

ROBIN DUNBAR

Reproductive Decisions

*An Economic Analysis of Gelada Baboon
Social Strategies*



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Reproductive Decisions

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Reproductive Decisions: An Economic Analysis of
Gelada Baboon Social Strategies, *by R. I. M. Dunbar*

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An Economic Analysis
of Gelada Baboon
Social Strategies

R.I.M. DUNBAR

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x ■ ACKNOWLEDGMENTS

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Reproductive Decisions

1

Introduction

As our knowledge of the behavior of particular species has increased with time, it has become apparent that the traditional ethological notion of "species-specific behavior" is often inappropriate for social behavior. More than anything else, field workers have come to appreciate that the degree of variability in the behavior of natural populations of animals is quite extraordinary. Concomitantly, we have seen a shift in emphasis over the past two decades from the early ethologists' view of animals responding more or less automatically to stimuli to one where animals are seen as decision-makers engaged in a process of evaluating strategic options.

This book is concerned with decision-making by animals. In it, I analyze the social behavior of gelada baboons (*Theropithecus gelada*) as a complex set of alternative strategies among which an individual has to choose. I ask the question: given that the gelada have the social system and ecological niche they do, how does an individual animal set about maximizing its personal reproductive output?

I also have an ulterior motive in that I use the gelada to illustrate a methodological approach to the study of social systems that is now beginning to yield increasing dividends. This approach takes the view that social behavior is concerned ultimately with reproduction and can most usefully be interpreted in terms of strategic decision-making aimed at maximizing an individual's contribution to its species' gene pool (see for example Daly and Wilson 1983). Of course, not everything an animal does during social interactions is immediately concerned with reproduction. Most behavior is concerned directly with objectives that are logically more proximate. For this reason, it is particularly important to distinguish between proximate and ultimate explanations of behavior. These can, perhaps, best be viewed as a series of increasingly direct influences on an individual's reproductive prospects and, at one further remove, on its contribution to the species' gene pool (see Dunbar 1983a). Reproduction, in a word, is the central problem in the life sciences, for it is the issue around which all other aspects of biology hinge.

I shall argue that such a view is becoming increasingly necessary if we are ever to understand social behavior completely. This is because it is essential to know not just what an animal does, but also what it is

“trying” to do in order to understand why, in the end, it does what it does (see also Seyfarth 1980). This inevitably demands a much more sophisticated approach to the problems of social behavior: indeed, the success of such a program is dependent on the existence of a body of theory capable of making detailed predictions about behavior. That theoretical framework now exists in what has come to be known as sociobiology, while the analytical techniques have long been available in economics and operations research (McFarland and Houston 1982).

The perspective I adopt is strictly sociobiological, though I hasten to add that I do not espouse narrow “socio-genetical” arguments: the decisions made by the animals are too complex and too deeply nested in a hierarchical network to constitute a case of simple genetic determinism. Nonetheless, a broad sociobiological viewpoint is heuristically valuable in that it provides a powerful Darwinian explanatory basis for observed behavior. I take it as axiomatic that an animal’s genetic inheritance obliges it to strive to maximize its contribution to its species’ gene pool, but that the actual choice of means to achieve that end is a consequence of the evaluation of the relative costs and benefits of different strategies.

In this respect, I shall make frequent use of the language of conscious decision-making in defiance of Lloyd Morgan’s proscription of anthropomorphisms. I do so partly because this is much the easiest way to discuss the animals’ behavior, but also partly because fifteen years of field work have made it abundantly clear to me that strategy evaluation is precisely what the animals are doing (see also Kummer 1978, 1982).

Theory of Reproductive Strategies

Evolution occurs as a result of a number of processes that influence a species’ gene pool. One of the most important of these is the production of offspring, since it is through offspring that an animal usually makes its main genetic contribution. Naive Darwinian considerations lead us to expect that animals will seek to maximize, by one means or another, the number of offspring they produce. As with most biological phenomena, however, sheer maximization is often counter-productive: the more offspring an individual produces, the less parental care can be given to each and the more likely it is that a high proportion of the young will fail to reach maturity. Lack (1966) gives examples from birds showing that the number of fledgling young peaks at intermediate

clutch sizes. In reproductive terms, more does not always mean greater success in the long run.

