

Below is the unedited preprint (not a quotable final draft) of:
Dunbar, R. I. M. (1993). Coevolution of neocortical size, group size and language in humans. *Behavioral and Brain Sciences* 16 (4): 681-735.

The final published draft of the target article, commentaries and Author's Response are currently available only in paper.

€ For information about subscribing or purchasing offprints of the published version, with commentaries and author's response, write to: journals_subscriptions@cup.org (North America) or journals_marketing@cup.cam.ac.uk (All other countries). €

CO-EVOLUTION OF NEOCORTEX SIZE, GROUP SIZE AND LANGUAGE IN HUMANS

R.I.M. Dunbar
Human Evolutionary Biology Research Group
Department of Anthropology
University College London
London WC1E 6BT

Keywords

Neocortical size, group size, humans, language, Macchiavellian Intelligence

Abstract

Group size is a function of relative neocortical volume in nonhuman primates. Extrapolation from this regression equation yields a predicted group size for modern humans very similar to that of certain hunter-gatherer and traditional horticulturalist societies. Groups of similar size are also found in other large-scale forms of contemporary and historical society. Among primates, the cohesion of groups is maintained by social grooming; the time devoted to social grooming is linearly related to group size among the Old World monkeys and apes. To maintain the stability of the large groups characteristic of humans by grooming alone would place intolerable demands on time budgets. It is suggested that (1) the evolution of large groups in the human lineage depended on the development of a more efficient method for time-sharing the processes of social bonding and that (2) language uniquely fulfills this requirement. Data on the size of conversational and other small interacting groups of humans are in line with the predictions for the relative efficiency of conversation compared to grooming as a bonding process. Analysis of a sample of human conversations shows that about 60% of time is spent gossiping about relationships and personal experiences. It is suggested that language evolved to allow individuals to learn about the behavioural characteristics of other group members more rapidly than is possible by direct observation alone.

1. Introduction

Primates are, above all, social animals. This has inevitably led to the suggestion that such intense sociality is functionally related to the exceptional cognitive abilities of these animals, as reflected in their unusually large brains (Jolly 1969, Humphrey 1976, Kummer 1982, Byrne & Whiten 1988). This claim is supported by the finding that mean group size is directly related to relative neocortical volume in nonhuman primates (Sawaguchi & Kudo 1990, Dunbar 1992a). These analyses suggest that although the size of the group in which animals live in a given habitat is a function of habitat-specific ecologically-determined costs and benefits (see for example Dunbar 1988, 1992b), there is a species-specific upper limit to group size which is set by purely cognitive constraints: animals cannot maintain the cohesion and integrity of groups larger than a size set by the information- processing capacity of their neocortex.

The group size identified by this relationship appears to refer to the maximum number of individuals with whom an animal can maintain social relationships by personal contact. It is not necessary that all these individuals live in the same physical group: chimpanzees (among a number of other species) have a fission/fusion form of social system in which at any one time the community (the group in the sense defined above) is divided into a number temporary foraging parties whose composition changes repeatedly (see for example Wrangham 1986). Nor does it follow that a species' social system consists only of a single type of group: it is now clear that most primate species live in complex multi-tiered social systems in which different layers are functional responses to different environmental problems (e.g. the gelada and hamadryas baboons: see Dunbar 1988, 1989a). Rather, the neocortical constraint seems to be on the number of relationships that an animal can keep track of in a complex, continuously changing social world: the function subserved by that level of grouping will depend on the individual species' ecological and social context.

It is important to appreciate that the causal relationship between group size and neocortex size depends on the explanatory perspective (or level) adopted. In evolutionary terms, the size of a species' neocortex is set by the range of group size required by the habitat(s) in which it typically lives. However, seen in proximate terms from an individual animal's point of view, current neocortex size sets a limit on the number of relationships that it can maintain through time, and hence limits the maximum size of its group. This means that although the evolution of neocortex size is driven by the ecological factors that select for group size, we can use the relationship in reverse to predict group sizes for living species (Dunbar 1992a).

It is generally accepted that the cohesion of primate groups is maintained through time by social grooming (see Dunbar 1988). Social grooming is used both to establish and to service those friendships and coalitions that give primate groups their unique structure. As might be anticipated, the amount of time devoted to social grooming correlates well with group size, notably among the catarrhine primates (Old World monkeys and apes) (Dunbar 1991).

However, the relationship between group size and time devoted to grooming appears to be a consequence of the intensity with which a small number of key "friendships" (the primary network) is serviced rather than to the total number of individuals in the group (Dunbar 1991; Kudo et al, in preparation). These primary networks function as coalitions whose primary purpose is to buffer their members against harassment by

the other members of the group. The larger the group, the more harassment and stress an individual faces (see for example Dunbar 1988) and the more important those coalitions are. It seems that a coalition's effectiveness (in the sense of its members' willingness to come to each other's aid) is directly related to the amount of time its members spend grooming each other (see Cheney & Seyfarth 1984, Dunbar 1984). Hence, the larger the group, the more time individuals devote to grooming with the members of their coalitionary clique.

The mean size of the primary network is, however, related to the mean group size for the species. This suggests that groups are built up by welding together sets of smaller primary networks (see also Cheney 1992) and that the total size of the group is ultimately limited not by the number of networks that can be welded together but rather by the size of the networks themselves.

In this paper, I ask what implications these two sets of results have for modern humans (*Homo sapiens sapiens*). If we extrapolate from the nonhuman primate regression, what group size would we predict for anatomically modern humans, given our current neocortex size? I then ask whether there are any observed human group sizes that correspond to this predicted value. Since the relationships that maintain group cohesion among nonhuman primates are serviced by social grooming, I use the regression equation for primates to determine how much time humans would have to spend grooming each other if they were to maintain group cohesion in this way for groups of the size predicted from neocortex size. Finally, I ask what implications this might have had for the evolution of language.

2. Methods

A number of different measures have been used in comparative analyses to provide unbiased estimates of relative differences in brain size. These have included the Extra Cortical Neurons Index (the ratio of the observed number of cortical neurons over and above those required for somatic maintenance, as estimated from body size, brain size and neural density: Jerison 1973), the cerebral Progression Index (the ratio of observed brain or neocortical volume to that predicted for a basal Insectivore of the same body size: Stephan 1972), the Encephalisation Quotient (the residual of brain volume, or neocortex volume, regressed against body weight: Jerison 1973, Clutton-Brock & Harvey 1980, Sawaguchi & Kudo 1990) and the Neocortex Ratio (neocortex volume divided by the volume of the rest of the brain or the volume of the hindbrain: Dunbar 1992a).

In examining the relationship between neocortex size and group size in nonhuman primates, I found that all these measures are reasonable predictors of group size. However, Neocortex Ratio (measured against the rest of the brain excluding the neocortex) gives much the best fit, accounting for 76% of the variance in mean group size among 36 genera of Prosimian and Anthropoid primates (using data on neocortex volume provided by Stephan et al 1981) (see Dunbar 1992a).

This analysis was based on the mean group size observed for a given genus rather than the maximum group size. The main justification for using the mean group size in these analyses lies in the nature of primate social groups. In contrast to the relatively simple aggregations typical of many birds and herbivores, primate groups are highly

structured with individual animals embedded in a complex set of social and kinship networks (see Dunbar 1988, 1989a). Whereas bird flocks can shed individuals through trickle migration as soon as they exceed their optimal size, primate groups cannot: they have to wait until the group is large enough to permit it to fission into two or more daughter groups of a minimum size necessary to ensure the safety and survival of their members. This means that primate groups tend to oscillate in size over quite a wide range around the optimal value. At the point of fission (by definition, their maximum observed size), groups tend to be unstable and close to social disintegration: this, of course, is why they undergo fission at that point. Hence, maximum group size is likely to represent the point of complete social collapse rather than the maximum size of group that the animals can maintain as a cohesive social unit. Consequently, mean group size is likely to be a better estimate of the limiting group size for a species than the maximum ever observed in any population (for further discussion, see Dunbar 1992a).

3. Results

3.1. Group Size in Modern Humans

The best-fit reduced major axis regression equation between neocortex ratio and mean group size for the sample of 36 primate genera shown in Fig.1 was found to be:

$\log(N) = 0.093 + 3.389 \log(CR)$ (1) ($r^2=0.764$, $t_{34}=10.35$, $p<0.001$), where N is the mean group size and CR is the ratio of neocortex volume to the volume of the rest of the brain (i.e. total brain volume minus neocortex) (Dunbar 1992a). Use of both major axis and least-squares regression, as well as alternative indices of relative neocortex size, all yield equations that are of about this same magnitude.

