

Coevolution of vocal communication and sociality in primates

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Understanding the rules that link communication and social behaviour is an essential prerequisite for discerning how a communication system as complex as human language might have evolved. The comparative method offers a powerful tool for investigating the nature of these rules, since it provides a means to examine relationships between changes in communication abilities and changes in key aspects of social behaviour over evolutionary time. Here we present empirical evidence from phylogenetically controlled analyses indicating that evolutionary increases in the size of the vocal repertoire among non-human primate species were associated with increases in both group size and time spent grooming (our measure of extent of social bonding).

Keywords: repertoire size; non-human primates; language; comparative method

1. INTRODUCTION

Although there is intense interest in the evolution of language (Christiansen & Kirby 2003), the evolutionary basis for increases in the size of the vocal repertoire among non-human mammals has rarely been explored, and then only subsets of calls within the repertoire have been examined (Blumstein & Armitage 1997). No previous studies have investigated whether there is evidence that changes in the size of the entire vocal repertoire over evolutionary time have been associated with changes in key aspects of social living. Given the central role of social behaviour in theories of language evolution (e.g. Dunbar 1993; Pinker 2003), it is critical to address these questions.

Here we use data extracted from the literature to conduct phylogenetically controlled analyses that examine evolutionary relationships between vocal repertoire size and social behaviour in non-human primates. Since the methods that primatologists have used to determine the number of acoustically different calls that a species gives (its vocal repertoire size) vary widely, we devised rules for making comparisons between species as systematic as possible (see below). Inconsistencies in the way that authors group or differentiate calls inevitably remain and these would be expected, *a priori*, to add noise to the data. However, if vocal repertoire sizes were linked to levels

of social bonding, we would expect evolutionary increases in repertoire size to predict increases in group size and/or increases in the amount of time that individuals spend in key bonding activities.

2. MATERIAL AND METHODS

We extracted data on vocal repertoire sizes in non-human primates from the literature (table 1). In assessing repertoire size, we only considered papers in which calls from the whole adult repertoire were systematically described, and which distinguished calls on the basis of their acoustic structure (in order to provide the most objective measure that would be most comparable across studies). This resulted in the omission of papers in which only part of the repertoire was documented, or in which calls were described simply by the context in which they were given. Furthermore, since only some papers gave a description of calls from infants and juveniles as well as adults, we based our analyses on the size of the adult vocal repertoire, excluding calls given by infants or juveniles unless an explicit statement was made that the call also occurred in the adult repertoire. Lip smacking, teeth chattering/grinding and vomiting were excluded from our total, while coughing, hiccupping and sneezing, which might have constituted vocal utterances, were included. Finally, several authors included in the repertoire vocalizations that consisted of multiple units. We only included such vocalizations in our total if any of these units had not previously been described as distinct calls in the repertoire. For example, if call types A and B had already been described, a multiple unit call consisting of a composite of units A and B would not be counted as an extra call type, but one consisting of A and C would result in call type C being added to the repertoire. Furthermore, because the song of gibbons is such an unusual vocalization type, and it is unclear what status units of the song should be given in the repertoire, we excluded from the analysis the one gibbon species for which an assessment of full adult repertoire size had been published (*Hylobates agilis*: Gittins 1984). As a result of applying these systematic rules to each species we considered, our standardized measure of repertoire size often differed from the total stated by the authors of the study (which regularly included calls that we had excluded, such as infant and juvenile calls).

In order to assess whether evolutionary changes in vocal repertoire size are linked to key components of social living, we collected data on two indices of social bonding. The first of these, social group size, reflects the number of partners that individuals form social bonds with; we did not consider what social roles individuals had within the group, as this could not be systematically and objectively assessed across different primate species (c.f. Blumstein & Armitage 1997). The second, time spent grooming, provides a measure of the strength of social bonding between individuals in the group. Our aim in using these two measures was to take account of both the quantity and quality of relationships within social groups.

Group sizes were taken from a single standardized reference (Rowe 1996) except in two specific cases (see table 1); group size data for *Galago senegalensis* were not available in this reference, and it also gave no data for *Mandrillus sphinx* on reproductive unit size (the measure of group size we considered most appropriate for mandrills and gelada baboons because it reflects the number of social partners that each individual will interact with on a regular basis). Systematic data on percentage of time spent grooming has been published for a large number of non-human primate species and we collated all available information on the species in our dataset (table 1).

