

## Variability and Stability in the Rank Relations of Nonhuman Primate Females: Analysis by Computer Simulation

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This paper summarizes results of simulation analyses aimed at elucidating the way in which two important dimensions of female rank orders—nepotism and age-gradedness—are affected by variation in individual strategies of rank acquisition on the one hand and by variation in population-wide demographic parameters (eg, birth rate, death rate, etc) on the other. Female rank orders in simulated primate groups were characterized by substantial variability on a year-to-year basis in both nepotism and age-gradedness owing to stochastic processes alone. Although, in general, groups characterized by strongly nepotistic rank orders were not also strongly age-graded, quantitative measures of these two rank-order dimensions for individual groups showed little stability over intervals of time exceeding 3 years. Surprisingly, changes in birth and death rates did not strongly affect either nepotism or age-gradedness so long as average group size remained constant. However, in populations characterized by expanding or declining group size, variation in demographic parameters did indeed exert a powerful influence on the structure of female rank orders. Both nepotism and age-gradedness were also strongly affected, and in quite different ways, by changes in the rules of rank acquisition by females. In sum, the present analyses suggest that differences between species in the degree of nepotism and age-gradedness characteristic of their female rank orders does not in and of itself constitute evidence that the females of those species use markedly different strategies of rank acquisition.

**Key words:** dominance relations, rank orders, Amboseli baboons, nepotism, demography

### INTRODUCTION

In a variety of nonhuman primate species, the position occupied by a female within the dominance order of her group has been shown to markedly affect her survival and reproduction [Sade et al, 1977; Altmann, 1980]. Hence, the way in which rank positions are acquired and retained by females constitutes a topic of

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long standing interest and importance within primatology. For many nonprimate mammals (eg, wolves [Mech, 1970]; mountain sheep [Geist, 1971]), rank is merely a matter of age, with younger individuals generally being subordinate to older individuals of the same sex. Thus, one might expect that this would also be the case for female primates. However, to the best of our knowledge, such a positive association between age and rank has not been reported for females of any anthropoid primate species. More importantly, in those few cases in which an association between age and rank has been reported, the relationship has actually been a negative one; ie, young females are dominant to older females rather than vice versa. For example, within groups of Hanuman langurs (*Presbytis entellus*) and howling monkeys (*Alouatta palliata*), females assume a high rank position shortly after maturation and then move to successively lower rank positions as they advance in age [Hrdy & Hrdy, 1976; Jones, 1980].

In contrast, the rank position acquired by maturing females in most other species of monkeys and apes appears to be influenced primarily by their maternal genealogical affiliation [Walters, 1980]. For example, among macaques and baboons, a daughter, upon reaching maturity, generally assumes a position in the rank order of adult females very close to—and usually immediately below—that of her mother [Kawamura, 1965; Sade, 1967; Silk et al, 1981; Hausfater et al, 1982]. Of course the previous occupant of the rank position obtained by a maturing female under these circumstances will quite frequently be an older sister of that female who herself underwent such a rise in rank within the previous few years. Thus, one important consequence of this maturational rank ascendancy of younger sisters is that within any given matriline adult daughters generally come to be ranked in reverse order of their age [Sade, 1972].

One would hope that the comparative method might reveal distinct habitat differences between species with genealogically based (ie, nepotistic, *sensu* [Hrdy & Hrdy, 1976]) female rank orders and those with rank orders based on age independent of matriline. Unfortunately this is not the case. In their natural environment, groups of langur monkeys—a reverse age-ordered species—are frequently found living side-by-side with rhesus macaques (*Macaca mulatta*), the paradigmatic nepotistically organized species [Jay, 1965]. Thus, the distribution among species of these two different female rank acquisition systems is not readily explained by any simple ecological correlate. Similarly, several more global evolutionary explanations of patterns of rank acquisition by primate females also fail to account for observed variability between species in this phenomenon. For example, Hrdy and Hrdy [1976] have suggested that the reverse age-ordering of adult females in langur groups is an adaptive feature of group organization resulting in allocation of high rank positions to females of high reproductive value (see also discussion by Hrdy [1981]). Yet precisely this same argument has been invoked by other authors to explain the nepotistic pattern of rank acquisition of female macaques [Schulman & Chapais, 1980; Chapais & Schulman, 1980].

Given the above convergence of both ecological and evolutionary explanations, it is perhaps worthwhile to consider whether nepotistic and age-reversed systems of rank acquisition are, in fact, as separate and distinct as they at first appear. For example, consider that if groups of some nepotistically organized species were relatively small in size and composed of females all of whom were descendants of a single matriarch, then a largely age-reversed rank order would arise in groups of this hypothetical species merely as a consequence of their unique demographic structure. Unfortunately, it seems very unlikely that groups of either howling monkeys or langurs are composed exclusively of single extended matriline since migration of females between groups is relatively common in both species [Jones,

1980; Hrdy, 1977; Moore, 1984]. Nevertheless, it remains an open question as to what extent differences among nonhuman primate species in rank acquisition systems, or other aspects of social structure, can in fact be accounted for merely by variation in the demographic parameters of those species.

