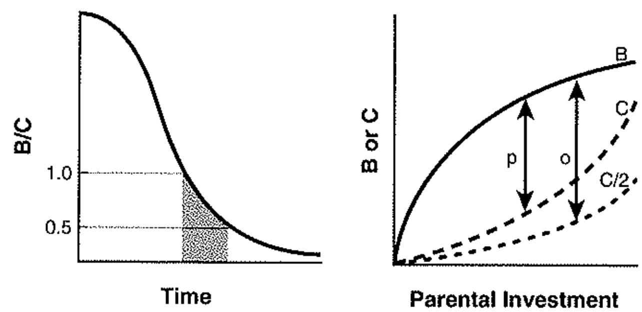
A graphical representation of how the *B/C* ratio of a mother's milk is expected to change with the offspring's age is shown in Figure 6.7. The same argument applies, of course, to any other kind of parental care, such as protecting the young from predators, cleaning them, helping them in competition with others (relatives and nonrelatives), and teaching them how to fend for themselves.

Pursuing this reasoning further, there should be a progressive change in parent-offspring interactions because the benefit/cost ratio decreases as the offspring matures. Immediately after birth, when an offspring is small and cannot feed itself, a small amount of the mother's milk greatly benefits its chances of survival, so the *B/C* ratio is very high, and the mother will anticipate and be responsive to its offspring's needs. As the offspring grows in size, the amount of milk (i.e., the cost of production) needed to benefit the offspring by the same amount increases, so the *B/C* ratio decreases. As the *B/C* ratio reaches 1, we expect the mother to curtail nursing by refusing its offspring's demands and decreasing the secretion of milk. At this point and beyond, when the *B/C* falls below 1, the mother should resist nursing. If the offspring can cause the mother to continue nursing, the *B/C* ratio may eventually fall to 0.5, at which point the offspring should stop nursing because further benefits to itself are less than the benefits to its genes in full siblings. Proximate causes of behavioral change include a developing ability to utilize other sources of food.



(*A*) (*B*)

FIGURE 6.7 (A) Weaning conflict in mammals can be understood in an evolutionary perspective. Just after birth the ratio of the benefit (B) to cost (C) of a mother's milk is high: a little milk makes a big difference as to whether the offspring survives and reproduces (B), whereas the cost (C), in terms of how much that milk detracts from her investment in other offspring, is small. Because the youngster values his siblings relative to himself half as greatly as does his mother, there is a period (shaded) when there is parent-offspring conflict over the delivery of goods and services—when the youngster is eager to have more than the parent is easily willing to provide.

(B) A similar disagreement exists over the *amount* of parental investment provided by the mother. A small parental investment to any one offspring provides a big benefit and entails a small cost, but a large investment carries with it a smaller benefit and a larger cost. From the offspring's perspective, however, the costs will be devalued by a factor of 2. The parent will be inclined to withhold further investment when the difference between benefit and cost is maximal (short arrow labeled *p*), but the offspring will demand more until the difference between benefit and ½ cost is maximal (longer arrow labeled *o*). Remember that in this analysis cost and benefit relate to the lifetime reproductive success of the parent, but the offspring's "interests" in the outcome are influenced by effects on close kin as well as itself.

This sort of change in parent-offspring interactions is seen, in one form or another, in virtually all animals in which the young depend upon their parents for food and protection between birth and adulthood. Parents of birds and mammals are typically very protective and solicitous toward their newborn young, and as the young mature the parents become progressively less responsive. Finally, the young, now grown in size, become so physical and emotional in their demands for investment that the parent's rebuff may not be gentle. In the case of nursing mammals these behaviors are so striking that they have their own descriptive name: "weaning conflict." These interactions have previously been seen as the parents' way of preparing its young to fend for themselves, but this argument does not make much evolutionary sense. Why should young animals resist what is good for them?

By this point you may have recognized ways in which this description of parent-offspring conflict applies to the interactions between human parents and their young. This should not be surprising, for parental investment in humans extends for longer than in any other species and therefore can become complex and intense. Trivers extended his analysis to provide insight into many other aspects of parent-offspring conflict, and a number of these insights follow quite logically from the concept as we have outlined it to this point.

PSYCHOLOGICAL ADAPTATIONS OF OFFSPRING AND PARENTS

Young animals cannot physically coerce their larger parents into extending investment, but psychological manipulations can be used to accomplish the same end. Parents are adapted to respond to the distress cries of offspring, but offspring may feign greater hunger or dependence on the parent than is actually the case, or they may become so loud, disruptive, and interfering in their attention-getting behavior as to "blackmail" the parent into acceding to their demands. A psychological arms race ensues, in which the parent must distinguish between real and exaggerated needs.

