

The Reproductive Consequences of Infanticide in Langurs: A Mathematical Model

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Summary. 1. An analysis of the factors influencing the reproductive success of infanticidal and noninfanticidal adult males in populations of langur monkeys (Genus *Presbytis*) is presented. Male tenure, defined as an adult male's length of residency in a one-male bisexual group, is demonstrated to be an important factor in any reproductive advantage accruing to infanticidal males. Other factors include the lengths of the female interconception intervals, the time at which adult male replacement occurs relative to the start of any such interval, and whether or not the subsequent replacement male is also infanticidal.

2. Infanticide is found always to confer a reproductive advantage on the resident male in a bisexual group under conditions of subsequent replacement by a noninfanticidal male. Infanticide would thus be expected to spread when introduced into an otherwise noninfanticidal population. Under conditions of subsequent replacement by an infanticidal male, infanticide is found to be advantageous for the resident male only a particular lengths of tenure. Infanticide would thus become fixed only in populations where the distribution of tenure lengths is advantageous for infanticidal males. Accordingly, it is predicted that average or modal tenure length in populations fixed for infanticide should coincide with those tenure lengths theoretically yielding a reproductive advantage for infanticidal males. Three direct estimates of average male tenure obtained from field studies of langur populations are consistent with the predictions of the model.

Introduction

Until recently, infant killing in any animal species was generally considered a rare and aberrant event. After observing several cases of infanticide by adult

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males in one-male groups of Hanuman langurs (*Presbytis entellus*), Sugiyama (1965) suggested that infant killing might be a regular occurrence in this species. Subsequently, infanticide by adult males has been reported for several other primates (Angst and Thommen, 1977; Hrdy, 1974, 1977a; Struhsaker, 1977; Wolf and Fleagle, 1977) as well as some nonprimate species (Bertram, 1973, 1975). This phenomenon has been studied most extensively in langur populations, however, and for this reason infanticide is discussed in the present paper with primary reference to this genus of colobine monkeys.

Langurs are commonly found in groups containing a single adult male, several adult females, and their offspring (Rudran, 1973; Sugiyama, 1964; Sugiyama et al., 1965; Yoshiba, 1968). Periodically, the resident male in such groups is replaced by a new individual, usually from a neighboring all-male group (Hrdy, 1974, 1977a; Sugiyama, 1965, 1966). Although the particular events surrounding male replacement may vary, the resident male of the bisexual group is typically driven out by the invading all-male group. One of the former bachelor males then attacks and eventually expels all the other males. Having thus eliminated his rivals, the new male begins to stalk and harass females carrying unweaned infants and within a short time bites to death all unweaned infants in the group (Hrdy, 1974, 1977b; Sugiyama, 1965, 1966). Females make only limited and unsuccessful attempts to defend their offspring (Hrdy, 1977b; Hrdy and Hrdy, 1976; Sugiyama, 1965) and resume sexual cycling a few days after the death of their infants (Hrdy, 1974). Infants born even a short time after male replacement are apparently unharmed by the new male (Hrdy, 1974, 1977b; Sugiyama, 1965; Yoshiba, 1968).

Previous discussions of infanticide in langurs have interpreted the phenomenon, at one extreme, as a behavioral pathology arising only under abnormal environmental conditions (Curtin and Dolhinow, 1978), or, at the other extreme, as an adaptive reproductive strategy for adult males under nearly all environmental conditions (Angst and Thommen, 1977; Hrdy, 1974, 1977a and b; Sugiyama, 1965). Those advocating the hypothesis of infanticide as a reproductive strategy have pointed out that since the death of an infant presumably brings its mother quickly into estrus, a new male who kills a female's infant effectively reduces the waiting time until she would have weaned the infant and become fertile again. In this way he may increase the number of offspring he is likely to conceive during his tenure, or length of residency in the bisexual group. This hypothesis has not been stated in a testable or quantifiable form, however, and the precise relation between tenure length and the differential reproduction of infanticidal and noninfanticidal males has not previously been determined.

This paper presents an analysis of the variables influencing the reproductive success of infanticidal and noninfanticidal males and a general mathematical model expressing reproductive success for infanticidal and noninfanticidal males as a function of tenure length under various reproductive and social conditions. The overall objectives of the paper are to determine the specific importance of tenure length in the evolution and maintenance of infanticide in natural populations of langurs and other animal species, and to derive quantitative and testable implications from the hypothesis that infanticide is reproductive strategy.

The Model

Variables and Assumptions

The primary variables in the following analysis are (1) male tenure, T , defined as the interval between successive replacements of the resident adult male in a bisexual group of langurs or other appropriate species, (2) the interval, I , between successive conceptions for an individual female, referred to hereafter as the interconception interval, (3) the month, m , at which replacement occurs relative to the interconception interval of a particular female, and (4) whether the new resident male in a bisexual group will himself be replaced by an infanticidal or noninfanticidal male. The purpose of the analysis is to determine the effects of these variables on the number of offspring that are sired by the resident male with a particular female and that survive his subsequent replacement. This number of offspring is referred to in the present paper as the male's reproductive success, r , with respect to that female and as such is a per capita measure.