The idea that apparent differences in social structure between groups, populations, or species may reflect demographic differences between those units rather than differences in the social or reproductive strategies of individuals is certainly not a new one in primate sociobiology. In fact, Wrangham [1979] has argued that differences in social organization among the great apes primarily reflect differences in the ecological and demographic constraints faced by males and females of those species rather than in the social and reproductive strategies pursued by individuals of each sex. At a higher level of abstraction, Hinde and his students [Hinde, 1983] have frequently discussed primate social organization in terms of "deep" and "surface" structures, and Wilson [1975] introduced the concept of "behavioral scaling" to deal with precisely these same concerns.

In this study, a simulation model was used to quantitatively evaluate the way in which the rank ordering of nonhuman primate females within groups would be affected both by differences between those groups in demographic parameters and by differences between groups in the rules or strategies that govern female social behavior. Our approach to this problem was essentially the same as that used by Seyfarth [1977] in his analysis of the grooming behavior of nonhuman primate females. Specifically, we constructed a model social group in which rank acquisition by females took place according to a few simple and explicitly stated rules and in which birth and death rates for females were distributed randomly around predetermined means. Thus, by varying social rules on the one hand, or birth and death rates on the other, we were able to assess the way in which the rank order of females was influenced, respectively, by changes in the behavioral strategies of females or by changes in the demographic parameters of the population in which those females lived.

## THE MODEL

### Overview and Terminology

This paper summarizes results of discrete system simulation analyses aimed at elucidating sources of between-group variation in rank relations among nonhuman primate females. For the purposes of analysis we conceptualized female rank orders as resulting from the interaction of two sets of variables: (1) population-wide demographic parameters such as birth and death rates and (2) "social rules" that govern the rank acquisition behavior of individual females within their groups. Although most workers [eg, Altmann & Altmann, 1979; Dunbar, 1985] presume that over evolutionary time there will be feedback between demographic parameters and social processes—such as rank acquisition—in a way that produces group organizations that are "adaptive," the present analysis concerns variability in female rank orders over ecological time and thus treats demographic parameters as independent of group-level social processes.

Although the meaning of demographic parameters (eg, birth rate, death rate, etc) as used in this work is straightforward, the concept of "rules of rank acquisition" requires more detailed explication. Consider, for example, the case of a young female who comes to rank above her older sisters within a nepotistically organized group of macaques or baboons. Given that this female has just defeated one or more individuals (ie, her sisters) who are both closely related to herself and older than herself, why does she then not go on to defeat her mother, a female who, after all, shares precisely these same characteristics? In fact, it is quite difficult to account for the

failure of maturing females to do so without invoking some form of socially or developmentally imposed constraints on their rank acquisition behavior, and it is such constraints, whatever their precise nature, that are referred to as "social rules" within the present model.

In particular, rank acquisition by females in the model was programmed to conform to those rules that are generally assumed to underlie the nepotistic rank orders of female macaques and baboons [Sade, 1972; Schulman & Chapais, 1980; Hausfater et al, 1982]. Hence, daughters at maturity initially moved to the rank position held by their mother at the time of their births. However, if the mother still occupied the daughter's "targeted" rank position [Walters, 1980], then the daughter assumed the position immediately beneath that of her mother and thus "pushed" its current occupant (and all females beneath her) one position lower in the overall rank order of their group.

Of course, maturations are not the only events that change female rank orders within real-life groups of macaques and baboons. Thus, although such groups are generally characterized by marked stability of rank relations among fully adult females, it is nevertheless the case that rank changes do occur with some frequency among such individuals [Chikazawa et al, 1979; Silk et al, 1981; Gouzoules et al, 1982; Samuels et al, in press]. Although the precise factors leading to these spontaneous rank reversals are not fully understood [Samuels & Henrickson, 1983; Chepko-Sade & Sade, 1979], the age of the females involved does appear to be an important variable, with older females generally falling in rank to younger ones [Silk et al, 1981; Hausfater et al, 1982]. Hence, the present model also allowed for spontaneous rank-change attempts among females, other than mother-daughter pairs, occupying positions adjacent to each other in the rank order. Except as noted below, the outcome of such rank change attempts was decided solely on the basis of age, ie, in favor of the younger of the two females.

### Simulation Structure and Parameter Values

The present simulation model was written in the FORTRAN language and run under the WATFIV compiler on a variety of IBM and Amdahl mainframe computers. The simulation itself used event-scan time management procedures [Graybeal & Pooch, 1980], and the simulated events in each run included (1) births of females; (2) deaths of females; (3) maturations to adulthood of females (always accompanied by a rise to the maternal rank position); and (4) spontaneous rank reversals among fully adult females as described above. In any time interval, the occurrence of an event of one type did not directly affect the probability of occurrence of another event of either the same or different type. Thus, although the average rate of births, deaths, and spontaneous rank reversals was established in advance of each run of the model, the actual frequency of these events within the run, and the particular females they affected, were essentially the result of several mutually independent stochastic (ie, random) processes.

Each run of the simulation began with a seed population of ten unrelated females rank ordered from 1 to 10; females entered the simulated group only through birth and departed only through death. Neither the current rank or previous rank history of females affected their probabilities of reproduction or survival. Rather, females in each simulated group experienced rates of birth and death that varied over time in roughly Poisson fashion around certain prespecified mean values. In particular, mean birth and death rates for females in the model corresponded, as best as could be estimated, to the rates actually experienced by female yellow baboons (*Papio cynocephalus*) in the Amboseli National Park of Kenya [Altmann et

al, 1981]. Thus, interbirth intervals for females in the basic version of the model varied in length from 17 to over 30 months. In actual practice each interbirth interval was calculated as the sum of three independently determined components: (1) a period of lactational amenorrhea drawn from a uniform distribution of range 10 to 16 months; (2) a period of sexual cycling drawn from a geometric distribution with mean of 5 months; and (3) a period of gestation set constant at 6 months.