To investigate evolutionary relationships between the size of vocal repertoires and our measures of social interaction, while controlling for the non-independence of species, phylogenetically controlled analyses were carried out by the independent contrasts method (Purvis & Rambaut 1995) using Purvis' composite phylogeny of the primates (Purvis 1995) with equal branch lengths. This method calculates differences in character states (contrasts) between sister taxa at each node in the phylogeny. These contrasts, unlike species values, are statistically independent of each other. A significant relationship between contrasts in an independent and the dependent variable indicates correlated character change during evolution. In our analysis contrasts in vocal repertoire size were entered as the predictor variable, with contrasts in each of (1) group size and (2) grooming time as dependent variables. In addition, as evolutionary changes in time spent grooming could be a direct product of changes in group size, we entered contrasts in repertoire size and contrasts in group size as independent variables in a multiple regression, with contrasts in grooming time as the

Table 1. Repertoire size, group size and percentage grooming time among non-human primate species.

species	repertoire size	group size ^a	grooming time ^b	reference for repertoire size
<i>Alouatta palliata</i>	22	12.6	7	Baldwin & Baldwin (1976)
<i>Arctocebus calabarensis</i>	2	1.5	—	Charles-Dominique (1977)
<i>Callicebus moloch</i>	11	3.5	0.1	Robinson (1979)
<i>Callimico goeldii</i>	28	5	6	Masataka (1982)
<i>Callithrix jacchus</i>	13	8.9	—	Epple (1968)
<i>Cebuella pygmaea</i>	16	6.4	—	Pola & Snowdon (1975)
<i>Cebus olivaceus</i>	11	21.5	3	Robinson (1984)
<i>Cercocebus torquatus</i>	18	95	—	Range & Fischer (2004)
<i>Cercopithecus aethiops</i>	25	40.5	5	Strushaker (1967)
<i>Cercopithecus cephus</i>	16	20	—	Gautier (1978)
<i>Daubentonia madagascariensis</i>	9	1.5	0	Stanger & Macedonia (1994)
<i>Euoticus elegantulus</i>	6	4	—	Charles-Dominique (1977)
<i>Galago alleni</i>	5	2.5	—	Charles-Dominique (1977)
<i>Galago senegalensis</i>	18	2	—	Zimmermann (1985)
<i>Galagoides demidoff</i>	8	3.5	—	Charles-Dominique (1977)
<i>Gorilla gorilla</i>	16	9	1	Harcourt <i>et al.</i> (1993)
<i>Lagothrix lagotricha</i>	6	33	—	Casamitjana (2002)
<i>Lemur catta</i>	22	17	5	Macedonia (1993)
<i>Leontopithecus rosalia</i>	16	5.8	—	MacLanahan & Green (1977)
<i>Macaca fascicularis</i>	17	29	8.3	Palombit (1992)
<i>Macaca fuscata</i>	34	117	11.8	Green (1975)
<i>Macaca nemestrina</i>	16	27.5	—	Grimm (1967)
<i>Macaca radiata</i>	21	27.5	14	Hohmann (1991)
<i>Macaca silenus</i>	15	17	2	Hohmann (1991)
<i>Macaca sylvanus</i>	14	24	—	Fischer & Hammerschmidt (2002)
<i>Mandrillus sphinx</i>	10	22.5	—	Kudo (1987)
<i>Miopithecus talapoin</i>	12	45	1.9	Gautier (1974)
<i>Pan paniscus</i>	38	125	—	Bermejo & Omedes (1999)
<i>Pan troglodytes</i>	29	26.5	6.2	Goodall (1986)
<i>Perodicticus potto</i>	5	1.5	—	Charles-Dominique (1977)
<i>Petterus fulvus</i>	20	15.5	8.3	Paillette & Petter (1978)
<i>Petterus macaco</i>	13	8.5	—	Gosset <i>et al.</i> (2003)
<i>Petterus mongoz</i>	9	3.5	—	Curtis (1997)
<i>Pongo pygmaeus</i>	10	2	0	MacKinnon (1974)
<i>Presbytis entellus</i>	16	37.5	4.4	Hohmann (1991)
<i>Presbytis johnii</i>	16	17	—	Hohmann (1991)
<i>Procolobus badius</i>	17	49.5	3.8	Strushaker (1975)
<i>Saguinus fuscicollis</i>	16	5.9	—	Moody & Menzel (1976)
<i>Saguinus oedipus</i>	33	7.4	—	Cleveland & Snowdon (1982)
<i>Saimiri sciureus</i>	21	32	1.5	Newman (1985)
<i>Theropithecus gelada</i>	22	11.5	18.3	Aich <i>et al.</i> (1990)
<i>Varecia variegata</i>	13	10.5	—	Pereira <i>et al.</i> (1988)