Initial assumptions of the analysis concern the reproductive characteristics of females and the effects of infant mortality from sources other than infanticide. Specifically, it is assumed that lactational amenorrhea terminates simultaneously with the death or weaning of an infant and that the time elapsed between the death or weaning of an infant and resumption of sexual cycling by its mother is therefore negligible. Under this simplifying assumption, the interconception interval may be thought of as composed of three nonoverlapping segments: gestation, a period of lactational amenorrhea terminated by weaning, and one or more month-long menstrual cycles prior to the next conception. It is further assumed that the rates of miscarriage, spontaneous abortion, and infant mortality from causes other than infanticide are independent of any infanticidal or noninfanticidal tendencies of the resident male. Since these sources of mortality would thus affect the reproductive success of infanticidal and noninfanticidal males equally, they are ignored.

In order to illustrate the interaction and importance of the above variables, the number of offspring sired per female by infanticidal and noninfanticidal males will be compared with successive interconception intervals for females held constant at 22 months, composed of 7 months of gestation, 13 months of amenorrhea, and two month-long menstrual cycles prior to conception. (Each of these values as well as the total interconception interval is within the ranges for these reproductive parameters reported in field studies of langurs. See below.) This initial analysis will be carried out under the assumption that both infanticidal and noninfanticidal males will themselves eventually be replaced by a noninfanticidal male.

Replacement During Amenorrhea

Figure 1 compares the number of offspring sired per female by an infanticidal male (Fig. 1a) and a noninfanticidal male (Fig. 1b) with successive interconception intervals fixed at 22 months. Both figures have been drawn with the assumption that each male will eventually be replaced by a noninfanticidal male. Briefly, this figure indicates that only at certain lengths of tenure (e.g., between 2 and 14 months after male replacement) does the infanticidal male obtain a reproductive advantage. This advantage is never more than one additional offspring per female and is always attributable to the fact that infanticide at the time of replacement advances the onset of the female's estrus by some number of months.

Replacement Outside of Amenorrhea

In Fig. 1, adult male replacement is depicted as occurring during the female's lactational amenorrhea. An infanticidal male obtains a reproductive advantage at some values of T because infanticide following shortly after replacement advances the onset of estrus in the female. If replacement occurred during the two other segments of the female's interconception interval, during sexual cycling or gestation, the female would not be carrying an unweaned infant, infanticide would not occur, and no special reproductive advantage would accrue to an otherwise infanticidal male. In short, replacement during sexual cycling or gestation would result in identical reproductive success for both infanticidal and noninfanticidal males at all values of T .

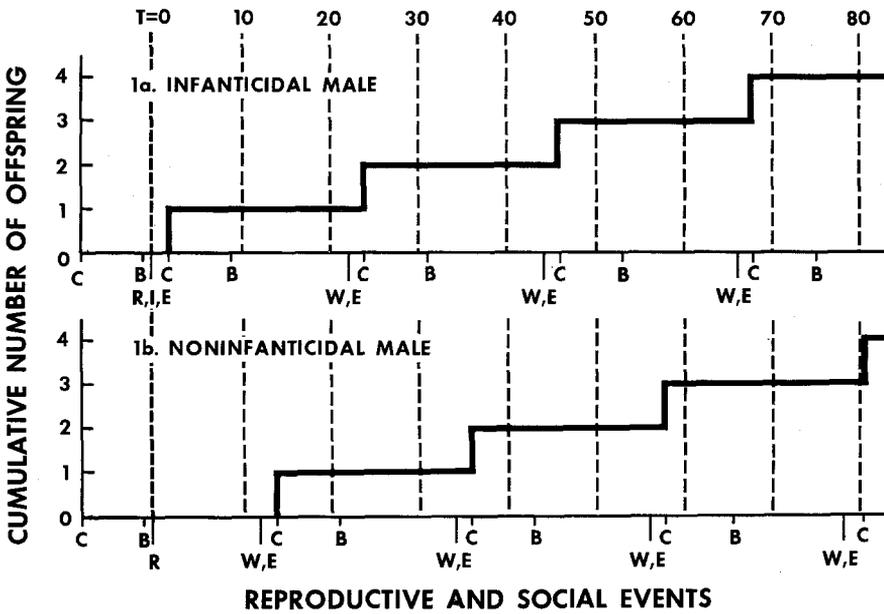


Fig. 1a and b. Cumulative number of offspring sired by an infanticidal (a) and a noninfanticidal (b) male with a given female in relation to male tenure, T , in months. Both figures are drawn under the assumption that each male will subsequently be replaced by another male who is noninfanticidal. The letters C , B , R , I , E , and W along the horizontal axis represent conception, birth, adult male replacement, infanticide, resumption of sexual cycles and estrus, and weaning, respectively. These reproductive and social events are spaced appropriately with respect to an adult male replacement occurring 1 month after birth in the first of a series of consecutive interconception intervals of 22 months duration. Various time intervals after the adult male replacement, each a potential value of T , are shown across the top of the figure and are further demarcated by broken vertical lines