Both the strategies that an animal can pursue and their relative efficiencies (in terms of generating mature offspring) are determined by the interaction of ecological, demographic, and social factors (Dunbar 1982a). The components of this system place conflicting demands on an animal's limited time and energy budgets and its morphological characteristics (Goss-Custard et al. 1972, S. Altmann 1974). Consequently, the optimal solution to one problem will often be incompatible with the preferred solutions to other problems. The resulting conflicts of interest will force the animal to re-evaluate its priorities and so to compromise on its original objectives.

The ways in which the various components of each subsystem interact are, in general, well understood. In contrast, the ways in which the subsystems themselves relate to each other have barely been touched on as yet. In particular, the important part played by demographic structure in determining the options available to an animal seems to be less widely appreciated than might be expected (Dunbar 1979a, Altmann and Altmann 1979). Demographic factors determine not only the social and reproductive opportunities available to an animal, but also the level of competition from conspecifics that it will have to face in acquiring whatever resources are relevant.

The system is also subject to density-dependent and frequency-dependent effects. These feedback effects make the "constraint-free strategy" less profitable as more individuals pursue it and are largely responsible for the generation of alternative strategies (Dunbar 1982a and references therein). By *constraint-free strategy*, I mean the strategy that would (other things being equal and in the absence of any constraints due to increased costs) be the preferred strategy in that particular socio-ecological system because it yields the highest net gain in terms of reproductive output. (In Dunbar 1982a, I refer to this by the less satisfactory terms "primary" or "normal" strategy for the species.) Note that a constraint-free strategy is not the same as an "ideal free strategy": as originally defined by Fretwell (1972), the ideal free distribution is that to which the population evolves (in a non-Darwinian sense) once the frequency-dependent and other constraints are imposed on the constraint-free strategy.

Within the context of the constraints imposed by these factors, animals can choose among a range of strategies. The degree to which the set of strategies is stable in an evolutionary sense depends on the extent to which their profitabilities equilibrate in the long term: that is to say,

on the extent to which they yield similar numbers of offspring (or genes) when summed over a lifetime (see Dunbar 1982a, 1983a).

In general, an animal may be expected to pursue those options that are most profitable to it, where profitability may be measured in terms of, for example, expected lifetime reproductive output. Of course, animals do not assess the numbers of offspring that any given strategy is worth: that would require an absurd degree of sophistication even for humans. Rather, they base their decisions on more proximate cues that, over evolutionary time, have come to be correlated with lifetime reproductive output. These proximate cues can take a variety of forms, ranging from overt events (such as the number of matings or mates acquired per unit time) to less easily quantified psychological values (such as general feelings of "contentment" or security). McFarland and Houston (1982) refer to the decision rules based on these cues as "rules of thumb." The correlations between these cues and ultimate profitability (measured in terms of genes contributed to future generations) are rarely one-to-one (Dunbar 1982b). Consequently, we cannot necessarily expect individual animals to make decisions that are evolutionarily optimal, though we can expect them to make decisions that are within a degree of latitude of those optimal decisions on the average.

Reproductive Strategies of Gelada Baboons

My immediate concerns in this book are (1) to describe the range of reproductive strategies pursued by gelada baboons, (2) to identify the proximate factors that give rise to these strategies and, where possible, (3) to evaluate their relative efficiencies.

As is well known, gelada reproductive units contain only one breeding male, and this defines and limits the range of reproductive strategies open to individuals of either sex. Male strategies are mainly related to methods of acquiring control over reproductive units. Females, on the other hand, face a more diffuse set of problems, and the range of strategies open to them is in consequence both more closely tied to their social relationships and less easily discerned by the observer. Thus, as is often the case, the problems faced by males and females are quite different, and the optimal solutions they would prefer are commonly in direct conflict with each other's interests. Part of my task here will be to determine how these strategy sets interrelate in order to understand how one sex's options limit the other sex's behavior.

To be able to do this, we need to know a great deal about the animals' background biology, both ecological and social. As far as the

gelada are concerned, most of the relevant information has now been published in monographs (Dunbar and Dunbar 1975, Kawai 1979a) and an extensive series of papers. Because few people will be familiar with all these publications, I take the liberty of summarizing the most relevant details from this literature in the first few chapters. In doing so, I have tried to avoid providing a general overview of gelada biology. Instead, I have concentrated on those aspects that bear directly on the animals' reproductive strategies. Without this information, the naive reader is apt to raise all sorts of obviously inappropriate alternative explanations for particular phenomena. Those who require more detailed discussions are referred to the original sources cited in the text. This is especially important with respect to many of the causal statements in these chapters: these will often seem to be based on correlations, when reference to the original sources will reveal that the causal inferences are based on very much more detailed logical and evidential analyses.

