Appendix 3 / A Numerical Method for Estimating Coefficients of Relationship in a Langur Troop, by Jon Seger

The average coefficient of relationship (r_{ij}) among the members of a social group is expected to influence the evolution of any trait that affects the average fitness of group members other than the bearer of the trait. It is usually impossible to write a general expression for r_{ij}, because it depends on a large number of variables, including the means and variances of group size, age-specific reproduction and mortality for males and females (l_x and m_x schedules), and migration rates (both into and out of the group, for males and females, by age), as well as other features of the mating system such as patterns of assortative or disassortative mating. Fortunately, tractable numerical methods are easy to devise for some special cases. This appendix describes a method that was used to estimate r_{ij} among the adult females of a hypothetical troop modeled after the langurs of the Mount Abu region.

Simplifying Assumptions   Time is reckoned in two-year "epochs." The troop always contains eight adult females, each two years older than the next younger; at the beginning of an epoch they are 5, 7, 9, 11, 13, 15, 17, and 19 years of age. Two years later, at the beginning of the next epoch, the eldest female (now 21) dies, and a female aged 5 years enters the adult population out of the pool of juveniles belonging to this troop. Thus the mother of the new recruit must now be aged 11, 13, 15, 17, 19, or is deceased (21, 23, or 25). This corresponds to an extreme form of "type 1" survivorship, in which all female mortality takes place before and after the ages of reproduction. Although not strictly realistic, such an age distribution appears to fit adult female langurs surprisingly well, and allows the calculation of all intratroop coefficients of relationship (r_{ij}) by the very simple procedure described below. The probabilities that each eligible female is the mother of the recruit were arbitrarily set as follows:

$$p(11) = 0.20$$
$$p(13) = .20$$
$$p(15) = .20$$
$$p(17) = .15$$
$$p(19) = .10$$

$$p(21) = .10$$
$$p(23) = .05$$
$$p(25) = 0 \qquad (1)$$

These are proportional to age-specific fertilities five years previously if infant and juvenile mortalities are not heavily dependent on the mother's age. Because $p(25) = 0$, the eldest female alive in the troop is nonreproductive.

Juvenile males are assumed to leave the troop before reaching adulthood and are ignored in the model. Incoming adult males may remain in the troop 2, 4, or 6 years, and therefore father one, two, or three surviving female offspring. Different distributions of male tenure were employed, and these significantly affected r_{ij} among the females, as was expected. A critical assumption is that *adult males are unrelated to females and to each other.* This may be unrealistic, since the actual amount of inbreeding at Mount Abu, if any, is not known.

The Model   Construct a 10-by-10 matrix **R** with entries r_{ij}. Let the subscripts index females by their ages (5 to 23 in steps of 2) and the entries be their coefficients of relationship. Then $r_{ii} = 1$ and $r_{ij} = r_{ji}$; the matrix is symmetric. The population is progressed at each two-year "epoch" as follows. First advance each female one age-grade and introduce the new female in the upper lefthand cell.

$$r'_{i+2, \, j+2} = r$$
$$r'_{5,5} = 1 \qquad (2)$$

where primes indicate elements of the matrix being formed out of the previous (unprimed) matrix. Then select one from among the females eligible to be the mother of the incoming female, according to the distribution of probabilities (equations 1). Call this female i. It follows from the rules for calculating coefficients of relationship in diploid species that the new female is related through her mother to every other female by

$$r'_{5,j} = \tfrac{1}{2} r'_{i,j}$$
$$r'_{j,5} = r'_{5,j} \qquad (j = 7, 9, \ldots, 23) \qquad (3)$$

which completes the upper row and the lefthand column. If the new female's father was also the father of the previous recruit,

$$r'_{5,7} = r'_{5,7} + \tfrac{1}{4}$$
$$r'_{7,5} = r'_{5,7} \qquad (4)$$

where "=" is understood to mean "replace the lefthand side with

the righthand side." If he was the father of the *two* previous recruits, it is true in addition that

$$r'_{5,9} = r'_{5,9} + \tfrac{1}{4}$$
$$r'_{9,5} = r'_{5,9} \qquad . \tag{5}$$

The paternal (half) sibling relationship between females 7 and 9 was established at the previous epoch by equations 4, and since by assumption successive males are unrelated, the matrix is complete.

