Parent-Offspring Conflict

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SYNOPSIS. When parent-offspring relations in sexually reproducing species are viewed from the standpoint of the offspring as well as the parent, conflict is seen to be an expected feature of such relations. In particular, parent and offspring are expected to disagree over how long the period of parental investment should last, over the amount of parental investment that should be given, and over the altruistic and egoistic tendencies of the offspring as these tendencies affect other relatives. In addition, under certain conditions parents and offspring are expected to disagree over the preferred sex of the potential offspring. In general, parent-offspring conflict is expected to increase during the period of parental care, and offspring are expected to employ psychological weapons in order to compete with their parents. Detailed data on mother-offspring relations in mammals are consistent with the arguments presented. Conflict in some species, including the human species, is expected to extend to the adult reproductive role of the offspring: under certain conditions parents are expected to attempt to mold an offspring, against its better interests, into a permanent nonreproductive.

In classical evolutionary theory parent-offspring relations are viewed from the standpoint of the parent. If parental investment (PI) in an offspring is defined as anything done by the parent for the offspring that increases the offspring's chance of surviving while decreasing the parent's ability to invest in other offspring (Trivers, 1972), then parents are classically assumed to allocate investment in their young in such a way as to maximize the number surviving, while offspring are implicitly assumed to be passive vessels into which parents pour the appropriate care. Once one imagines offspring as *actors* in this interaction, then conflict must be assumed to lie at the heart of sexual reproduction itself—an offspring attempting from the very beginning to maximize its reproduc-

tive success (RS) would presumably want more investment than the parent is selected to give. But unlike conflict between unrelated individuals, parent-offspring conflict is expected to be circumscribed by the close genetic relationship between parent and offspring. For example, if the offspring garners more investment than the parent has been selected to give, the offspring thereby decreases the number of its surviving siblings, so that any gene in an offspring that leads to an additional investment decreases (to some extent) the number of surviving copies of itself located in siblings. Clearly, if the gene in the offspring exacts too great a cost from the parent, that gene will be selected against even though it confers some benefit on the offspring. To specify precisely how much cost an offspring should be willing to inflict on its parent in order to gain a given benefit, one must specify how the offspring is expected to weigh the survival of siblings against its own survival.

The problem of specifying how an individual is expected to weigh siblings against itself (or any relative against any other) has been solved in outline by Hamilton (1964), in the context of explaining the evolution

of altruistic behavior. An altruistic act can be defined as one that harms the organism performing the act while benefiting some other individual, harm and benefit being defined in terms of reproductive success. Since any gene that helps itself spread in a population is, by definition, being selected for, altruistic behavior in the above sense can be selected only if there is a sufficiently large probability that the recipient of the act also has the gene. More precisely, the benefit/cost ratio of the act, times the chance that the recipient has the gene, must be greater than one. If the recipient of the act is a relative of the altruist, then the probability that the recipient has the gene by descent from a common ancestor can be specified. This conditional probability is called the *degree of relatedness*, r_o. For an altruistic act directed at a relative to have survival value its benefit/cost ratio must be larger than the inverse of the altruist's r_o to the relative. Likewise an individual is expected to forego a selfish act if its cost to a relative, times the r_o to that relative, is greater than the benefit to the actor.

The rules for calculating degrees of relatedness are straightforward for both diploid and haplodiploid organisms, even when inbreeding complicates the relevant genealogy (see the addendum in Hamilton, 1971). For example, in a diploid species (in the absence of inbreeding) an individual's r_o to his or her full-siblings is $\frac{1}{2}$; to half-siblings, $\frac{1}{4}$; to children, $\frac{1}{2}$; to cousins, $\frac{1}{8}$. If in calculating the selective value of a gene one not only computes its effect on the reproductive success of the individual bearing it, but adds to this its effects on the reproductive success of related individuals, appropriately devalued by the relevant degrees of relatedness, then one has computed what Hamilton (1964) calls *inclusive fitness*. While Hamilton pointed out that the parent-offspring relationship is merely a special case of relations between any set of genetically related individuals, he did not apply his theory to such relations. I present here a theory of parent-offspring relations which follows directly from the key concept of inclusive fitness and from the assumption that the offspring

is at all times capable of an active role in its relationship to its parents. The form of the argument applies equally well to haplodiploid species, but for simplicity the discussion is mostly limited to diploid species. Likewise, although many of the arguments apply to any sexually reproducing species showing parental investment (including many plant species), the arguments presented here are particularly relevant to understanding a species such as the human species in which parental investment is critical to the offspring throughout its entire prereproductive life (and often later as well) and in which an individual normally spends life embedded in a network of near and distant kin.

PARENT-OFFSPRING CONFLICT OVER THE CONTINUATION OF PARENTAL INVESTMENT

Consider a newborn (male) caribou calf nursing from his mother. The benefit to him of nursing (measured in terms of his chance of surviving) is large, the cost to his mother (measured in terms of her ability to produce additional offspring) presumably small. As time goes on and the calf becomes increasingly capable of feeding on his own, the benefit to him of nursing decreases while the cost to his mother may increase (as a function, for example, of the calf's size). If cost and benefit are measured in the same units, then at some point the cost to the mother will exceed the benefit to her young and the net reproductive success of the mother decreases if she continues to nurse. (Note that later-born offspring may contribute less to the mother's eventual RS than early-born, because their reproductive value may be lower [Fisher, 1930], but this is automatically taken into account in the cost function.)

The calf is not expected, so to speak, to view this situation as does his mother, for the calf is completely related to himself but only partially related to his future siblings, so that he is expected to devalue the cost of nursing (as measured in terms of future sibs) by his r_o to his future sibs, when comparing the cost of nursing with its benefit to himself. For example, if fu-

ture sibs are expected to be full-sibs, then the calf should nurse until the cost to the mother is more than twice the benefit to himself. Once the cost to the mother is more than twice the benefit to the calf, continued nursing is opposed by natural selection acting on both the mother and the calf. As long as one imagines that the benefit/cost ratio of a parental act changes continuously from some large number to some very small number near zero, then there must occur a period of time during which $\frac{1}{2}<B/C<1$. This period is one of expected conflict between mother and offspring, in the sense that natural selection working on the mother favors her halting parental investment while natural selection acting on the offspring favors his eliciting the parental investment. The argument presented here is graphed in Figure 1. (Note, as argued below, that there are specialized situations in which the offspring may be selected to consume *less* PI than the parent is selected to give.)

