



Uncertainty of Paternity Can Select Against Paternal Care

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NOTES AND COMMENTS

UNCERTAINTY OF PATERNITY CAN SELECT
AGAINST PATERNAL CARE

Trivers (1972) proposed that uncertainty of paternity would favor male desertion. This hypothesis was later criticized by Maynard Smith (1978) on the ground that, if a male is uncertain of his paternity in the current batch of young, he is equally uncertain of his paternity in the future young. In other words, if the current reproductive success of a male is reduced by uncertainty of paternity, then the future reproductive success of the male is reduced by exactly the same factor. Therefore uncertainty of paternity alone cannot select against paternal care. With the same, but perhaps independent, reasoning, Krebs and Davies (1987) reached the same conclusion. I will demonstrate in this note that this reasoning, insightful as it seems, is fallacious.

In order to show the fallacy in Maynard Smith (1978) and Krebs and Davies (1987), let me represent their reasoning in symbolic form. Suppose there is an avian species in which females always provide maternal care to their young of fixed clutch size of w (same as in Maynard Smith 1977). Denote by P_2 and P_1 the probabilities of young's surviving to adulthood with and without paternal care, respectively ($P_2 > P_1$). If a male deserts, then he can mate n extra times ($n > 0$). Let P_c be certainty of paternity, which is defined as the probability of a male's fathering the offspring produced by a female that the male has mated with ($0 \leq P_c \leq 1$). Given these assumptions, a paternal male and a deserting male will have equal fitness if

$$0.5 \times w \times P_2 \times P_c = 0.5 \times w \times P_1 \times (1 + n) \times P_c, \quad (1)$$

where the term on the left side of equation (1) is the fitness of the paternal phenotype and the term on the right is the fitness of the deserting phenotype. Canceling out identical terms, we have

$$P_2 = P_1 \times (1 + n), \quad (2a)$$

or

$$P_1 = P_2 / (1 + n). \quad (2b)$$

Evidently, P_c , which is found on both sides of equation (1), cancels out; that is, P_c does not play any role in determining whether a male should provide paternal

care. This is the reasoning that leads Maynard Smith (1978) and Krebs and Davies (1987) to conclude that uncertainty of paternity alone does not select against paternal care. The reasoning is correct as long as P_c is a constant, no matter what specific value P_c takes between 0 and 1.

But P_c is not a constant by definition. The uncertainty of paternity implies not that P_c is some specific value less than 1, but that P_c is a random variable varying between 0 and 1, with its own mean (\bar{X}) and variance (σ^2). This makes a difference because now a paternal male and a deserting male will have equal fitness only if

$$P_2 \times P_{c1} = P_1 \times P_{c1} + P_1 \times P_{c2} + \dots + P_1 \times P_{cn+1}, \quad (3)$$

or

$$P_2 \times P_{c1} = P_1 \times (P_{c1} + P_{c2} + \dots + P_{cn+1}). \quad (4)$$

If $P_{c1} = P_{c2} = \dots = P_{cn+1}$, then equation (4) is reduced to equation (2). But now that P_c is a random variable, not a constant, equations (4) and (2) are no longer the same. The difference between equations (2) and (4) can be seen by substituting P_1 with $P_2/(1+n)$ (see eq. [2b]) into equation (4). Now we have

$$P_2 \times P_{c1} = \frac{P_2}{(n+1)} \times (P_{c1} + P_{c2} + \dots + P_{cn+1}), \quad (5)$$

or

$$P_2 \times P_{c1} = P_2 \times \frac{(P_{c1} + P_{c2} + \dots + P_{cn+1})}{(n+1)}. \quad (6)$$

Now it becomes clear that the equation no longer holds because P_{c1} , which is a single value sampled from the distribution of $P_c(\bar{X}, \sigma^2)$, is not the same as

$$\frac{(P_{c1} + P_{c2} + \dots + P_{cn+1})}{(n+1)},$$

which is the arithmetic mean of $(n+1)$ values sampled from the distribution of $P_c(\bar{X}, \sigma^2)$. The term on the right of equation (6) and the term on the left have the same arithmetic mean, but the one on the right is $(n+1)$ times less variable than the one on the left. Because mean fitness of a gene over N generations is the geometric mean (Gillespie 1977, and literature cited therein), not arithmetic mean, over these N generations, the paternal gene loses in a finite population because of greater fluctuation of its fitness over generations. Readers not familiar with selection for reduced fluctuation of fitness over time should consult Seger and Brockmann (1987, and literature cited therein).

I should emphasize here that the above cost for the paternal gene decreases with increasing population size, for the following reason. Although fitness over many generations should be measured by the geometric mean, it is not the geometric mean fitness of individual genes but instead is the geometric mean of mean fitness averaged in each generation over all individuals of the same genotype. For purpose of illustration (which implies the use of simplifying assumptions that I do not intend to defend), suppose that a paternal gene will have a fitness variance

of σ^2 over many generations and that a deserting male will always mate with n females so that the deserting gene will have a fitness variance n times smaller than that of the paternal gene (i.e., σ^2/n). Given this, the difference in fitness variance between that particular paternal gene and that particular deserting gene is

$$D_{\sigma^2} = \sigma^2 - \sigma^2/n = \sigma^2 \times (n - 1)/n. \quad (7)$$

When there are N copies of the paternal gene and N copies of the deserting gene in the population, then the variance of both genotypes is reduced by N and the difference in fitness variance between the paternal genotype and the deserting genotype becomes N times smaller; that is,

$$D_{\sigma^2} = \sigma^2/N - \sigma^2/(nN) = \sigma^2 \times (n - 1)/(nN). \quad (8)$$

Apparently, for very large populations, the cost of being paternal due to uncertainty of paternity becomes trivial. This is a case in which an individual copy of the paternal gene has a lower longtime fitness than an individual copy of a deserting gene, but an infinitely large "population" of the paternal gene would have the same longtime fitness as a population of the deserting gene. This has two implications. First, a mutant deserting gene has little selective advantage, in terms of reduced fitness variance, in invading a large population of the paternal gene. Second, males in a large population are more likely paternal than those in a small population, everything else being equal.

In summary, uncertainty of paternity increases fitness variance of the paternal gene relative to the deserting gene and therefore can select against paternal care, but this effect decreases rapidly with increasing population size. Thus, Trivers's (1972) assertion (but not his reasoning) that uncertainty of paternity can select against paternal care appears to be correct, although the cost of being paternal due to uncertainty of paternity may be trivial in a large population.

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