With a neocortex volume of 1006.5 cc and a total brain volume of 1251.8 cc (Stephan et al 1981), the neocortex ratio for humans is $CR=4.1$. This is about 50% larger than the maximum value for any other primate species (see Dunbar 1992a). Strictly speaking, of course, extrapolation from regression equations beyond the range of the X-variable values on which they are based is frowned on. However, we can justify doing so in this case on the grounds that our concern at this stage is exploratory rather than explanatory. We do so, therefore, in the knowledge that the confidence limits around any predictions are likely to be wide.

Equation (1) yields a predicted group size for humans of 147.8. Because the equation is log-transformed and we are extrapolating well beyond the range of neocortex ratios on which it is based, the 95% confidence limits around this prediction (from formulae given by Rayner 1985) are moderately wide (100.2- 231.1). Equations based on alternative indices of neocortex size (see Dunbar 1992a, Table 2) yield predicted group sizes that range from 107.6 (EQ residual of neocortex volume regressed against body weight) to 189.1 (Jerison's Extra Neocortical Neurons index) and 248.6 (absolute neocortex volume), all of which are within (or close to) the 95% confidence limits on the neocortex ratio equation.

In trying to test this prediction, we encounter two problems. One is deciding just what counts as the "natural" condition for *H. s. sapiens*; the other is the problem of defining the appropriate level of grouping for human societies living under these conditions.

It is generally accepted that human cultural evolution has proceeded at a very much faster pace than our anatomical evolution during the past few millennia. Given that our brain size has its origins in the later stages of human evolution some 250,000 years ago (Martin 1983, Aiello & Dean 1990), we may assume that our current brain size reflects the kinds of groups then prevalent and not those now found among technologically advanced cultures. The closest we can get to this is to examine those modern humans whose way of life is thought to be most similar to that of our late Pleistocene ancestors. These are generally presumed to be the hunter-gatherers (Service 1962, Sahlins 1972).

Given that hunter-gatherers are the only appropriate source of information, we then face the problem of deciding what constitutes the appropriate level of grouping within hunter-gatherer societies. There has, however, been considerable debate within anthropology as to the precise structure of these societies (see Service 1962, Birdsell 1970, Williams 1974, Morris 1982, Lee 1982). Irrespective of how this debate is eventually resolved, it is nonetheless clear that most hunter-gatherers live in complexly structured social universes that involve several different levels of grouping.

Thus, the !Kung San of southern Africa live in camps whose composition can change from day to day, but whose membership is mostly drawn from a distinct set of individuals whose foraging area is based on a number of more or less permanent waterholes; several of these "regional groups" make up a much larger tribal grouping typically based on a common dialect and occupancy of a given geographical area (see Lee 1982). The temporary living groups are drawn together into their larger regional groupings for up to three months each year when they congregate at traditional dry season camps based on what is often the only permanent waterhole in the region.

Lee (1982) refers to this as a concentration/dispersal social system and suggests that its origins lie in the unpredictable nature of food and water sources in typical Bushman habitats. He also argues that this form of flexible social system is typical of most (if not all) modern hunter-gatherers: rather similar patterns of social organisation have been documented, for example, among the Australian aboriginals (Meggitt 1965, Strehlow 1947), various Eskimo societies (Spencer 1959, Damas 1968), many of the North American Indian tribes (Helm 1968, Leacock 1969, Steward 1938, Drucker 1955) and among the Congo pygmies (Turnbull 1968, Hewlett 1988).

Given this complexity, any attempt to determine the "true" group size in hunter-gatherers would almost certainly be challenged by anthropologists on innumerable ethnographic grounds. In addition, two other more general objections might be raised. One is that most surviving hunter-gatherers occupy marginal habitats, and this may well influence both the size and the structure of their social systems (as is known to be the case with baboons, for example: Dunbar 1992a, in press). The second is that most living hunter-gatherer societies have been seriously disrupted, either directly or indirectly, by contact with modern colonial cultures.

In view of these caveats, and rather than get involved in the kind of fruitless argument about definitions that has so often clouded the literature in this area, I will proceed more cautiously and simply ask whether we find any groups at all that are consistently of the size predicted for modern humans by equation (1). Given the definition of

grouping elaborated in the Introduction, the central issue is not whether a particular form of grouping occurs in every social system but whether a particular size of grouping does so.

Unfortunately, ethnographers have not often regarded censuses as an important feature of their investigations: although most studies allude to groupings of different kinds and often describe the structural relationships between them in great detail, they seldom provide quantitative data on the sizes of these groupings. Table 1 summarises all the data I have been able to find in the ethnographic literature for a number of historical and contemporary hunter-gatherer and swidden horticulturalist societies. I have included swidden horticulturalists since these may reasonably be considered to be settled hunter-gatherers (see Johnson & Earle 1987).

The data in Table 1 suggest that group sizes fall into three quite distinct size classes: small living groups of 30-50 individuals (commonly measured as overnight camps, but often referred to as bands in some of the hunter-gatherer literature), a large population unit (the tribe or in some cases sub-tribe) that typically numbers between 500 and 2500 individuals and an intermediate level of grouping (either a more permanent village or a culturally defined clan or lineage group) that typically contains 100-200 people. In a few cases (e.g. the Mae Enga and the Kaluli of New Guinea), more than three grouping layers were identified by the ethnographer. Most such groupings are, however, organised in a hierarchically inclusive fashion and I have therefore identified the groupings that are closest to the senses defined above.

Plotting these values on a graph produces what appears to be a clear trimodal distribution of group sizes with no overlap between grouping levels (Fig. 2). The average size of the smallest and largest grouping levels (means of 37.7 and 1154.7, respectively) correspond quite closely to the figures for bands (30-50) and tribal groups (1000-2000) that are widely quoted in the anthropological literature (e.g. Steward 1955, Service 1962). The level of grouping that appears to lie between these two has, however, been given little more than passing attention (even though the social significance of such groupings as clans have been discussed extensively). This is reflected in the large number of ? entries in Table 1, indicating that the ethnographer discussed such a grouping but gave no indication of its actual size.

The average size of the intermediate level groups for those societies for which accurate census data are available is 148.4 (range 90-221.5, N=9). If all the available data are considered (taking median values in cases where only ranges are given), the mean is 134.8 (N=15); if only nomadic hunter-gatherers are considered, the mean is 156.4 (N=4). None of these estimates differs significantly from the predicted value ($z < +0.431$, $P > 0.667$ 2-tailed). Indeed, with one exception (the Mae Enga of New Guinea), all the values given in Table 1 lie within the 95% confidence limits of the predicted value (and even the exception is only just outside the lower 95% confidence limit). More importantly, in no case does the mean size of any temporary camp or tribal grouping (i.e. the smaller and larger grouping types) lie within the 95% confidence limits on the predicted group size. Indeed, the mean values for the band and tribal level groupings are significantly different from the predicted value ($z = 6.401$ and $z = 9.631$, respectively, $P < < 0.0001$).

Note that the coefficient of variation for the intermediate level grouping is considerably smaller than those for either of the other two groupings (Table 1). This suggests that the constraints on the former are greater than those on the latter, as might be expected if the former is subject to an intrinsic (e.g. cognitive) constraint whereas the latter are more often determined by extrinsic environmental factors. The size of hunter-gatherer "bands" (or night camps), for example, is known to be particularly unstable and to be seasonally adjusted to the group's resource base (Turnbull 1968, Lee 1982, Johnson & Earle 1987). In contrast, the greater variability in the size of the tribal level groupings almost certainly reflects the impact of contact with modern (especially European) cultures and their attendant diseases; in many cases, these have drastically reduced the size of indigenous tribes.

It is important to note that the intermediate level groupings do not always have an obvious physical manifestation. Whereas overnight camps can readily be identified as demographic units in time and space and the tribal groupings can be identified either by linguistic homogeneity or geographical location (and often both), the intermediate level groupings are often defined more in terms of ritual functions: they may gather together once a year to enact rituals of special significance to the group (such as initiation rites), but for much of the time the members can be dispersed over a wide geographical area and, in some cases, may even live with members of other clan groupings. Nonetheless, what seems to characterise this level of grouping is that it constitutes a subset of the population that interacts on a sufficiently regular basis to have strong bonds based on direct personal knowledge. My reading of the ethnographies suggests that knowledge of individuals outside this grouping is generally less secure and based more on gross categories (a "Them" and "Us" basis as opposed to identifying individuals by name). More importantly, perhaps, in the case of New Guinea horticulturalists at least, the intermediate level grouping seems to provide an outer network of individuals who can be called on for coalitionary support during raids or the threat of attack by other groups (see Meggitt 1965b, Hallpike 1977). Thus, this intermediate level of grouping in human societies seems to correspond rather precisely in both size and social function to what we would expect on the basis of the nonhuman primate data.

It is of interest to note that estimates of the size of Neolithic villages in Mesopotamia are of about the same magnitude. Oates (1977), for example, gives a figure of 150-200, based on the fact that 20-25 dwellings seems to be the typical size of a number of village sites dated to around 6500-5500 BC.