This argument applies to all sexually reproducing species that are not completely inbred, that is, in which siblings are not
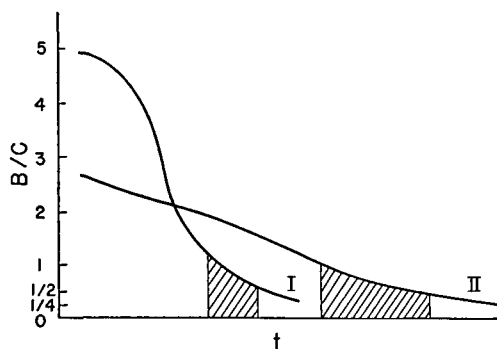

FIG. 1. The benefit/cost ratio (B/C) of a parental act (such as nursing) toward an offspring as a function of time. Benefit is measured in units of reproductive success of the offspring and cost in comparable units of reproductive success of the mother's future offspring. Two species are plotted. In species I the benefit/cost ratio decays quickly; in species II, slowly. Shaded areas indicate times during which parent and offspring are in conflict over whether the parental care should continue. Future sibs are assumed to be full-sibs. If future sibs were half-sibs, the shaded areas would have to be extended until $B/C = 1/4$.

identical copies of each other. Conflict near the end of the period of PI over the continuation of PI is expected in all such species. The argument applies to PI in general or to any subcomponent of PI (such as feeding the young, guarding the young, carrying the young) that can be assigned a more or less independent cost-benefit function. Weaning conflict in mammals is an example of parent-offspring conflict explained by the argument given here. Such conflict is known to occur in a variety of mammals, in the field and in the laboratory: for example, baboons (DeVore, 1963), langurs (Jay, 1963), rhesus macaques (Hinde and Spencer-Booth, 1971), other macaques (Rosenblum, 1971), vervets (Struhsaker, 1971), cats (Schneirla et al., 1963), dogs (Rheingold, 1963), and rats (Rosenblatt and Lehrman, 1963). Likewise, I interpret conflict over parental feeding at the time of fledging in bird species as conflict explained by the present argument: for example, Herring Gulls (Drury and Smith, 1968), Red Warblers (Elliott, 1969), Verreaux's Eagles (Rowe, 1947), and White Pelicans (Schaller, 1964).

Weaning conflict is usually assumed to occur either because transitions in nature are assumed always to be imperfect or because such conflict is assumed to serve the interests of both parent and offspring by informing each of the needs of the other. In either case, the marked inefficiency of weaning conflict seems the clearest argument in favor of the view that such conflict results from an underlying conflict in the way in which the inclusive fitness of mother and offspring are maximized. Weaning conflict in baboons, for example, may last for weeks or months, involving daily competitive interactions and loud cries from the infant in a species otherwise strongly selected for silence (DeVore, 1963). Interactions that inefficient *within* a multicellular organism would be cause for some surprise, since, unlike mother and offspring, the somatic cells within an organism are identically related.

One parameter affecting the expected length (and intensity) of weaning conflict is the offspring's expected r_0 to its future

siblings. The lower the offspring's r_o to its future siblings, the longer and more intense the expected weaning conflict. This suggests a simple prediction. Other things being equal, species in which different, unrelated males commonly father a female's successive offspring are expected to show stronger weaning conflict than species in which a female's successive offspring are usually fathered by the same male. As shown below, however, weaning conflict is merely a special case of conflict expected throughout the period of parental investment, so that this prediction applies to the intensity of conflict prior to weaning as well.

CONFLICT THROUGHOUT THE PERIOD OF PI OVER THE AMOUNT OF PI

In Figure 1 it was assumed that the amount of investment for each day (or moment in time) had already been established, and that mother and young were only selected to disagree over when such investment should be ended. But it can be shown that, in theory, conflict over the amount of investment that should at each moment be given, is expected throughout the period of PI.

At any moment in the period of PI the female is selected to invest that amount which maximizes the difference between the associated cost and benefit, where these terms are defined as above. The infant is selected to induce that investment which maximizes the difference between the benefit and a cost devalued by the relevant r_o. The different optima for a moment in time in a hypothetical species are graphed in Figure 2. With reasonable assumptions about the shape of the benefit and cost curves, it is clear that the infant will, at each instant in time, tend to favor greater parental investment than the parent is selected to give. The period of transition discussed in the previous section is a special case of this continuing competition, namely, the case in which parent and offspring compete over whether any investment should be given, as opposed to their earlier competition over how much should
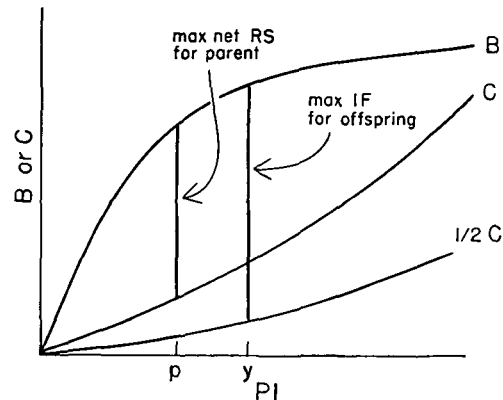

FIG. 2. The benefit, cost, and half the cost of a parental act toward an offspring at one moment in time as a function of the amount the parent invests in the act (PI). Amount of milk given during one day of nursing in a mammal would be an example of PI. At p the parent's inclusive fitness (B - C) is maximized; at y the offspring's inclusive fitness (B - C/2) is maximized. Parent and offspring disagree over whether p or y should be invested. The offspring's future siblings are assumed to be full-siblings. IF = inclusive fitness.

be given. Since parental investment begins before eggs are laid or young are born, and since there appears to be no essential distinction between parent-offspring conflict outside the mother (mediated primarily by behavioral acts) and parent-offspring conflict inside the mother (mediated primarily by chemical acts), I assume that parent-offspring conflict may in theory begin as early as meiosis.