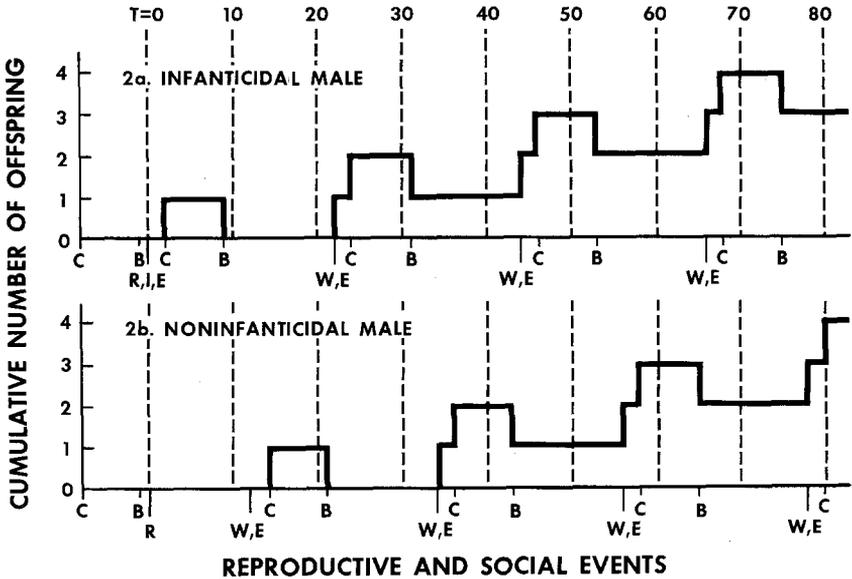


Fig. 2a and b. Cumulative number of offspring that are sired by an infanticidal (a) and a noninfanticidal (b) male with a given female and that survive subsequent male replacement, shown in relation to male tenure, T , in months. Both figures are drawn under the assumption that each male will subsequently be replaced by a male who is infanticidal

Subsequent Replacement by an Infanticidal Male

Another important factor influencing the relative reproductive success of infanticidal and noninfanticidal males is whether the subsequent replacement male will be infanticidal. Figure 2 depicts the cumulative number of offspring sired by an infanticidal male (Fig. 2a) and a noninfanticidal male (Fig. 2b) when each is subsequently replaced by an infanticidal male. In this figure, the infanticidal male again obtains a reproductive advantage beginning at $T=2$. If he is in turn replaced at $T=9$ through $T=22$, however, the infant sired at $T=2$ will be unweaned and subject to infanticide by the next replacement male so that an infanticidal male loses all reproductive advantage with respect to a noninfanticidal male at these values of T . At some values (e.g., $T=15$ through $T=22$) the infanticidal male will in fact be at a reproductive disadvantage compared to his noninfanticidal counterpart. This pattern of alternating advantage and disadvantage recurs cyclically for higher values of T such that at some values infanticidal and noninfanticidal males have equal reproductive success, at some values infanticidal males have a reproductive advantage of one or two offspring, and at some values noninfanticidal males have an advantage of one offspring.

As before, the reproductive success of infanticidal and noninfanticidal males differs only when replacement occurs during amenorrhea. Replacement at any other time does not lead to infanticide and thus results in equal reproductive success for infanticidal and noninfanticidal males.

A General Model of Infanticide

Calculation of the reproductive success of infanticidal and noninfanticidal males at each value of T is straightforward when, as in Figs. 1 and 2, interconception intervals are of fixed length and only one time of initial replacement is considered. A more general method is necessary if the model is to be applied to real animal populations in which females show variation in interconception interval lengths. To this end, the reproductive success of infanticidal and noninfanticidal males can be expressed as a function of particular combinations of values for tenure length, length of interconception intervals, and time of initial replacement through a series of conditional equations.

Consider first the case of a noninfanticidal male subsequently replaced by a noninfanticidal male. If the initial replacement occurs during the m th month after conception in the reproductive cycle of a given female, and if the male is in turn replaced after T months, then that male's reproductive success, r , with respect to a particular female can be determined from the following set of conditional equations:

$$\text{If } T < I_1 - (m - \frac{1}{2}), \quad r = 0; \tag{1}$$

$$\text{If } I_1 - (m - \frac{1}{2}) \leq T < I_1 - (m - \frac{1}{2}) + I_2, \quad r = 1; \tag{2}$$

⋮

$$\begin{aligned} \text{If } I_1 - (m - \frac{1}{2}) + I_2 + \dots + I_{n-1} \leq T < \\ I_1 - (m - \frac{1}{2}) + I_2 + \dots + I_n, \quad r = n - 1; \end{aligned} \tag{3}$$

where $I_{1, 2, \dots, n}$ are n consecutive interconception intervals of any length such that I_1 is the interconception interval in progress at the time of initial male replacement and I_n is the interval in progress when the resident male is himself replaced, and where the quantity $I_1 - (m - \frac{1}{2})$ is equal to the portion of I_1 remaining after the initial replacement. One-half is subtracted from m in these and subsequent equations as a correction for continuity in replacement times: Replacement is conceived as occurring midway during the m th month of I_1 .