Anyone who has watched the interactions between young birds or farm animals and their parents has seen how loud, aggressive, and persistent the young's begging can be and how infantile are their postures and cries. To a young animal the arrival of a new sibling is a sure signal that its parents' investments and attentions will be divided; the behavior often triggered by this event is so intense and characteristic in humans that, like weaning conflict in animals, it has its own name, "regression." Most, if not all, human parents have seen what they consider attention-getting and interfering behavior by their young children; indeed, the descriptive terms themselves imply that the behavior is excessive, a sure sign that there is conflict. But the theory of parent-offspring conflict sees parents as potential psychological manipulators as well. As Trivers notes, the parental argument that curtailment of investment benefits young by preparing them for adult independence could itself be seen as usefully manipulative and self-deceiving.

SOCIAL BEHAVIOR OF OFFSPRING TOWARD NEAR RELATIVES

Why do young siblings so often fight, misbehave, resist control, and in general behave more egoistically than their parents want them to? Why do parents have to threaten, coerce, and preach? The socialization of young animals, especially humans, is often thought of as a learning process that enables them to acquire the behaviors they will need as adults in order to be successful in their family and social groups. If this process is strictly in the best interests of the young, as in the case of weaning conflict, it is a mystery why it is so often disharmonious.

It therefore isn't sufficient to provide answers solely in terms of proximate cause. Johnny snitched his brother's cake because he thought he didn't get a fair share or because his brother did the same thing to him yesterday; or Johnny misbehaved because his parents are not always there and he feels insecure. These kinds of explanation have an immediate validity in the domain of psychology, but an explanation in terms of evolutionary cause can provide a deeper, albeit complementary perspective by addressing why Johnny and his siblings persist in their squabbling, no matter how well-provisioned or secure their lives really are. The theory of parent-offspring conflict provides such an insight.

Just as with weaning conflict, we refer to Johnny's degree of relatedness to himself ($r = 1$) and to his siblings ($r = \frac{1}{2}$). In any perceived conflict over resources, from cake to parental attention, Johnny is therefore inclined to behave in a manner that parents find egoistic. As the parents' r with all their children is $\frac{1}{2}$, they are inclined to view these squabbles not only as disruptive, but they will wish to see the cake and attention apportioned equitably. In other words, in social conflicts with siblings, Johnny's sense of the appropriate B/C ratio (although he will not conceptualize the problem like this!) will differ by a factor of 2 from that of everyone else in the family. The traditional view of developmental psychologists that children must be socialized out of such egoistic behavior is not incorrect; it just doesn't address the question of why in evolutionary terms the problems of socialization take the form that they do. The case of sibling rivalry is thus an example of how an evolutionary explanation can complement an explanation that is cast solely in terms of proximate cause.

DEPENDENCE ON THE MATING SYSTEM

The examples of parent-offspring conflict we have so far discussed pertain to a monogamous mating system in which all offspring are full siblings and therefore $r = \frac{1}{2}$. Under these conditions conflict is predicted for the period when $1 > B/C > 0.5$. If the mating system is at the other extreme, in which each sibling is fathered by a different male and r between them is therefore $\frac{1}{4}$, more prolonged and intense conflict is expected, namely when $1 > B/C > 0.25$. Indeed, comparisons of the intensity of sibling conflict and parent-offspring conflict in species with known degrees of sibling relatedness have shown that both kinds of conflict increase with decrease in r. In humans, children usually know (or frequently wish to discover) who their genetic parents are. In comparison with families in which there are full siblings, those with half-sibs and stepparents have additional sources of conflict between siblings, between parents and offspring, and between the parents themselves, especially if both bring to their marriage children from previous marriages (Chapter 14).

CONFLICT DURING PREGNANCY

How parents allocate their resources influences their lifetime reproductive success.

> 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 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.

This prescient prediction made in 1974 by Robert Trivers suggested that parent-offspring conflict might begin *in utero* with a fetus attempting to maximize the benefits it receives. Indeed, the evolutionary geneticist David Haig has recently described evidence for parent-offspring conflict during human gestation. The measures and countermeasures seem so clearly antagonistic that he has likened these mother-fetus interactions to a confrontation between two armies. At the very least, they suggest evolutionary compromises reflecting the somewhat different genetic interests of the two parties.