It must be emphasized that the cost of parental investment referred to above (see Fig. 2) is measured only in terms of decreased ability to produce future offspring (or, when the brood size is larger than one, decreased ability to produce other offspring). To appreciate the significance of this definition, imagine that early in the period of PI the offspring garners more investment than the parent has been selected to give. This added investment may decrease the parent's later investment in the offspring at hand, either through an increased chance of parental mortality during the period of PI, or through a depletion in parental resources, or because parents have been selected to make the appropriate

adjustment (that is, to reduce later investment below what otherwise would have been given). In short, the offspring may gain a temporary benefit but suffer a later cost. This self-inflicted cost is subsumed in the benefit function (B) of Figure 2, because it decreases the benefit the infant receives. It is not subsumed in the cost function (C) because this function refers only to the mother's future offspring.

THE TIME COURSE OF PARENT OFFSPRING CONFLICT

If one could specify a series of cost-benefit curves (such as Fig. 2) for each day of the period of PI, then the expected time course of parent-offspring conflict could be specified. Where the difference in the offspring's inclusive fitness at the parent's optimum PI (p in Fig. 2) and at the offspring's optimum PI (y) is large, conflict is expected to be intense. Where the difference is slight, conflict is expected to be slight or nonexistent. In general, where there is a strong difference in the offspring's inclusive fitness at the two different optima (p and y), there

will also be a strong difference in the parent's inclusive fitness, so that both parent and offspring will simultaneously be strongly motivated to achieve their respective optimal values of PI. (This technique of comparing cost-benefit graphs can be used to make other predictions about parent-offspring conflict, for example that such conflict should decrease in intensity with increasing age, and hence decreasing reproductive value, of the parent; see Figure 3.) In the absence of such day-by-day graphs three factors can be identified, all of which will usually predispose parent and offspring to show greater conflict as the period of PI progresses.

1) *Decreased chance of self-inflicted cost.* As the period of PI progresses, the offspring faces a decreased chance of suffering a later self-inflicted cost for garnering additional investment at the moment. At the end of the period of PI any additional investment forced on the parent will only affect later offspring, so that at that time the interests of parent and offspring are maximally divergent. This time-dependent change in the offspring's chance of suffering a self-
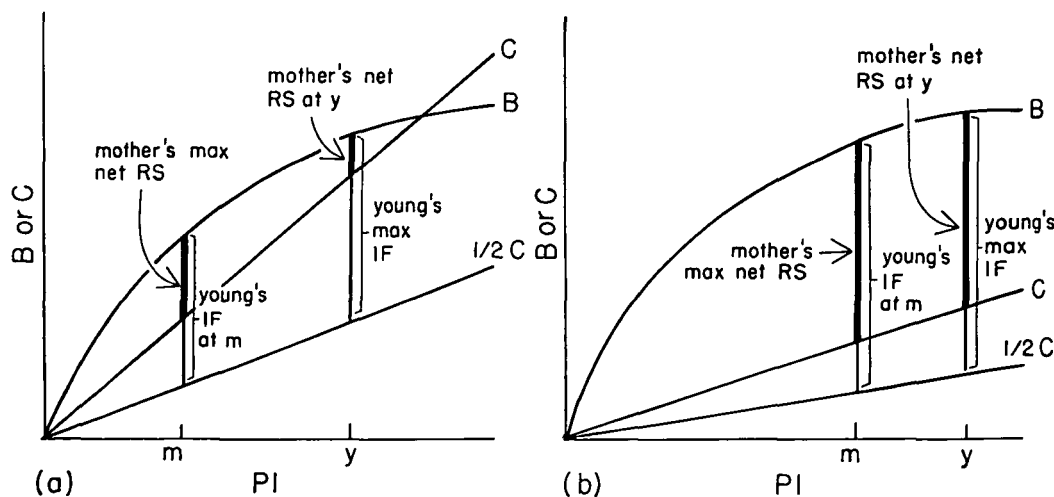

FIG. 3. The benefit and cost of a parental act (as in Fig. 2) toward (a) an offspring born to a young female and (b) an offspring born to an old female. One assumes that the benefit to the offspring of a given amount of PI does not change with birth order but that the cost declines as a function of the declining reproductive value (Fisher, 1930) of the

mother: she will produce fewer future offspring anyway. The difference between the mother's inclusive fitness at m and y is greater for (a) than for (b). The same is true for the offspring. Conflict should be correspondingly more intense between early born young and their mothers than between late born young and their mothers.

inflicted cost will, other things being equal, predispose parent and offspring to increasing conflict during the period of PI.

2) *Imperfect replenishment of parental resources.* If the parent is unable on a daily basis to replenish resources invested in the offspring, the parent will suffer increasing depletion of its resources, and, as time goes on, the cost of such depletion should rise disproportionately, even if the amount of resources invested per day declines. For example, a female may give less milk per day in the first half of the nursing period than in the second half (as in pigs: Gill and Thomson, 1956), but if she is failing throughout to replenish her energy losses, then she is constantly increasing her deficit (although at a diminishing rate) and greater deficits may be associated with disproportionate costs. In some species a parent does not feed itself during much of the period of PI and at least during such periods the parent must be depleting its resources (for example, female elephant seals during the nursing period: LeBoeuf et al., 1972). But the extent to which parents who feed during the period of PI fail to replenish their resources is usually not known. For some species it is clear that females typically show increasing levels of depletion during the period of PI (e.g., sheep: Wallace, 1948).

3) *Increasing size of the offspring.* During that portion of the period of PI in which the offspring receives all its food from its parents, the tendency for the offspring to begin very small and steadily increase in size will, other things being equal, increase the cost to the parent of maintaining and enlarging it. (Whether this is always true will depend, of course, on the way in which the offspring's growth rate changes as a function of increasing size.) In addition, as the offspring increases in size the relative energetic expense to it of competing with its parents should decline.