In the case of an infanticidal male subsequently replaced by a noninfanticidal male, the same equations (1) through (3) apply when the initial replacement occurs during gestation or during sexual cycling. Replacement during these segments of I_1 results in equal reproductive success for infanticidal and noninfanticidal males; only when replacement occurs during amenorrhea do they differ. Under the latter conditions, the number of offspring sired by an infanticidal male may be determined from the following conditional equations:

$$\text{If } T < I_1 - (G_1 + A_1), \quad r = 0; \tag{4}$$

$$\text{If } I_1 - (G_1 + A_1) \leq T < I_1 - (G_1 + A_1) + I_2, \quad r = 1; \tag{5}$$

⋮

$$\begin{aligned} \text{If } I_1 - (G_1 + A_1) + I_2 + \dots + I_{n-1} \leq T < \\ I_1 - (G_1 + A_1) + I_2 + \dots + I_n, \quad r = n - 1; \end{aligned} \tag{6}$$

where G_1 and A_1 , respectively, represent the length of gestation and amenorrhea in I_1 , such that the quantity $I_1 - (G_1 + A_1)$ is equal to the period of sexual cycling in I_1 .

The effect of subsequent replacement by an infanticidal male on the reproductive success of the current male may also be represented by conditional equations. The equations for a noninfanticidal male subsequently replaced by an infanticidal male are as follows:

$$\text{If } T < I_1 - (m - \frac{1}{2}), \quad r = 0; \quad (7)$$

$$\text{If } I_1 - (m - \frac{1}{2}) \leq T < I_1 - (m - \frac{1}{2}) + G_2, \quad r = 1; \quad (8)$$

$$\text{If } I_1 - (m - \frac{1}{2}) + G_2 \leq T < I_1 - (m - \frac{1}{2}) + G_2 + A_2, \quad r = 0; \quad (9)$$

$$\text{If } I_1 - (m - \frac{1}{2}) + G_2 + A_2 \leq T < I_1 - (m - \frac{1}{2}) + I_2, \quad r = 1; \quad (10)$$

⋮

$$\text{If } I_1 - (m - \frac{1}{2}) + I_2 + \dots + I_{n-1} \leq T < I_1 - (m - \frac{1}{2}) + I_2 + \dots + I_{n-1} + G_n, \quad r = n - 1; \quad (11)$$

$$\text{If } I_1 - (m - \frac{1}{2}) + I_2 + \dots + I_{n-1} + G_n \leq T < I_1 - (m - \frac{1}{2}) + I_2 + \dots + I_{n-1} + G_n + A_n, \quad r = n - 2; \quad (12)$$

$$\text{If } I_1 - (m - \frac{1}{2}) + I_2 + \dots + I_{n-1} + G_n + A_n \leq T < I_1 - (m - \frac{1}{2}) + I_2 + \dots + I_{n-1} + I_n, \quad r = n - 1. \quad (13)$$

Briefly, these equations denote the fact that infants sired by the resident male and either unborn (11) or past weaning (13) at the time of his replacement are unharmed by a subsequent infanticidal male; only infants that are unweaned at the time of replacement (12) are killed by the subsequent male.

When the initial replacement occurs during gestation or sexual cycling, Eqs. (7) through (13) also apply for an infanticidal male subsequently replaced by another infanticidal male. As before, when initial replacement occurs during amenorrhea, a different set of equations apply:

$$\text{If } T < I_1 - (G_1 + A_1), \quad r = 0; \quad (14)$$

$$\text{If } I_1 - (G_1 + A_1) \leq T < I_1 - (G_1 + A_1) + G_2, \quad r = 1; \quad (15)$$

$$\text{If } I_1 - (G_1 + A_1) + G_2 \leq T < I_1 - (G_1 + A_1) + G_2 + A_2, \quad r = 0; \quad (16)$$

$$\text{If } I_1 - (G_1 + A_1) + G_2 + A_2 \leq T < I_1 - (G_1 + A_1) + I_2, \quad r = 1; \quad (17)$$

⋮

$$\text{If } I_1 - (G_1 + A_1) + I_2 + \dots + I_{n-1} \leq T < I_1 - (G_1 + A_1) + I_2 + \dots + I_{n-1} + G_n, \quad r = n - 1; \quad (18)$$

$$\text{If } I_1 - (G_1 + A_1) + I_2 + \dots + I_{n-1} + G_n \leq T < I_1 - (G_1 + A_1) + I_2 + \dots + I_{n-1} + G_n + A_n, \quad r = n - 2; \quad (19)$$

$$\text{If } I_1 - (G_1 + A_1) + I_2 + \dots + I_{n-1} + G_n + A_n \leq T < I_1 - (G_1 + A_1) + I_2 + \dots + I_{n-1} + I_n, \quad r = n - 1. \quad (20)$$

Application to Langurs

In applying the model of infanticide represented in the above conditional equations to langurs, several additional assumptions were made regarding times of replacement and female reproductive parameters. These assumptions were necessary because the relevant information regarding langurs was lacking or incomplete; they are not intrinsic to the model.

