi & Wrangham 1999). It has not been recorded for western chimpanzees, in spite of studies of longer duration (and thus likelihood of detection) than at Kanyawara, Ngogo, and Budongo.

Decreased female sociality and increased prevalence of

infanticide in eastern chimpanzees are associated with differences in habitat. The two eastern sites are characterized by increased seasonality of rainfall, that is, an increased number of dry season months per year, relative to the two western chimpanzee and central African bonobo sites. Increased seasonality of rainfall is likely to result in greater seasonal variance in fruit availability, although phenological data are not currently available to test this hypothesis. Mean chimpanzee party size is known to be limited by the availability of ripe fruit; chimpanzees, and in particular female chimpanzees, respond to reduction in ripe fruit availability by reducing party size (for review see Doran 1997). Permanent female affiliation with males has been hypothesized to be a female counter-strategy to infanticide (van Schaik 1996; van Schaik & Kappeler 1997). Thus, it is possible that the costs (in terms of feeding competition) of female association with males on a more permanent basis may be too great to permit it to serve as an effective counter-strategy to infanticide in habitats with considerable annual variance in fruit production (as measured in this study by rainfall). As a result, in eastern chimpanzees, male-female association occurs less frequently and infanticide occurs (relatively) more often than in more stable environments, such as at Tai and Bossou, where female chimpanzees may benefit from more frequent male-female association with a reduction in infant mortality though infanticide. Thus, we hypothesize that for chimpanzees in more seasonal environments, seasonality of rainfall results in greater variance in fruit availability which, in turn, necessitates more independent female foraging, leaving females more vulnerable to infanticide. Thus, seasonality of rainfall may have a potentially profound impact on infanticidal behavior in fission-fusion species.

Interrelationship of behavior, ecology, habitat, and life history/demography

ECOLOGICAL FACTORS

Resource density and distribution have been hypothesized as influencing female competitive regimes and resultant social behavior (e.g. van Schaik 1989). Ecological explanations have figured heavily in the discussion of the evolution of chimpanzee and bonobo behavior. Reduced female feeding competition (for bonobos relative to chimpanzees) has been hypothesized as enabling the formation of more stable bonobo parties, which in turn permitted greater female sociality, an important step in the evolution of bonobo sociality (Wrangham 1986a). Among the hypotheses that have been proposed to account for reduced feeding competition in bonobos are bonobos' (1) greater reliance on herbs in diet (Wrangham 1986a); (2) use of larger fruit trees (White 1986; Badrian & Badrian 1988); and (3) more constant source of fruit, as a result of release from fluctuation in fruit availability as a result of their restricted geographical distribution relative to chimpanzees (Malenky 1990).

Results from this study indicate that although there are clear species-specific differences in behavior, there is no species-specific difference in basic diet. Bonobos do not consume, or at least spend more time eating, a greater amount of herbs and leaves compared to chimpanzees. In fact, although all chimpanzees and bonobos are highly frugivorous, bonobos (along with Taï chimpanzees) had the highest percentage of fruit in their diet, implying that herb use does not decrease their reliance on fruit. Thus, it is unlikely that bonobo herb use significantly reduces feeding competition relative to chimpanzees and, therefore, may not be a major factor in the evolution of bonobo party stability (and subsequent sociality).

The most significantly correlated variable distinguishing chimpanzees and bonobos in this study is the average number of dry season months per year, with bonobos having no, or few, dry months per year. This finding is concordant with Malenky's (1990) hypothesis that bonobo sociality may result from their release from the fluctuation in fruit availability that is common at chimpanzee sites, if seasonality of rainfall is considered a proxy for seasonality in fruit production (as discussed above). Phenological data from a wide range of chimpanzee and bonobo sites, which are not currently available, are necessary to make a direct test of this hypothesis. Additionally, to examine this hypothesis more fully it will be important to examine whether variation in

fruit availability is greater in a more southern (and seasonal) end of bonobo distribution (see Myers-Thompson, Chapter 4) and, if so, whether its impact on behavior is predictable (smaller parties and more variation in party size).

The phylogenetic analysis offers an additional way to test for consistent causal relationships between ecological and behavioral variables by looking for consistent patterns of associated change between individual characters, for example diet and group size (Eggleton & Vane Wright 1994). In this study, for example, Lomako, but not Wamba bonobos, are characterized by increased herbivory. The typical bonobo patterns of sociality (increased female-female and male-female association and affiliation) actually precede the occurrence of herbivory, appearing on the branch leading to the bonobo lineage (Figure 1.6). Another example relates to causal factors of infanticide. Differences in the degree of home range overlap are not associated with differences in the prevalence of infanticide, since the prevalence of infanticide differs remarkably at Mahale, Gombe, and Taï, in spite of a similar degree of home range overlap.