At each epoch, $\bar{r}_{ij}$ among living adult females is simply the average of the 56 off-diagonal elements of the 8-by-8 matrix derived from **R** by deleting the last two columns and rows (21 and 23). For the sake of simplicity, and to distinguish it from other averages that will be mentioned, the $\bar{r}_{ij}$ particular to a given epoch will subsequently be referred to as $\bar{r}$. Thus

$$\bar{r} = \frac{1}{N(N-1)} \sum_{\substack{j \neq i \\ i \neq j}} r_{ij} \tag{6}$$

where N is the number of females in the troop (here $N=8$).

The matrix contains additional information of potential interest. In particular, $\bar{r}(i)$ can be calculated, giving a female's average relatedness to her troopmates as a function of her age.

$$\bar{r}(i) = \frac{1}{N-1} \sum_{j \neq i} r_{ij} \tag{7}$$

Also, the average relatedness of two females as a function of their *difference* in age (D) can be found.

$$\bar{r}(D) = \frac{1}{N-D/d} \sum_{i=a}^{b-D} r_{i,i+D} \tag{8}$$

where d is the difference in age of successive females (here 2 years), a is the age of the youngest female (here 5 years), and b is the age of the oldest living female ($b = a + d\,(N\text{-}1)$, here 19 years).

Results   If this method works correctly, the *cumulative* average r_{ij} should converge to definite limits as the number of successive epochs through which the population is progressed approaches infinity. In particular, the cumulative r (that is, $\bar{r}$), should approach a fixed limit equal to the expected coefficient of relationship $E(r_{ij})$ between two females who know nothing about each other except that they belong to the same troop. As figure A shows, this convergence rapidly occurs from either of two extreme initial distributions
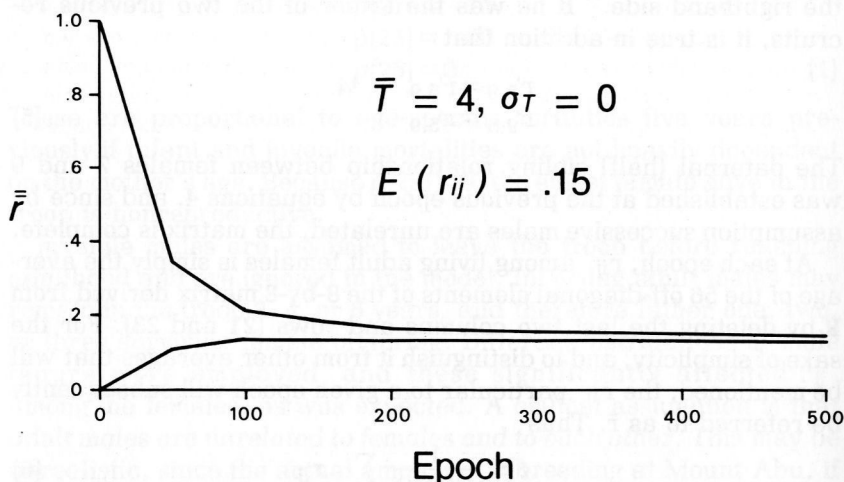
Figure A. Convergence of $\bar{\bar{r}}$ to $E(r_{ij})$. This graph shows the cumulative average $\bar{r}_{ij}$ within the model troop as a function of time, for one of the four sets of parameters of male tenure. The upper curve represents a run beginning from $\bar{r}_{ij} = 1$ (all individuals perfectly related), and the lower curve is from $\bar{r}_{ij} = 0$ (all individuals unrelated). Convergence is rapid, and the calculations were always terminated after 500 epochs. Replicates produced very similar results (see table E).

of r_{ij}, either $r_{ii} = 1$, $r_{ij} = 0$ ($\bar{r} = 0$, females entirely unrelated), or $r_{ij} = 1$ ($\bar{r} = 1$, females perfectly related). Since the average generation time in this model (given the fertility schedule in equations 1) is 9.5 years or 4.75 epochs, the 500 epochs for which each set of calculations was continued is equivalent to 1,000 years or more than 100 generations.

Eight different sets of initial conditions and parameters of male reproductive success were used, and each of these was twice replicated. Table E gives the estimates derived from each set of conditions for $E(r_{ij})$, its standard deviation across time, and the average standard deviation of r_{ij} within the troop at any given time.

