Why Mothers do not Resist Infanticide?
A Cost-benefit Genetic Model

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Abstract ——————— Infanticide has recently been observed in several primate species. A question of why mothers do not resist infanticide intensely is investigated by the haploid two-locus model. A hypothesis that mothers can recover loss of offspring by more gain of grandchildren is rejected in most cases, and it is shown that costs and benefits both for males and females have the strongest influence on the evolution of infanticide and obedience to it. The model may give rise to coexistence of infanticidal and non-infanticidal males and obedient and resistant females. Actual observations and data of primate infanticide are discussed in the light of results of the model.

INTORDUCTION

Since infanticide was first reported in a wild primate population of hanuman langurs (*Presbytis entellus*) by Sugiyama (1965), it has been so far observed in as many as 14 species of natural populations (Hiraiwa-Hasegawa, 1988). In most cases among them, the basic social

units are single-male groups, each group containing only one reproductive male, several females, and their offsprings. When an adult male, not belonging to any group, replaced a harem leader, it was observed that the male killed unweaned infants in that group and then mated with the infants' mothers. This resulted in that the infanticidal male had his first offspring earlier than if he did not kill infants. While interpretation of such infanticide has been one of the most controversial topics in recent primatology, accumulating evidence strongly suggests that it is a reproductive strategy for infanticidal males to promote their own fitnesses (Hausfater and Hrdy, 1984; Struhsaker and Leland, 1987).

Although infanticide may be advantageous to males, obviously it is not to females. Therefore, the fact that intense females' resistance to infanticidal males was not observed is an evolutionary question to be investigated (Sugiyama, 1965). To solve this problem, we will be required to analyze quantitatively costs and benefits of infanticide both for males and females. In such analysis of coevolution in male and female traits, consideration of the budget in only one generation is insufficient. For example, a female receiving infanticide suffers from some decrease in the number of her offspring, but she may have more sons sired by the infanticidal male compared than females resisting infanticide. The sons will inherit the infanticidal trait and may have more offsprings owing to that trait (Hrdy, 1981, p. 94). Thus the obedient female may recover the loss of offspring by the more gain of grandchildren (Itô, 1987, p. 138).

Recently, coevolution of apparent maladaptive traits of males and female preference to those traits has been intensively investigated (Lande, 1981; Kirkpatric, 1982, 1986; Segar and Trivers, 1986;

Pomiankowsky, 1987). The similar coevolution problem, called the "sexy son", has been also studied (Kirkpatric 1985). In those analysis, two kinds of genetic models, the quantitative genetics and the haploid two-locus model, were applied and the both models gave the similar results. Here we use the latter simpler model to investigate theoretically under what conditions the male infanticide and the female obedience could evolve. Actual observations and data of primate infanticide are discussed in the light of results of the model.

THE MODEL

The model supposes the following structure of a population with non-overlapping generations. In the population, there are two types of males, infanticidal and non-infanticidal, and two types of females, obedient and resistant. Mature females form a group of a certain size. The group size does not affect results of the current analysis. Each group includes one reproductive male at a time. Males other than reproductive males constitute a reservoir of bachelors. All females in a group produce their broods simultaneously and the number of broods in their life is n. Every time after the females produce their broods, the reproductive male in the group is always replaced by another male. The replacing males as well as the first reproductive male appear randomly from the reservoir of bachelor males. If the replacing male is an infanticidal male, a part of the brood of each female is killed by the male, and the size of the following brood is increased. When a female is obedient, the relative decrease and increase of the broods are designated by c and b, respectively. The

"relative" means that the sizes are measured so that the brood size of a pair of an non-infanticidal male and an obedient female is took as the unit. When a female is resistant, they are designated by c' and b', respectively. The resistant females may pay additional costs of decreasing the current brood (c'') to warn against infanticide. We will consider both cases of $c''>0$ and $c''=0$. In the pair of an obedient female and an infanticidal male, the balance of the female is minus ($b<c$) and the gain of the male is plus ($b>0$). Resistant females can reduce the number of killed offspring ($c'<c$), and therefore, the gain of infanticidal males is reduced ($b'<b$). Assuming cases in which resistance results in reducing the next brood, the value of b' may be negative.