After the embryo implants in the mother's uterine wall, its specialized trophoblast cells invade the uterus, break down the smooth constrictor muscles of the adjacent arteries, and form the "front line" of placental tissue in contact with the mother's circulatory system (Fig. 6.8) As a result of this initiative, the fetus gains control over several important parameters that later affect its supply of nutrients from the mother. First, the uterine arteries cannot respond to substances that are secreted by the mother into her blood to constrict the flow of blood to the uterine wall. She therefore loses this control over the flow of nutrients across the placenta. Second, the fetus can secrete substances directly into the mother's blood that increase the flow of blood and thus the flow of nutrients. Third, the fetus can regulate how much of certain substances in the maternal blood reach the fetus.

The maternal tissues that line the uterus—collectively called the "decidua" because they are shed at birth with the placenta—respond to the fetal cells in a way that looks more like defensive countermeasures than an opened-arm welcome. The stromal cells of the uterine lining secrete macromolecules that form a tough extracellular barrier or capsule around the arteries and in the path of the invading placenta. In their turn, the fetal cells secrete digestive enzymes that break down the barrier, and the uterine cells reply by secreting inhibitors of these enzymes.

Further evidence for *in utero* conflict between the mother and the fetus is seen in the regulation both of glucose concentration in the maternal blood and of maternal blood pressure. During early pregnancy, the mother's blood glucose level between meals falls, but after twelve weeks it stabilizes at a new low level until the baby is delivered. This lowering of glucose, which causes tiredness during early pregnancy, does not seem to be due to the fetus, because its early demands for energy are low and do not increase until later when the maternal supply of glucose has stabilized at the lower level. It appears instead that early in pregnancy the mother resets her blood glucose level to a low value in

