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Age Cohorts as Paternal Sibships

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Summary. Characteristics of a population's reproductive system affect the degree of relatedness within the age cohorts and maternal sibships of that population. Two consequences of a small litter size, particularly of size one, a relatively polygynous mating system at any one time period, and frequent replacement of reproductively active males over successive periods, are that (1) the set of offspring that each female produces (a maternal sibship) will usually consist of half-siblings, and (2) within a social group the members of each age cohort will be closely related, either all forming one paternal sibship (half-siblings) if there is only one reproductively active male at a time, or in the case of several reproductively active males, a set of individuals whose mean relatedness is somewhat lower than in the one-father case. In the present paper, degree of relatedness within each of these two subgroups is calculated on the basis of a simple model. I then examine effects of the various reproductive parameters on this relatedness and compare maternal sibships and age cohorts in the relative degree of relatedness within them. Age cohorts will often be identifiable, closely related units, paternal sibships in the extreme case. Age cohorts may be important in the evolution of family altruism. They differ from maternal sibships in interesting ways that may affect the kinds of behaviors that are likely to evolve.

Introduction

The purpose of this note is to consider certain commonly occurring conditions among group-living animals in which age cohorts will form a readily identified subgroup of closely related individuals, the extreme case being a paternal sibship. I phrase the following discussion in terms of mammals and primates in particular, but the argument applies to any

group-living animal with small litters, long dispersal stage, and a relatively polygynous mating system.

The consequences for relatedness of the different mating systems of such group-living animals have not been considered in formal theoretical treatments (e.g., Charlesworth, 1978; Wade, 1979) and have been only rarely treated in empirical studies (Bertram, 1976; Packer, 1979), except in the context of infanticide (e.g., Hrdy, 1974, and references therein). Yet, many mammals, of which primates are an excellent example, have very small litters with a long immature stage; most primates have only one infant per litter and the prereproductive and predispersal period lasts several years – on the order of two or three interbirth intervals. Only a few primate species are monogamous (e.g., marmosets, *Callitrix* sp.), some are polygynous (hamadryas baboons, *Papio hamadryas*; geladas, *Theropithecus gelada*; patas monkeys, *Erythrocebus patas*; some langurs, *Presbytis* sp. for example), and others live in multimale, multifemale groups. The last were originally thought to possess promiscuous mating systems, but as in many such multimale mammalian groups, only a few males, sometimes only one, leave offspring in any one year (cf., Hausfater, 1975; Packer, 1979, for savannah baboons, *Papio cynocephalus* and *Papio anubis*). That is, to varying degrees the system is effectively a polygynous one. Moreover, male tenure in a reproductive role may be relatively short (e.g., Bertram, 1976, for lions, *Panthera leo*; Hausfater, 1975; Packer 1979), often of the order of one or two interbirth intervals, compared to the reproductive span of the females in the group.

Two consequences of a small litter size, particularly of size one, a polygynous mating system at any one period, and frequent replacement of reproductive males over successive periods, are that (1) the set of offspring that each female produces (a maternal sibship) will usually consist of half-siblings, and (2) within a social group the members of each age cohort

will be closely related, either all forming one paternal sibship (half-sibs) if there is only one reproductively active male at a time, or in the case of several males fathering a cohort, a set of individuals whose mean relatedness is somewhat lower than in the one-father case. The second consequence is often ignored. To the contrary, it is usually assumed, implicitly or explicitly, that male lineages are undetectable by the observers and by the animals themselves and further that no other likely mechanism (such as social bond to a common mother for maternal sibships) would exist to enable the operation of sibling altruism within paternal sibships. Yet age cohorts are often distinguishable units and, as I show below, under some circumstances the average relatedness within these cohorts may be even greater than among maternal siblings.

Model and Results

The average coefficient of relatedness (Li, 1955) among maternal siblings and among cohort members of a group can be calculated under the following assumptions and definitions of parameters characterizing the reproductive system of a group.

Let:

S = the average number of offspring produced per female in her lifetime, $S \geq 2$

C = the average number of infants per age cohort, no more than one per mother, $C \geq 2$

T = the average tenure, in number of offspring that a male produces, by the same female. (Note that if males change mates in successive reproductive periods, this is equivalent to shorter tenure. If, for example, the same two males father all infants of two successive cohorts, but in the second cohort each fathers the infants of the females whose infants the second one fathered the first time, then $T=1$.) One could of course refine the model to include a stochastic component for T , but this hardly seems warranted at the present stage.

f = the coefficient of relatedness among the females (mothers), $f < 1$. Thus, cohort members will be related by $1/4f$ through their mothers (Li, 1955). In many species emigration from the natal group is common for males but not for females, resulting in relatedness among mothers of a group and thereby increasing the degree of relatedness among cohorts.

M = the number of reproductively active males fathering a cohort in a group at any one time. I shall assume that these M males share equally in the production of the cohort. Unequal contribution, for example as a function of dominance rank, could be accommodated, as Packer (1979) and Nozawa (1972) have done for considerations of inbreeding and effective group size in primates.

I assume that the reproductive males are unrelated. (A term could be added for the degree of relatedness among those M males reproducing at the same time, and one for those who constitute the

fathers of a maternal sibship.) I also assume that the fathers are unrelated to the mothers. Again, appropriate modifications could be made to accommodate exceptions to this assumption.