Chapters 6 through 15 constitute the meat of the book and present both new data and previously unpublished analyses relating to gelada reproductive strategies. The first four of these chapters deal with female strategies, the remainder with those of the males. The inferential process will generally be very much more explicit here. Finally, in Chapter 16, I reconsider certain theoretical issues in the light of these analyses.

It should be noted that I make no attempt to evaluate the adaptive significance of the gelada social system. Rather, I am concerned with just one component of that system, namely, reproductive strategies within the constraints imposed by a social system that is assumed to have been determined by other factors. The general form of the social system and the species' ecological niche can be considered as constraints within which the individual animals make their decisions, even though in reality it is a two-way process. For present purposes, we can assume an explanation for the system's evolution along the lines suggested by the classical socio-ecological literature (see, for example, Crook and Gartlan 1966, Crook 1970, Denham 1971, Goss-Custard et al. 1972), even though these explanations are almost certainly incorrect.

One other point needs to be made explicit. Genetic evolution is a consequence of fitness, a population genetic concept defined in terms of selective advantage (i.e. the rate at which an allele spreads in a population relative to the rates of spread of other alleles at the same locus: see references quoted in Dunbar 1982b). In practice, we are invariably obliged to use more easily quantified measures such as reproductive success, even though the relationship between these meas-

ures and fitness itself is not necessarily one-to-one. For practical reasons, I shall in general assume that lifetime reproductive output is a sensitive index of fitness (see also Grafen 1972) unless a particular context forces me to do otherwise.

Most of the data on which this volume is based were obtained from gelada living in the Sankaber area of the Simen* Mountains National Park in northern Ethiopia during field studies in 1971–72 and 1974–75. Additional data derive from the Bole Valley some 500 km to the south (based on field work in 1972 and 1974) and from the Gich area of the Simen Mountains (based on our own brief study there in 1971 and the more extensive project carried out by M. Kawai and co-workers in 1973–74). Detailed descriptions of the study areas can be found in Dunbar and Dunbar (1974a, 1975) and Kawai (1979a).

The data themselves derive from three main sources.

The demographic data were obtained from repeated censuses of the study populations. All the members of 11 of the 31 reproductive units of the two main bands in 1971–72 and of 15 of the 17 units in the 1974–75 study were known individually, at least within the context of their particular units. A number of other adults in the remaining units were individually recognizable under any circumstances. Almost every unit in the population (five bands in each study) could be instantly identified, either from its composition or by individually recognizable members. A detailed discussion of demographic methods can be found in Dunbar and Dunbar (1975) and Dunbar (1980a). Terminology and symbols for demographic variables follow standard practice (e.g. Caughley 1977).

The data on the structure of social relationships within units (especially those discussed in Chapter 10) derive from detailed studies of individual units. Scan censuses of non-agonistic interactions were used to determine the overall pattern of social relationships for 11 units in 1971–72 and 14 units in 1974–75. In order to standardize the time base, sampling was carried out on a whole unit as long as there was at least one dyad interacting. This time base is referred to as *potential social time*. In the gelada, most social activity is confined to the first and last hours of the day, with the period between 1000 hrs and 1700 hrs being devoted more or less continuously to feeding (see Dunbar 1977a, Iwamoto 1979). Most of the data derive from the morning and evening

* Those familiar with earlier publications on the Simen gelada will notice differences in the spelling of place names. *Geech*, for example, is now spelt *Gich*, while what used to be *Simien* is now *Simen*. Our original spellings followed those in use in 1971–72. A standard English–Amharic transliteration system (Lewis 1959) has recently been introduced (see Stahl and Zurbuchen 1978) and it now seems preferable to use this.

social periods. More detailed sampling of interactions was carried out for 11 of the units during the 1974–75 study: these were used to study dominance relationships, coalition formation, oestrous behavior and the behavioral bases of social relationships. Details of the methods and sample sizes can be found in Dunbar (1980b, 1983c).

The final set of data concerns events associated with the reproductive strategies themselves, especially those of the males. These include events (such as takeover fights and entry by males into units as followers) that occur rarely and at unpredictable intervals. It is impossible to sample these events and the behavior that occurs during them other than by opportunistic recording of all observed occurrences (i.e. by *ad libitum* sampling, *sensu* J. Altmann 1974). Usually, once such an event had been detected, the unit was intensively sampled for 2–3 hours each day until things had settled down again. This usually involved scan-sampling of all interacting dyads and *ad libitum* recording of all interactions involving the main individuals concerned.

