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MODELS OF STATUS-CORRELATED BIAS IN OFFSPRING SEX RATIO

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Abstract.—We study a simple model describing the genealogic structure of a population in which the sex ratio of offspring varies with a parent's position in a social hierarchy. This model is based on species in which one sex disperses and in which rank in a stable social hierarchy for the other sex is "inherited" by the offspring of that sex. We find that biased production of offspring in such a social system has important implications for group-size regulation, for the genetic relationships among individuals at any given time and across generations, and for the disparity between the social environment experienced by a parent and its offspring. The general model predicts that group size is tightly regulated and that group size is unstable in groups with underproduction by high-ranking mothers. We then further examine the particular case of the model in which the nondispersing sex (females) is overproduced by higher-ranking parents. In this case, we find that females are unusually closely related; all females in a group have a common female ancestor 5–10 generations back. Moreover, daughters of mothers in the middle of the hierarchy experience the largest intergenerational disparity. In contrast to daughters of high- and low-ranking females, they occupy ranks much lower than their mothers'.

Sex biases in offspring production may evolve, although overall parental investment in offspring of the two sexes will be one to one in diploid organisms (Fisher 1958; Hamilton 1967). Furthermore, facultative adjustment of offspring sex ratio may result in systematic variability in offspring ratios within populations. In the biological literature, attention on facultatively biased offspring sex ratios has focused on questions of the ultimate evolutionary result (e.g., Trivers and Willard 1973; Clark 1978; Clutton-Brock et al. 1981; Clutton-Brock and Iason 1986) and, to a lesser extent, on proximate mechanisms that would produce facultatively biased primary sex ratios (e.g., James 1971, 1983; Myers 1978; Myers et al. 1985). However, biased offspring production has several striking intergenerational effects, and any selective advantage of biased ratios must persist over a sufficient number of generations for the evolutionary consequences to be realized or maintained. It is surprising, therefore, that evolutionary models of behavior and social structure rarely focus on effects over the time course of several generations, and we know of no such examination in the case of offspring biases. In this article, we investigate these intergenerational consequences through a simple mathematical model that was initially motivated by the demography and social structure of cercopithecine primates. A mathematical approach is particularly useful for long-

lived, slowly maturing species such as primates because empirical data are available for at most a single generation for such animals, and even then only for a few species.

Almost all cercopithecine primates live in permanent semiclosed and matrilocal social groups: females remain within their natal group and reproduce there, whereas males disperse as adults and, if they are successful, reproduce in one or more groups in the subsequent years (review in Pusey and Packer 1987). Females can be ordered in clear dominance hierarchies that are usually stable throughout adulthood, and as a daughter matures she assumes her mother's relative dominance rank. Even if the relative rank relationship among females stays constant throughout their lives, however, the absolute rank of a female, by which we mean one more than the number of females above her in the hierarchy, changes as some higher-ranking females mature and others die. Female rank sometimes, though not invariably, confers reproductive advantage through earlier age of first reproduction, shorter interbirth intervals (i.e., higher birth rates), or lower infant mortality. Although male dominance rank often correlates with reproductive success in the short term, males, in contrast to females, change dominance rank often during adulthood, and mother's rank seems little related to initial or lifetime differences in rank or reproductive success (review in Fedigan 1983; Silk 1987; Walters and Seyfarth 1987; but see Meikle et al. 1984).

THE MODEL

Below, we model mathematically the relationships between maternal dominance rank and offspring sex ratio and the intergenerational consequences of such relationships. The model focuses on the female component of a group that is assumed to have the following biological characteristics: (1) a female stays in her natal group and reproduces there; (2) a daughter assumes her mother's relative position in the social hierarchy, or, if her mother is alive, she occupies a position directly below her mother (the ordering among sisters is immaterial for our purposes); and (3) the number of mature daughters produced by a female depends on the number of females above her in the hierarchy. This could arise in a variety of ways; the rank-related differences could arise from secondary sex ratios (i.e., through differential mortality) or from differences in number of offspring. Equivalently, the number of offspring that a female produces could be independent of her rank, but with the sex ratio of the offspring dependent on the number of females above her in the hierarchy. It is the terminology for this last situation that we use for the remainder of our explorations.