The organism has a haploid genetic system with two loci, T and P. The recombination rate between the two loci is designated by r ($0<r\leq1/2$). The value of $1/2$ corresponds to free recombination and the value near to 0 corresponds to tight linkage of the two loci. The T locus has two alleles, I and N, which code for the infanticidal and non-infanticidal traits of males, respectively. The P locus has also two alleles, O and R, which code for the obedient and resistant traits of females, respectively. Frequencies of genotypes, IO, IR, NO, and NR, are identical in the two sexes because the loci are autosomal. They are designated by x_1, x_2, x_3, and x_4, respectively. Thus, the allele frequencies of the infanticidal trait and the obedient trait are

$$t = x_1 + x_2 \quad \text{and} \quad p = x_1 + x_3 , \tag{1}$$

respectively. Under the above assumptions, we will deduce a system of equations which represent temporal changes in t and p.

The average number of the first brood of an obedient female, whose genotype is IO or NO, is $1-ct$ because the probability that the mate of the second brood is an infanticidal male is t. The average number of the second brood is $1+b-ct$ when the second mate is infanticidal (IO or IR) and $1-ct$ when the mate is non-infanticidal (NO or NR). The average brood sizes from the third to the $(n-1)$-th brood are the same as that of the second brood. The last n-th brood size is $1+b$ when the mate is infanticidal, and 1 when non-infanticidal. The average number of each brood of a resistant female (IR or NR) is given by replacing c and b by c' and b', respectively, and subtracting the warning costs c''. Resistant females are assumed to be unable to discriminate in advance between infanticidal males and non-infanticidal males, and therefore, they pay the same warning costs for either type of males. The average brood sizes described above are summarized in Table 1.

According to the Mendelian segregation law, the probability that offspring of each combination of parental genotypes becomes each one of genotypes IO, IR, NO, and NR can be calculated, and they are shown in Table 2. Using Tables 1 and 2, we can write down the relative average numbers of individuals with the four genotypes in next generation, W_1, W_2, W_3, and W_4, as shown in Table 3.

The sum of W_i's in the table can be reduced to a simple form, which is represented only by allele frequencies t and p in equations (1), without using x_i's directly:

$$W = \sum_{j=1}^{4} W_j$$

$$= n - (n\text{-}1)\{(c\text{-}b)p + (c'\text{-}b')(1\text{-}p)\}t - (n\text{-}1)c''(1\text{-}p) \ . \quad (2)$$

Genotype frequencies in next generation are thus given as

$$x_i' = \frac{W_i}{W} \quad (i = 1, 2, 3, 4) \ . \tag{3}$$

These equations are a set of recursion equations which determine temporal changes in genotype frequencies.

Allele frequencies in next generation are $t'=x_1'+x_2'$ and $p'=x_1'+x_3'$. Using equations (1), (2), and (3), and Table 3, the following formulation representing changes in p' and t' can be deduced:

$$\Delta p = p' - p = -\frac{p(1\text{-}p)}{2W}(n\text{-}1)B + \frac{D}{2W}(n\text{-}1)A \tag{4a}$$

$$\Delta t = t' - t = \frac{t(1\text{-}t)}{2W}(n\text{-}1)A - \frac{D}{2W}(n\text{-}1)B \tag{4b}$$

where

$$A = bp + b'(1\text{-}p) \tag{4c}$$

$$B = (c\text{-}b\text{-}c'+b')t - c'' \tag{4d}$$

$$D = x_1x_4\text{-}x_2x_3. \tag{4e}$$

Here, A represents the relative average benefit per brood of an infanticidal male against a non-infanticidal male, and B represents the relative average overall costs per brood of an obedient female against a resistant female. And D is so called the linkage disequilibrium,

which is a measure of nonrandom association between alleles at the T and P loci. We can see that the equations (4) are constituted of direct fitness differences in the first terms and indirect effects through the linkage of the loci in the second terms. It should be remarked that equation (4) are not closed as a recursion equation of t and p because D changes temporarily and it cannot be represented only by t and p. By these equations, however, the temporal changes in t and p can be analyzed to a certain degree as follows.