The argument advanced here is only meant to suggest a general tendency for conflict to increase during the period of PI, since it is easy to imagine circumstances in which conflict might peak several times during the period of PI. It is possible, for example, that weight at birth in a mammal such as humans is strongly associated with the offspring's survival in subsequent weeks, but that the cost to the mother of bearing a large offspring is considerably greater than some of her ensuing investment. In such circumstances, conflict *prior* to birth over the offspring's weight at birth may be more intense than conflict over nursing in the weeks after birth.

Data from studies of dogs, cats, rhesus macaques, and sheep appear to support the arguments of this and the previous section. In these species, parent-offspring conflict begins well before the period of weaning and tends to increase during the period of PI. In dogs (Rheingold, 1963) and cats (Schneirla et al., 1963) postnatal maternal care can be divided into three periods according to increasing age of the offspring. During the first, the mother approaches the infant to initiate parental investment. No avoidance behavior or aggression toward the infant is shown by the mother. In the second, the offspring and the mother approach each other about equally, and the mother shows some avoidance behavior and some aggression in response to the infant's demands. The third period can be characterized as the period of weaning. Most contacts are initiated by the offspring. Open avoidance and aggression characterize the mother.

Detailed quantitative data on the rhesus macaque (Hinde and Spencer-Booth, 1967, 1971), and some parallel data on other macaques (Rosenblum, 1971), demonstrate that the behavior of both mother and offspring change during the period of postnatal parental care in a way consistent with theory. During the first weeks after she has given birth, the rhesus mother's initiative in setting up nipple contacts is high but it soon declines rapidly. Concurrently she begins to reject some of the infant's advances, and after her own initiatives toward nipple contact have ceased, she rejects her infant's advances with steadily increasing frequency until at the end of the period of investment all of the offspring's advances are rejected. Shortly after birth, the offspring leaves the mother more

often than it approaches her, but as time goes on the initiative in maintaining mother-offspring proximity shifts to the offspring. This leads to the superficially paradoxical result that as the offspring becomes increasingly active and independent, spending more and more time away from its mother, its initiative in maintaining mother-offspring proximity increases (that is, it tends to approach the mother more often than it leaves her). According to the theory presented here, this result reflects the underlying tendency for parent-offspring conflict to increase during the period of PI. As the interests of mother and offspring diverge, the offspring must assume a greater role in inducing whatever parental investment is forthcoming.

Data on the production and consumption of milk in sheep (Wallace, 1948) indicate that during the first weeks of the lamb's life the mother typically produces more milk than the lamb can drink. The lamb's appetite determines how much milk is consumed. But after the fourth week, the mother begins to produce less than the lamb can drink, and from that time on it is the mother who is the limiting factor in determining how much milk is consumed. Parallel behavioral data indicate that the mother initially permits free access by her lamb(s) but after a couple of weeks begins to prevent some suckling attempts (Munro, 1956; Ewbank, 1967). Mothers who are in poor condition become the limiting factor in nursing earlier than do mothers in good condition, and this is presumably because the cost of a given amount of milk is considerably higher when the mother is in poor condition, while the benefit to the offspring remains more or less unchanged. Females who produce twins permit either twin to suckle on demand during the first three weeks after birth, but in the ensuing weeks they do not permit one twin to suckle unless the other is ready also (Ewbank, 1964; Alexander, 1960).

DISAGREEMENT OVER THE SEX OF THE OFFSPRING

Under certain conditions a potential off-spring is expected to disagree with its parents over whether it should become a male or a female. Since one can not assume that potential offspring are powerless to affect their sex, sex ratios observed in nature should to some extent reflect the offspring's preferred value as well as the parents'.

Fisher (1930) showed that (in the absence of inbreeding) parents are selected to invest as much in the total of their daughters as in the total of their sons. When each son produced costs on average the same as each daughter, parents are selected to produce a sex ratio of 50/50. In such species, the expected reproductive success (RS) of a son is the same as that of a daughter, so that an offspring should be indifferent as to its sex. But if (for example) parents are selected to invest twice as much in a typical male as in a typical female, then they will be selected to produce twice as many females as males, and the expected RS of each son will be twice that of each daughter. In such a species a potential offspring would prefer to be a male, for it would then achieve twice the RS it would as a female, without suffering a comparable decrease in inclusive fitness through the cost forced on its parents, because the offspring is selected to devalue that cost by the offspring's expected r_0 to the displaced sibling. For the example chosen, the exact gain in the offspring's inclusive fitness can be specified as follows. If the expected RS of a female offspring is defined as one unit of RS, then, in being made male, the offspring gains one unit of RS, but it deprives its mother of an additional daughter (or half a son). This displaced sibling (whether a female or half of a male) would have achieved one unit of RS, but this unit is devalued from the offspring's standpoint by the relevant r_0. If the displaced sibling would have been a full sibling, then this unit of RS is devalued by $\frac{1}{2}$, and the offspring, in being made a male, achieves a $\frac{1}{2}$ unit net increase in inclusive fitness. If the displaced sibling would have been a half sibling, the offspring, in being made a male, achieves a $\frac{3}{4}$ unit net increase in inclusive fitness. The parent, on the other hand, experiences

initially only a trivial decrease in RS, so that *initially* any gene in the offspring tending to make it a male against its parents' efforts would spread rapidly.