A great emphasis is placed on female kin relationships throughout this book. Without the benefit of a very long-term study, it is usually not possible to know which females are related. However, as with many other species of Old World monkeys, gelada females remain in their natal units and do not normally desert them. Analyses of the pattern of grooming interactions suggest that closely related females (mothers, daughters, sisters) form strong grooming partnerships; these were therefore used to determine matrilineal relationships (see Dunbar 1979b). Walters (1981) has shown that grooming frequencies are a good indicator of known mother-daughter relationships in *Papio cynocephalus*. This was subsequently shown to be true of a small group of captive gelada as well (Dunbar 1982c). There seems little reason to doubt the validity of the mother-daughter assignments we have made for the Sankaber gelada: to do so would require a set of even more complex hypotheses to account for the peculiar age distributions observed in the grooming dyads at Sankaber (and, incidentally, at Gich and elsewhere). In this book, the term *matriline* refers to the set of females whose extension is defined by the reproductively mature female descendants of a living female (or one that has only recently died). It does not refer to the extended lineages of the kind found in the literature on *Macaca mulatta* and *M. fuscata*, where the founding matriarchs were generally defined as the set of adult females present in the group when studies were first started two to three decades ago (most of whom are now long since dead). Thus, while matriline in the macaque literature often refer to sets of 20 or 30 females of all age classes (only half of

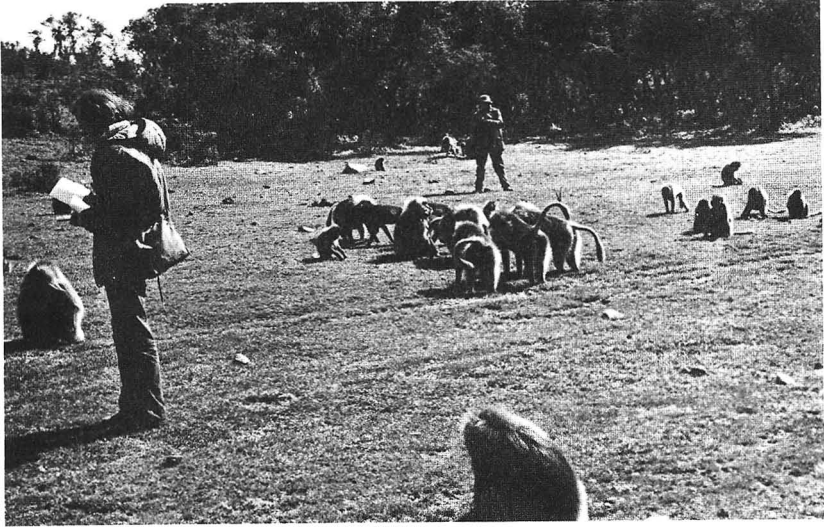


Figure 1 Observation conditions at Sankaber.

whom may still be living), in this book the term refers to sets of 1–6 (average 2) living reproductive females.

Dominance relationships among the members of individual reproductive units were determined from analyses of wins and losses in approach-retreat encounters that occurred in non-social contexts. The members of each unit could be ranked in a simple linear hierarchy on the basis of these data (for details, see Dunbar 1980b). It should be noted that dominance relationships between members of *different* reproductive units are in general irrelevant to the present story and are not considered here.

The detail into which we will be able to go in unfolding the gelada story has been possible because of two important factors. First, the unique structure of gelada society (small reproductive units that associate closely in large herds) made it possible to obtain unusually large sample sizes very rapidly. Not only could a very large number of individuals be observed and censused regularly, but the exceptional observation conditions made it possible to do this with minimum effort. We could expect to see 15–25 reproductive units comprising 250–350 animals on any given day (Fig. 1). This made it more likely that not only would we see rare events, but that we would see enough of them to have a statistically useful sample. Second, the fact that we could observe and sample the behavior of a large number of units meant that

we could do something that has never been done before, namely, analyze the social structure of those units on a quantitative basis in relation to their demographic structure. This has provided profound insights into the dynamics of the gelada social system that would otherwise probably not have been possible without at least two decades of continuous field work. The importance of this factor in the analyses that follow cannot be overestimated; it shows how valuable the comparative method can be when applied across groups and populations of the same species. Of course, the gelada are in many logistic respects unique. Nonetheless, even the comparisons that we have made for as few as three populations have yielded invaluable insights into the dynamics of the species' ecology and demography (although this has been possible with such a small sample only because the populations differed markedly on the environmental variables under consideration).