In fact, it turns out that figures in the region of 150 occur frequently among a wide range of contemporary human societies. Thus, the mean size of the 51 communities (or Bruderhoefe) in the Schmedenleut section of the Hutterites (a fundamentalist group who live and farm communally in South Dakota and Manitoba) is 106.9 individuals (Mange & Mange 1980). According to Hardin (1988), the Hutterites regard 150 individuals as the limiting size for their farming communities: once a community reaches this size, steps are taken to split it into two daughter communities. Bryant (1981) provides another example from an East Tennessee rural mountain community (all of whom claim to be related to each other and regard themselves as a single social group): the total number of living members was 197 when the community was censused at the end of the 1970s. Even academic communities appear to abide by this rule. Price & Beaver (1966), for example, found that research

specialities in the sciences tend to consist of up to 200 individuals, but rarely more. Becher (1989) sampled network sizes (defined as the number of individuals whose work you pay attention to) in 13 academic sub-disciplines drawn from both the sciences and the humanities and concluded that the typical size of the outer circle of professional associates that defines a sub-discipline is about 200 (with a range between 100-400). It seems that disciplines tend to fragment with time as their numerical size (and, of course, literature) grows.

In addition, it turns out that most organised (i.e. professional) armies have a basic unit of about 150 men (Table 3). This was as true of the Roman Army (both before and after the reforms of 104BC) as of modern armies since the sixteenth century. In the Roman Army of the classical period (350-100 BC), the basic unit was the maniple (or "double-century") which normally consisted of 120-130 men; following the reforms instituted by Marius in 104BC, the army was re-organised into legions, each of which contained a number of semi-independent centuries of 100 men each (Haverfield 1955, Montross 1975). The smallest independent unit in modern armies (the company) invariably contains 100-200 men (normally three or four rifle platoons of 30-40 men each, plus a headquarters unit, sometimes with an additional heavy weapons unit) (Table 3). Although its origins date back to the German mercenary Landsknechts groups of the sixteenth century, the modern company really derives from the military reforms of the Swedish king Gustavus Adolphus in the 1620s. Despite subsequent increases in size to accommodate new developments in weaponry and tactics, the company in all modern armies has remained within the 95% confident limits of the predicted size for human groups. The mean size of 179.6 for the twentieth century armies listed in Table 3 does not differ significantly from the 147.8 predicted by equation (1) ($z=0.913$, $P=0.361$ 2-tailed).

This fact has particular significance in the context of the present argument. Military units have to function very efficiently in coordinating men's behaviour on the battlefield: the price of failing to do so is extremely high and military commanders cannot afford to miscalculate. Given that the fighting power of a unit is a function of its size, we might expect there to be considerable selection pressure in favour of units that are as large as possible. That the smallest independent unit should turn out to have a maximum size of about 200 even in modern armies (where technology presumably facilitates the coordination of planning) suggests that this upper limit is set by the number of individuals who can work effectively together as a coordinated team. Military planners have presumably arrived at this figure as a result of trial and error over the centuries.

In the context of the present analysis, the reason given by the Hutterites for limiting their communities to 150 is particularly illuminating. They explicitly state that when the number of individuals is much larger than this, it becomes difficult to control their behaviour by means of peer pressure alone (Hardin 1988). Rather than create a police force, they prefer to split the community. Forge (1972) came to a rather similar conclusion on the basis of an analysis of settlement size and structure among contemporary New Guinea "neolithic" cultivators. He argued that the figure 150 was a key threshold in community size in these societies. When communities exceed this size, he suggested, basic relationships of kinship and affinity were insufficient to maintain social cohesion; stability could then be maintained only if formal structures developed which defined specific roles within society. In other words, large

communities were invariably hierarchically structured in some way, whereas small communities were not.

Similarly, in an analysis of data from 30 societies ranging from hunter-gatherers to large-scale agriculturalists, Naroll (1956) demonstrated that there was a simple power relationship between the maximum settlement size observed in a given society and both the number of occupational specialities and the number of organisational structures recorded for it. His analyses suggest that there is a critical threshold at a maximum settlement size of 500 beyond which social cohesion can only be maintained if there is an appropriate number of authoritarian officials. Bearing in mind that Naroll's threshold is expressed as the maximum observed settlement size, it seems likely that the equivalent mean settlement size will not be too far from the value of 150 suggested by the above analyses.

Other evidence suggests that 150 may be a functional limit on interacting groups even in contemporary western industrial societies. Much of the sociometric research on industrial and other comparable organisations, for example, has demonstrated that there is a marked negative effect of group size on both group cohesion and job satisfaction (as indicated by absenteeism and turnover in posts) within the size range under consideration (i.e. 50-500 individuals: see, for example, Indik 1965, Porter & Lawler 1965, Silverman 1970). Indeed, an informal rule in business organisation identifies 150 as the critical limit for the effective coordination of tasks and information-flow through direct person-to-person links: companies larger than this cannot function effectively without sub-structuring to define channels of communication and responsibility (J.-M. Delwart, pers. commun.). Terrien & Mills (1955), for example, found that the larger the organisation, the greater the number of control officials that is needed to ensure its smooth functioning.

Other studies have suggested that there is an upper limit on the number of social contacts that can be regularly maintained within a group. Coleman (1964) presented data on friendships among print shop workers which suggest that the likelihood of having friends within the workplace reaches an asymptote at a shop size of 90-150 individuals. (The small size of the sample for large groups makes it difficult to identify the precise point at which "saturation" is reached.) Coleman explicitly argued that this was a consequence of the fact that there is a limit to the number of individuals within a shop that any one person can come into contact with. Moreover, his results also seemed to suggest that the large number of regular interactants that an individual can expect to have within a large work group limits the number of additional friendships that can be made outside the workplace.

Most studies of social networks in modern urban societies have tended to concentrate on specific sub-sets (e.g. "support networks") within the wider network of "friends and acquaintances" (see Mitchell 1969, Milardo 1988). One exception to this has been the study by Killworth et al (1984) who used a "reversed small world" protocol to determine the total network size (i.e. the total number of individuals that are known by name with whom a respondent has a degree of personal contact). Forty subjects were each given a dossier containing 500 fictitious (but realistic) target individuals living in different parts of the world and asked to name an individual among their own acquaintances who (either directly or via a chain of acquaintances of their own) would be able to pass a message to each of the targets. The number of different

acquaintances listed was assumed to be an index of the subject's total social network. The mean number of acquaintances selected was 134 (though the variance around this figure was considerable). Since the number of nominated acquaintances seems to increase more slowly as the number of targets increases, Killworth et al (1984) suggested that the asymptotic network size could be determined by extrapolation from the rate at which the curve of nominated acquaintances increases with increasing numbers of targets. They calculated this value to be about 250. Though just outside the 95% confidence limits on the predicted value ($z=2.29$, $P=0.022$ 2-tailed), this latter estimate is not so far outside the range of likely values as to be seriously worrying. For one thing, the difference between the mean and asymptotic values may well reflect the difference between the functional norm (i.e. the number of personal friends that an individual has) and the maximum network size when more peripheral acquaintances are included. More research in this area is clearly needed to clarify this.

3.2. Grooming and the Evolution of Language

Given that primate groups are held together by social grooming, time budget constraints on group size become an important consideration (Dunbar 1992b). Even if a species has the cognitive capacity to manage all the relationships involved in large groups, there may be circumstances under which the animals simply do not have the time available to devote to servicing those relationships through social grooming. Relationships that are not serviced in this way will cease to function effectively; as a result, the group will tend to disperse and the population will settle at a new lower equilibrium group size (Dunbar 1992b).

A comparative analysis of the determinants of time spent grooming by primates has demonstrated that grooming time is a linear function of group size, at least within the catarrhine primates (Dunbar 1991). The distribution of the data suggests that grooming does not necessarily function in such a way that each individual grooms with every other group member: rather, as noted earlier (p.000), it suggests that the intensity of grooming with a small number of "special friends" (or coalition partners) increases in proportion to increasing group size. Irrespective of precisely how grooming functions to integrate large primate groups, we can use the relationship between group size and grooming time to predict the grooming time required to maintain cohesion in groups of the size predicted for modern humans.

Since our main concern is with how time spent grooming functions to maintain group cohesion, I have considered only those catarrhine species which do not have fission-fusion social systems. For the 22 species listed in Dunbar (1991, Table 1) that are described as living in stable cohesive groups, the reduced major axis regression equation is:

$G = -0.772 + 0.287 N$ (2) where G is the percentage of time devoted to social grooming during the day ($r^2=0.589$, $t_{20}=5.36$, $P<0.001$: Fig. 3). (Logging the data does not affect the value of r^2 , but produces impossibly high values of grooming time for some primate populations as a direct result of the transformation.) The highest recorded value for any individual species is 18.9% for one group of *Papio papio* baboons (Sharman 1981), but a number of other baboon and macaque groups exhibit grooming time allocations in the range 15-18% (see for example Iwamoto & Dunbar

1983). A figure of around 20% seems to be an absolute upper limit on the amount of time that primates can afford to devote to social interaction.