As a hypothetical gene for offspring control of sex begins to spread, the number of males produced increases, thereby lowering the expected RS of each male. This decreases the gain (in inclusive fitness) to the offspring of being made a male. If the offspring's equilibrial sex ratio is defined as that sex ratio at which an offspring is indifferent as to whether it becomes a male or a female, then this sex ratio can be calculated by determining the sex ratio at which the offspring's gain in RS in being made a male is exactly offset by its loss in inclusive fitness in depriving itself of a sister (or half a brother). The offspring's equilibrial sex ratio will depend on both the offspring's expected r_o to the displaced siblings and on the extent to which parents invest more in males than in females (or vice versa). The general solution is given
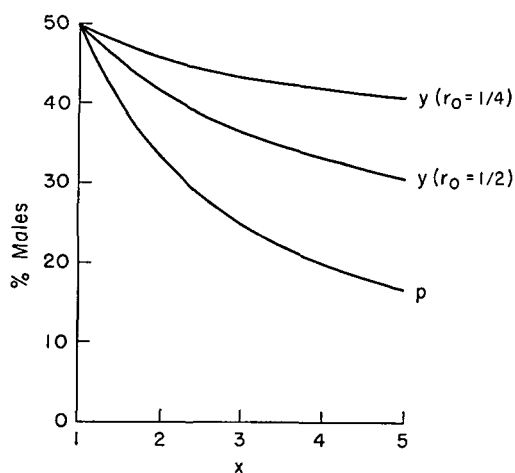

FIG. 4. The optimal sex ratio (per cent males) for the mother (m) and the young (y) where the mother invests more in a son than in a daughter by a factor of x (and assuming no paternal investment in either sex). Two functions are given for the offspring, depending on whether the siblings it displaces are full-siblings ($r_o = 1/2$) or half-siblings ($r_o = 1/4$). Note the initial rapid divergence between the mother's and the offspring's preferred sex ratio as the mother moves from equal investment in a typical individual of either sex (x = 1) to twice as much investment in a typical male (x = 2).

in the Appendix. Parent and offspring equilibrial sex ratios for different values of r_o and different values of x (PI in a typical son/PI in a typical daughter) are plotted in Figure 4. For example, where the r_o between siblings is $1/2$ and where parents invest twice as much in a son as in a daughter (x = 2), the parents' equilibrial sex ratio is 1:2 (males:females) while that of·the offspring is 1:1.414.

As long as all offspring are fathered by the same male, he will prefer the same sex ratio among the offspring that the mother does. But consider a species such as caribou in which the female produces only one offspring a year and assume that a female's successive offspring are fathered by different, unrelated males. If the female invests more in a son than in a daughter, then she will be selected to produce more daughters than sons. The greater cost of the son is not borne by the father, however, who invests nothing beyond his sperm, and who will not father the female's later offspring, so the father's equilibrial sex ratio is an equal number of sons and daughters. The offspring will prefer some probability of being a male that is intermediate between its parents' preferred probabilities, because (unlike the father) the offspring is related to the mother's future offspring but (unlike the mother) it is less related to them than to itself.

In a species such as just described (in which the male is heterogametic) the following sort of competitive interaction is possible. The prospective father produces more Y-bearing sperm than the female would prefer and she subjects the Y-bearing sperm to differential mortality. If the ratio of the sperm reaching the egg has been reduced to near the mother's optimal value, then the egg preferentially admits the Y-bearing sperm. If the mother ovulated more eggs than she intends to rear, she could then choose which to invest in, according to the sex of the fertilized egg, unless a male egg is able to deceive the mother about its sex until the mother has committed herself to investing in him. Whether such interactions actually occur in nature is at present unknown.

One consequence of the argument advanced here is that there is an automatic selective agent tending to keep maternal investment in a son similar to that in a daughter, for the greater the disparity between the investment in typical individuals of the two sexes, the greater the loss suffered by the mother in competitive interactions with her offspring over their preferred sex and in producing a sex ratio further skewed away from her preferred ratio (see Fig. 4). This automatic selection pressure may partly account for the apparent absence of strongly size-dimorphic young (at the end of PI) in species showing striking adult sexual dimorphism in size.

The argument presented here applies to any tendency of the parent to invest differentially in the young, whether according to sex or some other variable, except that in many species sex is irreversibly determined early in ontogeny and the offspring is expected at the very beginning to be able to discern its own sex and hence the predicted pattern of investment it will receive, so that, unlike other forms of differential investment, conflict is expected very early, namely, at the time of sex determination.

THE OFFSPRING AS PSYCHOLOGICAL MANIPULATOR

How is the offspring to compete effectively with its parent? An offspring can not fling its mother to the ground at will and nurse. Throughout the period of parental investment the offspring competes at a disadvantage. The offspring is smaller and less experienced than its parent, and its parent controls the resources at issue. Given this competitive disadvantage the offspring is expected to employ psychological rather than physical tactics. (Inside the mother the offspring is expected to employ chemical tactics, but some of the analysis presented below should also apply to such competition.) It should attempt to induce more investment than the parent wishes to give.

Since an offspring will often have better knowledge of its real needs than will its parent, selection should favor parental attentiveness to signals from its offspring that

apprize the parent of the offspring's condition. In short, the offspring cries when hungry or in danger and the parent responds appropriately. Conversely, the offspring signals its parent (by smiling or wagging its tail) when its needs have been well met. Both parent and offspring benefit from this system of communication. But once such a system has evolved, the offspring can begin to employ it out of context. The offspring can cry not only when it is famished but also when it merely wants more food than the parent is selected to give. Likewise, it can begin to withhold its smile until it has gotten its way. Selection will then of course favor parental ability to discriminate the two uses of the signals, but still subtler mimicry and deception by the offspring are always possible. Parental experience with preceding offspring is expected to improve the parent's ability to make the appropriate discrimination. Unless succeeding offspring can employ more confusing tactics than earlier ones, parent-offspring interactions are expected to be increasingly biased in favor of the parent as a function of parental age.

In those species in which the offspring is more helpless and vulnerable the younger it is, its parents will have been more strongly selected to respond positively to signals of need emitted by the offspring, the younger that offspring is. This suggests that at any stage of ontogeny in which the offspring is in conflict with its parents, one appropriate tactic may be to revert to the gestures and actions of an earlier stage of development in order to induce the investment that would then have been forthcoming. Psychologists have long recognized such a tendency in humans and have given it the name of regression. A detailed functional analysis of regression could be based on the theory presented here.