We report on the simplest stochastic model for the situation described above: we break time into discrete generations, and at each generation, a female is replaced by a random number of daughters, who are all considered the same age. These numbers are independent for different females and different generations. Our investigation then focuses on three aspects of the system. Specifically, we first ask what are the implications for group size of different relationships between dominance rank and offspring sex ratio; that is, is group-size regulation affected by whether the proportion of female offspring is an increasing or a decreasing

function of dominance rank? Next, using the results of this examination, we restrict subsequent investigations to the case in which the proportion of female offspring decreases with decreasing dominance rank, and we ask several questions about the number and identity of the original matriline that are represented in the group in subsequent generations. Finally, we examine the relationship between the absolute rank of a mother and her daughters.

We take a function $f_{i,k}$ that gives the probability that a female of rank i leaves k daughters in the next generation. The values of this function completely specify our model. Note that, following the convention in the biological literature, the highest-ranking individual is assigned rank number one, rank two is assigned to the next highest-ranking individual, and so on. We then define R_i as the expected numbers of adult daughters left by a female of rank i :

$$R_i = \sum_{k=1}^{\infty} k f_{i,k}.$$

GROUP-SIZE REGULATION

We show that for a species in which dominance rank is passed from mother to daughter, group size is tightly regulated if the high-ranking mothers overproduce daughters, and group size is unstable if they overproduce sons.

Suppose there are initially s females in a group. The i th produces an average of R_i daughters such that Δ_s , the average change in the group size after the next generation, is

$$\Delta_s = \left(\sum_{i=1}^s R_i \right) - s,$$

where here, and elsewhere, the size of the group means the number of females in the group. By definition Δ_s is positive when the group is expanding and is negative when the group is shrinking (see fig. 1). The sizes at which the graph of Δ crosses the horizontal axis ($\Delta = 0$) are the stationary group sizes; that is, there is no change in group size between successive generations, and a stationary size is stable under small perturbations if the graph crosses the axis with a negative slope. If the group declines slightly from the stationary size, then Δ is positive and the group increases in the next generation; if the group grows slightly, then Δ is negative and the group shrinks back toward the stationary point (see fig. 1).

Quite a different situation occurs if high-ranking mothers leave relatively fewer daughters (and, therefore, relatively more sons) than do low-ranking mothers. In this case, Δ is negative for small s , and Δ would cross the axis from below at its first crossing (see the inset to fig. 1). This implies that the nonzero stationary group size is unstable; any perturbation would tend to move the group size away from the stationary size, either down to extinction or up to infinity (realistically, other biological processes such as group fissioning would probably occur).

Consequently, offspring biases in which high-ranking females disproportionately produce sons and low-ranking ones disproportionately produce daughters

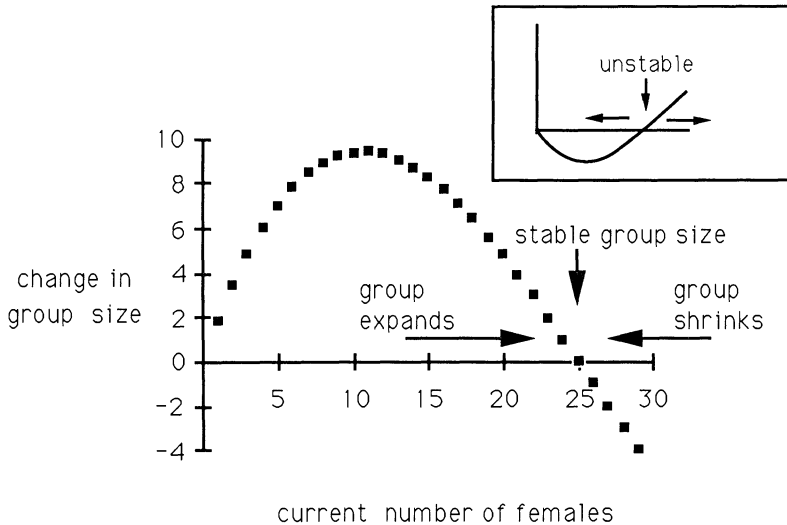


FIG. 1.— Δ , The change in group size (number of females) after one generation, as a function of current group size. Calculations for the main graph used the baseline reproductive values. Horizontal arrows, the direction of change in group size. Vertical arrow, the stationary group size, which is stable in this case. The inset shows that the horizontal arrows would be reversed if high-ranking mothers underproduced daughters, making the stationary size unstable.

lead to a much higher degree of instability of group size and impermanence of groups than would unbiased offspring production with stochastic variability (Cohen 1969). Conversely, if high-ranking females leave more daughters than do low-ranking females, then rank-specific sex-ratio biases provide an indirect mechanism for the regulation of group size, without any implication that the stable size is itself adaptive. This result invites a number of novel analyses and future research investigations, some of which we return to in the discussion.