Females born into the group had only a 50% chance of surviving to 2 years of age, in part because such females were removed from the group along with their mother in the event of the mother's death. Females then had uniformly high age-specific probabilities of survival not only from age 2 to 4, at which time sexual maturation occurred, but also over the next 10 years of life. Thereafter, age-specific mortality rates increased sharply so that females only very rarely exceeded 20 years of adulthood. Although the number of maturations in any set of runs was approximately equal to the number of deaths in those runs, the stochastic nature of birth and death processes in the model meant that groups potentially could become unrealistically large or small in size. Hence, in its final form the simulation incorporated a limited degree of size-dependent buffering of birth and death rates so as to prevent chance extinction of groups on the one hand or exaggerated growth on the other hand.

Within each simulated group, the rank order of females was affected not only by the above demographic processes but also by spontaneously occurring rank change attempts among adjacently positioned females, not all of which actually resulted in a rank reversal as explained above. Specifically, rank reversals among fully adult females took place in the basic version of the model at a mean rate of .07 changes per female per year, equivalent to just under three such changes every 4 years in a group of ten females. Although this value is somewhat higher than the long-term average for Amboseli females [Hausfater et al, 1982], rank reversals in Amboseli groups in certain years have in fact exceeded the above rate by almost an order of magnitude [Samuels et al, in press].

Finally, in each run of the model, no output statistics (ie, measures of nepotism or age-gradedness; see below) were obtained until the original "seed" females and their first cohort of daughters had passed through the group. This convention was adopted to assure that results of analyses would not be affected by either the fixed size or randomly determined age distribution of initial groups. Subsequent to this prespecified delay interval, each run of the model continued until 200 simulation years had elapsed or until an additional 50 females had passed through the group, whichever came first.

### Measures of Age-Grading and Nepotism

Analysis of the model proceeded in three phases, the first of which was intended to answer the question: Given an invariant set of social rules and fixed mean demographic parameters, to what extent will the female rank order within a group vary from year-to-year simply owing to chance alone? Results of this analysis were not only of interest in their own right but also provided a baseline against which results from subsequent modified versions of the model could be evaluated. Thus, for example, in the second phase of analysis, demographic parameters—but not social rules—were varied between runs so as to simulate expanding, declining, and high turn-over rate populations. In essence, these modified versions of the model were intended to answer the question: To what extent will rank orders differ between groups simply owing to demographic differences between those groups? Conversely, the third phase of analysis was intended to answer the question: Given a uniform

demographic environment, to what extent will rank orders differ between groups as a result of slight differences in the social rules that govern rank acquisition by females in those groups?

Obviously, the answer to each of the above questions depended not only on the specific parameter values used in any analysis, but also on the particular measures used to describe and compare female rank orders. In the present study the dependence of female rank position on age was measured simply by calculating a Spearman rank correlation coefficient ( $r_s$ ) between these two variables. Specifically, in the discussion that follows we refer to females as being ranked in reverse age order within their group if the value of  $r_s$  for that group fell between +0.50 and +1.00 inclusive, ie, low rank number (referred to as "high" rank position) associated with low age.

Surprisingly, despite extensive discussion of the nepotistic nature of female rank relations, we were unable to find in the literature on nonhuman primates any previous attempt to rigorously quantify this dimension of group organization. At a minimum, one might consider as nepotistically organized any group in which genetically related individuals occupy adjacent rank positions. In a group so organized, the ranks of individual members of any given matriline will be tightly clustered around the mean rank for that matriline, and furthermore the sum of squared deviations of the rank positions for all females in the group from their mean matrilineal rank will be at a minimum compared to the sum resulting from any alternative arrangement. Hence, the measure of nepotism used in the present study was obtained by comparing the observed sum of squared deviations for each simulated group to the sum expected under conditions of rank assignment without regard to genealogical affiliation.

Specifically, consider a group composed of  $n$  females distributed among  $k$  matriline. If  $R_{ij}$  equals the rank of the  $j$ th female in the  $i$ th matriline in that group, then the mean rank,  $\bar{R}_i$ , for the  $n_i$  females in the  $i$ th matriline will be equal to:  $[1/n_i] \sum R_{ij}$ . Furthermore, for the group as a whole, the sum of squared deviations of each female's rank from the mean for her matriline will be as follows:

$$\sum_{i=1}^k \sum_{j=1}^{n_i} (R_{ij} - \bar{R}_i)^2 . \quad (1)$$

Additionally, it can be readily shown that if those same  $n$  females were assigned to rank positions without regard to genealogical affiliation, then the expected value for the above sum of squared deviations would be:

$$\frac{(n - k)(n)(n + 1)}{12} . \quad (2)$$

Therefore, to obtain a measure of nepotism that was independent of group size and number of matriline, we merely divided equation (1) above by equation (2) above, yielding:

$$\frac{\sum_{i=1}^k \sum_{j=1}^{n_i} (R_{ij} - \bar{R}_i)^2}{\frac{(n - k)(n)(n + 1)}{12}} , \quad (3)$$

which can be rewritten in simplified computational form as:

$$\frac{4n + 2}{n - k} - \frac{12}{(n - k)(n)(n + 1)} \sum n_i \bar{R}_i^2. \quad (4)$$

(A complete derivation of this measure is available on request to the first author.)