The normal course of parent-offspring relations must be subject to considerable unpredictable variation in both the condition of the parent and (sometimes independently) the condition of the offspring. Both partners must be sensitive to such variation and must adjust their behavior appropriately. Low investment coming

from a parent in poor condition has a different meaning than low investment coming from a parent in good condition. This suggests that from an early age the offspring is expected to be a psychologically sophisticated organism. The offspring should be able to evaluate the cost of a given parental act (which depends in part on the condition of the parent at that moment) and its benefit (which depends in part on the condition of the offspring). When the offspring's interests diverge from those of its parent, the offspring must be able to employ a series of psychological maneuvers, including the mimicry and regression mentioned above. Although it would be expected to learn appropriate information (such as whether its psychological maneuvers were having the desired effects), an important feature of the argument presented here is that the offspring cannot rely on its parents for disinterested guidance. One expects the offspring to be pre-programmed to resist some parental teaching while being open to other forms. This is particularly true, as argued below, for parental teaching that affects the altruistic and egoistic tendencies of the offspring.

If one event in a social relationship predicts to some degree future events in that relationship, the organism should be selected to alter its behavior in response to an initial event, in order to change the probability that the predicted events will occur. For example, if a mother's lack of love for her offspring early in its life predicts deficient future investment, then the offspring will be selected to be sensitive to such early lack of love, whether investment at that time is deficient or not, in order to increase her future investment. The best data relevant to these possibilities come from the work of Hinde and his associates on groups of caged rhesus macaques. In a series of experiments, a mother was removed from her 6-month-old infant, leaving the infant in the home cage with other group members. After 6 days, the mother was returned to the home cage. Behavioral data were gathered before, during, and after the separation (see points 1 and 2 below). In a parallel series of experiments,

the infant was removed for 6 days from its mother, leaving her in the home cage, and the same behavioral data were gathered (see point 3 below). The main findings can be summarized as follows:

1) *Separation of mother from her offspring affects their relationship upon reunion.* After reunion with its mother, the infant spends more time on the mother than it did before separation—although, had the separation not occurred, the infant would have reduced its time on the mother. This increase is caused by the infant, and occurs despite an increase in the frequency of maternal rejection (Hinde and Spencer-Booth, 1971). These effects can be detected at least as long as 5 weeks after reunion. These data are consistent with the assumption that the infant has been selected to interpret its mother's disappearance as an event whose recurrence the infant can help prevent by devoting more of its energies to staying close to its mother.

2) *The mother-offspring relationship prior to separation affects the offspring's behavior on reunion.* Upon reunion with its mother, an infant typically shows distress, as measured by callings and immobility. The more frequently an infant was rejected *prior* to separation, the more distress it shows upon reunion. This correlation holds for at least 4 weeks after reunion. In addition, the more distressed the infant is, the greater is its role in maintaining proximity to its mother (Hinde and Spencer-Booth, 1971). These data support the assumption that the infant interprets its mother's disappearance in relation to her predeparture behavior in a logical way: the offspring should assume that a rejecting mother who temporarily disappears needs more offspring surveilance and intervention than does a nonrejecting mother who temporarily disappears.

3) *An offspring removed from its mother shows, upon reunion, different effects than an offspring whose mother has been removed.* Compared to an infant whose mother had been removed, an infant removed from its mother shows, upon reunion, and for up to 6 weeks after reunion, less distress and more time off the mother.

In addition, the offspring tends to play a smaller role in maintaining proximity to its mother, and it experiences less frequent maternal rejections (Hinde and Davies, 1972a,b). These data are consistent with the expectation that the offspring should be sensitive to the *meaning* of events affecting its relationship to its mother. The offspring can differentiate between a separation from its mother caused by its own behavior or some accident (infant removed from group) and a separation which may have been caused by maternal negligence (mother removed from group). In the former kind of separation, the infant shows less effects when reunited, because, from its point of view, such a separation does not reflect on its mother and no remedial action is indicated. A similar explanation can be given for differences in the mother's behavior.

PARENT OFFSPRING CONFLICT OVER THE BEHAVIORAL TENDENCIES OF THE OFFSPRING

Parents and offspring are expected to disagree over the behavioral tendencies of the offspring insofar as these tendencies affect related individuals. Consider first interactions among siblings. An individual is only expected to perform an altruistic act toward its full-sibling whenever the benefit to the sibling is greater than twice the cost to the altruist. Likewise, it is only expected to forego selfish acts when $C > 2B$ (where a selfish act is defined as one that gives the actor a benefit, B, while inflicting a cost, C, on some other individual, in this case, on a full-sibling). But parents, who are equally related to all of their offspring, are expected to encourage all altruistic acts among their offspring in which $B > C$, and to discourage all selfish acts in which $C > B$. Since there ought to exist altruistic situations in which $C < B < 2C$, parents and offspring are expected to disagree over the tendency of the offspring to act altruistically toward its siblings. Likewise, whenever for any selfish act harming a full-sibling $B < C < 2B$, parents are expected to discourage such behavior and offspring are expected to be relatively refractory to such

discouragement.

This parent-offspring disagreement is expected over behavior directed toward other relatives as well. For example, the offspring is only selected to perform altruistic acts toward a cousin (related through the mother) when $B > 8C$. But the offspring's mother is related to her own nephews and nieces by $r_o = \frac{1}{4}$ and to her offspring by $r_o = \frac{1}{2}$, so that she would like to see any altruistic acts performed by her offspring toward their maternal cousins whenever $B > 2C$. The same argument applies to selfish acts, and both arguments can be made for more distant relatives as well. (The father is unrelated to his mate's kin and, other things being equal, should not be distressed to see his offspring treat such individuals as if they were unrelated.)

The general argument extends to interactions with unrelated individuals, as long as these interactions have some effect, however remote and indirect, on kin. Assume, for example, that an individual gains some immediate benefit, B, by acting nastily toward some unrelated individual. Assume that the unrelated individual reciprocates in kind (Trivers, 1971), but assume that the reciprocity is directed toward both the original actor and some relative, e.g., his sibling. Assuming no other effects of the initial act, the original actor will be selected to perform the nasty act as long as $B > C_1 + \frac{1}{2}(C_2)$, where C_1 is the cost to the original actor of the reciprocal nastiness he receives and C_2 is the cost to his sibling of the nastiness the sibling receives. The actor's parents viewing the interaction would be expected to condone the initial act only if $B > C_1 + C_2$. Since there ought to exist situations in which $C_1 + \frac{1}{2}(C_2) < B < C_1 + C_2$, one expects conflict between offspring and parents over the offspring's tendency to perform the initial nasty act in the situation described. A similar argument can be made for altruistic behavior directed toward an unrelated individual if this behavior induces altruism in return, part of which benefits the original altruist's sibling. Parents are expected to encourage such altruism more often than the offspring is expected to undertake on his own. The

argument can obviously be extended to behavior which has indirect effects on kin other than one's sibling.