Figure B shows that $E(r_{ij})$ varies considerably as a function of the difference in age (D) between two females and that this pattern is affected by the standard deviation of male tenure. The especially low $\bar{r}(D)$ between two females who are separated by four years in age is presumably due to the fact that they are less likely than are adjacent females to share a common father, but cannot be mother and daughter. Two females separated by six years can be mother and daughter, but cannot have the same father. The youngest and

TABLE E. Summary of numerical results. Four distributions of male tenure and two initial distributions of female relatedness were employed. $\bar{T}$ is average male tenure in years, and σ_T is its standard deviation. Entries under $\bar{\bar{r}}_0$ are final cumulative average r_{ij} for runs beginning from populations of unrelated females $(r_{ij} = 0)$, while those under $\bar{\bar{r}}_1$ are for initial populations of perfectly related females $(r_{ij} = 1)$. $E(r_{ij})$ is the average of the four $\bar{\bar{r}}$ corresponding to a given distribution of male tenure; it is the value toward which the r appear to be converging. The average sample standard deviation of within-troop r_{ij} (s_I) is approximately 0.16 in all cases, indicating the wide range of relationships that exists even in a troop with only eight adult members. The variability of $\bar{\bar{r}}$ across epochs is low, however, as indicated by $s_E \approx .03$.

T	σ_T	$\bar{\bar{r}}_0$	$\bar{\bar{r}}_1$	$E(r_{ij})$	s_I	s_E
3	1	0.120	0.137	0.132	0.162	0.030
		.127	.142			
4	0	.147	.154	.149	.163	.028
		.144	.150			
4	1	.155	.161	.160	.160	.031
		.158	.165			
4	2	.168	.177	.174	.159	.029
		.170	.179			

oldest females have lower average coefficients of relationship to their troopmates, or $\bar{r}(i)$, than do middle-aged females, but the difference is slight.

Figure C illustrates the strong and highly significant positive correlation that exists between the standard deviation of male tenure and r.