(Alternative forms for equation [2] using least-squares regression and/or the full Catarrhine data-set yield equations that are very similar in form, but whose coefficients vary somewhat. Although this affects the absolute values for the grooming time requirement, it does not affect their relative values; hence, the argument itself is unaffected. Equation [2] seems to give a generally better fit to the primate data; in particular, it yields a more accurate prediction of the amount of time devoted to social grooming in the very large groups typical of the gelada. I have preferred to use it here mainly for this reason.)

The group size predicted for modern humans by equation (1) would require as much as 42% of the total time budget to be devoted to social grooming. (The 95% confidence limits on predicted group size would yield grooming times that range from 28% to 66%.) This is more than double that observed in any population of nonhuman primates. Bearing in mind that this figure refers to the average group size, and that many groups will be substantially larger than this, the implications for human time budgets are clearly catastrophic. A group of 200, for instance, would have to devote 56.6% of its day to social grooming. For any organism that also has to earn a living in the real world, this would place a significant strain on its ability to balance its time budget. This problem would clearly be compounded if thermoregulatory considerations forced individuals to take time out to rest in shade during the hottest parts of the day: among baboons at least, temperature-driven resting appears to be incompatible with social interaction (Dunbar 1992b).

To place this in perspective in relation to relative neocortex size in the hominoids, I have calculated the equivalent figures for predicted group size and grooming time for all the genera of hominoids (Table 3). (The fact that only the chimpanzees live in groups of the size predicted by equation [1] is not of significance in the present context: this point is discussed in more detail in Dunbar [1992a].) The question I want to ask here is whether the neocortex size of non-human hominoids is large enough to yield group sizes that would lead to a time-budgetting crisis if the group's relationships had to be serviced by social grooming alone. Table 3 suggests that, although group size increases steadily through the hominoids, in no case is the grooming time requirement predicted by equation (2) excessive by the standards of other catarrhine primates. The figure of around 15% social time predicted for orang utans and chimpanzees compares very favourably with the values actually observed among baboons and macaques (see Dunbar 1991). Although larger bodied apes would need to spend a rather higher proportion of their day foraging than smaller-bodied baboons, the predicted grooming time requirement is not such as to suggest that it would place excessive pressure on their time budgets. Data summarised by Wrangham (1986) indicate that the various chimpanzee populations spend 25-43% of their time in non-foraging activities (mainly resting and social interaction). None of these populations would be forced to forgo any foraging time were they to spend as much as 20% of their time in social grooming.

The situation for modern humans is clearly very different and such high grooming time requirements simply could not be met. In baboons, it has been shown that when the actual amount of time devoted to social interaction is less than that predicted for a

group of the observed size, the group tends to fragment easily during foraging and often subsequently undergoes fission (Dunbar 1992b). Faced with this problem, there are, in principle, only two solutions: either reduce group size to the point where the amount of grooming time is manageable or use the time that is available for social bonding in a more efficient way.

Given that minimum group sizes are ecologically imposed (see Dunbar 1988), there may be little that a particular species can do to manipulate its group size in a particular habitat. The only option will thus be a more efficient use of the time available for social bonding. In this context, the main problem with grooming as a bonding mechanism is that it is highly inflexible: it is all but impossible to do anything else while grooming or being groomed. In addition, grooming is an essentially dyadic activity: only one other individual can be groomed at a time.

Modern humans do, however, possess a form of social communication that overcomes both of these limitations very effectively: not only can speech be combined with almost every other activity (we can forage and talk at the same time), but it can also be used to address several different individuals simultaneously. Thus, language introduces major savings by allowing an individual to do two different things at once. My suggestion, then, is that language evolved as a "cheap" form of social grooming, so enabling the ancestral humans to maintain the cohesion of the unusually large groups demanded by the particular conditions they faced at the time.

3.3. Language as a Bonding Mechanism

That language (and hence speech) might have evolved as a consequence of the need to increase group size raises the question of just how it functions as a bonding mechanism. Conventionally, language has always been interpreted in terms of the exchange of information, and this has usually been understood as being the exchange of information about the environment (e.g. the location of prey, the coordination of behaviour during the hunt). However, the social intelligence hypothesis for the evolution of large brain size in primates (see Byrne & Whiten 1988) implies that the acquisition and manipulation of social knowledge is the primary consideration. The fact that language can be interpreted as fulfilling the same role as social grooming suggests that, rather than being the selective factor driving brain evolution, ecologically-related information-exchange might be a subsequent development that capitalised on a window of opportunity created by the availability of a computer with a substantial information-processing capacity.

How might language function as a mechanism for social bonding? There would appear to be at least two possibilities. One is by allowing individuals to spend time with their preferred social partners, thereby enabling them to acquire information about each other's behaviour by direct observation. This appears to be one way in which social grooming itself might work (Dunbar 1988). That the intellectual content of human conversations is often trivial (and, indeed, many conversations are highly formulaic and ritualised) lends some support to this argument. The second possibility is that language permits the acquisition of information about third party social relationships, thereby enabling an individual to acquire knowledge of the behavioural characteristics of other group members without actually having to observe them in action. (I am grateful to R.W.Byrne for pointing this out to me.) This would have the

effect of considerably widening an individual's sphere of social knowledge relative to what would be possible from direct personal observation. This suggestion meshes well with the social intelligence hypothesis, and is given some support by the extent to which humans seem to be fascinated by gossip about other people's behaviour.

It is rather difficult to test unequivocally between these two alternatives. In any case, it is not obvious that they are necessarily mutually exclusive. However, it is clear that, if the second explanation is true, gossip about third party social relationships must constitute an important component of human conversations. Table 4 summarises data on the content of conversations in a university refectory. Approximately 38% of conversation content was devoted to personal relationships (either of those present or of third parties) and a further 24% involved discussion of personal experiences of a more general kind, both topics being clearly related to social knowledge. Considering the potential importance of academic and other intellectual topics of conversation in a university environment, these are remarkably high values. The acquisition and exchange of information about social relationships is clearly a fundamental part of human conversation. I suggest that it implies that this was the function for which it evolved.

3.4. Efficiency of Language as a Bonding Mechanism

If language evolved purely as a form of vocal grooming in order to facilitate the evolution of larger social groups, its design properties should be of about the right efficiency relative to grooming to allow an increase in group size from the largest observed in nonhuman primates to those predicted for modern humans. By "efficiency" here, I mean the number of interactants that can be simultaneously reached during a social interaction. In social grooming, this is necessarily one, because grooming can only be a one-to-one interaction. Language would thus need to allow proportionately as many individuals to be interacted with at the same time as is necessary to raise the size of nonhuman primate groups up to that predicted for modern humans.

The observed mean group size for chimpanzees (presumably the closest approximation to the ancestral condition for the hominid lineage) is 53.5 (Dunbar 1992a). Since the predicted size for human groups is 147.8, this implies that language (the human bonding mechanism) ought to be $147.8/53.5=2.76$ times as efficient as social grooming (the nonhuman primate bonding mechanism). (The figure would be 2.27 if we used the neocortex-predicted group size of 62.5 given in Table 3 for chimpanzees.) In terms of the argument outlined here, this means that a speaker should be able to interact with 2.8 times as many other individuals as a groomer can. Since the number of grooming partners is necessarily limited to one, this means that the limit on the number of listeners should be about 2.8. In other words, human conversation group sizes should be limited to about 3.8 in size (one speaker plus 2.8 listeners).

Table 5 summarises data on small group sizes from a number of studies. Cohen (1971), for example, censused the distribution of group sizes from the reservations book for Novak's Restaurant in Brookline (Mass.) over a 98 day period in 1968. Although the distribution was double-peaked (with near equal modes at 2 and 4, as might be expected), the mean size of 3070 groups was 3.8. (If groups of less than

three people are excluded on the grounds that they have other concerns that social interaction, then the mean of 2020 groups is 4.8, but the modal group size is just 4 with a highly skewed distribution.) James (1952) collated information on the size of committees in a number of national and local government institutions in the USA, as well as four business corporations: mean size varied from 4.7 to 7.8 with distributions that were highly skewed towards the low end. In a study of freely forming groups in Portland (Oregon), James (1953) found a mean group size of 2.7 (solitary individuals excluded) on a public beach area. Group sizes were slightly smaller, but comparable, in a variety of other social contexts (shopping precincts, open streets, bus depots, school play grounds).