Note that when genealogically related females within a group of any given size show no greater clustering in their rank positions than would be expected were ranks assigned at random, the above nepotism statistic will take on a value of 1. That is, the observed sum of squared deviations for the group as a whole, as calculated by formula (1) above, will be the same as the expected value of that sum under the random assignment model, as given by formula (2) above. In contrast, a value of this nepotism measure much less than 1 indicates that genealogically related females are in general clustered among adjacent positions in the rank order of their group, while a value much greater than 1 indicates that related females are overdispersed with respect to present rank position.

Additionally, it is important to note that the above measure will show an equally high degree of nepotism in the rank order of any given group regardless of whether all daughters are ranked in reverse age order immediately beneath their mothers or whether mothers and their daughters are intermixed among adjacent rank positions in some other fashion. Hence, the measure of nepotism used in the present study was sensitive to what one might call "generic" nepotism and, importantly, was not specifically influenced by the degree of age-ordering, or lack thereof, within matriline. Furthermore, in making these nepotism calculations, the present model treated pairs of females for whom the coefficient of relatedness was less than 1/16 (eg, first cousins in most primate species) as if they were effectively unrelated. Although this convention was adopted primarily to reduce demands on computer time, there is in fact some evidence that first cousin is the lowest level of relatedness at which mammalian species can make a "kin/nonkin" distinction [Holmes & Sherman, 1983].

## RESULTS

### Stochastic Variation in Female Rank Orders

Each run of the model simulated births, deaths, maturations, and rank changes in a single group of females over a number of years of its history. Output from each run included a roster of the demographic and rank change events affecting each female as well as nepotism and age-gradedness scores for the group calculated on the last day of each simulation year. Figure 1 summarizes the distribution of these annual age-gradedness and nepotism scores generated by five runs of the model. The mean nepotism score for these runs, 0.59, indicated a tight clustering of related females within adjacent rank positions as was expected given the particular rules of rank acquisition embodied in the model. Nevertheless, the rank ordering of females within groups was still quite strongly affected by stochastic variation in demographic and social processes. Thus, in nearly 20% ( $N = 257$ ) of all simulation years, groups failed to show even a weakly nepotistic rank order, ie, a nepotism score marginally less than 1, and related females were actually strongly overdispersed among rank positions in about 4% of all years.

Figure 1 also demonstrates how frequently even a strictly nepotistic rank acquisition system would be expected to produce a strongly age-reversed female rank order. Thus, the mean age-rank correlation coefficient for all runs combined was +0.35, indicating a strong tendency for young females to be found in high rank

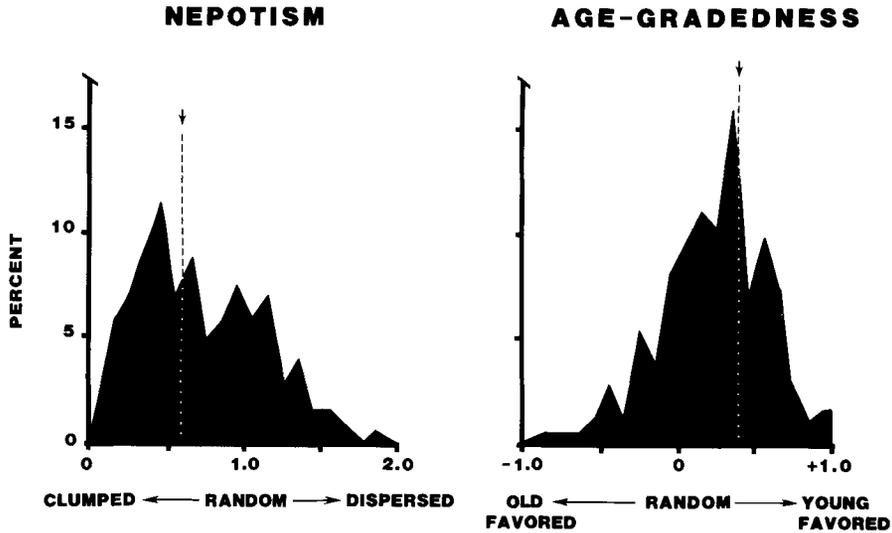


Fig. 1. Frequency distribution of annual nepotism scores and age-rank correlation coefficients obtained in five runs of the initial version of the model ( $N = 257$  simulation years). Broken vertical lines indicate the median score for each measure. See test for further explanation.

positions. Nevertheless, annual age-rank correlation coefficients generated by these five runs spanned the full range of potential values from  $-1.0$  to  $+1.0$ , and in fact the simulated groups were characterized by some degree of positive, as opposed to reverse, age-ordering in nearly 30% of all years ( $N = 257$ ). In sum, Figure 1 indicates that both the degree of nepotism and the degree of age-grading in female rank orders were strongly influenced by stochastic (ie, chance) variation in the demographic and social processes affecting those females.