First, it was assumed that male replacement occurs independently of the reproductive states of females in a bisexual group. Under this assumption, there is an equal probability that a male replacement will occur during any month in the first interconception interval following male replacement, and this probability is equal to $1/I_1$, the reciprocal of the length of that interval.

Second, in order to estimate the distributions of the duration of female reproductive cycles, it was assumed: (1) that the lengths of gestation and lactational amenorrhea were constant, fixed at 7 and 13 months, respectively; (2) that the waiting time before conception during sexual cycling was

geometrically distributed with a probability of conception of 1/3 for each occurrence of estrus. The assumption of zero variance for gestation was considered reasonable, since gestation for langurs and many other primates shows little variability relative to the time units of this analysis. The fixed gestation length of 7 months used in the present analysis was consistent with field data (Hrdy, 1974, 1977b; Roonwal and Mohnot, 1977). In natural populations, the length of lactational amenorrhea almost certainly varies by a number of months, but there is little data on the distribution of this parameter. The fixed value of 13 months used in this analysis was also consistent with most estimates of average length of amenorrhea under natural conditions (Hrdy, 1977b; Jay, 1963).

The distribution of the length of sexual cycling depends on the length of each cycle and the probability of conception for each occurrence of estrus. For langurs, the menstrual cycle is almost exactly 1 month in duration (Hill, 1937; Hrdy, 1974, 1977b), but no information is available specifically concerning the monthly probability of conception. A probability of 1/3 is consistent with information on several other primate species (Czaja et al., 1975; Hendrickx and Kraemer, 1969), and for purposes of analysis it was assumed that this probability applied to all occurrences of estrus for langurs as well. The number of menstrual cycles prior to conception was thus geometrically distributed such that the probability of conception on the *i*th occurrence of estrus was equal to (1/3)(2/3)^{*i*-1}. Under the earlier assumption that estrus immediately follows the death or weaning of an infant, the above expression also represents the probability that *i*-1 months of sexual cycling precede conception and that the total interconception interval is therefore equal to 7+13+(*i*-1) months. The expected length of interconception intervals by this method is 22 months, a reasonable estimate for langurs (Jay, 1963).

Computation of Expected Reproductive Success

For each of the conditional Eqs. (1) through (20) above, reproductive success, *r*, may be derived from tenure length, *T*, given specific values for the time of initial male replacement relative to the female's reproductive cycle, and the length of the various segments of *n* consecutive interconception intervals following replacement. With fixed values for gestation and amenorrhea, the derivation of *r* depends only on replacement time *m* and the total lengths of the consecutive interconception intervals *I*₁ through *I*_{*n*}. Given the probability distributions for these variables as estimated above, the computation of expected reproductive success for langur males is straightforward.

Let $\prod_{j=1}^n P(I_j)$ represent the joint probability of *n* consecutive interconception intervals *I*_{1,2,...,n} such that $k \leq I_j \leq K$, and let *P*(*m*) equal the probability that initial male replacement occurs during the *m*th month following conception in the first of these interconception intervals. Then the expected reproductive success, *E*(*r*_{*T*}), for an infanticidal or noninfanticidal male at any value of *T* may be determined from:

$$E(r_T) = \sum_{I_1, 2, \dots, n=k}^K \sum_{m=1}^{I_1} \prod_{j=1}^n P(I_j) P(m) r_{m, T, I_1, 2, \dots, n}, \tag{21}$$

where *r*_{*m, T, I*_{1,2,...,n}} is obtained from the appropriate conditional equation above for particular values of *m*, *T*, and *I*₁ through *I*_{*n*}.

Probabilities for lengths of individual interconception intervals, *P*(*I*_{*j*}), and for times of replacement, *P*(*m*), were evaluated according to the estimation procedures described above. Given the assumptions regarding langur reproductive parameters, the minimum length *k* of an interconception interval was 20 months. The maximum length *K* considered was 31 months, since the probability (<0.008) that an interconception interval should exceed this value was judged negligible. Under the assumption that time of replacement is independent of the reproductive states of group females, the results of this model do not depend on the degree of synchrony of females' reproductive states: Given *n* females in a bisexual group, the male's total expected reproductive success for tenure *T* is simply *nE*(*r*_{*T*}), regardless of the reproductive synchrony or asynchrony of the *n* females.