The most direct evidence, however, comes from a study of conversation group sizes carried out in a university refectory. Dunbar & Duncan (submitted) censused conversational cliques that formed freely within interacting groups that varied in size from 2-10 individuals. They found that the average number of people directly involved in a conversation (as speaker or attentive listener) reached an asymptotic value of about 3.4 (one speaker plus 2.4 listeners) and that groups tended to partition into new conversational cliques at multiples of about four individuals (Fig. 4).

It turns out that there is, in fact, a psycho-physical limit on the size of conversation groups. Due to the rate at which speech attenuates with the distance between speaker and hearer under normal ambient noise levels, there is a physical limit on the number of individuals that can effectively take part in a conversation. Sommer (1961), for example, found that a nose-to-nose distance of 1.7m was the upper limit for comfortable conversation in dyadic groups; this would yield a maximum conversation group size of five individuals with a shoulder-to-shoulder spacing of 0.5m between adjacent individuals standing around the circumference of a circle.

Theoretical and empirical studies of signal-attenuation rates suggest that, as the circle of interactees expands with increasing group size, the distances between speaker and listeners across the circle rapidly become too large for conversations to be heard (Beranek 1954, Webster 1965, Cohen 1971). In addition, Webster (1965) found that a doubling of the distance between speaker and hearer reduces by about 6 Db the level of background noise that can be tolerated for any given criterion of speech recognition accuracy, with the reduction being proportionately greater for those with lighter voices (e.g. women). Cohen's (1971) analyses of these results suggested that at background noise levels typical of both offices and city streets, conversational groups will be limited to a maximum of seven individuals if they maintain a spacing distance of about 0.5m apart even when they speak in a raised voice; groups of five would be the limit with normal voice levels.

Although background noise levels in natural environments are unlikely to approach those found on busy city streets, comparably high noise levels are commonly found in large interacting human groups. Legget & Northwood (1960) measured maximum noise levels at cocktail parties of 120-640 people (including a coffee party for librarians!): they found noise levels that were typically in the region 80-85 Db in the mature stages of these parties. This is considerably in excess of the noise levels recorded in city streets and only just below the level sufficient to induce hearing impairment. At such levels, speech recognition is close to zero, conversation becomes impossible and maximum group size approaches one (see Cohen 1971, Fig. 7.1). Such

noise levels may not be untypical of the periodic ritual social gatherings of primitive societies at which relationships are renewed and social gossip about third parties exchanged.

In summary, these results suggest that conversation does meet the requirements of a more efficient bonding mechanism, and that it does so at about the level relative to social grooming that is required to facilitate an increase in group size from those observed in nonhuman primates. Moreover, the psycho-physical properties of human speech provide some evidence to suggest that they are correlated with these demographic characteristics of human groups.

4. Discussion

The essence of my argument has been that there is a cognitive limit to the number of individuals with whom any one person can maintain stable relationships, that this limit is a direct function of relative neocortex size, and that this in turn limits group size. The predicted group size for humans is relatively large (compared to those for nonhuman primates), and is close to observed sizes of certain rather distinctive types of groups found in contemporary and historical human societies. These groups are invariably ones that depend on extensive personal knowledge based on face-to-face interaction for their stability and coherence through time. I argued that the need to increase group size at some point during the course of human evolution precipitated the evolution of language because a more efficient process was required for servicing these relationships than was possible with the conventional nonhuman primate bonding mechanism (namely, social grooming). These arguments appear to mesh well with the social intelligence hypothesis for the evolution of brain size and cognitive skills in primates.

Three points should be noted. One is that there is no obligation on particular human societies to live in groups of the predicted size: the suggestion here is simply that there is an upper limit on the size of groups that can be maintained by direct personal contact. This limit reflects demands made on the ancestral human populations at some point in their past history. Once neocortex size has evolved, other factors may of course dictate the need for smaller groups. Precisely this effect seems to occur in gibbons and orang utans: in both cases, neocortex size predicts groups substantially larger than those observed for these species, but ecological factors apparently dictate smaller groups (Wrangham 1979). Thus, the observation that Australian Aboriginal tribes living in the central desert regions lack the larger clan-like groups does not necessarily disprove the hypothesis. The marginal habitats occupied by these peoples seems to dictate a foraging strategy based on small dispersed groups living in very large territories; this almost certainly creates communication problems that preclude the formation of larger social networks. The hypothesis would be invalidated, however, if there was no evidence for clan-like groupings in more productive environments.

(It is, incidentally, worth observing that we might expect the upper limit on group size to depend on the degree of social dispersal. In dispersed societies, individuals will meet less often and will thus be less familiar with each, so group sizes should be smaller in consequence; in spatially concentrated societies, on the other hand,

individuals will see each other more often and group sizes should be proportionately larger.)

The second point is that the limit imposed by neocortical processing capacity is simply on the number of individuals with whom a stable inter-personal relationship can be maintained. This in no sense commits us to any particular way of structuring those groups (e.g. via kinship). Although the layers of grouping listed in Table 1 are often based on biological relatedness (involving the successive fission of what are usually termed segmentary lineages: see for example Meggitt 1965b), there is no requirement that groups necessarily have to be organised on genetic principles. Kinship is one dimension of primate societies that is relevant to individuals' decisions about whom to group with, and it often provides a convenient means for structuring a hierarchically inclusive pattern of grouping (see Dunbar 1988). However, even among nonhuman primates, it is not the only basis on which individuals choose whom to form groups and/or alliances with (see Cheney 1983). Primate groups are, strictly speaking, coalitions based on common interest and any number of biological, economic and social dimensions besides kinship may be relevant in individual cases (see, for example, de Waal & Luttrell 1986).

Finally, it should be noted that this explanation clearly stands in direct contrast to the conventional wisdom that language developed in the context of hunting to enable early hominids to communicate about the location of possible prey and to plan coordinated hunting expeditions. Indeed, the explanation for the increase in brain size within the hominid lineage on which my argument is based itself stands in contradiction to the conventional wisdom that these large brains evolved to enable humans to hunt and/or manufacture tools. Others (e.g. Wynn 1988; see also Blumenberg 1983) have already pointed out that the evolution of large brain size within the hominid lineage does not correlate well with the archaeological record for changes in tool construction. The markedly improved tool designs of the Upper Palaeolithic can thus be better interpreted as a consequence rather than a cause of enlarged brain size.

This analysis raises a number of additional questions. (1) At what point during the process of human evolution from the common pongid ancestor did such unusually large groups (and hence language) evolve? (2) How is it that, despite these apparent cognitive constraints on group size, modern human societies are nonetheless able to form super-large groups (e.g. nation states)? (3) To what extent is language a uniquely novel solution confined to the hominid lineage?

The fossil evidence (see Aiello & Dean 1990) suggests that brain size increased exponentially through time within the hominid lineage, being well within the pongid range for the Australopithecus species and not showing a marked increase until the appearance of Homo sapiens. This would tend to suggest that neocortex sizes are unlikely to have been sufficiently large to push the grooming time requirement through the critical threshold at about 25-30% of the time budget until quite late in hominid evolution. Application of equations (1) and (2) to all the fossil hominids for which cranial capacity estimates are available identifies the appearance of archaic Homo sapiens at about 250,000 years BP as the point at which language most likely evolved (Aiello & Dunbar, submitted). (It turns out that neocortex ratio is a simple allometric function of cranial capacity in all primates, including humans, with a very

high coefficient of determination, thus allowing us to determine group sizes even for extinct species.) Language would thus have been a rather late evolutionary development. Just why early humans should have found it necessary to evolve such large groups remains uncertain, however, and there is little that can usefully be said to clarify this point at present (for further discussion, see Aiello & Dunbar, submitted).

(Let me forestall at least one line of criticism at this point by observing that the fact that we cannot identify a functional explanation to account for the evolution of a trait does not invalidate the fact that such a trait has evolved: it merely signals our limited knowledge. Humans clearly have larger group sizes than nonhuman primates, and groups of that size cannot have appeared by magic for no good reason. Whether we can ever answer that question will ultimately depend on whether we can extract the relevant information from the fossil record. It will also, however, depend on our developing theories of sufficient complexity to allow us to understand the interactions between the various components within what is inevitably a complex socio-ecological system (Tooby & DeVore 1987, Dunbar 1989b).)

The second issue concerns the fact that contemporary human societies are able to maintain very large groupings indeed (in the order of several hundred million individuals in a modern nation state). Two observations are worth making here. One is that the structure of these super-large groupings is not particularly stable through time, as has repeatedly been demonstrated in history by the eventual collapse of most large empires. The other is that language has two unusual properties that make it possible to form groups that are substantially larger than the 150-200 predicted by neocortex size: it allows us (1) to categorise individuals into types and (2) to instruct other individuals as to how they should behave towards specific types of individuals within society. Thus, we can specify that individuals identified as a class by a particular badge (for example a clerical collar or a sherrif's badge) should be treated in a certain rather specific way (e.g. with great deference). A naive individual will thus know how to respond appropriately to a member of that class on first meeting even though s/he has never previously encountered that particular individual before. This may be especially important in the case of those types of individuals (e.g. royalty, bishops, etc) that the average citizen does not normally have the opportunity to meet. Subsequent more intimate interactions may, of course, allow the relationship to be fine-tuned in a more appropriate way, but conventional rules of this kind at least make it possible to avoid the initial risk of souring a potential relationship by inappropriate behaviour at the first meeting.

