Paternity and the Evolution of Male Parental Cace

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It is generally believed that level of paternity (the proportion of zygotes in a brood that were fertilized by the male providing parental care) has an important role in the evolution of parental care. We have used population genetics models to investigate this role. The models indicate that *only in mating systems where a parental male "sacrifices" promiscous matings can paternity influence the evolution of male parental care.* This is because level of paternity can reflect the number of opportunities for these promiscuous fertilizations. For example, high paternity can mean few opportunities and therefore a low cost for paternal care.

Certain behaviors may preadapt a species for the evolution of male parental care because they decrease the costs of providing care. For example, in fish species where male care has evolved from spawning territories, the very establishment of territories may have precluded males from gaining promiscuous matings, thereby eliminating the promiscuity costs and facilitating the evolution of care. Without a promiscuity cost, level of paternity will not have influenced the evolution of male care in fishes.

Because paternity has limited influence in the evolution of male care, differences in reliability of parentage between males and females are unlikely to explain the prevalence of female care. Our analysis suggests that paternity differences between species cannot serve as a general explanation for the observed patterns of parental care behavior.

1. Introduction

Parental care, defined here as investment into offspring after fertilization, is commonly shown by males in fishes, amphibians and birds, but rarely in mammals, invertebrates and reptiles (Breder & Rosen, *1966;* Salthe & Mecham, *1974;* Lack, *1968;* Kleiman, *1977;* Milne & Milne, *1976;* Wilson, *1975;* Fitch, *1970;* Pooley & Gans, *1976).* There has been considerable recent interest in the evolution of male care in these groups (e.g. Trivers, *1972;* Williams, *1975;* Dawkins & Carlisle, *1976;* Maynard Smith, *1977,*

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1978; Ridley, 1978; Perrone & Zaret, 1979; Gross & Shine, 1979): One factor of possible importance is the genetic relatedness between a male that provides parental care and the brood receiving that care. This is a special case of Hamilton's (1964) kinship theory, in which the fitness accruing from an act depends on the resulting benefits (here, increased zygote survival), costs (e.g. lost opportunities for additional matings, decreased male survivorship), and the relatedness of the participants. It has variously been termed "confidence of paternity" (Alexander, 1974; Perrone & Zaret, 1979), "certainty of paternity" (Trivers, 1972; Maynard Smith, 1978; Ridley, 1978), and "reliability of paternity" (Gross & Shine, 1979).

In general, a male of a given reproductive strategy in a population of animals will have an *average level of genetic relatedness* to the offspring resulting from a mating in which he participates. Several factors determine this level of relatedness. For example, if sperm competition occurs (Parker, 1970) the relatedness between a male and the offspring from a female he has inseminated may be quite low. At the same time, the occurrence of sperm competition can simultaneously *increase* the number of matings from which the male is likely to father at least some offspring. This is a condition of low reliability of paternity (henceforth, "low paternity"). For the problem of paternal care evolution, we define paternity as the *proportion of zygotes in a brood that were fertilized by the male providing parental care.* In the above example, a male showing parental care after mating contributes to the survivorship of genetically unrelated zygotes in addition to his own; and with lower paternity, fewer of the offspring receiving care are fathered by the parental male. Defined in this manner, paternity can vary on a scale from 0 to 1, ranging from a condition in which none of the brood belong genetically to the parental male to where all the brood are genetic offspring.

The concept of paternity has been appealing to biologists and several authors have applied paternity as an explanation for patterns of parental care evolution (e.g. Barash, 1977; Ridley, 1978; Loiselle & Barlow, 1978; Perrone & Zaret, 1979; Alexander *et al.,* 1979). The general argument is that animal groups or breeding systems in which males face low paternity, will not evolve parental care. However, there is some question as to whether paternity can play a role. Gross and Shine (1979) have tested predictions from a paternity model against patterns of care in fishes and amphibians, and found little correspondence. Maynard Smith (1978) has argued that since low paternity will, on average, have an equal effect on all matings, paternity should not be an influence on whether a male deserts his brood.