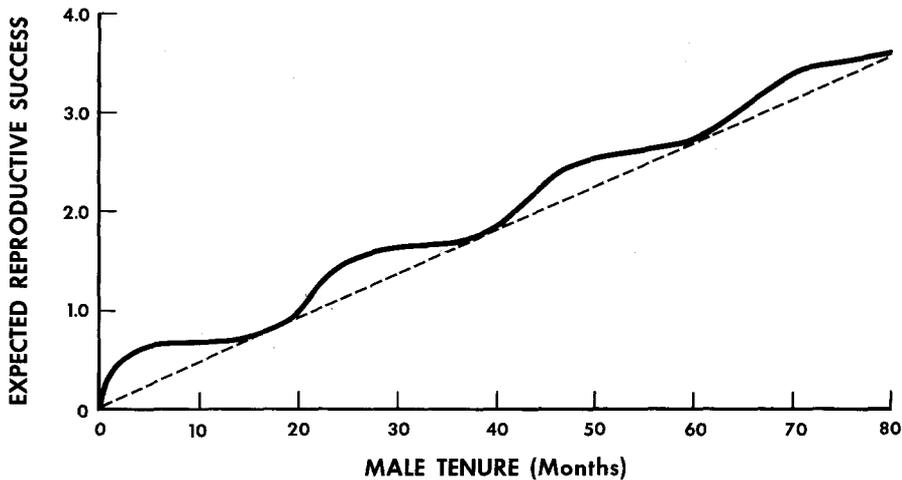


Fig. 3. Expected reproductive success with respect to a given female for infanticidal (*solid line*) and noninfanticidal (*broken line*) males as a function of their tenure, T , in months. Subsequent replacement is by a noninfanticidal male

Results

Patterns of Expected Reproductive Success

Figure 3 compares the expected reproductive success per female of infanticidal and noninfanticidal male langurs as calculated from Eq. (21) under conditions of subsequent replacement by a noninfanticidal male. This figure may be thought of as demonstrating the reproductive consequences of infanticide at the time of origin of the behavior, i.e., when nearly all adult males in a population are noninfanticidal and even the rare infanticidal male is likely to be replaced by a noninfanticidal male. Under these conditions, the expected reproductive success of an infanticidal male exceeds that of a noninfanticidal male at all values of T , although the difference is greatest at values of 3, 26, 48, and 70 months. Even at values of 15–19, 38–40, and 60–61, where the two curves appear to touch in Fig. 3, infanticidal males have a slight advantage. In short, an infanticidal male always has a reproductive advantage compared to other males in a predominantly noninfanticidal population.

Figure 4 compares the expected reproductive success of infanticidal and noninfanticidal males under conditions of subsequent replacement by an infanticidal male. This figure may be thought of as demonstrating the reproductive consequences of infanticide once the behavior is fully established in a population, i.e., when a resident male of either type will almost always be replaced by an infanticidal male. Under these conditions, infanticide is not reproductively advantageous at all values of T : At values between 8 and 19, between 32 and 40, between 54 and 61, and between 77 and 80 inclusive, infanticidal males have a lower expected reproductive success than their noninfanticidal counterparts. These intervals demarcate tenures that terminate at times when the current

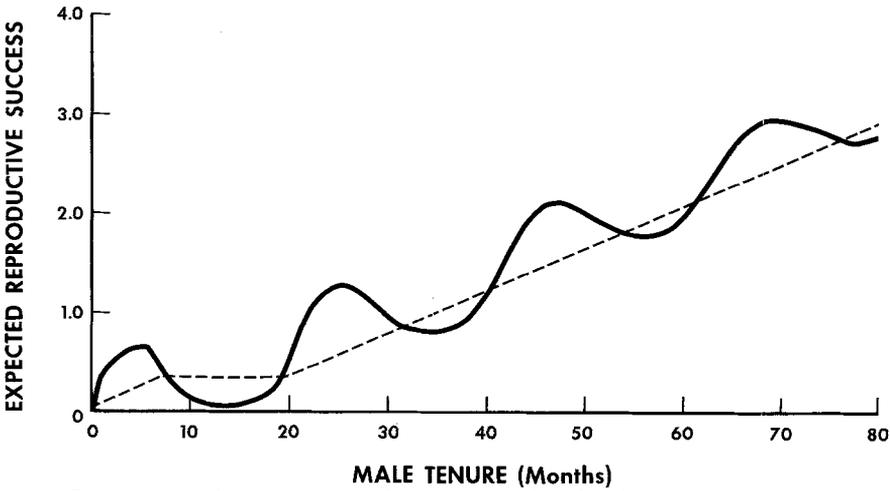


Fig. 4. Expected reproductive success with respect to a given female for infanticidal (solid line) and noninfanticidal (broken line) males as a function of their tenure, T , in months. Subsequent replacement is by an infanticidal male

male's infants are likely to be unweaned and subject to infanticide by the subsequent male. In contrast, at values of T near 26, 47, and 69 months, infanticidal males are at a substantial reproductive advantage relative to noninfanticidal males. In short, when infanticide is disadvantageous it is only slightly so, but when it is advantageous it is greatly so.