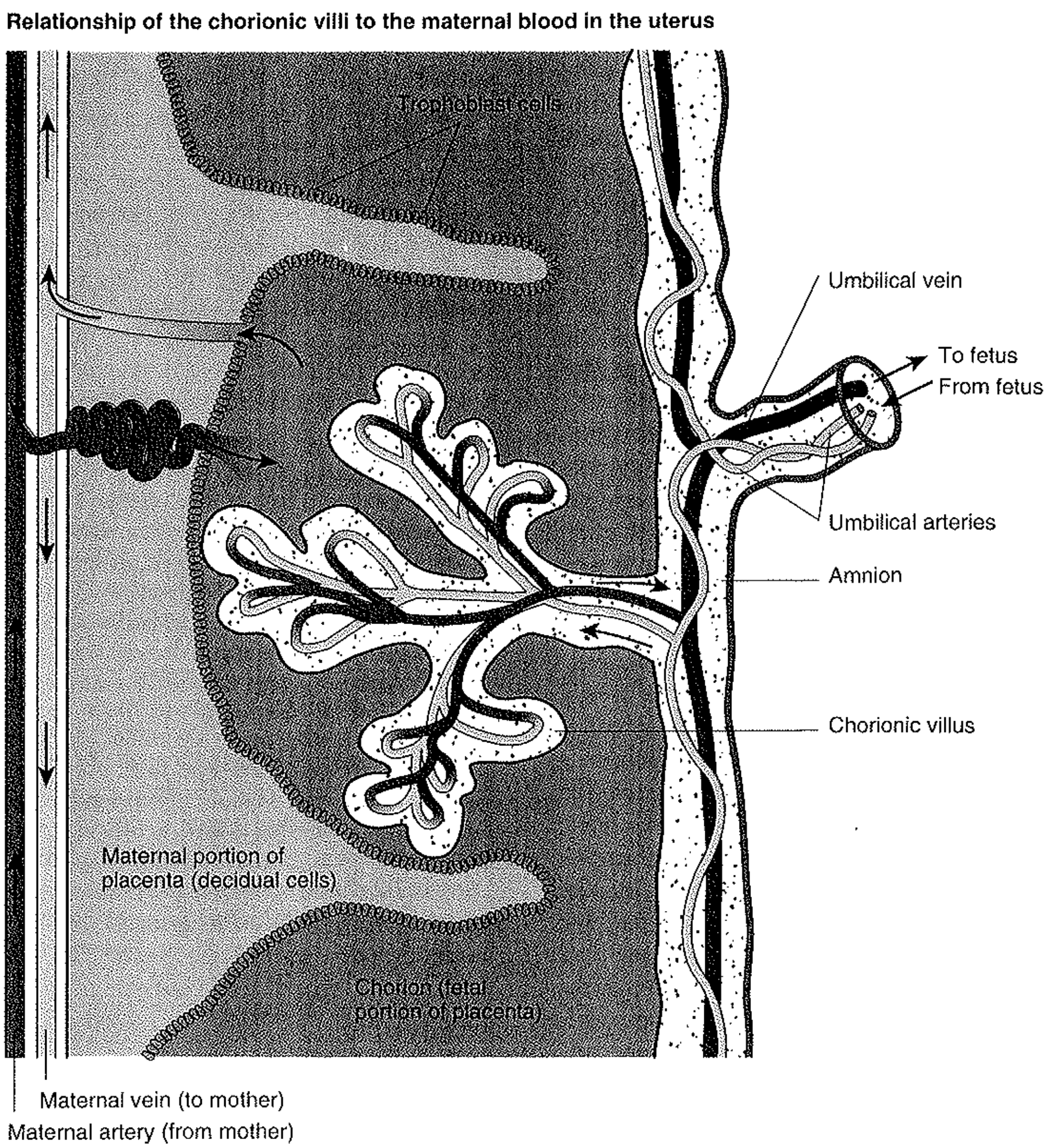


FIGURE 6.8 The relation between the maternal and fetal blood supply. Fetal blood vessels are bathed by blood from the mother's circulatory system.

anticipation of the fetus's demands, so that the fetus cannot remove more than it needs and more than is in the mother's genetic interest.

The fetus, operating from its advantageous placental beachhead, employs countermeasures. During the third trimester of pregnancy, the mother's blood level of insulin (the hormone that promotes removal of glucose from her blood) increases in concentration and at the same time becomes much less effective in removing glucose, especially after meals. This leads to higher glucose levels in her blood, and in extreme cases to gestational diabetes. There is good evidence that two hormones released by the fetus into the mother's blood, placental lactogen and placental growth hormone, interfere with the mechanism by which the mother's insulin lowers her blood glucose. The placental secretion of these hormones cannot be regulated by the mother, and despite their high concentrations neither is essential for a successful outcome of pregnancy. It appears that these hormonal interactions between the fetus and its mother are designed for interactions other than efficient and cooperative communication. As David Haig puts it: "If a message can be conveyed in a whisper [low concentrations of hormones], why shout? Raised voices are frequently a sign of conflict."

REPRODUCTIVE FUTURE OF THE PARENT

In many animals for which the supply of food varies during the rearing of young, the parents produce more offspring than are likely to survive to adulthood if food should become scarce. Under such conditions, some of the eggs or young may be abandoned or cannibalized by the parents and/or the siblings. Examples are found among hawks and owls, whose young grow rapidly in early spring. At this time of year, a late winter storm can make food difficult to find. There may be three young in the nest, one of which is smaller because it hatched last and because its larger siblings frequently monopolize the food as it is brought to the nest by the parents. If one of the young is cannibalized by parents or siblings, it is always the smallest.

We can readily see why and how natural selection has favored this behavior. Conditional infanticide, exercised when food is scarce and the entire brood is threatened, can rescue reproductive success for the current season. From the genetic perspective of the parents, benefits exceed costs ($B > C$) if the sacrifice of one offspring substantially increases the chances that at least some of the young will survive. The argument is equally clear from the genetic perspective of the larger of the nestlings: kin selection will favor siblicide when $B > \frac{1}{2} C$. But even from the perspective of the victim, kin selection should support the behavior if $B > 2C$.

Observations thus demonstrate that parents can assess the reproductive prospects of their offspring and redirect their parental investment so as to maximize the number of grand-offspring they leave, even if it requires reducing the number of young in the immediate future. Once again we must caution you about the simple language we are using. Do not read the word "assess" as implying conscious calculation of probabilities. We simply do not have many common English words that characterize the effects of behaviors without also suggesting human mental processes (Chapter 11).

As an organism ages, its potential for reproduction declines. In time it will not have enough resources or live long enough or be physiologically capable of producing another offspring. (In women this line is crossed at the time of menopause.) If at this juncture the organism has dependent young in its care, selection should favor parents who invest their remaining energies and resources in those last offspring. Such a pattern of behavior has been found: older animals generally feed, protect, and accede to the demands of their offspring more than do younger parents, and parent-offspring conflict is correspondingly less. This pattern of indulging the last child or a grandchild is familiar to humans as "doting."

SEXUAL SELECTION

Males and females are defined on the basis of primary universal differences related to the production of different kinds of gametes: males produce small motile gametes called *sperm*, whereas females produce larger, less-mobile gametes called *eggs*. Eggs are many times larger than sperm because they contain virtually all the cytoplasm that will be present in the zygote as well as nutrients that sustain growth during the early development of the embryo. Eggs can be enormous, particularly in birds. The need to make large gametes containing sufficient reserves to launch development was a by-product of the evolution of multicellular life. To be multicellular is to be larger, and how are gametes to find each other over a distance, particularly if they are big cells? The evolutionary solution was for

FIGURE 6.9 Bull elk following cow. The males of elk, deer, and many other hoofed mammals have large antlers or horns that are the product of sexual selection.