Definitions

Definitions of the terms used for social units and the various levels of gelada society are given in the next chapter. I here define the terms used to refer to types of animals within these units. (For more detail, see Kawai et al. 1983.)

Males who "own" harems of females (in that they associate continuously with and have exclusive mating access to those females) are termed *harem-holders* (or just harem males). Other adult males who associate regularly with a reproductive unit (but do not, in general, have sexual access to the females) are termed *followers*. Followers may be either young adult males or old males well past their prime (see Dunbar and Dunbar 1975). Terms for the age classes for each sex are defined in Kawai et al. (1983) (see also Dunbar 1980a). Males are considered to be reproductively mature at 6 years of age (though they undergo puberty at the age of 3–4 years); they continue to put on weight until 8–9 years old, which is taken to be the dividing line between young and old adults. Females are considered to be reproductively mature at puberty (ca. 3 years of age): they are classed as juveniles until they are 4 years old, as subadults between 4 and 6 years of age, as young adults from the ages of 6 (when they complete physical growth) to 8, and as old adults thereafter. (Females more than 11 years old are sometimes distinguished as very old adults.) The female's paracallosal skin, normally slate grey in immature animals, turns purplish at puberty; it remains this color until the female is about 6 years old, when it gradually begins to turn pink, a process that takes 18–24 months (see

Dunbar 1977b). Thus, the color of a female's paracallosal skin provides a reliable guide to her approximate age.

In the chapters that follow, I distinguish between the total number of animals of all ages and both sexes in a reproductive unit and the number of reproductive females in that unit. I refer to the first as *unit size* and the second as *harem size*. *Reproductive females* refers to all post-puberty females, whereas *mature females* refers to all females older than 4 years of age.

Pairs of individuals who spend more than 10% of their potential social time interacting with each other are referred to as *grooming partners*, the dyad they form being termed a *grooming dyad* (see Dunbar 1983b).

To avoid confusion over the names of reproductive units, the units censused in the two studies were given different prefixes: 1971–72 units have the letter *H* (e.g. H21), while 1974–75 units have *N* (e.g. N21). Owing to demographic changes between the two studies (notably fissions and takeovers), only a small proportion of the units observed in the first study were genealogically the same as those observed in the second study. Consequently, the identification numbers following the study year prefixes are quite independent: N21 is not the same unit as H21 two years later. Although some of the 1974–75 units were known (from the presence of identifiable members) to be specific units from the 1971–72 study, the proportion of known identities was too small to make the use of the same numbering system worthwhile.

Use of Modeling

The function of modeling in all sciences is to allow complex systems to be studied by isolating the minimum set of variables that describes the behavior of that system. Within this framework, modeling can take a variety of forms and can be used for several, quite different, purposes. I use modeling (1) to generate null hypotheses against which to evaluate observed distributions, (2) to study the long-term consequences of particular behavioral strategies, and (3) to determine the relative importance of the variables that give rise to particular patterns of behavior. The second and third are often two sides of the same coin and, in some cases, involve fairly complex models.

One of the key problems in studying the functional and evolutionary aspects of the behavior of large, relatively long-lived mammals is that direct estimates of the consequences of different behavioral strategies in terms of lifetime reproductive output can seldom be obtained. In the

case of the gelada, for example, such a study would require about 20 years, while chimpanzees or gorillas would require studies on the order of 30–40 years to ensure that all the members of one cohort were followed through a complete lifetime (see Teleki et al. 1976). However, in those cases where we know enough about the animals under study to be able both to specify the relationships between all relevant variables *and* to quantify these relationships, we can use modeling to study the consequences of behavior under circumstances where we have no prospect of being able to carry out proper empirical studies.

If we do not do this, we must either accept that our knowledge of the world about us will always remain incomplete or we must use simpler, more short-lived species as models of larger, less easily studied taxa. Neither strategy is an encouraging prospect, least of all the second because of the number of assumptions involved in deducing conclusions about the behavior of one species from the behavior of another. Each species is the unique outcome of a particular set of biological and environmental interactions over time; consequently, one species' responses to a given set of environmental conditions will often be quite different from those of another (see Dunbar 1984a). These will, in turn, impose quite different constraints and selection pressures on the animals' reproductive and social behavior.