This ability to categorise individuals into types clearly makes it possible to create very much larger groups than is possible by direct interaction. It is only necessary to learn how to behave towards a general type of individual, rather than having to learn the nature of each individual relationship. By structuring relationships hierarchically in this way, social groups of very substantial size can in principle be built up. The obvious example is, once again, the hierarchical structuring of military units. Notice that, even in this case, members of different groupings are often given distinctive badges or uniforms in order to allow them to be identified easily: this applies not only to categories of individuals who are considered to be "important" (e.g. officers) but also to members of different types of unit who are of equivalent status in the hierarchy (e.g. military policemen, marines, different regiments, etc).

It is significant, however, that larger groupings of this size appear to be very much less cohesive than groups that are smaller than the critical limit. Language seems to be a far from perfect medium for acquiring detailed social knowledge about other individuals: secondhand knowledge, it seems, is a poor substitute for the real thing. Indeed, it is conspicuous that when we do want to establish very intense relationships, we tend to do so through the much more primitive medium of physical contact rather than through language. The kind of "mutual mauling" in which we engage under these circumstances bears a striking resemblance to social grooming in other primates -- and suffers from all its disadvantages. One study of social grooming in a natural human population, for example, found that 92% of all grooming interactions were dyadic (Sugawara 1984). In this context, it is relevant to note that sociometric studies of "sympathy groups" suggest that we are only able to maintain very intense relationships with 10-12 other individuals at any one time (Buys & Larson 1979).

The final issue is the purely phylogenetic one of where language might have evolved from within the natural communication patterns of primates. Can we identify any features of nonhuman primate vocal communication that could function as a natural precursor for human language? The obvious analogy lies in the contact calls used extensively in many species of anthropoid primates to coordinate spacing between individuals of the same group. Although these calls have traditionally been interpreted as a mechanism for maintaining contact during movement (hence their generic name), it has become clear in recent years that there may be more subtle layers of meaning to these calls. Cheney & Seyfarth (1982), for example, found that vervet monkeys use contact calls to comment on events or situations as they occur. They were able to show experimentally that slight differences in the acoustical form of the calls allow the audience to infer a great deal about the event or situation on which the caller is commenting, even in the complete absence of any visual information.

So far, rather little work has been done on the phonetic structure of primate contact calls. The one exception here has been the gelada, whose vocalisations have been analysed in considerable detail by Richman (1976, 1978, 1987). Richman (1976) found that gelada are able to produce sounds that are synonymous with the vowel and consonant sounds (notably fricatives, plosives and nasals, as well as sounds articulated in different parts of the vocal tract such as labials, dentals and velars) that were hitherto thought to be distinctive features of human speech. Furthermore, Richman (1987) has pointed out that the gelada's highly synchronised exchanges of contact calls (see also Richman 1978) possess many of the rhythmic and melodic properties of human speech patterns. The conversational nature of these exchanges led Richman (1987) to suggest that gelada use these musical qualities to designate utterance acts so as to permit hearers to parse the sound sequence into smaller units in just the way that humans do when talking. He specifically related this ability to the social context, in particular the need to resolve the emotional conflicts inherent in many social situations. It is significant that, in the gelada, calling and counter-calling between individuals is closely related to the strength of the relationship between them (see Kawai 1979, Dunbar 1988, p.251).

We do not at present know whether the acoustic features identified by Richman are unique to the gelada. They might well not be. However, the conversational properties of gelada contact calls (in particular their use in highly synchronised bouts, often involving intense emotional overtones) do seem to be unusual. It may therefore be

significant that gelada live in the largest naturally occurring groups of any nonhuman primate: the average size of their rather loosely structured bands (a high level grouping within an extended hierarchically organised social system based on a very much smaller stable reproductive unit) is about 110 (see Iwamoto & Dunbar 1983).

Clearly, the gelada have in no sense evolved language in the sense we would use this term of humans, but then neither have they developed the large cohesive groups characteristic of our species. However, it may be that the large groups in which this species sometimes gathers forced the evolution of a supplementary vocal mechanism for servicing relationships in a context where they are already at the limit of available grooming time (see Iwamoto & Dunbar 1983, Dunbar 1991). It is worth noting that this much has been achieved without the need to increase neocortex size: indeed, the gelada have a rather small neocortex compared to their baboon cousins (genus *Papio*) which probably explains the lack of cohesiveness in their larger-scale groups compared to those of the baboons.

This would seem to suggest that many of the basic properties of speech and language were already available in the more advanced nonhuman primates. What was required was their close integration and elaboration, and this may have been dependent on a significant increase in neocortex size in order to provide the necessary computing capacity. I simply suggest that the evolution of this increased capacity arose out of the need to coordinate the large number of inter-personal relationships necessary to maintain the cohesion and stability of larger than normal groups.

Acknowledgments

I am grateful to a large number of individuals with whom I have discussed the ideas presented in this paper over the past four years, but in particular I thank Leslie Aiello, Dick Byrne and Henry Plotkin for their encouragement and advice.

References

- Aiello, L.A. & Dean, C. (1990). *An Introduction to Human Evolutionary Anatomy*. Academic Press: London.
- Aiello, L.A. & Dunbar, R.I.M. (submitted). Neocortex size, group size and the evolution of language in the hominids. *Current Anthropology*.
- Becher, T. (1989). *Academic Tribes and Territories*. Open University Press: Milton Keynes.
- Beranek, L.L. (1954). *Acoustics*. McGraw-Hill: New York.
- Birdsell, J.B. (1970). Local group composition among the Australian aborigines: a critique of the evidence from fieldwork conducted since 1930. *Current Anthropology* 11: 115-142.
- Blumenberg, B. (1983). The evolution of the advanced hominid brain. *Current Anthropology* 24: 589-623.

- Bryant, F.C. (1982). *We're All Kin: A Cultural Study of a Mountain Neighbourhood*. University of Tennessee Press: Knoxville.
- Buys, C.J. & Larsen, K.L. (1979). Human sympathy groups. *Psychological Report* 45: 547-553.
- Byrne, R. & Whiten, A. (eds) (1988). *Machiavellian Intelligence*. Oxford University Press: Oxford.
- Chagnon, N.A. (1979). Mate competition, favouring close kin and village fissioning among the Yanomano Indians. In: N.Chagnon & W.Irons (eds) *Evolutionary Biology and Human Social Behaviour*, pp. 86-131. Duxbury Press: North Scituate (Mass.).
- Cheney, D. (1983). Extrafamilial alliances among vervet monkeys. In: R.A.Hinde (ed) *Primate Social Relationships*, pp. 278- 286. Blackwell Scientific Publishing: Oxford.
- Cheney, D.L. (1992). Within-group cohesion and inter-group hostility: the relation between grooming distributions and inter-group competition among female primates. *Behavioural Ecology* (in press).
- Cheney, D. & Seyfarth, R.M. (1982). How vervet monkeys perceive their grunts. *Animal Behaviour* 30: 739-751.
- Clutton-Brock, T.H. & Harvey, P.H. (1980). Primates, brains and ecology. *Journal of Zoology (London)* 190: 309-323.
- Cohen, J.E. (1971). *Casual Groups of Monkeys and Men*. Harvard University Press: Cambridge (Mass.).
- Coleman, J.S. (1964). *Introduction to Mathematical Sociology*. Collier-Macmillan: London.
- Damas, D. (1968). The diversity of Eskimo societies. In: R.Lee & I.DeVore (eds) *Man the Hunter*, pp.111-117. Aldine: Chicago.
- Dunbar, R.I.M. (1984). *Reproductive Decisions: An Economic Analysis of Gelada Baboon Social Strategies*. Princeton University Press: Princeton.
- Dunbar, R.I.M. (1988). *Primate Social Systems*. Chapman & Hall: London and Cornell University Press: Ithaca.
- Dunbar, R.I.M. (1989a). Social systems as optimal strategy sets: the costs and benefits of sociality. In: V.Standen & R.Foley (eds) *Comparative Socioecology*, pp. 73-88. Blackwells Scientific: Oxford.
- Dunbar, R.I.M. (1989b). Ecological modelling in an evolutionary context. *Folia Primatologica* 53: 235-246.
- Dunbar, R.I.M. (1991). Functional significance of social grooming in primates. *Folia Primatologica* 57: 121-131.