Discussion   These results suggest that in troops structured as those near Mount Abu seem to be, adult females are related on average by at least 1/8 (0.125), and quite possibly by 1/7 (0.143) to 1/6 (0.167). But these estimates may be low, because the model used to derive them does not account for several processes, each of which would tend to raise $E(r_{ij})$. One of these processes is inbreeding. If males ever remain with a troop long enough to mate with their daughters, and are accepted by them, resulting offspring would be especially highly related to their mothers, and the offspring of such an inbred individual would be more highly related among them-
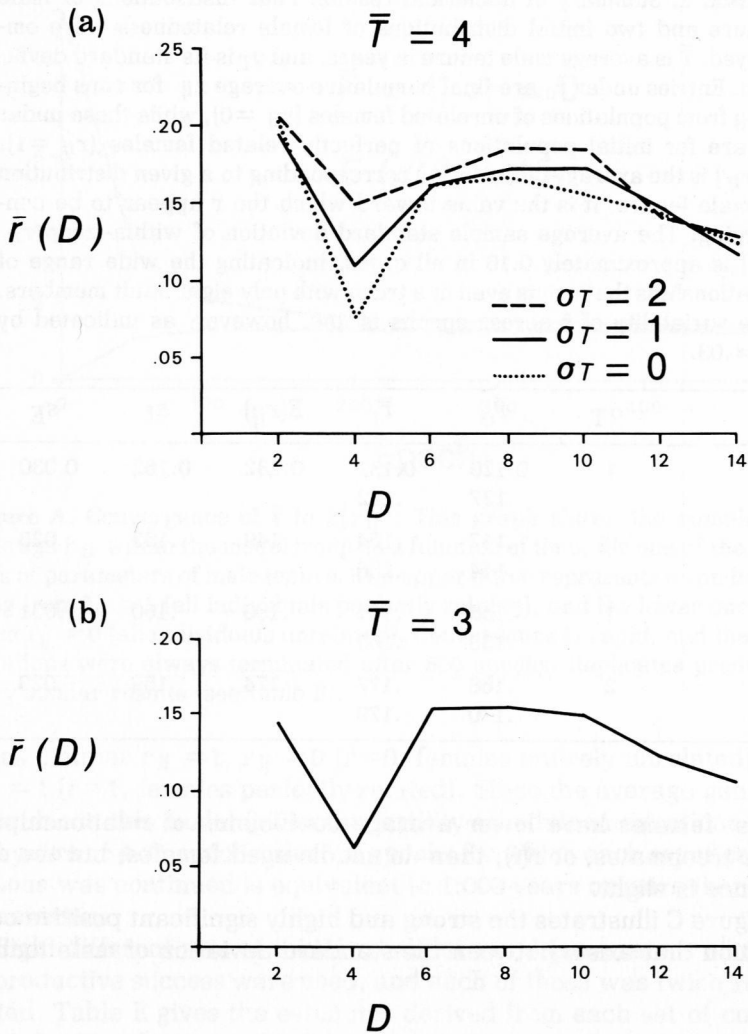
Figure B. Expected r_{ij} as a function of difference in age between females. Individuals four years apart may be typically only half as related to each other as they are on average to their other troopmates, given the assumptions of the model. (a) Increasing the variance of male tenure partly erases this anomaly because a greater proportion of males father three successive offspring, all of whom are therefore at least half siblings ($r_{ij} = 0.25$). (b) Where the average male tenure is three years each male fathers one or two offspring, never three. As a result, individuals four years apart are never siblings of any kind, and show an average r_{ij} of about 1/16, equivalent to that of half first cousins.
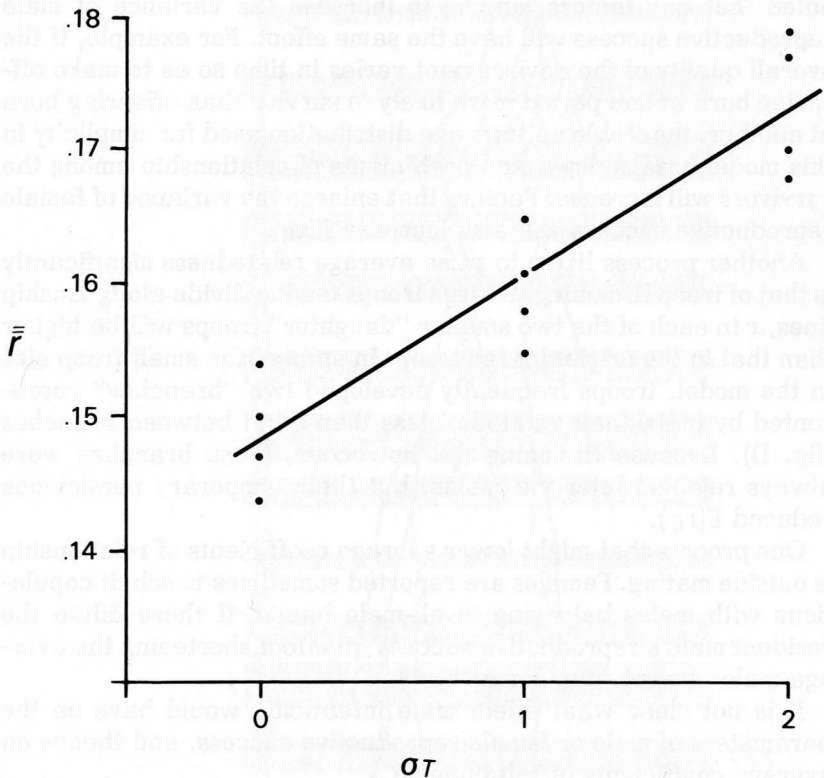
Figure C. Correlation between standard deviation of male tenure and average relatedness among Females, for $\bar{T}=4$. At each σ_T, the upper two points are from replicates beginning at $r_{ij}=1$, and the lower two are from corresponding replicates beginning at $r_{ij}=0$ (see table E). In all cases $\bar{r}$ is converging toward an $E(r_{ij})$ very close to the least-squares regression line. The correlation for these sample points 0.93, $P < 0.001$.

selves than are the equivalent offspring of an outbred individual. Even if daughters somehow know who their fathers are and refuse to mate with them, inbreeding will result if successive adult males are sometimes related to each other. Until detailed observational or biochemical genetic studies of the large-scale population structure are carried out for langurs, there will be no way to estimate the magnitude of this "background" inbreeding.