On the basis of this finding regarding instability in group size in the case of male-biased ratios for high-ranking females, we develop the model further for the case in which lower-ranking females leave fewer daughters. Indeed, this is the situation in a group of savanna baboons, *Papio cynocephalus*, in Amboseli Park, Kenya (Altmann et al. 1988), the site of a longitudinal study that has produced natality and mortality data that are used for illustrative purposes below.

We conducted a series of three sets of numerical simulations to investigate intergenerational changes in matrilineal structure arising from status-correlated offspring production. In each set of simulations, an exponential distribution was used to model the distribution of surviving daughters at each rank. In mathematical terms, $f_{i,k} = \alpha_i(1 - \alpha_i)^k$, where α_i is a parameter that depends on i ; this dependence was different in each set of simulations. The choice of an exponential distribution was motivated by evidence from the Amboseli population that per annum mortality and fertility are fairly constant for most of a female's reproductive career (Altmann et al. 1988). As our baseline, we chose α_i according to the

Amboseli data on sex ratio at birth and offspring survival. This data set provides an example with quite a strong correlation between rank and sex ratio. We additionally considered hypothetical populations in which the correlation was reduced to 50% and 33% of the baseline. This reduction, which can be thought of as multiplying Δ by a constant, maintains the same stable group size but decreases the correlation between rank and number of surviving daughters.

CONSOLIDATION

Computer simulations demonstrated that the entire group will be descended from a single ancestral mother within a small number of generations. We refer to this process as *consolidation*, and we consider here several aspects of the consolidation process.

If R_i is decreasing in i —that is, production of daughters is a decreasing function of rank—then eventually the entire group will be descended from a single female because the females at the top of the hierarchy are more than replacing themselves and thus their female descendants occupy a larger portion of the hierarchy than they did. We fix some generation as the beginning of time and treat each female in this generation as the progenitor of a distinct family tree. We say that the descendants of the female of rank i in this original generation are all members of the i th matriline. The picture the reader should have is that each generation of females is subdivided into distinct matriline and that after a period of time one of the matriline, usually one descended from a high-ranking ancestor, consolidates the entire group.

We define Q_i as the probability that the i th matriline consolidates the group, T_i as the average time until consolidation, conditioned on the i th matriline taking over, and $M_n + 1$ as the average number of distinct matriline present after n generations. (We define M_n this way because there is always at least one matriline present; M_n measures the number of excess matriline.) We present numerical results for the behavior of Q_i , T_i , and M_n and also show that it is fairly easy to calculate Q_i by solving a system of linear equations. Notice that Q_i is the only quantity considered in this article that truly depends on the stochastic nature of our model. One could consider Δ_i , T_i , and M_n even for a deterministic model and arrive at comparable results.

The Number of Matriline as a Function of Elapsed Generations

The simplest way to quantify the consolidation process and the consequential within-group loss in genetic variability through the maternal line is to count the number of distinct matriline that are present in each generation. Because R_i decreases in i , the matriline at the bottom of the hierarchy have a high probability of becoming “extinct” (no remaining female descendants), and thus we would expect M_n to approach zero quite quickly. Simulations showed that M_n decreases exponentially as n increases. For the values that we used from the Amboseli data, computer simulations showed that M_n decreased by a factor of about 2.4 in each generation (fig. 2). This means that only about 40% of the females in the present

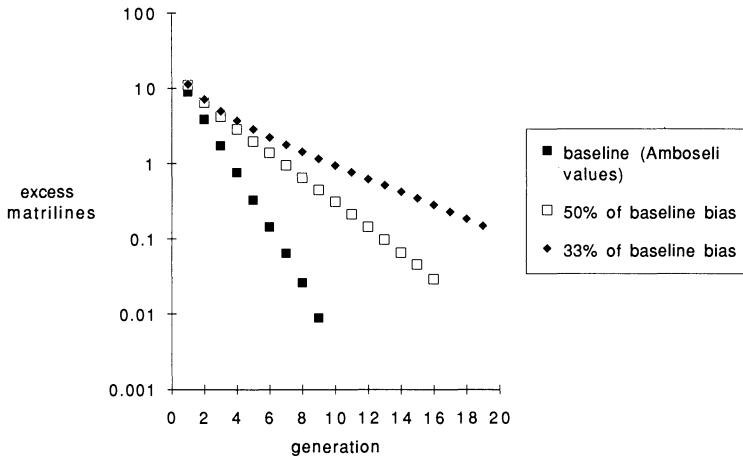


FIG. 2.—Number of matrilineal lines in excess of the one that consolidates the group as a function of time. Results shown for three levels of correlation between rank and sex ratio.