As it applies to human beings, the above argument can be summarized by saying that a fundamental conflict is expected during socialization over the altruistic and egoistic impulses of the offspring. Parents are expected to socialize their offspring to act more altruistically and less egoistically than the offspring would naturally act, and the offspring are expected to resist such socialization. If this argument is valid, then it is clearly a mistake to view socialization in humans (or in any sexually reproducing species) as only or even primarily a process of "enculturation," a process by which parents teach offspring their culture (e.g., Mussen et al., 1969, p. 259). For example, one is not permitted to assume that parents who attempt to impart such virtues as responsibility, decency, honesty, trustworthiness, generosity, and self-denial are merely providing the offspring with useful information on appropriate behavior in the local culture, for all such virtues are likely to affect the amount of altruistic and egoistic behavior impinging on the parent's kin, and parent and offspring are expected to view such behavior differently. That some teaching beneficial to the offspring transpires during human socialization can be taken for granted, and one would expect no conflict if socialization involved *only* teaching beneficial to the offspring. According to the theory presented here, socialization is a process by which parents attempt to mold each offspring in order to increase their own inclusive fitness, while each offspring is selected to resist some of the molding and to attempt to mold the behavior of its parents (and siblings) in order to increase its inclusive fitness. Conflict during socialization need not be viewed solely as conflict between the culture of the parent and the biology of the child; it can also be viewed as conflict between the biology of the parent and the biology of the child. Since teaching (as opposed to molding) is expected to be recognized by offspring as being in their own self-interest, parents

would be expected to overemphasize their role as teachers in order to minimize resistance in their young. According to this view then, the prevailing concept of socialization is to some extent a view one would expect adults to entertain and disseminate.

Parent-offspring conflict may extend to behavior that is not on the surface either altruistic or selfish but which has consequences that can be so classified. The amount of energy a child consumes during the day, and the way in which the child consumes this energy, are not matters of indifference to the parent when the parent is supplying that energy, and when the way in which the child consumes the energy affects its ability to act altruistically in the future. For example, when parent and child disagree over when the child should go to sleep, one expects in general the parent to favor early bedtime, since the parent anticipates that this will decrease the offspring's demands on parental resources the following day. Likewise, one expects the parent to favor serious and useful expenditures of energy by the child (such as tending the family chickens, or studying) over frivolous and unnecessary expenditures (such as playing cards)—the former are either altruistic in themselves, or they prepare the offspring for future altruism. In short, we expect the offspring to perceive some behavior, that the parent favors, as being dull, unpleasant, moral, or any combination of these. One must at least entertain the assumption that the child would find such behavior more enjoyable if in fact the behavior maximized the offspring's inclusive fitness.

CONFLICT OVER THE ADULT REPRODUCTIVE ROLE OF THE OFFSPRING

As a special case of the preceding argument, it is clear that under certain conditions conflict is expected between parent and offspring over the adult reproductive role of the offspring. To take the extreme case, it follows at once from Hamilton's (1964) work that individuals who choose not to reproduce (such as celibate priests) are not necessarily acting counter to their

genetic self-interest. One need merely assume that the nonreproducer thereby increases the reproductive success of relatives by an amount which, when devalued by the relevant degrees of relatedness, is greater than the nonreproducer would have achieved on his own. This kind of explanation has been developed in some detail to explain nonreproductives in the haplodiploid Hymenoptera (Hamilton, 1972). What is clear from the present argument, however, is that it is even more likely that the nonreproducer will thereby increase his *parents'* inclusive fitness than that he will increase his own. This follows because his parents are expected to value the increased reproductive success of kin relatively more than he is.

If the benefits of nonreproducing are assumed, for simplicity, to accrue only to full siblings and if the costs of nonreproducing are defined as the surviving offspring the nonreproducer would have produced had he or she chosen to reproduce, then parent-offspring conflict over whether the offspring should reproduce is expected whenever $C < B < 2C$. Assuming it is sometimes possible for parents to predict while an offspring is still young what the cost and benefit of its not reproducing will be, the parents would be selected to mold the offspring toward not reproducing whenever $B > C$. Two kinds of nonreproductives are expected: those who are thereby increasing their own inclusive fitness ($B > 2C$) and those who are thereby lowering their own inclusive fitness but increasing that of their parents ($C < B < 2C$). The first kind is expected to be as happy and content as living creatures ever are, but the second is expected to show internal conflict over its adult role and to express ambivalence over the past, particularly over the behavior and influence of its parents. I emphasize that it is not necessary for parents to be conscious of molding an offspring toward nonreproduction in order for such molding to occur and to increase the parent's inclusive fitness. It remains to be explored to what extent the etiology of sexual preferences (such as homosexuality) which tend to interfere with reproduction can be ex-

plained in terms of the present argument.

Assuming that parent and offspring agree that the offspring should reproduce, disagreement is still possible over the form of that reproduction. Whether an individual attempts to produce few offspring or many is a decision that affects that individual's opportunities for kin-directed altruism, so that parent and offspring may disagree over the optimal reproductive effort of the offspring. Since in humans an individual's choice of mate may affect his or her ability to render altruistic behavior toward relatives, mate choice is not expected to be a matter of indifference to the parents. Parents are expected to encourage their offspring to choose a mate that will enlarge the offspring's altruism toward kin. For example, when a man marries his cousin, he increases (other things being equal) his contacts with relatives, since the immediate kin of his wife will also be related to him, and marriage will normally lead to greater contact with her immediate kin. One therefore might expect human parents to show a tendency to encourage their offspring to marry more closely related individuals (e.g., cousins) than the offspring would prefer. Parents may also use an offspring's marriage to cement an alliance with an unrelated family or group, and insofar as such an alliance is beneficial to kin of the parent in addition to the offspring itself, parents are expected to encourage such marriages more often than the offspring would prefer. Finally, parents will more strongly discourage marriage by their offspring to individuals the local society defines as pariahs, because such unions are likely to besmirch the reputation of close kin as well.