This paper is an attempt to clarify the theoretical importance of paternity in the evolution of male parental care, from the ancestral condition of no parental care. The results from a few simple models indicate that paternity

can influence male parental care evolution, but only under conditions which are probably too restrictive to make paternity a general explanation for patterns of paternal care.

2. Models and Discussion

Our models are based on the evolutionarily stable strategy (ESS) technique discussed by Maynard Smith (1976) (see also Parker, 1978). A rare (low frequency) gene coding for a particular trait is mathematically introduced into a population not showing that trait, and under specified conditions it is determined whether or not the trait will increase in frequency. The conditions are then examined for the maintenance of the trait when common. Here we are interested in the trait of male parental care (MPC) and if its evolution is sensitive to degree of paternity.

There are three major variables to be considered: (1) the survival of zygotes receiving care relative to those without care (this is a measure of benefit to the parental behavior); (2) the cost to the parental male from providing care measured as the number of zygotes fertilized relative to those fertilized by nonparental males; and (3) the genetic relatedness or paternity of the parental male to the zygotes for which he provides care.

Maynard Smith (1978) has presented a reasoned argument for why paternity should be irrelevant in the evolution of male parental care. When paternity is equivalent for all matings independent of care behavior, then paternity will not itself effect selection for care. Our investigations of models indicate that the evolution of MPC is sensitive to assumptions about the nature of the mating system, and in particular the type of cost accrued by a parental male. We have found that some of these costs are influenced by degree of paternity, and therefore paternity may be important to care evolution in such situations. To show this, we first develop a model with specific assumptions about the mating system and then derive a more general model from which conclusions about paternity can be drawn.

(A) THE TERRITORIAL-MALE MODEL

Imagine an externally-fertilizing species with males establishing breeding territories in which females deposit eggs. By "territory" we mean a spatial site from which a resident male attempts to exclude nonspecific males. Males gain fertilizations both within their territory and, through sperm competition, in the territories of other males. Now suppose there is a rare dominant gene in the population, "A", which causes its male bearers to provide parental care. "Aa" males will provide care to the eggs in their territory, and

"aa" males will not (we can ignore "AA" males because they are, at least at first, extremely rare). Those zygotes receiving care have an increased survival relative to those not receiving care, but the parental males potentially suffer a fertilization cost because of providing care. This cost may affect the number of eggs a male fertilizes within his own territory (termed, "territory cost"), and/or the number he fertilizes outside his territory ("promiscuity cost"). This distinction of costs within vs. outside the parental male's territory is important because males may provide care to eggs within their territory but never to those outside.

In this mating system the conditions for the increase of a rare gene for MPC exist when the mean fitness of the "Aa" genotype is greater than that of the "aa" genotype,

$$W_{Aa} > W_{aa}$$

Let T = number of eggs in the territory of a non-parental male, $K \cdot T$ = number of eggs in the territory of a parental male, p = (paternity) the proportion of eggs in a male's territory which he actually fertilizes (let this be equal for parentals and non-parentals) S = survival of zygotes receiving care/survival of zygotes not receiving care, $C_n \cdot T$ = number of eggs fertilized by a non-parental male, outside of his territory, $C_r \cdot T$ = number of eggs fertilized by a parental male, outside of his territory. It follows from (1) that the conditions for the increase of MPC are,

$$TKSP + TC_r > TP + TC_n. \qquad (2)$$

Because "Aa" males are relatively rare, they have no significant effect upon the total number of fertilizations that males receive outside their territories. Therefore, the average number of fertilizations that a non-parental "aa" male receives outside his territory must be equivalent to what he loses within his territory. Hence,

$$C_n = 1 - P. \qquad (3)$$

Substituting for C_n and then solving for P gives,

$$P > \frac{1 - CP}{KS}. \qquad (4)$$

Notice that the territorial male has a specific paternity (P) towards the eggs within his territory, but that the model does not assign a paternity for matings the male receives outside his territory. A male's paternity to offspring of promiscuous matings may or may not be the same as his paternity to offspring within his own territory. Since the number of fertilized eggs a non-parental male receives outside his territory is 1-P, his average

paternity in promiscuous matings (P*) must vary inversely with the number of promiscuous matings (N) he receives, such that $P^*N = 1 - P$. Since P* and *N* do not affect the results of the models, they have not been included.