### Temporal Stability of Nepotism and Age-Gradedness

Despite variation in nepotism and age-gradedness scores both within and between runs, the simulated groups nevertheless showed considerable stability in these measures on a year-to-year basis. Thus, the autocorrelation coefficient between the nepotism score in each simulation year and that same score in the year immediately following averaged  $.77$  across all five runs of the model ( $p < .05$  for all runs). Similarly, for age-gradedness, the correlation coefficient between current year and previous year was  $.70$  averaged over the same five runs ( $p < .05$  for all runs). Viewed another way, these findings indicate that the nepotism or age-gradedness score of a group in any one simulation year accounted for 50–60% of the variance in that same measure in the following year.

However, this marked stability of nepotism and age-gradedness scores did not persist over intervals of time much greater than one to two years. Thus, the nepotism score of a group in any one year accounted for less than 30% of the variance in that group's nepotism score 3 years later. Similarly, less than 20% of the variance in the age-gradedness score for a particular year was accounted for by the comparable score 3 years earlier. At more distant time intervals, for example at lag-times of 5 years or more, autocorrelation coefficients for both scores were in all cases below  $.32$ , meaning that less than 10% of the variance in current score was explained by the comparable score 5 or more years earlier.

### Cross-Correlation of Nepotism and Age-Gradedness Scores

The scores summarized in Figure 1 were also used to test the assumption, implicit in most discussions of female rank acquisition systems, that age-gradedness and nepotism are mutually exclusive attributes of female rank orders. In fact, nepotism scores within years were significantly correlated with age-gradedness scores within years, indicating that strongly nepotistic rank orders were not, in general, also age-reversed rank orders. However, the actual magnitude of these correlations was quite low, and hence it was not possible to predict the nepotism score of a group with any precision from its age-gradedness score or vice versa. Specifically, the mean within-year correlation of nepotism and age-gradedness scores was only 0.31 indicating, as above, that less than 10% of the variance in one measure, say nepotism, was accounted for by variance in the other, ie, age-gradedness. Nevertheless, the fact remains that highly nepotistic groups were, in general, only very rarely also strongly reverse age-ordered, although strongly age-ordered groups in contrast showed no marked departures in their distribution of nepotism scores from the overall sample. In sum, results of this analysis suggest that while extremely strong nepotism precludes extremely strong reverse age-ordering within groups, the opposite is not the case.

### Demographically Induced Variation in Female Rank Orders

In the literature on rank relations among nonhuman primates, differences between species in the degree of nepotism and age-grading in female rank orders have typically been presumed to reflect differences between those species in the rules (or strategies) that govern female rank acquisition behavior. However, such an inference is likely to be correct only if the species in question do not differ in birth rates, death rates, and other demographic parameters. Alternatively, one might wish to argue that demographic differences between species are unimportant from the standpoint of understanding patterns of rank acquisition and stability among females. The second phase of analysis of the model was thus intended to determine the extent to which female rank orders might differ in nepotism or age-gradedness solely as a consequence of differences between groups in their demographic characteristics.

In carrying out the above analyses, the original model was modified in such a way that an initial group of ten females was allowed to grow at the rate of 5% per annum until it reached 100 females in size, or conversely, an initial group of 100 females was allowed to decrease in size (again at 5% p.a.) to a minimum of 10 females. Figure 2 summarizes output obtained from three runs of the model in each of these modified forms. Specifically, the right-hand panel of Figure 2 shows the proportion of simulation years in each set of runs for which the Spearman correlation coefficient between age and rank equaled or exceeded +0.50, indicating strong reverse age-ordering of females. Similarly, the left-hand panel of Figure 2 indicates the proportion of years in which simulated groups were characterized by a nepotism score of 0.50 or less, ie, percent of years in which related females showed extreme clumping in their rank positions.

In general, declining groups were characterized by a very high frequency (93.8%,  $N = 128$ ) of strongly nepotistic rank orders and by a virtual absence of reverse age-grading. In contrast, expanding groups showed strongly nepotistic female rank orders roughly only half as frequently (55.0%,  $N = 182$ ) as was the case for declining groups. Furthermore, female rank orders in expanding groups were more likely than those in declining groups to show strong reverse age-ordering, although in neither case was the actual proportion of years that groups showed this pattern particularly high (8.8% vs 0.6%). In sum, these results suggest that the degree of

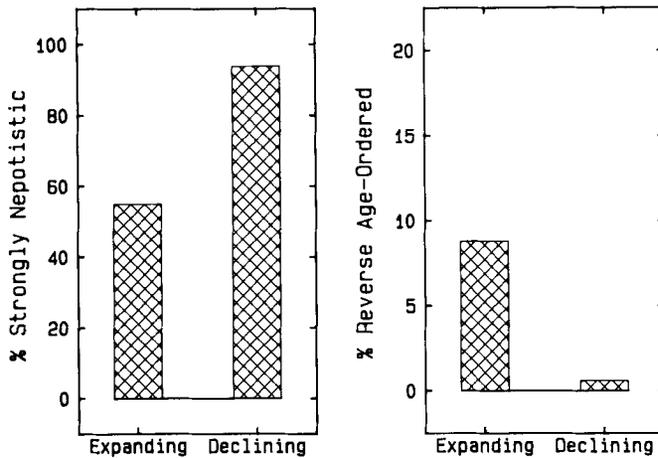


Fig. 2. Proportion of all years in which simulated groups showed strongly nepotistic rank orders (left panel) and strongly age-reversed rank orders (right panel), respectively, in populations expanding or declining at the rate of 5% per annum. Strongly nepotistic rank orders were those receiving a score of +0.5 or less on the nepotism measure; strongly age-reversed rank orders were those characterized by a Spearman correlation coefficient between age and rank of +0.5 or greater. Note differing axes in left and right panels. See text for further explanation.

nepotism, and to a much lesser extent the degree of reverse age-grading, observed in female rank orders is indeed dependent on the growth characteristics of the population in which those females live.