^a All data taken from Rowe (1996) except *Galago senegalensis* (Bearder 1969) and *Mandrillus sphinx* (Stammbach 1984).

^b All data taken from Dunbar (1991) except *Callimico goeldii* (Christen 1998), *Daubentonia madagascariensis* (Petter & Charles-Dominique 1979), *Macaca fuscata* (Watanuki & Nakayama 1993), *Macaca radiata* (Silk 1982), *Macaca silenus* (Kurup & Kumar 1993) and *Miopithecus talapoin* (Wolfheim 1977).

dependent variable. For comparison we also present the results of simple cross-species analyses, investigating present-day relationships between the three variables. Normalized data were used in all analyses (repertoire size was square root transformed, group size was log transformed and percentage grooming time was log+1 transformed).

3. RESULTS

Our phylogenetic analyses reveal a strong positive correlation between contrasts in repertoire size and contrasts in group size (figure 1a; $r=0.49$, $F_{1,39}=12.25$, $p<0.005$) and between contrasts in repertoire size and contrasts in time spent grooming (figure 1b; $r=0.75$, $F_{1,18}=23.76$, $p<0.0005$). The multiple regression revealed that evolutionary changes in time spent grooming were predicted by changes in repertoire size rather than changes in group size

($F_{2,17}=12.02$, $p<0.005$; adjusted $R^2=0.54$; contrasts in repertoire size: $\beta=0.68$, $t=3.77$, $p<0.005$; contrasts in group size: $\beta=0.15$, $t=0.83$, $p=0.419$). When only diurnal species were considered (excluding the six nocturnal species), significant relationships remained between contrasts in repertoire size and contrasts in group size ($r=0.45$, $F_{1,33}=8.22$, $p<0.01$), and between contrasts in repertoire size and contrasts in grooming ($r=0.72$, $F_{1,17}=18.42$, $p<0.0005$). The multiple regression conducted on this reduced dataset again identified contrasts in repertoire size as the key predictor of contrasts in grooming time ($F_{2,16}=8.92$, $p<0.005$, adjusted $R^2=0.47$; contrasts in repertoire size: $\beta=0.68$, $t=3.60$, $p<0.005$; contrasts in group size: $\beta=0.09$, $t=0.49$, $p=0.632$). Thus over evolutionary time increases in the size of the vocal repertoire were associated with increases in

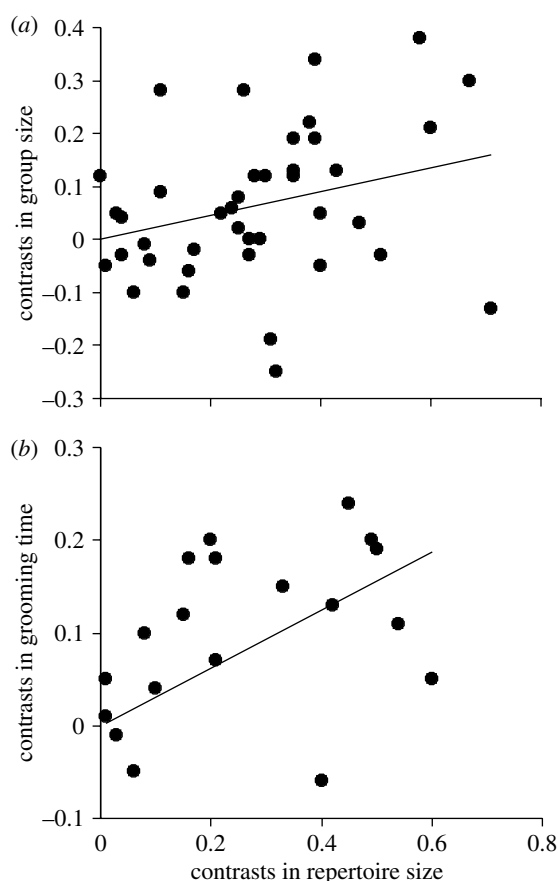


Figure 1. Relationships between (a) contrasts in repertoire size and contrasts in group size and (b) contrasts in repertoire size and contrasts in grooming time. Repertoire size was square root transformed, group size was log transformed and percentage grooming time was log+1 transformed.