generation could be expected to leave any female offspring. After five generations, M_n dropped below 0.5, which says that with an initial population of 25 females, only one female in most simulations had any descendants in the group after five generations. Our simulations with reduced sex-ratio bias showed qualitatively similar results (fig. 2). In all three sets, a negative exponential function fit M_n with an R^2 of at least 0.997. When the bias was reduced to 33% of baseline, 18% of the transient matrilineal lines disappeared in each generation.

Variation in the Time until Consolidation

The results of the preceding section indicate that the consolidation process can be extremely rapid, on the order of five generations. Because those analyses did not consider potential variability in consolidation time, depending on which matriline took over, we now turn to a consideration of T_i , the conditional average time until consolidation, conditioned on the i th matriline taking over. Intuitively, we would not expect T_i to depend strongly on i . If an initially low-ranking matriline (large i) is going to consolidate, all the higher matrilineal lines must die off. The most likely way for this to happen is for all the higher-ranking matrilineal lines to die off in the first one or two generations; otherwise they will probably grow too much. Once the higher-ranking matrilineal lines have died off, the low-ranking one is top ranking and therefore behaves in the same way as a matriline that was initially high-ranking. Therefore, we expect that the time until consolidation should be only slightly longer for consolidation by low-ranking matrilineal lines. This expectation is borne out for all three sets of simulations. The mean times until consolidation for the baseline amount of correlation and for 50% and 33% of baseline bias were 6.3, 9.9, and 14 generations, respectively. The coefficients of variation for the three sets of simulations were 0.091, 0.073, and 0.083.

Again, we see that for the baseline set, the group typically has a common

ancestor five generations back, independent of the rank of that ancestor. This provides a nice single index of the rate of genetic homogenization that can be used to compare two otherwise-similar groups.

For the sake of completeness, we note that T_i is also a function of the size of the initial generation. However, this dependence is extremely slight because stabilization of group size proceeds even more rapidly than does the consolidation process. After some initial experimentation, we always set the initial size as the stationary size for our simulations, and we believe that other initial conditions would have a very small effect on our conclusions.

The Probability of Consolidation

Finally, we estimate Q_i , the probability for each original female that her matriline consolidates the group. Although computer simulations again provide good estimates of the quantities, they can also be estimated by analytical methods, the details of which are available from the first author.

Figure 3 shows that across all ranks the probability of consolidation by any rank is a constant fraction of that for the next higher rank; that is, exponential decay in Q_i is a characteristic of all three sets of simulations (all three R^2 values exceeded 0.97), although the decay constants are quite different. For rank 4 and below (higher rank number), there is less than a 10% chance of any one matriline consolidating the group, but the sets differ markedly in the probability of consolidation by the higher ranking matriline; compare a 64% chance of consolidation for rank 1 in the baseline with 28% for rank 1 in the set with 33% of baseline correlation between rank and sex ratio. As the correlation increases, the disparity between high- and low-ranking females increases. Without going into details, we note that this exponential decay also arises for continuous-time models, where we can show that the decay constant is almost entirely determined by the sex-ratio bias at the highest ranks.

DOMINANCE RANK OF MOTHERS AND THEIR DAUGHTERS: THE GENERATION GAP

A considerable empirical literature assessing the stability of dominance rank, especially in baboons and macaques, has been reviewed by Silk (1987). In addition, Hausfater et al. (1987) have examined the effects of variability in demographic parameters on dominance structure within overlapping generations. Here, we investigate within-family changes in absolute dominance rank between successive generations when transmission of relative rank is perfect. Even if group size is stable, within-generation dominance rank is stable, and relative rank is perfectly transferable between generations from mother to daughter, overproduction of daughters by high-ranking females of the various ranks results in a difference between absolute ranks of mothers and daughters. An important consequence of the kind of rank-specific sex-ratio bias that we have been investigating is that some daughters have an absolute rank that is very close to their mother's, whereas others have ranks that are quite different from their mother's. This difference can be quantified as follows.