A case of no costs for resistance

As stated briefly in introduction, obedient females for infanticide may recover the loss of offspring by gaining the more grandchildren because their sons inherit the infanticidal trait more than sons of resistant females. In the scheme of the population genetics, this "grandchildren effect" is represented as the linkage disequilibrium between alleles at the T and P loci, D, in equation (4e). According to numerical calculations of equations (3), D becomes positive soon in most cases even if it starts from zero or negative values. Positive values of D mean that the allele combinations IO and NR is more frequent than those of IR and NO, compared with random association of the alleles. In other words, obedient females do come to carry infanticidal genes more frequently than resistant females.

In order to examine how influential this grandchildren effect is in the dynamics of allele frequencies, we consider a special case in which resistant females can perfectly defend their offspring against infanticide without any cost, *i.e.*, $b'=c'=c''=0$. Under this condition, resistant females are obviously more advantageous than obedient

females in respect of the number of offspring. Nevertheless, there are cases in which the allele frequency of the obedient trait, $p=x_1+x_3$, is increasing if the loss of obedient females, $c-b$, is rather small. An numerical example is shown in Fig.1a (a broken line), where $n=2$, $b=0.8$, $c=0.9$, and $r=0.5$ with initial genotype frequencies $(x_1,x_2,x_3,x_4)=(0.5,0,0,0.5)$. These x_i's gives the maximum linkage disequilibrium $D=0.25$. As $b>0$, the allele frequency of the infanticidal trait, $t=x_1+x_2$, increases. Although p also increases for a while, it reverses the direction to decrease after t attains a certain value. And finally, the trajectory approaches $(p, t)=(0,1)$. When more tight recombination is assumed instead of the above free recombination of $r=0.5$, p increases up to a more high level. A dotted line in Fig.1a represents a case of $r=0.1$. When initial genotype frequencies are 0.25 all together, where $(p, t)=(0.5,0.5)$ and $D=0$, D increases but the degree is so small that p does not increase at all. A solid line in Fig.1a represents the trajectory in case of $r=0.5$. In this case, the maximum attained value of D is 0.012. Other values of the recombination rate give almost the same trajectory, and D does not increase above 0.012. This may be because two operations of building and breaking the linkage disequilibrium have comparative effects whether the recombination rate is large or small.

So far as c is larger than b, any pair of c and b led to similar results. The obedient trait may substantially increase only when initial values of D are considerably large. As such initial large values are unnatural, we conclude that the grandchildren effect does not work influentially in usual cases. Even if the obedient trait increases temporarily, the final goal is always the fixation of the resistant trait.

Thus, in order to answer why mothers do not resist infanticide, consideration of resistant costs is inevitable.

Large D values produce another seemingly curious phenomenon. When $c-b$ is large with a small b, p decreases rapidly. If the initial value of D is large, t decreases although infanticidal males are more advantageous than non-infanticidal males. An example is shown in Fig.1b where $n=2$, $b=0.1$, and $c=0.9$ with initial genotype frequencies (x_1,x_2,x_3,x_4) =(0.5,0,0,0.5): a broken line for $r=0.5$ and a dotted line for $r=0.1$. However, the infanticidal trait increases monotonically when the initial value of D is 0 (a solid line). Once the resistant trait is fixed ($p=0$), t remains unchangeable because infanticidal and non-infanticidal males are equivalent against resistant females in this case.

Cases of finite costs for resistance

We will analyze mainly the case of positive warning costs ($c''>0$), and add briefly the case of no warning costs ($c''=0$) later. First, we examine the changes on the boundary of the (p, t) space (see Fig.2). The value of D on the boundary is 0 because either x_1 or x_4 is 0 and either x_2 or x_3 is 0. When $t=0$, $\Delta t=0$ and $\Delta p=p(1-p)(n-1)c''/(2W)>0$ in equations (4). Therefore, p increases along the $t=0$ axis. When $p=1$, $\Delta p=0$ and $\Delta t=t(1-t)(n-1)b/(2W)>0$, which means t increases along the $p=1$ axis. When $t=1$, $\Delta t=0$ and Δp is proportional to $(c'-b'+c'')-(c-b)$, which is the overall cost difference per brood between a resistant female and an obedient female when the new mate is an infanticidal male. We consider two cases, (1) $(c'-b'+c'')>(c-b)$ and (2) $(c'-b'+c'')<(c-b)$. The value of p increases in case (1) and decreases in case (2) along the $t=1$ axis. When $p=0$, $\Delta p=0$ and Δt is proportional to b'. The value of b'

represents benefits of an infanticidal male when the mate is a resistant female. We also consider two cases, (3) $b'>0$ and (4) $b'<0$. Corresponding to each case, the value of t increases or decreases along the $p=0$ axis. Combination of the above cases gives four different cases: I.(1) and (3), II.(1) and (4), III. (2) and (3), and IV. (2) and (4).