each of our measures of social bonding. Furthermore, evolutionary changes in grooming time were not simply a product of increases in group size but instead were closely associated with changes in repertoire size.

When present-day relationships between vocal repertoire size, group size and grooming were examined in the simple cross-species comparison, we found a strong positive correlation between repertoire size and group size ($r=0.58$, $F_{1,40}=20.44$, $p<0.0005$) and between repertoire size and time spent grooming ($r=0.75$, $F_{1,18}=22.69$, $p<0.0005$). In the multiple regression, time spent grooming was predicted by repertoire size rather than group size ($F_{2,17}=13.89$, $p<0.0005$, adjusted $R^2=0.58$; repertoire size: $\beta=0.59$, $t=3.40$, $p<0.005$; group size: $\beta=0.29$, $t=1.68$, $p=0.112$). All these present-day relationships remained unchanged when nocturnal species were removed from the dataset.

4. DISCUSSION

Despite inconsistencies in the methods that different researchers have used to assess vocal repertoire sizes in primate species, clear and strong relationships between social group size, grooming time and vocal repertoire size have emerged in our analyses. Independent contrasts analyses revealed that evolutionary

changes in repertoire size are a strong predictor of both changes in group size and changes in grooming time among non-human primates. Simple cross-species comparisons also indicate strong present-day relationships between repertoire size and the two measures of sociality. It is important to note that the direction of causality cannot be inferred from correlational analyses, therefore it is not possible to say whether evolutionary increases in vocal repertoire sizes directly preceded or followed increases in levels of sociality. However, our findings are consistent with the hypothesis that the vocal communication system may facilitate (or constrain) increases in group size and levels of social bonding within primate social groups. Moreover, they emphasize the key role that vocal communication can play in the evolution of social behaviour.

Dunbar suggested that language originally evolved to service social relationships when primate groups became too large for grooming to serve this function (reviewed in Dunbar 2003). Our analyses provide a more comprehensive insight—that the vocal repertoire itself may facilitate social bonding in non-human primates. Repertoire size too would have a restricted ceiling in an animal with characteristics typical of extant non-human primates, which both lack a descended larynx (limiting the number of different sounds that could be produced) and have very limited powers of vocal learning (Fitch 2000). Our findings also suggest that evolutionary changes in grooming are closely linked to evolutionary changes in repertoire size rather than being directly associated with group size. It seems likely that repertoire size and grooming have coevolved—increases in one creating a selection pressure for increases in the other.

Clearly there are radical differences between non-human primate vocal repertoires and human language (Pinker 1995; Bickerton 2003). While the number of even functionally referential calls in non-human primate vocal repertoires is strictly limited, humans have highly advanced capabilities for using sounds symbolically (Deacon 1997; Bickerton 2003). More fundamentally, non-human primates show little evidence of syntactic abilities and their vocal utterances certainly lack structural rules comparable with the duality of patterning (where phonemes are combined into words and words into sentences) that adds unprecedented diversity to the utterances that humans can produce (Pinker 1995; Bickerton 2003). Whether these critical steps in language evolution were a response to changes in social variables remains a crucial, and unanswered, question.

Until now use of the comparative approach in the study of language evolution has generally been limited to studying how specific linguistic and cognitive abilities compare between humans and non-human primates (Blumstein 1999; Hauser & Fitch 2003). Here we use comparative analyses in order to investigate more general relationships underlying changes in vocal communication in our closest relatives. A preliminary investigation of the relationship between gestural repertoire size and social organization in macaques (Maestripietri 2000) suggests that the evolution of gestural communication could also be

profitably explored in this way. New methods for producing objective and consistent measures of repertoire size (based on pattern recognition techniques) could provide a basis for future comparative studies to investigate potential interactions between vocal and gestural forms of signalling in the evolution of primate communication.

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