The question of demographic influences on female rank orders was also approached by changing both the birth and death rate parameters of the model commensurately. In these latter versions of the model, the number of maturations within each run was again closely matched to the number of deaths within that run. However, the overall rate of "turn-over" of females within groups differed substantially between runs. Specifically, three runs of the model were carried out with birth and death rates set so as to yield turn-over rates of 8% and 16% per annum, respectively; results of these runs were then compared to those from the original version of the model (Fig. 1) characterized by roughly a 12% p.a. turn-over rate. Output measures for all three turn-over rates are summarized in Figure 3, which, quite surprisingly, shows that neither nepotism (range: 41–47%) nor age-gradedness scores (range: 21–31%) differed markedly across this twofold range of birth and death rates. Hence it appears that the structure of female rank orders in stable populations is not directly affected by the absolute frequency of births and deaths in those populations.

### Socially Induced Variability in Female Rank Orders

In all previous analyses, rank acquisition by females was governed by three invariant social rules, namely: (1) at maturity a female rose to the rank position occupied by her mother at the time of the female's birth; (2) no female ever supplanted her mother from a rank position; and (3) in spontaneously occurring rank change attempts, younger females always defeated older females, except for their mothers. In the final phase of analysis, these constraints on female rank acquisition behavior were relaxed and in particular rules (2) and (3) above were made probabilistic rather than deterministic.

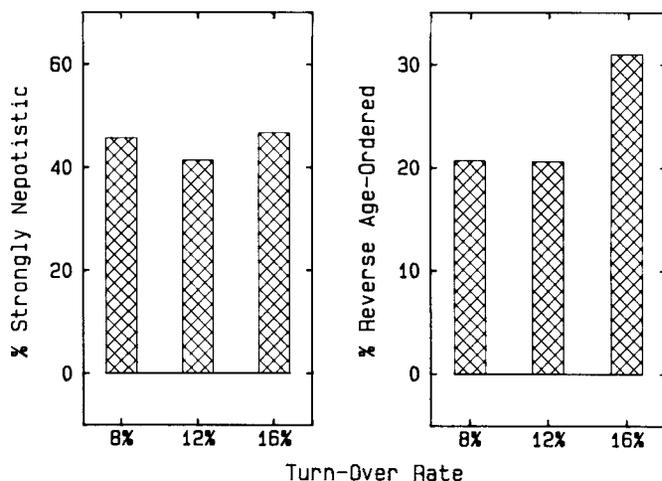


Fig. 3. Proportion of all years in which simulated groups showed strongly nepotistic rank orders (**left panel**) and strongly age-reversed rank orders (**right panel**), respectively, at each of three turn-over rates. "Turn-over" rate refers to the average proportion of females in the group who were replaced each year through birth and death processes. Conventions as in Figure 2; see text for further explanation.

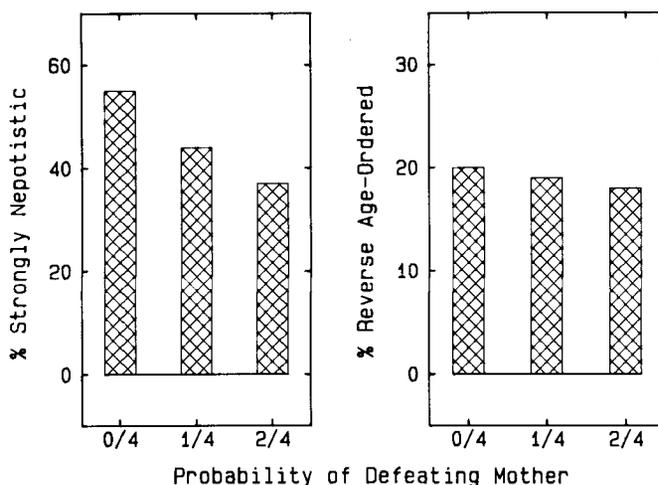


Fig. 4. Comparison of nepotism (**left panel**) and age-gradedness (**right panel**) scores for groups in which females had a probability of 0, 0.25, or 0.5 of defeating their mother in a spontaneously occurring rank change attempt. Conventions as in Figure 2; see text for further explanation.