We illustrated the above four cases in Fig.2, in which changes on the boundaries are shown by arrows. The directions of arrows in cases I and II suggest that $(p, t) = (1,1)$ is a stable equilibrium point (SEP) of equation (3), which means that starting from any point near to this point, the trajectory approaches the point. We can also presume that $(p, t)=(0,1)$ is a SEP in case III, and that there is no SEP on the boundary in case IV. Corners other than the SEP's are unstable equilibrium points (UEP), which means that starting from a point (actually almost all points) near an UEP, the trajectory departs the point. Through linearization of equations (4) with respect to the equilibrium points, it can be easily proved that the above statements are true.

We can also prove that only in case IV, there is an equilibrium point (EP) inside the boundary. Because there is only one SEP on the boundary and no EP inside the boundary in cases I, II, and III, we can expect that any trajectory finally approaches the SEP, i.e., those points are globally stable. Putting $A=B=0$ in equations (4), we have the inside equilibrium point in case IV:

$$(p, t) = (\frac{-b'}{b-b'}, \frac{c''}{c-b-c'+b'}) . \tag{5}$$

Trajectories are expected to run around this inside EP because the trajectory on the boundary does go around.

To get more detailed information, we have conducted numerical calculations of equations (3). As in the case of no costs, trajectories were barely dependent on values of the recombination rate and initial values of D unless the initial D values are unnaturally large. Therefore, all of examples given in the following are those in which $r=0.5$ and $D=0$ initially.

Case I: $c'-b'+c''>c-b$ and $b'>0$ ----- In this case, resistant females are less advantageous than obedient females for infanticide, and infanticidal males are more advantageous than non-infanticidal males for resistance. Numerical calculations for possible combination of parameters satisfying the above conditions always give monotonic increase of both p and t, with reaching finally to $(p, t) =(1,1)$. Thus (1,1) was confirmed to be a globally stable equilibrium point which has been suggested through the boundary analysis. An example is shown in Fig.1a, where $n=2$, $b=0.2$, $c=0.5$, $b'=0.1$, $c'=0.45$, and $c''=0.05$, with different initial points.

Case II: $c'-b'+c''>c-b$ and $b'<0$ ----- Resistance is less advantageous but it simultaneously brings costs for infanticidal males. In this case, t decreases when resistant females are common, but increases when rare. On the other hand, p always increases. The final result is that (p, t) approaches (1,1) as the same in case I (see Fig.2b).

Case III: $c'-b'+c''<c-b$ and $b'>0$ ----- Resistant females are more advantageous than obedient females for infanticide, and infanticidal males can obtain benefits even when their mates are resistant females. When t is small, p increases due to the warning costs of resistant females. As t increases, p comes to decrease, and (p, t) approaches (0,1), contrary to cases I and II (see Fig.2c).

Case IV: $c'-b'+c''<c-b$ and $b'<0$ ----- Resistance is more advantageous only when infanticidal males common, and Infanticide is more advantageous only when obedient females are common. In this case, trajectories go around an equilibrium point represented by equation (5), as suggested by the boundary analysis. Numerical calculations have shown that the *EP* is always weakly unstable, i.e., starting near an *EP*, the trajectory makes circles with its radius increasing gradually. An example is shown in Fig. 2d. Finally, the trajectory come to pass close to the boundary, and its period to complete one circle becomes enormously long.

In addition, we examined cases where a small number of males and females with equal genotype frequencies immigrate into the population in each generation. When the immigration rate is very small, trajectories approach a closed circle near the boundary, i.e., a limit cycle. An example is shown in Fig.3a where the immigration rate is 0.0001 per population size, and $b=0.2$, $c=0.5$, $b'=-0.2$, $c'=0$, $c''=0.05$, and $r=0.5$. In this case, the linkage disequilibrium D also fluctuated between 0.001 and 0.004. When the immigration rate is larger, the *EP* becomes stable and the final state is coexistence of the four genotypes. An example is shown in Fig.3b, where the immigration rate is 0.001, ten times as large as in Fig.3a. In this case, D approached a constant value of 0.007. Low magnitude of immigration rates (such as less than 0.001) did not change remarkably the results in cases I, II, and III, except that the *SEP* on the boundary move inside slightly.