LIFE HISTORY/DEMOGRAPHY

In this study, demographic factors do not uniformly have an impact on behavior. The behavior and demography ATD matrices were not significantly correlated. In the multivariate analyses, Taï and Mahale clustered together on the basis of demographic features, particularly on the basis of large community size, high adult female to male sex ratio, and relatively longer interbirth intervals. These demographic similarities were not associated with clear behavioral differences. The phylogenetic analysis reinforces the results from the multivariate analysis; there is a lack of clear causality between demographic/life history factors and behavior in this study. One of the more surprising results of the phylogenetic analysis was the relatively low consistency index (CI = 0.62) and retention index (RI = 0.11) of the life history/demography characters compared with the ecological and behavioral characters. Comparative biologists have debated the extent to which life history features are more (Alberch 1990; Vrba 1990) or less (Vrba 1990) likely to show extensive homoplasy (parallel evolution of similar features) relative to other aspects of an animal's biology. This study supports the view that these features are subject to extensive homoplasy, as most of the change in life history/demography characters takes place at the local population level. Of 21 reconstructed changes in demography/life history characters among chimpanzees, 15 were at the level of individual populations, two at the subspecies level, three at the

species level, and three at the generic level. It is worth noting, however, that this study, like most others, involved considerable preselection of characters to be analyzed. That is, characters were chosen specifically because they showed variation between species, subspecies, or populations, that is invariant characters were culled. Aspects of life history and demography that were the same for all African apes or all hominoids, such as a tendency for single births, were not included in the analysis.

The role of phylogeny

In recent years, primatologists have become increasingly aware that phylogeny is an important consideration in attempts to evaluate the evolution of adaptations (e.g. Fleagle 1992; DiFiore & Rendall 1994; Lee 1999; Nunn & Barton 2001). However, there is considerable debate as to the proper way to evaluate the role of phylogeny in the evolution of aspects of behavior and ecology, the significance of phylogenetic patterns in the distribution of behavioral and ecological characteristics, and in the appropriateness of even considering behavioral characteristics in a phylogenetic perspective (Robson-Brown 1999). Indeed, among the five coauthors of this paper, we probably embody many of the varied views of enthusiasm, utility, trepidation, skepticism, and confusion that are evoked among primatologists today during the discussion of phylogenetic considerations of behavior. Nevertheless, the results of this study illustrate quite clearly why phylogenetic considerations are both appropriate and valuable for understanding the evolution of behavior and ecology, as well as point to some of its limitations.

A common view of behavioral (and ecological) features is that they are so variable between populations (or within species and genera) that they do not generally reflect phylogenetic relationships. In other words, they show too much parallel evolution, compared to other aspects of an animal's biology (such as tooth structure or ear morphology) commonly used in taxonomic studies. However, the few formal attempts to compare levels of homoplasy among behavioral, cranial, postcranial, and biomolecular features, have not generally found a consistent pattern indicating greater homoplasy of behavioral features (see Lockwood & Fleagle 1999 and references therein). Indeed, among phylogenetic studies of primate behavior and morphology, the behavioral studies show some of the lowest levels of homoplasy – much lower than many studies of morphological or biomolecular evolution.

Features of behavior, ecology, and life history/demography used in this study and mapped onto the commonly accepted phylogeny of African great apes, show a CI of 0.75. This is almost exactly the level of homoplasy expected for seven taxa, according to a formula based on a broad analysis of a very large sample of phylogenetic studies from a wide range of organisms and many types of characters (Sanderson & Donoghue 1989). Thus, behavioral features show no more homoplasy than other aspects of an animal's biology. Indeed the CI of 0.75 shows that, in this study, a parsimonious reconstruction of the evolution of these behavioral features among the taxa being considered accords well with the accepted phylogeny of the taxa.