Parental care costs are represented by two terms in equation (4). *K* is the number of eggs that a parental male receives in his territory relative to those in the territory of a nonparental male. If *K < 1*, then there is a "territory cost". This might occur in several ways: (i) if parental males are less likely to survive to future reproductive periods because of the care they provide; (ii) if they are weaker, smaller, etc. in later reproductive periods, relative to nonparental males, and hence less attractive to females; (iii) if the time and energy required for care detracts from the time and energy other males are putting into courtship.

Secondly, a "promiscuity cost" is represented in the C, term, and occurs if C, < 1- P. The formula is somewhat more complicated because C, need not be independent of paternity (P). Exactly how C, varies with paternity depends upon the mating system. For example, when the paternity of nonparental males is low, the opportunities for promiscuous matings may be high. Alternatively, C, may be independent of paternity. This could occur if care giving prevented a male from garnering promiscuous matings outside of the territory, such that C, equals zero.

Equation (4) shows that MPC is likely to incrc ·⁻- when rare if (i) parental care greatly increases offspring survivorship (S); kii) territory costs (1-K) and promiscuity costs are small (C, is large); and (iii) paternity (P) is high. Notice, however, without any promiscuity cost (i.e. C, = C,, =1-P) the formula simplifies to,

$$KS > 1. \tag{5}$$

The important result here is if a parental male does not lose fertilizations outside of his territory, paternity will not play a role in the evolution of MPC. Conversely, *when there is a cost in promiscuous fertilizations, paternity can play a role in the evolution of* MPC. To illustrate, if the parental male receives *no* promiscuous fertilizations (i.e. C, = 0), then for parental care to evolve the following condition must be satisfied;

$$\mathbf{P} > \frac{1}{KS}$$

This relationship is shown in Fig. 1. Paternity could play a significant role in the evolution of MPC over moderate values of KS.

Once MPC *has* evolved, what are the conditions for its maintenance? Suppose males provide parental care and there arises in the population a dominant gene for being nonparental ("B"). Now "bb" males are parental,
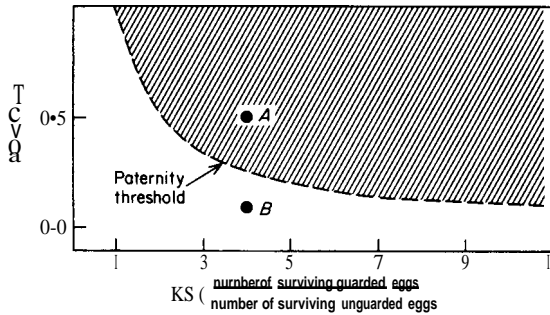
FIG. 1. Threshold for the evolution of parental care when the cost of care is no promiscuous matings $(C_p = 0)$ and territorial males do all the cuckolding. Populations exceeding the Paternity threshold will be selectively favored to show paternal care. The Fig. indicates that two populations (A and B) in which individuals derive similar benefits and suffer similar costs will differ in the evolution of MPC because of different degrees of paternity. Here A will evolve paternal care and B will not.

"Bb" males are nonparental, and "BB" males are too rare to warrant consideration. MPC will be maintained when,

$$TKSP + TKSC, > TP + TKSC, \qquad (7)$$

(where C, and C_n are redefined as relative to the clutch size of a parental male). In this case the parentals are the common genotype and $C_, = 1\text{-}P$. Substituting,

$$P < KS (1 - C_n). \qquad (8)$$

Here low paternity will favor maintenance of MPC, a rather unintuitive result. The range where paternity could be important is rather limited. If $C_n > 1$, then the nonparentals will invade regardless of P. This is equivalent to saying that a nonparental receives more fertilizations outside his territory than a parental receives in total. At the other extreme, when $C_n < (KS\text{ -}1)/KS$, a MPC strategy cannot be invaded. One could imagine that once MPC has evolved, KS will increase because (i) parental males should become more behaviorally proficient at providing care, (ii) offspring will become more dependent upon this care, and (iii) females may favour males which provide care. These factors would further stabilize MPC.