Specifically, Figure 4 summarizes nepotism and age-gradedness scores from the original version of the model (Fig. 1) as compared to scores obtained in three runs of each of two revised versions. In these latter versions, daughters had either one chance in four ( $p = 0.25$ ) or two chances in four ( $p = 0.50$ ) of supplanting their mother from an adjacent rank position, compared to a zero probability for such an event in the original model. Figure 4 shows that the proportion of years in which the simulated groups were characterized by strongly nepotistic female rank orders

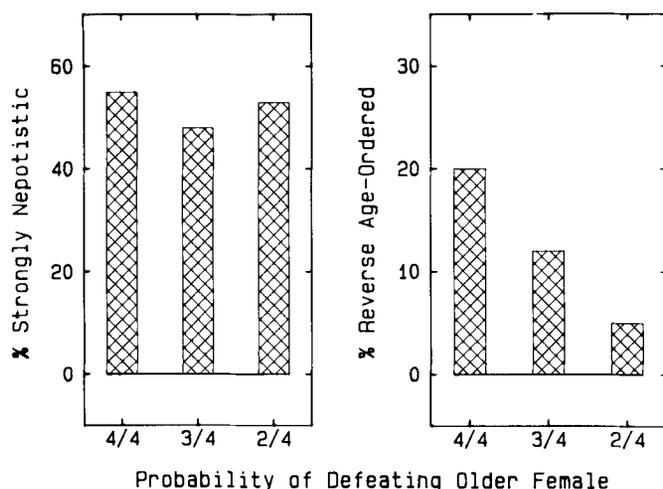


Fig. 5. Comparison of nepotism (left panel) and age-gradedness (right panel) scores for groups in which females had a probability of 1, 0.75, or 0.5 of defeating opponents older than themselves (other than their mother) in spontaneously occurring rank change attempts. Conventions as in Figure 2; see text for further explanation.

declined in direct relationship to the probability that mothers would be defeated by their daughters. Thus, female rank orders were scored as highly nepotistic in 55%, 44%, and 37% of all years, respectively, for groups in which daughters had probabilities of 0, 0.25, and 0.50 of defeating their mothers. In contrast, under these same conditions, the simulated groups showed marked reverse age-ordering of females in 20%, 19%, and 18% of all years, respectively. The obvious conclusion from this analysis is that changes in the probability of daughters supplanting their mothers from high rank positions strongly affected the nepotistic dimension of female rank orders but had only limited effect on age-gradedness.

On the other hand, the extent of age-gradedness of rank orders was itself strongly affected by changes in the probability that younger females would defeat older females—other than their mothers—during spontaneous rank change attempts. Thus, Figure 5 shows that in comparison to the original version of the model ( $p = 1.0$ ), those versions in which young females had either three chances in four ( $p = .75$ ) or two chances in four ( $p = .50$ ) of defeating an older female were characterized by a substantial reduction in the extent of age-grading. In particular, female rank orders were characterized by strong reverse age-grading in 20%, 13%, and 5% of all years, respectively, for versions in which younger females had probabilities of 1.0, 0.75, and 0.5 of defeating older females in spontaneous rank change attempts. As might be expected, however, addition of this probabilistic component to the outcome of rank change attempts had little effect on nepotism scores; at all three probability levels the simulated groups were characterized by strongly nepotistic rank orders in about 50% of all years.

Additionally, one further analysis demonstrated that the kind of decoupling of nepotism and age-gradedness shown in Figures 4 and 5 cannot be produced merely by changing the rate at which younger females attempt to supplant older females—other than their mother—from high rank positions, but rather depends specifically on changes in the outcome probabilities for those attempts. Thus, Figure 6 shows that as the rate of rank reversals was increased in a succession of runs of the basic

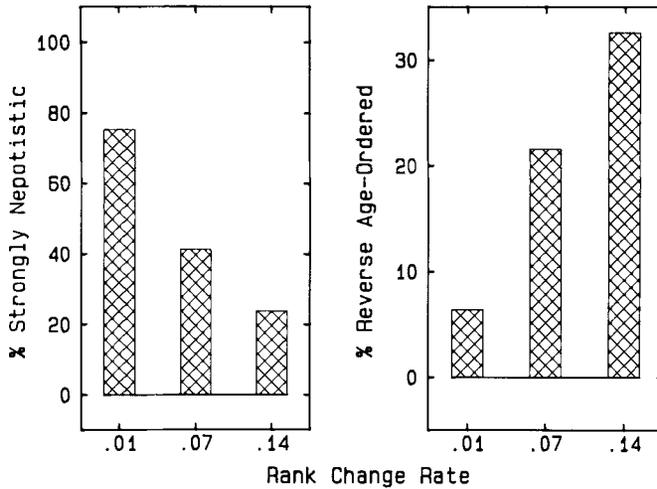


Fig. 6. Comparison of nepotism (left panel) and age-gradedness (right panel) scores for groups in which females underwent spontaneous rank reversals at rates of 0.1, .07, and .14 rank changes per female per year, respectively. Conventions as in Figure 2; see text for further explanation.

version of the model (minimum of three runs per rank change rate), the degree of nepotism within groups declined proportionately and the degree of age-gradedness increased proportionately. Hence, differences between groups in the rate at which females underwent rank reversals affected nepotism and age-gradedness scores in much the same way as demographic differences between groups and quite unlike that seen in the immediately preceding analyses.

## DISCUSSION

This paper has summarized results of a simulation analysis aimed at elucidating the effects of stochastic variation in demographic and social processes on the degree of temporal stability shown by female rank orders in small groups of nonhuman primates. Like any such modeling endeavor, this simulation was grounded in a few very simple (and explicitly stated) assumptions and led to commensurately simple conclusions. At the risk of belaboring the obvious, we will merely state that the social organization of real-life groups of nonhuman primates is almost certainly the product of much more complex interactions than was the case in the present model. Nevertheless, we believe that at least a few of the conclusions derived from this simulation analysis have important implications—both theoretically and methodologically—for the study of primate social organization.