What is the significance of all this? Essentially, it just documents that, overall, more closely related groups of chimpanzees tend to be more similar in behavior. There are some notable exceptions; there are some extremely divergent characters and some divergent taxa (discussed below). However, this general conclusion is a fairly routine expectation based on the assumption that species, subspecies, and populations have not been created *de novo*, but have evolved by modification from other chimpanzee species, subspecies, and populations. Thus, as we have discussed in the previous paragraphs, gorilla, bonobos, eastern chimpanzees, and western chimpanzees can each be characterized by clusters of shared features of behavior and ecology. This does not mean that the behavior of chimpanzees is 'constrained' by phylogeny in anything other than a retrospective sense. Rather, only that, by and large, the pattern of changes that are reconstructed to have evolved in these chimpanzee populations generally follow what is regarded as the phylogenetic history of the individual populations based on genetic studies. Indeed, as the comparisons of the different patterns of behavioral similarities and differences among eastern and western populations clearly demonstrate, individual populations show tremendous differences in the extent to which they resemble their closest relatives.

HOW IS BOSSOU UNIQUE, AND WHAT DOES THIS INDICATE ABOUT HOW DIFFERENT FACTORS MAY INFLUENCE BEHAVIOR IN AFRICAN APES?

The chimpanzees of Bossou provide an especially interesting case to consider in regard to the question of phylogeny because, although they share some features in common with Tai chimpanzees, the two populations are, in many ways, behaviorally, environmentally, and demographically distinct. As noted above, the demographic makeup of the

chimpanzee community of Bossou, a small community having only one adult male, is considerably different from that of the other three chimpanzee communities in this study, although not unique from all known communities (the Taï community has undergone recent demographic changes; only one adult male is currently present in the north community). Thus, by default, strong male bonds, and the traits associated with them that are generally considered 'chimpanzee traits,' are absent. Generally, male–male cooperation is important for territory defense through boundary patrolling. At some, but not all, other sites, community disintegration resulted when the number of males decreased as a result of active 'warfare' by males of adjacent communities (Goodall 1986, pp. 503–14; but see Nishida 1990b). The long-term stability (greater than 10 years) of a one–male group at Bossou may be due to the population's isolation from any close neighboring communities of chimpanzees, and a distance of at least 7 km of savanna between it and any adjacent chimpanzee dwelling forest (Sugiyama 1999). It would be especially informative to broaden this study by including recent behavioral results from Taï, based on data collected after the number of adult males in the community decreased. Looking at how (a wide variety of) behavior changes within a community through time, while maintaining roughly constant environmental features, would help to elucidate the effect that demographic versus environmental features have on the distinctive position Bossou occupies in this study.

As a result of its demographic distinction, Bossou shares many features in common with mountain gorillas, to the extent that when an outgroup (Karisoke mountain gorillas) is added in the UPGMA clustering of the ATDs based on all 82 variables, Bossou clusters with mountain gorillas, albeit distantly, leaving the underlying pattern of behavioral affinities of the other chimpanzee and bonobo taxa unchanged. Similarly, a phylogeny linking Bossou with gorillas rather than with the Taï chimps provides better resolution of the distribution of characters in this data set, even though it clearly does not correspond to the most probable phylogeny of these apes.

Far more interesting, however, is the evidence that Bossou provides as a test case for the association between different behavioral, demographic, and ecological features. Many of the distinctive features characterizing the Bossou population are, at least in part, causally related to the unusual demography (reduced number of adult males) and isolation of this population. As a one–male group, with the resulting

absence of strong male–male bonds and coalitions, Bossou chimpanzees are similar to gorillas and bonobos (and distinct from all other chimpanzees studied to date) in their absence of territoriality, lack of hunting of monkeys, lack of male–male affiliations, and potential occurrence of male dispersal. In spite of these considerable differences in demography, Bossou, in their reduced prevalence of infanticide in conjunction with more stable male–female association, is similar to Taï chimpanzees and unlike eastern chimpanzees. We propose that in seasonal environments, such as those of the eastern chimpanzees considered in this study, greater variation in fruit supply makes more permanent male–female association too costly for females. Finally, in spite of considerable differences in habitat, demography, and ecology, Bossou chimpanzees remain similar to all other chimpanzees (considered in this study) and distinct from bonobos in (1) their use of tools to acquire food; (2) the continued dominance of males over females, in spite of a reduction in the number of males present and an increase in female–female association; (3) a considerably longer time before resumption of estrus after parturition; and (4) the absence of a ventral–ventral mating pattern. Thus, these behavioral traits seem relatively invariant in chimpanzees despite considerable differences in habitat, demography, and ecology.

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NOTE

1. Data, statistical analyses and further references relevant to this chapter are available on Diane Doran's web site at <http://www.informatics.sunysb.edu.anatomy/IDPAS/Doran/>.

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