When there is no promiscuity cost $(C_n = 1\text{-}P)$, paternity drops from the equation and becomes irrelevant to MPC maintenance. That is, a promiscuity cost is necessary if paternity is to play a role in the maintenance of MPC.

(B) MULTI-MALE STRATEGY MODEL

In the previous model we had assumed that all males have territories. It is easy to imagine that some males might be favored by natural selection to not develop territories, but instead concentrate upon sneaking fertilizations in the territories of other males. Simply, a male will be favored to do so when he can gain more by that strategy than by being a parental. This could occur for individual males who were (i) unattractive to females, (ii) relatively less able to exclude males from cuckoldry, or (iii) less able to provide care. Such conditions may exist in species where the factors above are age, size, or health dependent. Small, young or unhealthy males may then be favored to pursue the "sneaker" strategy. For instance, "cuckolding" males exist in the fish *Lepomis macrochirus* (Gross, 1979), and they are invariably smaller than parental males, do not establish territories, and show colour patterns and behaviors which aid their sneaking into the territories of parental males (Gross, in prep.).

In the Territorial-Male model the fitness of the common genotype was independent of paternity because what the males lost to cuckoldry they equally gained from the territories of others. In systems with sneakers, or any alternative male strategies which preclude providing care, this will no longer be true since sneakers could account for a significant proportion of the cuckolding.

What are the conditions for the increase of a rare gene for MPC ("A") in a mixed population of both nonparental males and sneakers? If we assume that becoming a sneaker is independent of the "A" genotype (e.g. sneaking may be a size related strategy), and let Z = proportion of males that are sneakers; W_S = reproductive success of sneakers; $W_{...}$ = reproductive success of nonparental territorial males; W_P, = reproductive success of parental territorial males; then the parental gene will increase when rare if,

$$ZW_s +(1-Z)W_P, >ZW_S +(1-Z)W_{,,,} \tag{9}$$

or

$$W_P, > W_{..} \tag{10}$$

We can therefore disregard the fitness of the sneaker males.

In the simplest case, where sneakers account for all the cuckoldry, then the evolution of care is dependent upon

$$KS > 1. \tag{11}$$

Again, paternity drops from the equation when there is no promiscuity cost to the parental male[t].

The more general formula is

$$KSP + C_p > P + C_{,,}, \tag{12}$$

or

$$P(KS-1) > C_{,t} - C_{p} \tag{13}$$

This formula also gives the conditions for the maintenance of MPC when care is common.

Here it may be useful to introduce the concept of paternity towards promiscuous matings. If $P^* =$ paternity to promiscuous matings and $L =$ the number of promiscuous matings which a parental male loses, then $P^*L = C_{,,} - C_p$. Substituting,

$$\underset{\substack{\text{territory gains} \\ \text{and costs}}}{P(KS\text{-}1)} > \underset{\substack{\text{promiscuity} \\ \text{costs}}}{P^*L} \tag{14}$$

The total fitness a parental male gains from within his territory must be greater than what he loses from promiscuous matings outside his territory.

When a male has equal paternity towards promiscuous matings (P^*) as towards those within his territory (P) and L is a constant, then paternity drops from this equation, as noted in the arguments of Maynard Smith (1978). However, as the previous models have shown, promiscuity costs (P^*L) may actually decrease with increasing paternity, because of decreased opportunities. The maximum value that promiscuity costs can assume when territorial males do all of the cuckolding is the value 1-P. When territorial males do no cuckolding, its minimum value is zero. Figure 2 shows a few reasonable relationships between promiscuity costs and paternity. For example, if territorial males consistently account for a fixed proportion of the cuckoldry, then $P^*L = F(1-P)$, where F is the fraction of cuckoldry going to territorial males. In general, promiscuity costs must decrease with increasing paternity.

From these models can be drawn the following general conclusions.