- Dunbar, R.I.M. (1992a). Neocortex size as a constraint on group size in primates. *Journal of Human Evolution* 20: 469-493.
- Dunbar, R.I.M. (1992b). Time: a hidden constraint on the behavioural ecology of baboons. *Behavioural Ecology and Sociobiology* 31: 35-49.
- Dunbar, R.I.M. (in press). Ecological constraints on group size in baboons. In: P.Jarman & A.Rossiter (eds) *Animal Societies: Individuals, Interactions and Social Organisation*. Blackwell Scientific: Oxford.
- Dunbar, R.I.M. & Duncan, N. (submitted). Human conversational groups. *Ethology and Sociobiology*.
- Drucker, P. (1955). *Indians of the Northwest Coast*. Natural History Press: Garden City (N.Y.).
- Ellen, R. (1978). *Environment, Subsistence and System*. Cambridge University Press: Cambridge.
- Forge, A. (1972). Normative factors in the settlement size of Neolithic cultivators (New Guinea). In: P.Ucko, R.Tringham & G.Dimbelby (eds) *Man, Settlement and Urbanisation*, pp.363- 376. Duckworth: London.
- Hallpike, C.R. (1977). *Bloodshed and Vengeance in the Papuan Mountains*. Oxford University Press: Oxford.
- Harako, R. (1981). The cultural ecology of hunting behaviour among Mbuti pygmies in the Ituri Forest, Zaire. In: R.S.O.Harding & G.Teleki (eds) *Omnivorous Primates*, pp.499- 555. Columbia University Press: New York.
- Harcourt, A.H. (1988). Alliances in contests and social intelligence. In: R.Byrne & A.Whiten (eds) *Machiavellian Intelligence*, pp. 132-152. Oxford University Press: Oxford.
- Harcourt, A.H. (1989). Sociality and competition in primates and non-primates. In: V.Standen & R.Foley (eds) *Comparative Socioecology*, pp. Blackwells Scientific Publications: Oxford.
- Hardin, G. (1988). Common failing. *New Scientist* 102 (1635): 76.
- Haverfield, F.J. (1955). Roman Army. *Encyclopaedia Britannica* (14th edition) 19: 395-399.
- Helm, J. (1968). The nature of Dogrib socioterritorial groups. In: R.Lee & I.DeVore (eds) *Man the Hunter*, pp.118-125. Aldine: Chicago.
- Hewlett, B.S. (1988). Sexual selection and paternal investment among Aka pygmies. In: L.Betzig, M.Borgerhoff Mulder & P.Turke (eds) *Human Reproductive Behaviour*, pp. 263-276. Cambridge University Press: Cambridge.

- Humphrey, N.K. (1976). The social function of intellect. In: P.Bateson & R.Hinde (eds) *Growing Points in Ethology*, pp.303-317. Cambridge University Press: Cambridge.
- Indik, B.P. (1965). Organisation size and member participation: some empirical tests of alternative hypotheses. *Human Relations* 18: 339-350.
- Irwin, C.J. (1987). A study in the evolution of ethnocentrism. In: V.Reynolds, V.Falger & I.Vine (eds) *The Sociobiology of Ethnocentrism*, pp.131-156. Croom Helm: London.
- Iwamoto, T. & Dunbar, R.I.M. (1983). Thermoregulation, habitat quality and the behavioural ecology of gelada baboons. *Journal of Animal Ecology* 52: 357-366.
- James, J. (1952). A preliminary study of the size determinant in small group interaction. *American Sociological Review* 16: 474-477.
- James, J. (1953). The distribution of free-forming small group size. *American Sociological Review* 18: 569-570.
- Jerison, (1973). *Evolution of the Brain and Intelligence*. Academic Press: New York.
- Jolly, A. (1969). Lemur social behaviour and primate intelligence. *Science* 153: 501-506.
- Johnson, A.W. & Earle, T. (1987). *The Evolution of Human Societies*. Stanford University Press: Stanford (Calif.).
- Kawai, M. (1979). Auditory communication and social relations. In: M.Kawai (ed) *Ecological and Sociological Studies of Gelada Baboons*, pp. 219-241. Japan Science Press: Tokyo & Karger: Basel.
- Killworth, P.D., Bernard, H.R. & McCarty, C. (1984). Measuring patterns of acquaintanceship. *Current Anthropology* 25: 391- 397.
- Knauft, B. (1987). Reconsidering violence in simple human societies: homicide among the Gebusi of New Guinea. *Current Anthropology* 28: 457-500.
- Hudo, H., Bloom, S. & Dunbar, R. (in preparation). Neocortex size as a constraint on social network size in primates.
- Kummer, H. (1982). Social knowledge in free-ranging primates. In: D.Griffin (ed) *Animal Mind -- Human Mind*, pp.113-130. Springer: Berlin.
- Leacock, E. (1969). The Montagnais-Naskapi band. In: D.Damas (ed) *Band Societies*, pp.1-17. National Museum of Canada: Ottawa.
- Lee, R.B. (1982). *The !Kung San: Men, Women and Work in a Foraging Society*. Cambridge University Press: Cambridge.

Legget, R.F. & Northwood, T.D. (1960). Noise surveys of cocktail parties. *Journal of the Acoustical Society of America* 32: 16-18.

MacDonald, C.B. (1955). Company. *Encyclopaedia Britannica* (14th edition) 6: 143-144.

Mange, A. & Mange, E. (1980). *Genetics: Human Aspects*. Saunders: Philadelphia.

Martin, R.D. (1983). Human brain evolution in an ecological context. 52nd James Arthur Lecture. American Museum of Natural History: New York.

Meggitt, M.J. (1965a). *Desert People*. Chicago University Press: Chicago.

Meggitt, M.J. (1965b). *The Lineage System of the Mae-Enga of New Guinea*. Oliver & Boyd: Edinburgh.

Milardo, R.M. (1988). Families and social networks: an overview of theory and methodology. In: R.M. Milardo (ed) *Families and Social Networks*, pp.13-47. Sage: Newbury Park.

Mitchell, J.C. (ed) (1969). *Social Networks in Urban Situations*. University of Manchester Press: Manchester.

Montross, L. (1975). Tactics. *Encyclopedia Britannica* (15th edition) 19: 572-583.

Morris, B. (1982). The family, group structuring and trade among South Indian hunter-gatherers. In: E.Leacock & R.Lee (eds) *Politics and History in Band Societies*, pp.171-187. Cambridge University Press: Cambridge.

Naroll, R. (1956). A preliminary index of social development. *American Anthropologist* 58: 687-715.

Oates, J. (1977). Mesopotamian social organisation: archaeological and philological evidence. In: J.Friedman & M.J.Rowlands (eds) *The Evolution of Social Systems*. Duckworth: London.

Porter, L.W. & Lawler, E.E. (1965). Properties of organisation structure in relation to job attributes and job behaviour. *Psychological Bulletin* 64: 23-51.

Price, D. & Beaver, D. (1966). Collaboration in an invisible college. *American Psychologist* 21: 1011-1018.

Rayner, J.M.V. (1985). Linear relations in biomechanics: the statistics of scaling functions. *Journal of Zoology (London)* 206: 415-439.

Richman, B. (1976). Some vocal distinctive features used by gelada monkeys. *Journal of the Acoustical Society of America* 60: 718-724.

Richman, B. (1978). The synchronisation of voices by gelada monkeys. *Primates* 19: 569-581.

- Richman, B. (1987). Rhythm and melody in gelada vocal exchanges. *Primates* 28: 199-223.
- Sahlins, M. (1972). *Stone Age Economics*. Aldine: Chicago.
- Sawaguchi, T., & Kudo, H. (1990). Neocortical development and social structure in primates. *Primates* 31: 283-290.
- Service, E.R. (1962). *Primitive Social Organisation: An Evolutionary Perspective*. Random House: New York.
- Seyfarth, R.M. & Cheney, D.L. (1984). Grooming, alliances and reciprocal altruism in vervet monkeys. *Nature (London)* 308: 541-543.
- Sharman, M. (1981). *Feeding, Ranging and Social Organisation of the Guinea Baboon*. Ph.D. thesis: University of St. Andrews.
- Schieffelin, E.L. (1976). *The Sorrow of the Lonely and the Burning of the Dancers*. St Martin's Press: New York.
- Silberbauer, (1972). The G/wi bushmen. In: M.G.Bicchieri (ed) *Hunters and Gatherers Today*, pp.271-325. Holt Rinehart & Winston: New York.
- Silverman, D. (1970). *The Theory of Organisations*. Heinemann: London.
- Smuts, B., Cheney, D., Seyfarth, R., Wrangham, R. & Struhsaker, T. (eds) (1987). *Primate Societies*. Chicago University Press: Chicago.
- Spencer, R. (1959). The north Alaskan Eskimo: a study in ecology and society. *Burrell American Ethnology Bulletin* Vol. 171.
- Stephan, H. (1972). Evolution of primate brains: a comparative anatomical approach. In: R.Tuttle (ed) *Functional and Evolutionary Biology of Primates*, pp. 155-174. Aldine- Atherton: Chicago.
- Stephan, H., Frahm, H. & Baron, G. (1981). New and revised data on volumes of brain structures in insectivores and primates. *Folia Primatologica* 35: 1-29.
- Steward, J.H. (1936). The economic and social basis of primitive bands. In: R.H.Lowie (ed) *Essays in Anthropology Presented to A.L.Kroeber*, pp. 331-359. University of California Press: Berkeley.
- Steward, J.H. (1938). Basin-plateau aboriginal sociopolitical groups. *Burrell American Ethnology Bulletin* Vol. 120.
- Steward, J.H. (1955). *Theory of Culture Change: The Methodology of Multilinear Evolution*. University of Illinois Press: Urbana.
- Strehlow, T.G.H. (1947). *Aranda Traditions*. Melbourne University Press: Melbourne.