Because parents may be selected to employ parental investment itself as an incentive to induce greater offspring altruism, parent-offspring conflict may include situations in which the offspring attempts to terminate the period of PI *before* the parent wishes to. For example, where the parent is selected to retain one or more offspring as permanent "helpers at the nest" (Skutch, 1961), that is, permanent nonreproductives who help their parents raise

additional offspring (or help those offspring
to reproduce), the parent may be selected
to give additional investment in order to
tie the offspring to the parent. In this situ-
ation, selection on the offspring may favor
any urge toward independence which over-
comes the offspring's impulse toward addi-
tional investment (with its hidden cost of
additional dependency). In short, in species
in which kin-directed altruism is important,
parent-offspring conflict may include situ-
ations in which the offspring wants *less*
than the parent is selected to give as well
as the more common situation in which
the offspring attempts to garner *more* PI
than the parent is selected to give.

Parent-offspring relations early in on-
togeny can affect the later adult reproduc-
tive role of the offspring. A parent can
influence the altruistic and egoistic tenden-
cies of its offspring whenever it has influ-
ence over any variable that affects the costs
and benefits associated with altruistic and
egoistic behavior. For example, if becoming
a permanent nonreproductive, helping
one's siblings, is more likely to increase
one's inclusive fitness when one is small in
size relative to one's siblings (as appears
to be true in some polistine wasps: Eber-
hard, 1969), then parents can influence the
proportion of their offspring who become
helpers by altering the size distribution of
their offspring. Parent-offspring conflict
over early PI may itself involve parent-
offspring conflict over the eventual repro-
ductive role of the offspring. This theo-
retical possibility may be relevant to human
psychology if parental decision to mold an
offspring into being a nonreproductive in-
volves differential investment as well as
psychological manipulation.

THE ROLE OF PARENTAL EXPERIENCE IN PARENT-OFFSPRING CONFLICT

It cannot be supposed that all parent-
offspring conflict results from the conflict
in the way in which the parent's and the
offspring's inclusive fitnesses are maximized.
Some conflict also results, ironically because
of an overlap in the interests of parent and
young. When circumstances change, alter-

ing the benefits and costs associated with
some offspring behavior, both the parent
and the offspring are selected to alter the
offspring's behavior appropriately. That is,
the parent is selected to mold the appro-
priate change in the offspring's behavior,
and if parental molding is successful, it
will strongly reduce the selection pressure
on the offspring to change its behavior
spontaneously. Since the parent is likely to
discover the changing circumstances as a
result of its own experience, one expects
tendencies toward parental molding to ap-
pear, and spread, before the parellel tenden-
cies appear in the offspring. Once parents
commonly mold the appropriate offspring
behavior, selection still favors genes lead-
ing toward voluntary offspring behavior,
since such a developmental avenue is pre-
sumably more efficient and more certain
than that involving parental manipulation.
But the selection pressure for the appropri-
ate offspring genes should be weak, and if
circumstances change at a faster rate than
this selection operates, there is the possi-
bility of continued parent-offspring con-
flict resulting from the greater experience
of the parent.

If the conflict described above actually
occurs, then (as mentioned in an earlier
section) selection will favor a tendency for
parents to overemphasize their experience
in all situations, and for the offspring to
differentiate between those situations in
which greater parental experience is real
and those situations in which such experi-
ence is merely claimed in order to manipu-
late the offspring.

APPENDIX: THE OFFSPRING'S EQUILIBRIAL SEX RATIO

Let the cost of producing a female be
one unit of investment, and let the cost of
producing a male be x units, where x is
larger than one. Let the expected repro-
ductive success of a female be one unit of
RS. Let the sex ratio produced be $1:y$ (males:
females), where y is larger than one. At
this sex ratio the expected RS of a male is
y units of RS, so that, in being made a male
instead of a female, an offspring gains

y—1 units of RS. But the offspring also thereby deprives its mother of x—1 units of investment. The offspring's equilibrial sex ratio is that sex ratio at which the offspring's gain in RS in being made a male (y—1) is exactly offset by its loss in inclusive fitness which results because it thereby deprives its mother of x—1 units of investment. The mother would have allocated these units in such a way as to achieve a 1:y sex ratio, that is, she would have allocated x/(x+y) of the units to males and y/(x+y) of the units to females. In short, she would have produced (x—1)/(x+y) sons, which would have achieved RS of $y(x-1)/(x+y)$, and she would have produced $y(x-1)/(x+y)$ daughters, which would have achieved RS of $y(x-1)/(x+y)$. The offspring is expected to devalue this loss by the offspring's r_0 to its displaced siblings. Hence, the offspring's equilibrial sex ratio results when

$$y - 1 = \frac{r_0\, y\, (x - 1)}{x + y} + \frac{r_0\, y\, (x - 1)}{x + y}$$

$$= (2r_0 y)\, \frac{x - 1}{x + y}$$

Rearranging gives

$$y^2 + y\, (x - 2r_0 x + 2r_0 - 1) - x = 0$$
$$y^2 + (x - 1)\, (1 - 2r_0)\, y - x = 0$$

The general solution for this quadratic equation is

$$y = \frac{-(x - 1)\, (1 - 2r_0)}{2} +$$

$$\frac{\sqrt{(x - 1)^2\, (1 - 2r_0)^2 + 4x}}{2}$$

Where $r_0 = \frac{1}{2}$, the equation reduces to $y = \sqrt{x}$. In other words, when the offspring displaces full siblings (as is probably often the case), the offspring's equilibrial sex ratio if 1 : $\sqrt{x}$, while the parent's equilibrial sex ratio is 1:x. These values, as well as the offspring's equilibrial sex ratio where $r_0 = \frac{1}{4}$, are plotted in Figure 4. The same general solution holds if parents invest more in females by a factor of x, except that the resulting sex ratios are then reversed (e.g., $\sqrt{x}$: 1 instead of 1 : $\sqrt{x}$).

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