(i) If there is a promiscuity cost for providing care (loss in fertilizations of zygotes not receiving care), then paternity can be an important factor in the

t This equation also represents the conditions for the evolution of *female* care, where K is the egg production of parental females relative to nonparental females. It has been argued that the lower reliability of parentage faced by males (female parentage is certain) explains the prevalence of female care (e.g. Ridley, 1978; Perrone & Zaret, 1979). The model indicates that when there is no promiscuity cost for male care, the conditions are the same for male care evolution as for female care evolution. Which sex evolves care then becomes a question of ability to invest and cost differences between the sexes.
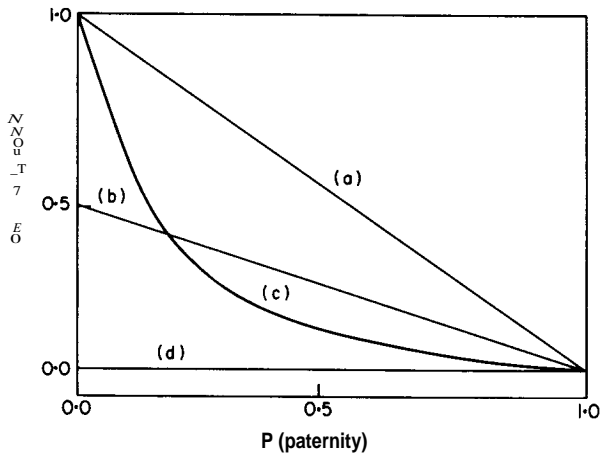
FIG. 2. **Some relationships between "promiscuity costs" and paternity: (a) there exists an upper limit to promiscuity costs where "territorial" males account for all cuckoldry and parentals do not cuckold; (b) costs may be a linearly declining function of paternity when territorial males account for a fixed proportion of cuckoldry and parentals do not cuckold; (c) if male behavior varies with level of paternity then a nonlinear relationship can result; (d) there are no promiscuity costs when territorial males do not cuckold other males.**

evolution of MPC. The larger this cost, the greater the potential importance of paternity.

(ii) The total gain in surviving offspring (KS) in the parental male's clutch must be greater with MPC than without MPC, for MPC to evolve.

(iii) The importance of paternity in the evolution of MPC when there is a promiscuity cost will depend upon the initial increase in offspring survival. The greater this, the less significant is paternity.

(iv) Paternity must be greater than zero, that is, care cannot be dispersed randomly with respect to parentage if MPC is to evolve.

3. General Implications

The models show that there are at least 2 possible consequences of paternity for male parental care evolution; paternity influences (1) the "genetic returns" a male obtains from providing care for a clutch and (2) the "genetic costs" resulting from lost promiscuous matings. The genetic returns *increase* with increasing paternity, but the genetic costs may *decrease* with increasing paternity because promiscuous matings are less available when paternity is high than when it is low. When there is no promiscuous mating cost, paternity will not determine whether or not MPC is selectively favored

$(P(KS -1) > 0)$, but only the *rate* at which the genes for MPC will spread throughout a population. *Only in mating systems where a parental male "sacrifices" promiscuous matings can paternity influence whether MPC is favored by natural selection.*

The hypothetical life-history in the models was fashioned after externally fertilizing fish where males establish spawning territories and attempt to exclude other males during spawning (see Breder & Rosen, 1966). As the models show, the ability of paternity to affect promiscuity costs depends upon the ecology of the mating system. For example, asynchronous spawning may result in a promiscuity cost if parental males remain with the clutch in their territory while non-parentals leave their clutch and attempt to cuckold those males which have attracted females. When spawning is synchronous, a promiscuity cost is less likely since neither parental nor nonparental males would have time to cuckold during the spawning period. Even where asynchronous spawning introduces a promiscuity cost, paternity will not be influential in MPC evolution when the survivorship gains to offspring receiving care are very large (see Fig. 1).

There is sometimes an implicit assumption made that patterns of parental care reflect an evolutionary tradeoff between the sexes (Dawkins & Carlisle, 1976; Perrone & Zaret, 1979). However, since fitness is relative only within a sex (Fisher, 1958), whether one sex evolves care is not dependent upon the advantages or disadvantages to the other sex. The only cases where one sex can be caught in a "cruel bind" by the other sex (Dawkins & Carlisle, 1976) are special cases where both sexes are favored to provide care in the absence but not the presence of the other sex. Such circumstances are much more likely to occur once biparental care has already evolved rather than from a situation of no parental care.