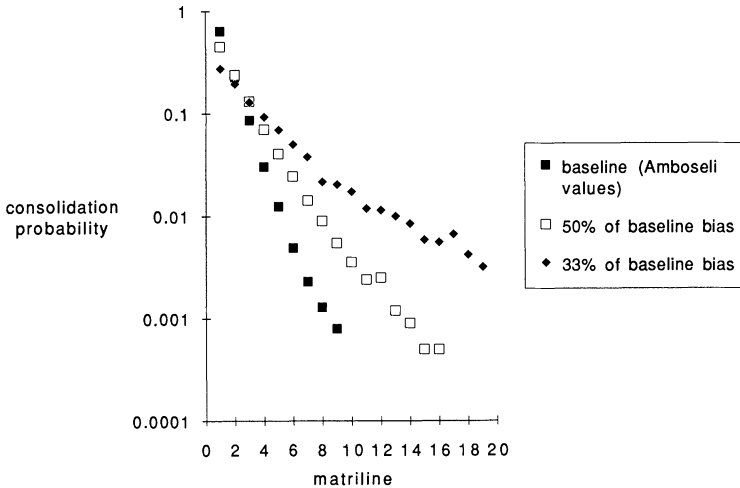


FIG. 3.—The probability that a matriline consolidates the group. Results shown for three levels of correlation between rank and sex ratio.

THEOREM: The expected difference in rank between a mother of rank i and a randomly selected daughter is approximately Δ_i , with an error term that is small for most choices of $f_{i,k}$.

PROOF: If the mothers in ranks 1 through $i - 1$ produce D daughters, and the mother of rank i produces d daughters, then these d daughters occupy ranks $D + 1, D + 2, \dots, D + d$. Therefore, a randomly selected one of these daughters has rank $D + (d + 1)/2$, and the difference between that and the maternal rank is $D + (d + 1)/2 - i$. It is not hard to see that the means of D and d (conditioned on d being greater than zero so that there is a daughter to select) are $\sum_{r=1}^{i-1} R_r$ and $R_i/(1 - f_{i,0})$. Some algebra shows that the average rank difference is

$$E\left(D + \frac{d + 1}{2} - i\right) = \frac{\Delta_{i-1} + \Delta_i}{2} + \frac{R_i f_{i,0}}{2(1 - f_{i,0})}. \quad (1)$$

If it were not for the factor of $1/(1 - f_{i,0})$ in the conditional expectation of d , the right-hand side of equation (1) would be exactly equal to interpolating Δ at a midpoint between $i - 1$ and i . The amount by which the average rank difference deviates from $(\Delta_i + \Delta_{i-1})/2$, the second term on the right of equation (1), could in theory be large, but for most reasonable choices of $f_{i,k}$, it stays small. The error is small because $f_{i,0}$ is usually small for the values of i for which R_i is large, and, when $1 - f_{i,0}$ is small, R_i is also small.

Thus, when the error term is small, the average daughter-mother rank difference is approximately Δ , and this rank difference is therefore greatest near the rank where Δ is greatest. This can be understood intuitively because the daughters of middle-ranking females are pushed very far down the hierarchy by the large overproduction of daughters from higher-ranking mothers. High-ranking daughters do not experience as much disparity simply because there are few higher-

ranking mothers, and low-ranking daughters are not displaced far because the overproduction among the high-ranking mothers is almost balanced by underproduction by mid- to low-ranking mothers.

Under our assumption that R_i is decreasing in i (higher-ranking females overproduce daughters), we know that Δ has the shape shown in the main part of figure 1. The first zero of Δ is the stable group size, and Δ peaks near the middle of the group. We can therefore conclude that daughters of mid-ranking mothers find the greatest disparity between their ranks and their mothers' ranks. For the parameter values in our examples, the error never exceeds half a rank. The rank difference is greatest at $i = 11$, about halfway down the hierarchy. Daughters of a rank 11 mother are, on the average, about nine and a half positions lower in the hierarchy than was their mother.