Cohort Relatedness. For each cohort member, we can calculate the number of paternal siblings he has in the cohort, which is $C/M-1$ and the proportion of the cohort that are his paternal half-siblings is then

$$\frac{C/M-1}{C-1} = \frac{C-M}{M(C-1)}.$$

An individual's expected relatedness to the other cohort members or, equivalently, the expected relatedness within the cohort, R_C , is just the proportion that are paternal siblings multiplied by the degree of relatedness among those siblings ($1/4 + 1/4f$) plus the proportion that are not paternal siblings multiplied by the degree of relatedness among them ($1/4f$).

$$\begin{aligned} R_C &= \frac{C-M}{M(C-1)} \left(\frac{1}{4} + \frac{1}{4}f \right) + \left(1 - \frac{C-M}{M(C-1)} \right) \left(\frac{1}{4}f \right) \\ &= \frac{1}{4} \left(f + \frac{C-M}{M(C-1)} \right). \end{aligned}$$

Note that:

$f/4 + 0.25 \geq R_C \geq f/4$ for all values of C and f ,

min. $R_C = f/4$ at $M=C$ for all C , and

max. $R_C = f/4 + 0.25$ at $M=1$ for all C .

Maternal Sibling Relatedness. In a similar fashion we can calculate for each member of a maternal sibship the number of maternal siblings that are full siblings = $T-1$ and the proportion of maternal siblings that are full siblings = $(T-1)/(S-1)$.

The expected relatedness of maternal siblings, R_S , is calculated as above.

$$R_S = \frac{T-1}{S-1} \left(\frac{1}{2} \right) + \left(1 - \frac{T-1}{S-1} \right) \left(\frac{1}{4} \right) = \frac{1}{4} \left(1 + \frac{T-1}{S-1} \right).$$

Note that:

$0.50 \geq R_S \geq 0.25$ for all values for S ,

min. $R_S = 0.25$ at $T=1$ for all S , and

max $R_S = 0.50$ at $T=S$ for all S .

In general, for the average relatedness within cohorts to be at least as great as that within maternal sibships, the proportion of paternal siblings in a cohort must be at least $1-f$ greater than the proportion of full siblings among the maternal siblings.

Consider the following special cases:

Case 1: If $M=1$ and $T=1$, then $f+1 \geq 1$, $R_C \geq R_S$.

That is, if one male in a group breeds at a time and there is male turnover for each subsequent conception, then cohort relatedness will be at least as great as relatedness in maternal sibships.

Case 2: If $f=0$, then $R_C \geq R_S$ only if $T=1$ and $M=1$. That is, if females are unrelated, the cohort relatedness will equal or exceed maternal sibship relatedness only if each cohort's infants are fathered by a different single male.

Notice, however, that within a multimale group for which there is more than one male fathering a cohort ($M > 1$), further behavioral and/or spatial structuring may be such as to produce essentially one-male multi-female subgroups, in which case the relatedness of cohorts within such subgroups would be higher than in the group as a whole.

Effects on relatedness of differences in some of these variables are worth comment.

For any given degree of relatedness among the mothers (f), cohort relatedness (R_C) will be maximum when only one male fathers a cohort ($M=1$) and will decrease as the number of reproducing males increases, dropping quite sharply at first. For $M=1$, cohort relatedness will be unaffected by cohort size, and for $M > 1$ the effects on relatedness of increases in cohort size will be extremely slight (an increase from $C=8$ to $C=12$ only results in R_C change of 0.01 for $M=4$, less for smaller values of M).

In general, cohort relatedness is primarily a function of the number of reproducing males, plus an additive term for the relatedness among females, and is little affected by cohort size.

Maternal sibship relatedness, R_S , on the other hand, is considerably decreased by increasing sibship size, for $T < S$, and relatedness is increased by increasing length of male tenure, T . Changes in length of tenure will have a greater effect on relatedness in populations with large maternal sibships. For any tenure length, T , a change to length $T+1$ will result in relatedness within maternal sibships increasing by $1/4 (S-1)$. This is in contrast to effects on R_C for an increasing number of reproducing males in which the change, for example, from one to two males fathering the cohort reduces cohort relatedness much more than does a change from three to four fathers.

Discussion

Clearly, the prevalent reproductive system in a population can have major effects on the degree of relatedness among identifiable subsets of the populations. Many studies in which altruistic or harmful behavior

is explained in terms of degree of relatedness among individuals cannot afford to ignore paternal relatedness, as seen from an examination of the consequences of different population parameters. In the absence of direct genetic information, estimates based on the reproductive system can provide first approximations to the prevailing conditions of relatedness in a study group.

Even in situations in which maternal sibships and cohorts are similar in degree of relatedness, these subgroups will differ in some interesting and potentially important ways in terms of the opportunities for interactions and expression of behaviors that may be significant in evolution through natural selection or in social evolution. First, paternal sibships will overlap in their life spans more than will maternal ones. In some sense, the *effective* potentially interacting sibship is larger in the case of paternal sibships. Thus, paternal sibships may provide more opportunity for evolution of sibling altruism or competition than do maternal sibships.

Second, some behaviors are primarily age-asymmetric, e.g., helpers at the nest (or den) in birds (e.g., Brown, 1978; Woolfenden, 1975) or jackals (Moehlman, 1979); others, e.g., cooperative defense, play, or hunting may require like-aged animals. The two kinds of sibships will differ in their suitability for the development of these asymmetric and symmetric behaviors. In slowly developing social animals, cohort identification and bonding through cohort-restricted activities, such as play, provide ample opportunity for selective interaction within peer groups which are, to varying degrees, paternal sibships.

In conclusion, even though cohort relatedness will rarely be as great as relatedness among a female's offspring in real populations, cohort relatedness is not negligible and, under a number of common kinds of mating systems and social structures, will be appreciable. Moreover, cohorts, even subgroup cohorts, are usually readily identifiable units within social groups, with considerable overlap in life spans, thereby providing ample opportunity for the expression of social behaviors that might have considerable evolutionary consequences.

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