In the case of no warning costs ($c''=0$), the effect of linkage disequilibrium was nearly analogous to those in the case of positive warning costs ($c''>0$). For cases I and III, the trajectories inside the boundaries are almost the same, except that all points on the t=0 axis

are equilibrium points (see Fig.4a, c). For case II, the final goals are different, depending on initial points, that is, there is a separatrix (Fig.4b). Starting from one side of the separatrix, trajectories approach a stable equilibrium point $(p,t)=(1,1)$, and starting from the other side, trajectories approach the $t=0$ axis. This case is somewhat interesting because either of two populations, infanticidal males with obedient females and non-infanticidal males with a mixture of resistant and obedient females, can occur in the same environmental condition. For case IV, trajectories starting from points inside the boundary always approach the $t=0$ axis finally, although the infanticidal trait may increase temporarily when the resistant trait is rare.

Above mathematical and numerical analysis shows that the evolutionary process is determined mainly by parameter values of costs and benefits. The number of broods per female n has influence only on the rate of evolution when measured by per generation. The recombination rate r has influence on the transient pass substantially only when initial values of the linkage disequilibrium are large. In conclusion, when we observe that the obedient trait is common among females in a population, the fact must be attributed to the lower costs of obedience than costs of resistance (case I or II), or to a transient state in a long cycle of male and female traits (case IV when $c''>0$).

DISCUSSION

In the model, we have assumed, for simplicity of explanation, that the reproductive male in a group is always replaced by another male after the females reproduce. This assumption can be relaxed so that

the male is replaced with a probability k. In this case, the model holds in the original formulation if all of b, c, b', c', and c'' are multiplied by k. Thus, inequalities classifying Cases I, II, III, and IV in the previous section holds for arbitrary values of k.

Actually, the frequency of male replacement will have correlation to the number of females in a group, because the reproductive male can hardly sustain a big group for a long time and the number of bachelors aiming replacement must be large when one male monopolizes many females. The group size may thus have indirect influence. Another more influential effect of the group size may be to reduce the resistant costs c' and c'' if females in a group resist infanticide cooperatively. Such cooperative resistance has been observed in some primate populations (Hrdy, 1977; Sommer, 1987).

Infanticide itself have been frequently observed in recent years (Hiraiwa-Hasegawa, 1988), but none of the observations are unfortunately sufficient for the costs and benefits to be analyzed under full quantitative data. We will, however, apply our model for data on hanuman langurs (*Presbytis entellus*) at Dharwar, India (Sugiyama, 1965), and try to estimate parameters in the model. The main purpose of this attempt is not only to show that the data and observations are explainable by our model, but also to demonstrate the method of how the model can be applied for future better data.

The hanuman langurs at Dwarwar constitute typical single-male groups (Sugiyama, 1965). The reproductive schedule of mature females is represented in Fig.5 where conception, birth, and weaning are represented by C_i, B_i, and W_i, respectively. The conception period, the suckling period and the time from weaning to next conception are estimated as 6.5, 13, and 4.5 months, respectively, and thus inter-birth

interval is 24 months. Although the population consists of overlapping generations and the birth time of females is not synchronous as the assumptions in the model, we try to estimate parameter values of costs and benefits rather forcingly as follows. When the replacing male is non-infanticidal, the offspring of the female grows uneventfully. When the male is infanticidal, unweaned infants of obedient females are killed but weaned infants are not. Even if the replacement occurs during conception, the infants assumed to be killed at their birth. Assuming that the male replacement occurs randomly during 24 months of one reproductive period, the probability that an infant is killed by the infanticidal male is $(6.5+13)/24=0.81$. We put this value as the costs of an obedient female, c. Obedient females mate with the infanticidal male and conceive new infants immediately after the infanticide. Females carrying weaned infants also mate immediately with the infanticidal males. Thus, the time of next birth is advanced, when the number of advanced months are dependent on the timing of the male replacement. In Fig. 5, those are shown and the average advanced months are calculated as $17.5\times(6.5/24)$ + $(17.5+0)/2\times(17.5/24)=11.12$. This advance of the birth time can increase the opportunity that the female, as well as the infanticidal male, produce more offspring in future. We put the ratio of this value to one reproductive period, $11.12/24=0.46$, as the benefits of an obedient female, b. Because $b=0.46>0$ and $c-b=0.81-0.46=0.35>0$, infanticide in this case is advantageous to males and not to females as assumed in the model.