In many fishes, it is probable that MPC has evolved from a mating system where males established spawning territories (Williams, 1975; Loiselle, 1978; Gross & Shine, 1979) in response to female discrimination of oviposition sites. Selection favoring site tenacity and exclusion of conspecific males reduces opportunities for promiscuous matings for all territorial males. In addition, territorial males are probably incidentally providing parental care (since conspecifics are often major egg predators-Loiselle & Barlow, 1978; Ridley, 1978; Gross & MacMillan, 1979) while remaining capable of multiple spawnings. Since there is little promiscuity cost for territorial males, paternity has probably been insignificant in the evolution of MPC in fishes. Further support for this conclusion is that known cuckoldry in some male parental care systems is done by nonparental males pursuing alternative reproductive strategies (Gross, 1979; Gross, in prep.), and that survivorship gains for brood with paternal care can be very large.

The models may be extended to other animals, for instance, birds and mammals. Many species of passerine birds have male territoriality with females laying eggs within the territories (Lack, 1968), and with cuckoldry occurring (Bray *et al.,* 1975). It is not known, however, whether cuckoldry is done by territorial males or nonterritorial "floaters". For mammals in which the males establish territories and are therefore associated with the young (many carnivores, Williams, 1975), or species which live in social groups such as some primates (Clutton-Brock & Harvey, 1977), there can be promiscuity costs for the male providing care if the females mate promiscuously. The establishment of a harem by exclusion of other adult males, as found in some primates (e.g. Patas monkey, Gelada baboon; Struhsaker, 1969), will both increase paternity and decrease opportunities for promiscuous matings because of the continued vigilance required in harem defense. A functional incompatibility between high paternity and promiscuous matings of this sort can create a correlation between high paternity and MPC, but the cause of the relationship may actually be an absence of promiscuity costs.

These examples indicate that certain behaviors can preadapt a species for MPC evolution because they incidentally minimize the costs of providing care, and not because they increase paternity. However, male care behavior will only evolve when there is environmentally induced selection for care, and males are capable of improving brood survivorship.

Variations in paternity within a species can have a significant effect upon male parental behavior. Males are always favored to increase paternity if it increases net reproductive success, whether or not care is provided (e.g. the "passive phase" of some insects-Parker, 1970; extended courtship behavior of some passerine birds-Trivers, 1972). Males which do provide care will be favored to prefer broods with higher paternity over broods with lower paternity (Trivers, 1972; Erickson and Zenone, 1976; Barash, 1977). This will occur whether or not there is a promiscuity cost. However, this argument cannot be extended to paternity variations between species. Many authors (e.g. Perrone & Zaret, 1979; Ridley, 1978; Barash, 1977; Blumer, 1979; Loiselle & Barlow, 1978; Alexander *et al.,* 1979) have argued that high paternity favors the evolution of MPC. They suggest that a correlation between external fertilization and male parental care may result from higher paternity in externally fertilizing species. Our analysis shows that high paternity will favor MPC evolution only in those mating systems where paternity can affect opportunities for promiscuous mating, and there is a promiscuity cost to providing care. It is clear that alternative mating opportunities will be determined by many ecological factors, such as synchrony of matings, dominance hierarchies, breeding density, adult sex ratio,

life span, number of reproductive bouts in a season, alternative male strategies, female promiscuity, etc. These variables probably occur independent of mode of fertilization, undermining any paternity explanation for an external fertilization relationship. Furthermore, in the teleost fishes, which account for a significant proportion of MPC in externally fertilizing species, it is questionable whether parental males suffer any promiscuity cost. The belief that paternity explains broad correlations between external fertilization and MPC can therefore be rejected. A similar conclusion was reached in an extensive analysis of the care patterns of ectothermic vertebrates, by Gross & Shine (1979). Since male care evolution is generally not influenced by the level of paternity, the often cited difference in reliability of parentage between males and females seems an inadequate explanation for the prevalence of female care in internally fertilized species.

In conclusion, although paternity has some theoretical importance for the evolution of MPC due to its relationship to alternative opportunities for matings, it is inadequate as a general explanation for the evolution of care behavior.

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