In addition to these comparisons of infanticidal and noninfanticidal males within replacement conditions, it is instructive to compare males across replacement conditions. For example, an infanticidal male replaced by an infanticidal male (solid line in Fig. 4) will generally have lower expected reproductive success than a noninfanticidal male replaced by a noninfanticidal male (broken line in Fig. 3), although the difference between the curves is minimal at a few values of T . Thus, the end result of the spread of infanticide in a population will be the reduction of expected reproductive success for all males in that population, although the extent of the reduction will depend on the tenure lengths characteristic of the population.

Implications and Predictions

From Fig. 3 it is clear that an infanticidal male in an otherwise noninfanticidal population will generally have a substantial reproductive advantage and will never be at a disadvantage compared to other males. Figure 4 indicates that in a predominantly infanticidal population, infanticide would still be advantageous at most values of T so that the behavior is likely to be maintained. Even if some males were replaced at disadvantageous values of T , infanticide would be maintained as long as the average fitness of males replaced at advantageous values of T exceeded that of males replaced at values disadvantageous for

infanticide. Even in the case of a population characterized by tenures disadvantageous for infanticidal males, one might expect a balanced polymorphism between infanticidal and noninfanticidal males to result rather than the complete elimination of infanticidal males from the population. In short, infanticide could become either a 'pure' or 'mixed' evolutionary stable strategy (ESS) as described by Maynard Smith (1974). The distribution of tenure lengths would determine whether the population would adopt a 'pure' strategy (fixation of infanticide) or a 'mixed' strategy (behavioral polymorphism or alternating infanticidal and noninfanticidal behavior within the life history of an individual male).

The results of the present model demonstrate that male tenure is indeed an important variable in the evolution and maintenance of infanticide in natural langur populations and provide the basis for the following prediction regarding infanticide and tenure length: Infanticide should become a fixed characteristic of adult males only in populations where tenure lengths typically yield a reproductive advantage for infanticidal males. Available data are insufficient to determine how tenure lengths are distributed in langur populations, but several estimates of mean tenure length are available for populations in which repeated occurrences of infanticide have been reported. Comparison of these estimates with Fig. 4 provides a very limited test of this prediction, assuming that estimated mean tenure lengths are representative of individual tenure lengths in the population.

Male Tenure in Natural Populations

Published demographic and reproductive data provide the basis for three independent direct estimates of average male tenure from infanticidal populations. The sources, derivation, and reliability of these estimates are discussed below.

From 1961 through 1963, Sugiyama (1964, 1965; Sugiyama et al., 1965) studied Hanuman langurs (*Presbytis entellus*) near the town of Dharwar in central India. Two independent estimates of male tenure can be derived from his data: (1) During June–December, 1961, Sugiyama (1964; Sugiyama et al., 1965) observed or inferred a total of five adult male replacements in a 180-day period involving 38 langur groups. This yields an estimate of one adult male replacement every 1368 days, or roughly 46 months, on the average ($38 \text{ groups} \times 180 \text{ days} \div 5 \text{ replacements}$). Data from Sugiyama (1964) and Sugiyama et al. (1965) yield individual estimates of 43 and 17 months, respectively, but since these estimates are based on subsets of the complete data they are not considered further here. (2) From April, 1962, through March, 1963, Sugiyama (1965) again censused and observed the Dharwar langur population. Adult male replacements were recorded in four of nine study groups with an estimated replacement rate of one every 821 days, approximately 27 months ($9 \text{ groups} \times 365 \text{ days} \div 4 \text{ replacements}$). This is the most widely cited estimate for the rate of adult male replacements among langurs (Sugiyama, 1967; Wilson, 1975; Yoshida, 1968). Three of the nine groups, however, were specifically chosen because of their

presumed susceptibility to male replacement, so that the above figure may overestimate the actual replacement rate (Sugiyama, 1965).

The only other demographic data sufficient to provide direct estimates of average tenure come from Hrdy's (1974, 1977b) observations of Hanuman langurs in the area of Mt. Abu, Rajasthan, India. (3) Long-term data from this site contain eight, or possibly nine male replacements over a period of 248 group-months (Hrdy, 1977b, and personal communication), yielding an estimated rate of one replacement every 28–31 months (248 group-months \div 8 or 9 replacements). Since observation during this period was not continuous, the above figure may underestimate the actual replacement rate. The estimate of one replacement every 35 months published by Hrdy (1974) was derived from a subset of the complete data and is not considered here.

The above estimates are based on directly observed or inferred incidences of infanticide during the observation period. In addition, several estimates of individual tenure lengths have been published based on a more indirect procedure in which the age of the oldest male juvenile plus 6 months for gestation was taken as a rough estimate of the time since the last adult male replacement accompanied by infant killing (Sugiyama, 1965; Rudran, 1973). These individual estimates yielded mean estimates of approximately 53 months (Sugiyama, 1965, Table 5) and 30 months (Rudran, 1973, p. 175). We consider these indirect estimates to be unreliable for several reasons: First, it is notoriously difficult to determine the exact ages of individuals in natural populations. Second, this method assumes that the oldest juvenile was conceived immediately following replacement, although it is possible that he would have been conceived shortly before or some time following replacement. Third, only those groups are considered in which replacement actually occurred during the observation period, so that estimates of male tenure may have been affected by sample selection bias.