Estimation of costs and benefits of resistant females is more difficult because most females seem to be obedient for infanticide. Actually, unweaned infants of most females are killed within half a

month. But, a female could escape from infanticide over one month. Regarding this female as a resistant female, we assume tentatively that resistant females can resist infanticide for 1.2 months. Then unweaned infants who will wean in less than 1.2 months are not killed, and c' is took as $(6.5+13-1.2)/24 =0.76$. The next conception of resistant females is delayed, compared with that of obedient females, due to the resistance for infanticide. The delay after infanticide is took as about 2.4 months, and then the total delay is $1.2+2.4=3.6$ months. The advance of the next conception of a resistant female corresponds to b' in the model. Thus $b'=b-3.6/24=0.46-0.15=0.31$. We put also $c''=0$ because the warning costs in this case is assumed to be not so severe.

The estimated parameter values correspond to case I in the model because $c'-b'+c''=0.45 > c-b=0.35$ and $b'=0.31 > 0$. Although the real situation does not fit exactly for assumptions of the model and the estimated parameter values are also inaccurate, we still consider the estimation is not so unreasonable to say that in the hanuman langurs at Dharwar, obedient females are more advantageous than resistant females and infanticidal males than non-infanticidal males. Of course, more extensive observational researches are required to make the suggestion conclusive.

Although infanticide has been often observed in many species (Hiraiwa-Hasegawa, 1988), the phenomenon is not common among general primates. When sexual activity is constrained by seasonality, and females do not resume receptivity until the following mating season such as *rhesus macaques*, there would be little reproductive gain ($b \approx 0$) for a male who killed an infant (Hrdy, 1979). Even if infanticide is advantageous for males ($b > 0$), resistant females will

suffer from less costs than obedient females (c'-b'+c'' < c-b) unless the sexual dimorphism of body size is extremely large. If cooperative resistance of females are made as observed in several primates (Hrdy, 1977; Sommer, 1987), this condition is easier to be satisfied. When infanticide still benefits for males (b'>0) instead of the female's successful resistance, the result is conflict between males and females. This situation corresponding to case III seems to be most prevailing situation in primates and other animals living in single-male or multi-male groups. If infanticide brings the loss for the infanticidal males by female's resistance (b'<0), the result may be a periodic fluctuation of different traits of males and females (case IV when c''>0). The period becomes enormously long if the population is perfectly isolated from other populations or migration rates between populations are very low. In the example in Fig.3a, the period of one cycle is about 600 generations. The phenomenon that frequencies of infanticide are different between populations in the same species (Hrdy, 1979) might be reasoned by an explanation that we observe different phases of analogously fluctuating cycles.

Hausfater (1984) discussed the condition of evolution of infanticide with a special reference to data of langurs at Jodhpur, India (Vogel and Loch, 1984). The analysis is based upon a model (Chapman and Hausfater, 1979) where fitnesses of males are frequency-dependent: non-infanticidal males may be more advantageous than infanticidal males in the population with most males being infanticidal. This depends on the key assumptions that the tenure period of reproductive males has a rigid constant value, that females do not abort, and that infanticidal males never kill new-born infants who were fetuses at the time of take-over. The model can thus explain

coexistence of infanticidal and non-infanticidal males in Jodhpur's population, but the assumptions are doubtful at least for us. Actually, several cases of abortion after male replacement have been reported in the more recent paper about the Jodhpur population (Sommer, 1987). Although counterstrategies of females are took into consideration in the model, coevolution of male and female traits is not. In our view, other various explanations are possible for the existence of the male dimorphism. For example, males may conduct infanticide conditionally, depending on ages of infants and/or their own expected tenure period. Our model also gives stable coexistence of infanticidal and non-infanticidal males in case IV with warning costs and migration. We regard that more investigations are necessary before giving any conclusion to the coexistence.