Figures B and C show how increased variance of male reproductive success, caused here by variance of tenure, leads to higher average coefficients of relationship among females. It should be

noted that *any* factors tending to increase the variance of male reproductive success will have the same effect. For example, if the overall quality of the environment varies in time so as to make off-spring born at one period more likely to survive than offspring born at another, the stable uniform age distribution used for simplicity in this model breaks down and coefficients of relationship among the survivors will increase. Factors that enlarge the variance of female reproductive success will also increase $E(r_{ij})$.

Another process likely to raise average relatedness significantly is that of troop fissioning. If large troops tend to divide along kinship lines, r in each of the two smaller "daughter" troops will be higher than that in the original large troop. In spite of the small troop size in the model, troops frequently developed two "branches" represented by individuals related at less than 0.001 between branches (fig. D). Because fissioning did not occur, these branches were always rejoined later via males, but their temporary persistence reduced $E(r_{ij})$.

One process that might *lower* average coefficients of relationship is outside mating. Females are reported sometimes to solicit copulations with males belonging to all-male bands. If these dilute the resident male's reproductive success (in effect shortening the average male tenure), they lower $E(r_{ij})$.

It is not clear what effect male infanticide would have on the parameters of male or female reproductive success, and thence on average coefficients of relationship.

Taken together, these considerations suggest that $\bar{r}$ probably lies somewhere between 1/8 and 1/4 among adult females in typical troops of the Mount Abu region. As table E shows, for a given mating system this average is reasonably stable across time. However, at any given time there is obviously considerable variance of r_{ij} *within* the troop (standard deviation approximately equal to the mean). If individuals know directly who are their closest kin (for instance, if females know their own adult offspring), selection may often favor particular acts conditioned on estimates of r_{ij} other than $\bar{r}$.
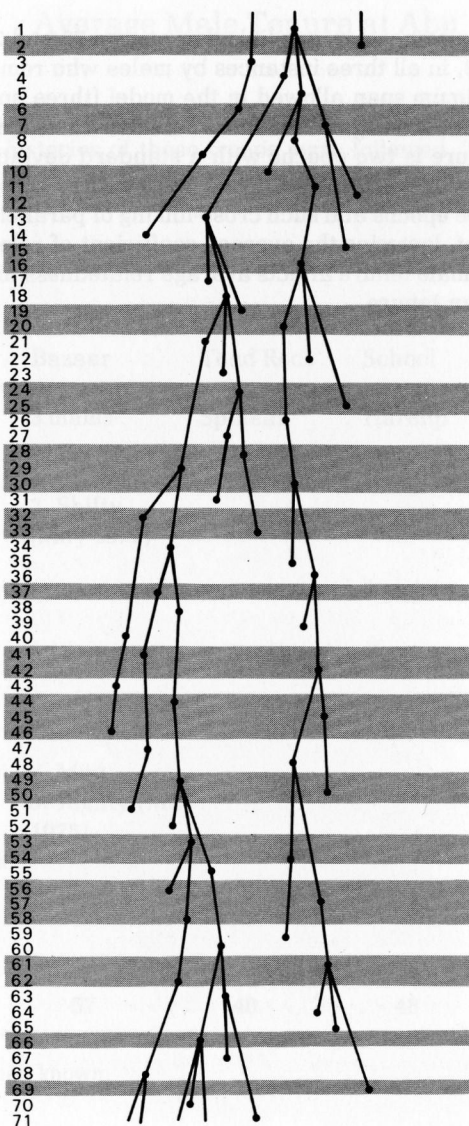
Figure D. Representative family tree, illustrating the development of extended parallel matrilines, and the effect of the variance of male tenure on the frequency of links between them. The diagram shows descent through females for seventy-one epochs near the end of a run. Alternating light and dark bands cover periods of tenure by successive unrelated males. Thus the females born at epochs 3, 4, and 5 have a common father, as do the females at 6 and 7. The tree's two continuous branches, which derive from

a single female ancestor, are linked at epochs 28 and 29, at 34 and 36, and at 57 and 58, in all three instances by males who remained with the troop for the maximum span allowed in the model (three epochs). Each of these links raises the average relatedness between the matrilines. In this run the average tenure is two epochs with a standard deviation of one; when the average was two with a standard deviation of zero, no males ever remained three epochs and such cross-linking of parallel female lineages was less frequent, lowering the average coefficient of relationship. Hence, the variance of male tenure affects average relatedness in the troop independently of mean tenure.