This is often assumed by the philosophically naive to mean that the life sciences have no universal principles and therefore lack predictive power. This, however, is to confuse different levels of explanation, and it is one of the fundamental assumptions of this book that such principles do exist. Biological problems are inherently complex because they involve the interaction of many component elements, each with its own predictive universal principle. Consequently, the key to understanding a species' behavioral biology lies in being able both to identify all these components and to evaluate their relative influences on the more general problem. Only then is it possible to make valid predictions as to what behavior is the most likely to evolve. In most cases, simulation modeling is the only means of handling such a complex network of causal relationships. The models I use here generally take the form of multivariate dynamic models of the kinds commonly found in economic and operations research contexts (see, for example, Thierauf and Klemp 1975, Jeffers 1978). The application of this approach to social behavior constitutes a powerful analytical tool that will permit rapid advances in our understanding of social systems at both the individual and the socio-ecological levels (see also Nagel 1979).

One final important advantage of modeling should be mentioned. In seeking to understand and explain behavior, we need to know not just

how to predict it, but also why a particular prediction occurs (Gale 1979). This requires us to go beyond a mere curve-fitting exercise to determine precisely why it is that any two variables are related in the way they are. Modeling forces us to axiomatize the network of hypotheses, and so to specify precise quantitative relationships (see Maynard Smith [1978], who stresses the importance of stating *all* assumptions clearly when modeling). Once a system has been modeled, sensitivity analysis can be used to determine which relationships contribute most to the predicted outcome. Sensitivity analyses are often used to demonstrate that models are robust—i.e. that the outcome occurs regardless of the precise shape of the quantitative relationships between the variables. This is a useful exercise for simple systems, but for systems that are inherently variable (and in which the variability itself is the object of study), it may tell us little we do not already know. What it can do, however, is tell us how important each variable is to the outcome. I shall make as much use of this second approach to sensitivity analysis as I shall of the first.

Statistical Analyses

The statistical procedures used in this book are taken from standard sources (usually Siegel 1956, Sokal and Rolf 1969, or Pollard 1977). Two-tailed tests are used throughout, except where specific hypotheses are being tested. I treat significance levels (i.e. p -values) as estimates of confidence in a Bayesian sense (following Salmon 1966, Lindley 1970, and others). This means that I tend to specify p -values rather more precisely than is normally considered necessary and that I do not accord the value $p = 0.05$ the magical property that is commonly associated with it. Rather, my belief in any one hypothesis is a simple function of the p -value associated with its statistical test, the more so when compared to the p -values obtained for alternative explanations of the same phenomenon. This should not be seen as an attempt to eke out significant results from dubious data, but rather as an attempt to place a more satisfactory interpretation on the meaning of statistical tests and the inferences drawn from them. Nonetheless, in the interests of minimizing confusion, I will use the term *statistically significant* in its conventional sense with reference to the $p = 0.05$ level.

It is worth observing here that a Bayesian approach to inference using multiple-hypothesis-testing is a powerful means of strengthening evolutionary and functional explanations of behavior (see also Platt 1964). A functional perspective itself is heuristically valuable because

it forces us to find an explanation for a phenomenon, thereby making us think more deeply about it. However, because functional explanations can easily degenerate to the point where they have no greater intrinsic justification than their own null hypotheses, it is essential that they be carefully evaluated and tested. Unfortunately, it is often not possible to carry out rigorous tests with observational studies. This problem can usually be circumvented by ensuring (1) that the explanation is consistent with as many other known aspects of the system as possible, (2) that all alternative explanations can be excluded, and (3) that a convincing physiological or behavioral mechanism can be shown to underlie the functional explanation.

In a number of cases where samples are too small to generate meaningful estimates of significance, a procedure due to R. A. Fisher can be used to pool the results of a number of independent tests of the same hypothesis (see Sokal and Rolf 1969, pp. 621–624). This allows us to determine how likely it is that a distribution of p -values as extreme as those observed would be obtained by chance. This procedure is particularly valuable when the proper unit of analysis is the set of individuals within a harem: in such a case, the sample size is often only 3–5 animals, but data may be available from as many as 10 such units.