DISCUSSION

The present investigation has departed from most earlier discussions in the evolutionary literature by modeling demographic and behavioral consequences of biased offspring sex ratios that vary systematically within internally structured groups. The effects we have examined, moreover, are ones that are realized after only a few generations, changing the social environment, and thus the context for evolution, within and among groups. Our models consider species in which the females of a group form ordered, stable dominance hierarchies, relative dominance is passed from mother to daughter, offspring sex ratios are a monotonic function of maternal dominance rank, and males, but not females, disperse from their groups of birth by adulthood.

One of the most striking results was the instability of group size for models in which high-ranking mothers overproduce sons. In sharp contrast, overproduction of daughters constitutes an indirect mechanism for stabilizing group size. Differing directions of bias or the absence of systematic bias in offspring sex ratios are reflected in the size distribution of groups within a population at any given time and of individual groups over a number of generations. Consequently, group-size distributions can provide a test of the prior history of offspring sex-ratio bias in a population. Appropriate tests, however, must be based on elaborations of existing models of group-size distributions (Cohen 1969, 1971, 1972) to incorporate offspring bias. These tests should be designed to use data from single groups over time and from group censuses within multigroup populations.

Does it matter if group size is unstable? The size of a group has consequences for day ranges, social coordination, minimal requirements for resources such as sleeping sites, and so on. If the group size or structure that an individual experiences during maturation is a poor predictor of the characteristics of the group that the individual will experience during adulthood, especially when raising its own offspring, then the potential advantages provided by learning during a long stage of immaturity might be diluted or totally negated by this lack of continuity. The wisdom of individuals and of their relatives in the group would be of little use in a situation of poor predictability, of moderate use in a neutral situation, and of considerable advantage when variability is low.

Overproduction of sons by high-ranking females relative to lower-ranking females would probably produce additional reduction in homeostasis of social environment beyond that caused by instability of group size, because low-ranking maternal lineages will expand within a group relative to high-ranking ones. This would increase the likelihood that coalitions of low-ranking relatives would be able to challenge successfully the dominance status of higher-ranking animals and thereby destabilize the social structure. The extent of intra- and intergenerational rank stability and the consequences of breakdowns in stability should suggest, albeit not provide as direct a test as would group sizes, the history of offspring sex-ratio biases or absence of persistent biases in a population. In the few primate populations for which there are appropriate data, instability of the female dominance hierarchy seems to be rare (reviews in Samuels et al. 1987; Silk 1987), suggesting that overproduction of sons by high-ranking females has not been persistent or pervasive.

The remaining predictions of the model that we explored incorporated the additional assumption that offspring sex ratios were a decreasing function of dominance rank, that is, that high-ranking females overproduced daughters rather than sons. We found that, although daughters assume their mothers' relative dominance status, the absolute rank of daughters can differ significantly from that of their mother. Daughters of the highest-ranking females and the rare daughters of low-ranking females have dominance ranks close to those of their mothers. In contrast, daughters of mid-ranking females will experience a large generation gap. If individuals that are faced with similar conditions as adults to those they experienced as immatures are at an advantage because they are better prepared (Fairbanks 1989), high-ranking females will be at an advantage, in this regard, relative to all but the rare lowest-ranking ones.

In additional analyses we explored the relationship between the rank-bias structure and the relatedness within the groups of a population using parameter values from data on baboons in Amboseli. We saw that in a few generations, the female component of a group was composed entirely of members of the same matriline (i.e., all descendants of a single female) and that before that "consolidation," the group experienced approximately a 60% reduction from one generation to the next in the number of matriline represented. The common female ancestor was usually the highest-ranking female in the starting generation; consolidation was rarely (14%) by a matriline other than one of the top two; and the identity (rank number) of the consolidating matriline had little effect on the time to takeover. When we examined a hypothetical example with a rank-specific sex-ratio bias that was much weaker than in Amboseli, we found an increased variability in which matriline consolidated the group and an increased time to takeover. Even for the Amboseli model, however—in which consolidation was usually within five generations and was by the highest-ranking matriline over 60% of the time—in any one generation, the highest-ranking female left the most female offspring less than 20% of the time. Calculations such as these are important to keep in mind when implications are drawn from empirical findings, and they are particularly important for taxa such as primates for which data rarely span a full generation and are usually available for only one group or at most one population.

Matrilineal aspects of these investigations have been explored in more detail using models that treat time and, to some extent, rank as continuous (M. Altmann 1988). Genetic data have been gathered for a few primate populations (e.g., Dugleby 1978; Melnick 1987), and other studies are underway. These empirical investigations are usually undertaken primarily with a focus on determining paternity or differential reproduction by males, but, if combined with behavioral data, they should be able to provide the data necessary for assessing evidence of persistent prior relationships between rank and offspring sex ratios.