- Sommer, R. (1961). Leadership and group geometry. *Sociometry* 24: 99-110.
- Sugawara, K. (1984). Spatial proximity and bodily contact among the central Kalahari San. *African Studies Monographs, Supplement*, 3: 1-43.
- Terrien, F.W. & Mills, D.L. (1955). The effect of changing size upon the internal structure of organisations. *American Sociological Review* 20: 11-13
- Tooby, J. & DeVore, I. (1987). The reconstruction of hominid behavioural evolution through strategic modelling. In: W.Kinzey (ed) *The Evolution of Human Behaviour*, pp. 183-237. State University of New York Press: Albany.
- Turnbull, C. (1968). The importance of flux in two hunting societies. In: R.Lee & I.DeVore (eds) *Man the Hunter*, pp.132-137. Aldine: Chicago.
- Webster, J.C. (1965). Speech communications as limited by ambient noise. *Journal of the Acoustical Society of America* 37: 692- 699.
- Whiten, A. & Byrne, R.B. (1988). The Machiavellian intelligence hypotheses. In: R.Byrne & A.Whiten (eds) *Machiavellian Intelligence*, pp. 1-9. Oxford University Press: Oxford.
- Williams, B.J. (1974). A model of band societies. *Memoires of the Society of American Archaeologists* Vol. 39, no. 4. de Waal, F. & Luttrell, L.M. (1986). The similarity principle underlying social bonding among female rhesus monkeys. *Folia Primatologica* 46: 215-234.
- Wrangham, R.W. (1979). On the evolution of ape social systems. *Social Science Information* 18: 335-368.
- Wrangham, R.W. (1986). Ecology and social relationships in two species of chimpanzees. In: D.Rubenstein & R.Wrangham (eds) *Ecological Aspects of Social Evolution*, pp. 352-378. Princeton University Press: Princeton, N.J.
- Wynn, T. (1988). Tools and the evolution of human intelligence. In: R.W.Byrne & A.Whiten (eds) *Machiavellian Intelligence*, pp.271-284. Oxford University Press: Oxford.

Legends to Figures

Fig. 1. Group size plotted against neocortex ratio for nonhuman primates. (Redrawn from Dunbar 1992a)

Fig. 2. Distribution of group sizes for traditional societies. Individual societies are placed along the abscissa in arbitrary order. The group size predicted by equation (1) is indicated by the horizontal line; 95% confidence limits around this value are indicated by the dotted lines. Source: Table 1.

Fig. 3. Mean percentage of time spent grooming plotted against mean group size for Old World monkeys and apes that do not have fission-fusion societies (based on data in Dunbar 1991).

Fig. 4. Mean size of conversational cliques (speaker plus attentive listeners) in groups of different size in a university refectory. Clique size was censused at 15- min intervals. Source: Dunbar & Duncan (submitted)

Table 1. Group sizes in modern hunter-gatherer societies.

Mean Size of: Society Location Overnight Band/ Tribe Source

camp village ----- Walbiri
 Australia c.25-30 221.5 886 Meggitt 1965a various New Guinea - 128.7b ? Ellen
 1978 Tauadec New Guinea 27.3 202.5 1237.3 Hallpike 1977 Mae Engad New Guinea
 48 90 (350) 2290 Meggitt 1965b Gebusi New Guinea 26.5e 53-159 450 Knauft 1987
 Kaluli New Guinea 60.0f 109.1 1200 Schieffelin 1976 Ruhua Nualu Indonesia -
 180.0b ? Ellen 1978 Bihar India 26.8 90-120 c.1625 Williams 1974 Andamanese
 Andaman Is 40-50 ? 471 Williams 1974 G/wi San S. Africa 21-85 ? 2000 Silberbauer
 1972 !Kung San Botswana 18.6 152.3 2693 Lee 1982 Mbuti Zaire - 60-150b ? Harako
 1981,

Turnbull 1968 Aka W. Congo 25-35 60-100 (c.1050+) Hewlett 1988 Ammassalik
 Greenland 31.8 ? 413 Service 1962 Inuit Canada ? 150.0 483 Irwin 1987 Central
 Eskimo Canada ? c.100 600 Damas 1968 Dogrib USA c.10-60 c.60-250f ? Helm 1968
 Shoshone USA 62.7 ? ? Service 1962 California Indians USA c.50-75 ? ? Steward
 1955 Yanomano Venezuela - 101.9b 663g Chagnon 1975 Ona Tierra del Fuego 40-
 120 ? ? Steward 1936

Table 1 (continued)

----- Meanh: 37.7 148.4i
 1154.7 Sample size: 8 9 13 Coefficient of Variation (%) 41.7 29.1 64.4

a) Some sources only give a range in group size. ? indicates

that the level of grouping is specifically mentioned by the

ethnographer, but no census data are given; - indicates

that the grouping specifically does not occur. b) Settled hunter-gatherers or traditional horticulturalists

living in permanent villages. c) The values are, respectively, the mean size of clans, tribes

and dialects, as defined by Hallpike (1977), from a total

language group of about 8700; this interpretation is closest to the usage in the present paper. d) The values are, respectively, the mean size of patrilineages, sub-clans (clans in parentheses) and phratries, as defined by Meggitt (1965b), from a total tribal group estimated at 60,000; see comment on footnote (c). e) Helm (1968) quotes sizes as numbers of "conjugal pairs"; I have assumed an average of 3 living children per conjugal pair. f) Mean number of residents in a longhouse. g) Mean size of "population blocs" of Chagnon (1979) from a total Yanomano population estimated to be about 15,000. h) For societies in which actual census data are given. i) The larger value for the Mae Enga would give a mean of 177.3; the median values would be 150.0 and 152.3, respectively.

Table 2. Sizes of the smallest independent unit (a "company") in selected professional armies.

Period National army Size

16th Cent Spain 100-300

England 100

17th Cent Sweden/Germany 106

England: c.1650 110

c.1670 80

20th Cent USA: 1940 223

1945 193

1960 212

Britain: 1940 124

USSR: 1940 139

France: 1940 185

Italy: 1940 198

Germany: 1940 185

1943 147

Japan: 1940 190

Source: MacDonald (1955)

Table 3. Grooming time requirements for hominoids, based on group sizes predicted by neocortex ratio.

Genus Neocortex Predicted Grooming time
ratioa group requirement

sizeb (%)c ----- Gibbon 2.08 14.8 3.4
Orang utan 2.99 50.7 13.8 Gorilla 2.65 33.6 8.8 Chimpanzee 3.2 65.2 17.9 Human
4.10 147.8 41.6 ----- a) Based on
neocortex and total brain volumes given by

Stephan et al (1978) or Dunbar (1992a). b) Predicted by equation (1) c) Predicted by equation (2)

Table 4. Topics of conversation in naturally formed groups in a university refectory.

Percent of Conversationa Topic males females
----- Personal relationships 35.1 41.2
Personal experiences 23.2 24.2 Future social activity 6.4 9.0 Sport/leisure 8.6 6.7
Culture (art, music etc) 4.6 4.7 Politics, religion, ethics 3.1 4.1 Academic-related
matters 19.0 10.1 ----- Sample size 453
614 ----- a) Based on conversations
sampled from 19 groups; the topic

of conservation was determined at 30-sec intervals

(for details, see Dunbar & Duncan [submitted])

Table 5. Human interactional group sizes.

Mean Type of Group group size Source
----- Freely interacting groupsa 2.7

Coleman (1964) Sub-committees (US Congress) 7.1 James (1952) State and city board committees 5.5 James (1952) Business corporation boards 5.3 James (1952) Restaurant reservations 3.8 Cohen (1971)

----- a) Individuals recorded
interacting in groups (solitary

individuals excluded) at the public beach picnic area in