For example, based on the foregoing analyses one would expect the rank orders of nonhuman primate females to be strongly influenced by the kind of year-to-year fluctuations in birth and death rates that occur in any small group of animals. More specifically, as a consequence of such demographic stochasticity even a strictly nepotistic system of rank acquisition would be expected to result in rank orders with the combined characteristics of strong reverse age-ordering (ie,  $r_s \geq 0.50$ ) and only negligible nepotism ( $> 0.50$ ) in nearly 1 out of every 5 years. Additionally, it seems clear that nepotism and age-gradedness as dimensions of female rank orders are at best loosely coupled and characterized by only short-term temporal stability.

Taken together, the above points suggest to us that any field study of less than approximately 5 years duration is unlikely to have accurately characterized either

the central tendency or range of variability in female rank relations for a given group, population, or species. Conversely, existing descriptions of species-specific patterns of female rank relations derived from short-term studies of single groups are almost certain to have grossly underestimated the extent of variability in this dimension of group organization.

In fact, these conclusions will come as no great surprise to anyone actually engaged in long-term investigations of the social behavior of nonhuman primates in their natural habitats. For example, concerning long-term stability of social organization among Amboseli baboons, Hausfater [1978] has written:

In sum, the data collected in Amboseli from 1971 through 1978 demonstrate a wide variety of social organizations for a single baboon group. Viewed another way, the recent history of Alto's Group is such that one can find a three-month period of time when the observed social organization of the group closely matched the social organization reported for nearly any other baboon group of any species in any habitat by any observer (p. 12).

Similar ideas have been proposed by Altmann and Altmann [1979], Bernstein [1981], Hinde [1983] and coworkers, Dunbar [1984], and several other investigators.

Obviously, not all of the variability in rank relations among nonhuman primate females arises solely as a consequence of the inherently stochastic nature of demographic and social processes in small groups of animals. Thus, the second phase of the present analysis examined the extent to which differences between populations in birth and death rates will result in differences between those populations in the characteristic structure of their female rank orders. Essentially, these later analyses showed that female rank orders in nonstable populations are likely to be strongly influenced by the birth rate, death rate, and other demographic parameters of those populations. In contrast, this was not the case in populations in which average group size remained constant over time.

These findings imply that differences between conspecific or allospecific primate populations in patterns of female rank relations should not be taken as indicative of between-population differences in female social strategies unless those populations are characterized by similar demographic parameters or stable group size distributions. In fact, this same point has been made by a number of other authors, most notably Dunbar [1984, 1985], who has recently stated: "we will never fully understand behaviour if we fail to take demographic processes into account" [1985:516].

In contrast, the third phase of analysis of the model served to elucidate exactly what kinds of differences in female rank orders one would expect as a consequence of differences between groups, populations, or species in the rules governing the social interactions of females within those units. This latter analysis showed that the extent of nepotism in female rank orders depended primarily on the probability that any given female would eventually assume a rank position higher than that of her mother at the time of the female's birth. Furthermore, changes in this probability had virtually no effect on the extent of age-gradedness in female rank orders. Rather, this latter dimension proved to be influenced primarily by the probability that spontaneously occurring rank challenges would be resolved in favor of the younger of the two participants. Interestingly, changes in the absolute rate of such spontaneous rank challenges did not similarly uncouple nepotism and age-gradedness; this could only be accomplished through changes in the specific probabilities mentioned above.

One implication of these latter findings is that descriptions of the structure and stability of female rank orders should be considered at best only indirect evidence

as to the precise social strategies and decision rules used by the individuals in those rank orders. In fact, based on results of the present model, one could plausibly argue that rank relations among adult females in virtually all Old and New World monkey species—baboons, macaques, langurs, and howler monkeys—are based on just a single set of social rules, the expression of which is modified by each species' unique population structure and ecology. At the very least, the present simulation analysis emphasizes the need for development within primatology of methodologies suitable for determining the extent to which between-population differences in patterns of female rank organization reflect demographic differences between those populations as opposed to substantive differences in female social strategies.

## CONCLUSIONS

Based upon analyses of a computer simulation of female rank relations within model primate groups, we have concluded:

1. That the degree of nepotism and of age-gradedness characteristic of female rank orders would be expected to show substantial year-to-year variation owing to stochastic factors alone.

2. That neither of the above dimensions of female rank orders would be expected to show appreciable temporal stability.

3. That changes in the birth and death rate of a population would affect the degree of nepotism and age-gradedness characteristic of female rank orders in that population only if those changes also result in an increase or decrease over time in average group size.

4. That changes in the probability of any female supplanting her mother from a high rank position would strongly affect the degree of nepotism characteristic of a rank order but would have little influence on age-gradedness.

5. That the obverse of the above result would be true given changes in the probability that younger females will supplant older females other than their mother from high rank positions.

More generally, the present analysis suggests that in the absence of appropriate long-term demographic and behavioral data, reported differences between nonhuman primate species in the degree of nepotism or age-gradedness characteristic of their female rank orders should not be accepted uncritically as evidence of species differences in the strategies of rank acquisition used by females.

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