It is interesting to note that the mathematical tools used in this analysis were originally developed in the context of a population in which reproduction potentially varied with social status (Galton and Watson 1874, reprinted in Keyfitz and Smith 1977). Galton and Watson were concerned with determining whether upper-class English family names were disappearing because of lower fertility among the upper class or simply because of random fluctuations. Unfortunately, they considered only the null hypothesis of a homogeneous population, and mathematical intractability led the subsequent mathematical theory of branching processes away from the original idea of socially determined reproduction. Consequently, few models of population growth have incorporated both social structure and reproductive behavior.

In the models analyzed here, we assumed that females have the ability to adjust facultatively the sex ratio of their offspring and that they do so based on their social status relative to the higher-ranking females. Facultative adjustment of sex ratios is advantageous for species in which there are conditional advantages of producing offspring of each sex and for which these conditions change during the reproductive span of a single individual, differ between parents and offspring, or differ among siblings. Heritable differences in sensitivity to conditional cues may be subject to selection. These cues may arise in several different milieus; ecological stress might favor a different offspring sex ratio than social stress. When the cues vary among closely related species or perhaps even populations of a single species, it is particularly difficult to identify the appropriate level for analysis.

Proximally, sex-ratio adjustment may be effected through mechanisms such as behavioral timing of conception or physiological changes that differentially affect male- and female-bearing sperm (e.g., Guerrero 1970; James 1971, 1983). Whether sex-ratio adjustment itself has been subject to selection or whether the adjustment is a by-product of mechanisms that have some other primary consequence is not at all clear.

When attention first focused on the evolution of facultative adjustment of offspring sex ratios, it was argued that the relationship between sex ratio and parental condition or quality "should" be positive (Trivers and Willard 1973), for example, that high-ranking females should overproduce sons rather than daughters. The reasoning was based on the assumption that many species are relatively polygynous, in which case, males typically have higher variance in reproductive success than do females. The implicit leap was then made to conclude that mothers in good condition could, therefore, influence the reproductive success of their sons more than that of their daughters, and empirical demonstration of a positive

relationship between maternal condition and sex ratio in a population was then equated with demonstration of adaptive sex ratio (but see Clark 1978; Myers 1978).

Subsequent authors (e.g., J. Altmann 1980; Silk 1983; van Schaik and van Noordwijk 1983, all focusing on cercopithecine primates) demonstrated that the model was much less general than originally supposed. They pointed out that sex differences in variability of reproductive success were overestimated by dependence on cross-sectional or short-term empirical studies, and that short-term differences in male and female reproductive success were probably considerably greater than lifetime ones precisely because of the instability of male life histories relative to those of females (e.g., Hausfater 1975; Samuels et al. 1987).

In addition, even relatively polygynous species often exhibit demographic systems and forms of social structure in which mothers potentially influence their daughters more than their sons (see, e.g., Silk 1983). The operation of opposing factors could result in predicted adaptive relationships between maternal quality and offspring sex ratio that are positive, negative, or zero, depending on the particular biological system under consideration. This calls into question studies in which "tests" of adaptive sex ratios were based on the fallacious assumption that a relationship had to be positive to be adaptive and in which a positive relationship was taken as *prima facie* evidence for the evolution of adaptive sex ratios. If one wanted to follow the general Trivers-Willard approach and ask which sex-ratio relationship might be favored in a given biological system, it would be necessary to evaluate the Trivers-Willard assumptions by obtaining estimates of the relative effects of mothers on their sons' and daughters' reproductive success (see, e.g., Clutton-Brock 1985; Hrdy 1987), data that have in general been unavailable for most species.

In the present series of investigations, we have approached the question of adaptive sex ratios from a totally different perspective. We have asked about the consequences of quality-bias relationships within certain types of biological systems, regardless of whether these relationships might on other bases, such as polygyny or sex differences in maternal effects on offspring, seem to be of selective advantage or disadvantage. Despite the apparent ultimate advantages of a quality-bias relationship, the relationship can persist only if it is compatible with the other behavioral, social, and demographic structures of the species. Models of effects on the levels and time scale that we have considered here are not only of intrinsic interest for studies of demography and social structure, but they also address the potential context for evolution of biased offspring sex ratios.

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