2

Structure of Gelada Populations

The gelada social system is a complex arrangement of hierarchically organized social groupings, each of which corresponds to a different functional unit. These groupings are analogous to those of the hamadryas baboon, *Papio hamadryas* (see Sigg et al. 1982), these two species apparently being unique among the primates in the degree of organizational complexity that they have evolved.

In this chapter, I describe the social units that make up the gelada system. The species' ecological niche and population dynamics will be outlined in Chapters 3 and 4, while the structure of social relationships between the individual animals will be discussed in Chapter 5.

Structure of Gelada Society

Traditionally, the basic social unit of the gelada is considered to be the one-male group (Crook 1966), and this is certainly the smallest independent grouping within the social system. These units, together with all-male groups of bachelor males, associate together in a series of higher-level groupings. Kawai et al. (1983) have viewed these patterns of association between units as ascending levels of clustering on a tree-dendrogram. Figure 2 shows this for a nominal group of units. The variable on the y-axis can be either of two equally good indices: (1) the probability of any two units being together on any given day or (2) the correlation between these two units' use of the habitat (i.e. the similarity in their ranging patterns). These association patterns, however viewed, are highly variable and, strictly speaking, they form a continuum over the unit probability range. However, the tendency for association probabilities to cluster at specific levels allows us to define groupings that possess some real significance for the animals themselves. The animals probably view the situation in terms of units whose members are more or less familiar to them, familiarity being a consequence of frequency of association. Frequency of association correlates strongly with similarity of home range, though whether units have similar home ranges because they associate together frequently or associ-

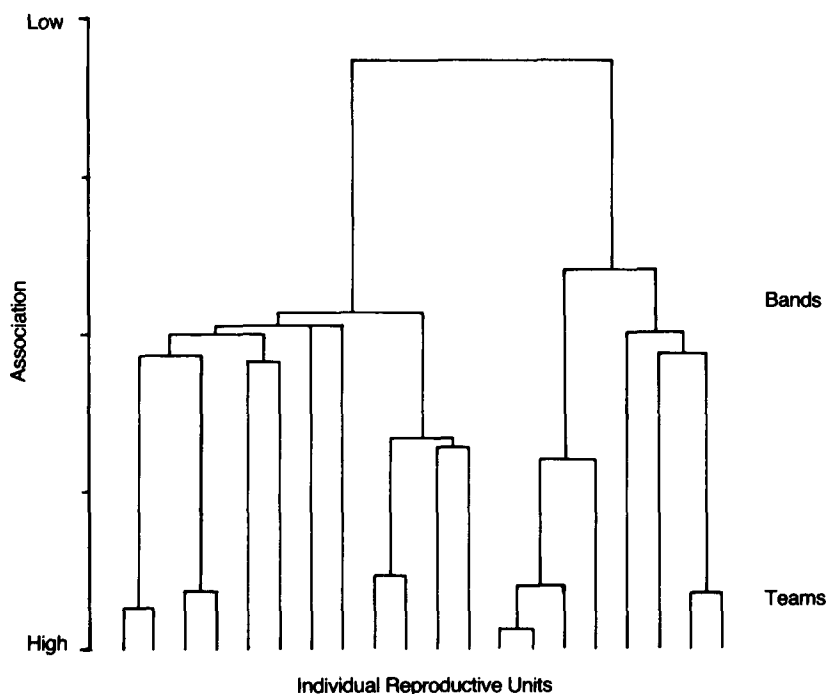


Figure 2 Cluster-analysis of association patterns among a nominal group of reproductive units belonging to two bands. The degree of association between any two units can be estimated either by the frequency with which they occur in the same herd or by the correlation between their respective ranging patterns. Tendencies for distinct clusters to form at specific levels of association reflect the grouping patterns within gelada society. These are identified on the right-hand side of the dendrogram. (Redrawn from Kawai et al. 1983, Fig. 1.)

ate together because they share a common range is a moot point. I am inclined to favor the view that units share a common range because they associate with each other frequently, and that they associate frequently because they are the product of the successive fission of units in the past (Dunbar and Dunbar 1975; see also Kawai et al. 1983).

The two main components of the system are the individual reproductive units and the clusters of units (termed *bands*) that share a common home range. The one-male units provide the context in which most social behavior and all reproductive activities take place, whereas the band is the basic *ecological* unit (being precisely analogous to the *Papio hamadryas* band). The band is a multimale unit that is ecologically equivalent to the typical *Papio* and *Macaca* troop. Studies by Sho-