In our model, we take direct resistance for infanticide as a strategy of females. Another counterstrategy of females for male infanticide will be abortion of fetuses in advance when the new-born infants have a high probability of suffering infanticide after their birth. Our model can apply also for this case if traits O and R are took as the aborting and non-aborting traits. Then c is the loss of offspring due to the abortion and b the increase in future reproduction, and c' is the loss from infanticide and b' the future reproductive gain when a female does not abort. Coevolution of the male infanticidal trait and the female aborting trait can be thus treated in the framework of the present model.

Theoretical researches on problems about coevolution of male and female traits has been intensively made recently. The haploid two-locus model as used here was powerful in every case for its simplicity. In the problem of evolution of a male trait which reduces own

survivorship but appeals more to females, the model suggested that the final result is dependent on initial states (Kirkpatric, 1982). In other words, a one-dimensional set in the space of male and female traits is the stable equilibrium of coevolution, with every point on the set being equivalent. Application of another model of quantitative genetics for the same problem gives almost the same but slightly different result: there is a one-dimensional equilibrium set but it may be either stable or unstable (Lande, 1981). On the evolution of infanticide, our model gives a result that there is no inside equilibrium, or if any, it is only one point and the point is unstable. The analysis by the quantitative genetics model will be useful to test the robustness of the present haploid two-locus model.

LITERATURE CITED

CHAPMAN, M., AND G. HAUSFATER. 1979. The reproductive consequences of infanticide in langurs: A mathematical model. Behav. Ecol. Sociobiol. 5:227-240.

HAUSFATER, G. 1984. Infanticide in langurs: Strategies, counterstrategies, and parameter values, pp.257-281. *In* G. Hausfater and S.B. Hrdy (ed.), Infanticide: Comparative and evolutionary perspectives, Aldine Publishing, N.Y.

HAUSFATER, G., AND S.B. HRDY. 1984. Infanticide:Comparative and Evolutionary Perspectives. Aldine Publishing, N.Y.

HIRAIWA-HASEGAWA, M. 1988. Adaptive significance of infanticide in primates. Trends in Ecology & Evolution 3:102-105.

HRDY, S.B. 1977. The Langurs of Abu. Harvard Univ. Press, Cambridge, Mass.

—————————.1979. Infanticide among animals: A review, classification, and examination of the implications for the reproductive strategies of females. Ethol. Sociobiol. 1:13-40.

—————————. 1981. The Woman That Never Evolved. Harvard Univ. Press, Cambridge, Mass.

ITô, Y. 1987. Animal Societies. Tokai Univ. Press, Tokyo, Japan (in Japanese).

KIRKPATRIC, M. 1982. Sexual selection and the evolution of female choice. Evolution 36:1-12.

—————————. 1985. Evolution of female choice and male parental investment in polygynous species: the demise of the "sexy son". Amer. Natur. 125:788-810.

—————————. 1986. The handicap mechanism of sexual selection dos not work. Amer. Natur. 127:222-240.

LANDE, R. 1981. Models of speciation by sexual selection on polygenic traits. Proc. Natl. Acad. Sci. USA 78:3721-3725.

POMIANKOWSKY, A. 1987. The costs of choice in sexual selection. J. theor. Biol. 128:195-218.

SEGAR, J., AND R. TRIVERS. 1986. Asymmetry in the evolution of female mating preferences. Nature 319:771-773.

SOMMER, V. 1987. Infanticide among free-ranging langurs (*Presbytis entellus*) at Jodhpur (Rajasthan/India): Recent observation and a reconsideration of hypotheses. Primates 28:163-197.

STRUHSAKER, T.T., AND L. LELAND. 1987. Colobines: Infanticide by adult males, pp.83-97. *In* B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham, and T.T. Struhsaker (ed.), Primate Societies, Univ. Chicago Press, Chicago.

SUGIYAMA, Y. 1965. On the social change of hanuman langurs (*Presbytis entellus*) in their natal condition. Primates 6:381-418.

VOGEL, C., AND H. LOCH. 1984. Reproductive parameters, adult-male replacements, and infanticide among free-ranging langurs (*Presbytis entellus*) at Jodhpur (Rajasthan), India, pp.237-255. *In* G. Hausfater and S.B. Hrdy (ed.), Infanticide: Comparative and evolutionary perspectives, Aldine Publishing, N.Y.