In summary, the three direct estimates of average male tenure listed under (1), (2), and (3) fall on or near peaks in Fig. 4 and are thus consistent with the predictions of the present model. The two indirect estimates fall in regions where infanticide is only slightly favored, but the reliability of this indirect estimation procedure must be questioned on several grounds.

Discussion

Female Counterstrategies

Since infanticide results in lowered reproductive success for females, it might be expected that they would evolve strategies to reduce the incidence of infant killing. Vigorous defense of unweaned infants following male replacement would seem to be the most direct counterstrategy against infanticide. In fact, adult females engage in only limited defense of their offspring and are rarely successful in preventing infant killing (Hrdy, 1974, 1977b; Hrdy and Hrdy, 1976; Mohnot, 1971; Sugiyama, 1964, 1965).

Another possible counterstrategy is the modification of certain female reproductive parameters. Since infanticide is advantageous for males only because it shortens the waiting time until conception following male replacement, females might reduce this advantage by delaying conception following the death of their infants (Hrdy, 1977a).

A third possible counterstrategy is pseudoestrous behavior when male replacement occurs while a female is pregnant (Hrdy, 1974, 1977a). As noted above, infanticidal males reportedly tolerate infants born shortly after replacement even though the infant may have been conceived before replacement. Hrdy (1974) pointed out that langur females solicit copulation from a new male even when pregnant and has argued that an infanticidal male may tolerate an infant born shortly after replacement only because he has already formed a consortship with the infant's mother.

A final possible female counterstrategy, specifically suggested by the present model, is the manipulation of the resident male's length of tenure. If females were successful in preventing male replacement except when many of them were pregnant or sexually cycling, the incidence of infanticide would be proportionally reduced.

At present, there is no clear evidence for any female counterstrategies except direct defense of infants, and the latter does not appear to be particularly effective. Females at best might reduce the incidence of infant killing; they are unlikely to succeed in eliminating it.

Conclusion

In *The Descent of Man*, Darwin concluded that infanticide was one of the most important Malthusian checks on human population growth, adding: "Our semi-human progenitors would not have practiced infanticide... for the instincts of the lower animals are never so perverted as to lead them regularly to destroy their own offspring" (1874, p. 52). The present analysis, however, has demonstrated that it can be to the selective advantage of adult male langurs regularly to kill infants of their own species, although not, to be sure, their own offspring. In particular, the tenure of adult males in bisexual groups has been shown to be a key determinant of any reproductive advantage accruing to infanticidal males.

Although the present model has been illustrated with reference to langur monkeys, with suitable modifications it is applicable to other primate or non-primate species living in similar one-male groups. Current debate has centered on the distribution of infanticide within the order Primates (Dolhinow, 1977; Hausfater, 1977; Hrdy, 1977c). Curtin and Dolhinow (1978) consider infanticide an aberrant behavior occurring only in a small number of langur populations living under abnormal environmental conditions. In contrast, advocates of the hypothesis that infanticide is a reproductive strategy have pointed out numerous, though isolated, reports of infanticide in Old World monkey species other than langurs (Angst and Thommen, 1977; Hrdy, 1977a). The relatively low frequency of such reports may reflect a lack of observation time, particularly for

typically reclusive and forest-dwelling species, rather than the absence of the behavior itself (Hrdy, 1977a; Struhsaker, 1977). The importance of the present model is that it yields predictions regarding the distribution of infanticide both within and among species as a function of male tenure.

It is even possible to question whether the one-male group structure is necessary for the evolution of infanticide. What is required is some means by which the infanticidal male avoids killing infants he himself has sired. In multimale primate groups such as those of baboons, even subordinate males have some likelihood of impregnating females within the group (Hausfater, 1975). Infanticide following displacement of a first-ranking male by a male from within the group would probably not be advantageous for the new first-ranking male, since some of the infants in the group are likely to be his own. This would not be the case when a first-ranking male was displaced by a male from outside the group, so that infanticide following first-rank replacements from outside the group might be expected to evolve even in species living in multimale groups. Consistent with this hypothesis, Angst and Thommen (1977) concluded from a number of reports from various primate species that infanticide is most likely to occur when an unfamiliar male becomes the first-ranking male in a group.

The present analysis demonstrates that discussions of the distribution of infanticide within and among species must take into account the particular combination of male tenure and female reproductive parameters characteristic of each species. Unfortunately, such demographic and reproductive data are not available even for otherwise well-studied populations. The importance of this analysis and others like it (e.g., Altmann, 1962; Hausfater, 1975; Saunders and Hausfater, 1978) may lie as much in pointing out precisely what information is necessary in order to answer meaningful questions regarding animal behavior as in providing answers to those questions. It is hoped that such analyses will stimulate observers of natural primate populations to obtain such information.

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