Does Mother Nature Punish Rotten Kids?

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1   Parent-Offspring Conflict in Economics and Biology

Economic Theories of the Family

The demand for children and for children's consumption goods have been central themes in the economics of the family.[1] Most economic studies of these topics are based on theory that would apply equally well to the demand for pets and the derived demand for pet food. Children are assumed to have no decision-making authority and hence their preferences are assumed to have no bearing on economic outcomes.

In 1974, Gary Becker [3] introduced an economic model of the household in which children are rational decision-making agents with interests distinct from those of their parents. Becker's model allows children to have economic spheres of influence where they can make decisions that influence their own well-being. Becker found a surprising result—which he called the "Rotten-Kid Theorem." The Rotten-Kid Theorem assumes that offspring care only about the money value of their consumption and that there is a benevolent "household head" who is so much wealthier than his children that he chooses to make gifts to each of them. Thus all "marginal" allocational decisions are made by the household head. Although children are entirely selfish and are able to influence the pre-transfer income distribution in the family, it will be in the interest of each to try to maximize total household income. The outcome is the same as the allocation that would have been selected by a benevolently dictatorial household head. According to Becker,

> . . .the head *automatically* internalizes the "external" effects of his actions on other family members. Indeed, because the head maximizes family income, he *fully* internalizes these externalities not only when the income of different members but also when their consumption . . . is directly affected."

Economists [4], [7], [23], have since demonstrated that the conclusions of the Rotten Kid Theorem depend critically on special assumptions that are likely

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[1]This literature is ably surveyed by Martin Browning [6].

to be violated in normal interactions among offspring and parents. In realistic environments, a child who is able to make the "first move" in interactions with a parent may be able to manipulate the parent to contribute more resources to the child than the parent would if the parent could control the child's actions.

Biological theories of Parent-Offspring Relations

Biologists, like economists, have found the language of game theory a useful way to study conflict and cooperation between parents and offspring. Evolutionary biologists bring two ideas to the study of the family that are new to economists. First, payoffs in games between family members are usually measured in the currency of reproductive success. Second, in biological models, the strategy that an individual uses in games with its relatives is programmed by its genes, which are passed from parent to offspring by the rules of Mendelian inheritance.

Almost all modern work on familial interaction (surveyed by T. H. Clutton-Brock [9] and H. J. C. Godfray [17]) has been influenced in one way or another by the fundamental contribution of William D. Hamilton [20] to the theory of *kin selection.* Hamilton demonstrated that evolution will favor siblings who are neither totally altruistic nor totally selfish toward each other. Hamilton stated the following proposition, which has come to be known as "Hamilton's Rule"[2].

> The social behavior of a species evolves in such a way that in each distinct behavior-evoking situation the individual will seem to value his neighbors' fitness against his own according to the coefficients of relationship[3] appropriate to that situation."

Robert Trivers [25] explicitly applied Hamilton's theory of kin selection to parent-offspring conflict. Trivers advanced the view that since in sexually reproducing species the genetic interests of offspring do not coincide with those of their parents, offspring will frequently act in ways that are not in their parents' genetic interests.[4]

Trivers' view that children are likely to find ways to exploit their parents was not universally shared by evolutionary biologists. In the same year that Gary Becker introduced the Rotten Kid Theorem, biologist Richard Alexander, [1] offered a theory of parent-offspring relations that is more in accord with Becker's ideas. Alexander proposed that evolutionary theory would lead us to expect

parents to be able to manipulate their offspring to act in the parental genetic interest.

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[2]Hamilton's original model focused on the special class of interactions in which the costs and benefits of each behavior are "additive." Hamilton's theory has since been extended to broader classes of interactions, by L. Luca Cavalli-Sforza

and Marcus Feldman [8] [13], Gordon Hines and John Maynard Smith [22], Alan Grafen [18], Theodore Bergstrom [5], and others.

[3]A definition of the *coefficient of relationship* between two individuals appears later in this paper. (Definition 7)

[4]Trivers' textbook *Social Evolution* [26] devotes a chapter to parent-offspring conflict, with several engaging descriptions of efforts by bird and mammal offspring to manipulate their parents and *vice versa.*

Alexander supported his view with two arguments; the first of which does not seem to have occurred to economists. Alexander reasoned that a gene that leads a child to act against reproductive interests of its parents will not spread because when such a child gene grows up, its own children will act against its reproductive interests, and hence in the long run such a "rotten kid" will generate fewer descendants.

Richard Dawkins [10], [11] disputed Alexander's genetic argument for the primacy of parental interests. Dawkins agreed that Alexander was correct in pointing out that one of the costs of being a selfish child was "the disadvantage of one's selfishness spreading to one's own children" but argued that this cost is not decisive in the conflict between the reproductive interests of parent and child. Appealing to Hamilton's theory of kin-selection, Dawkins asserts that for sexual diploids, "a selfish child will still do well to be selfish so long as the net benefit to him is at least half of the cost to close relatives." Alexander [2] later agreed to the view expressed by Dawkins and recanted his genetic explanation for parental dominance.

But Alexander had in store a second argument for the dominance of parental interests. This argument is more direct and is similar to that made by Gary Becker in the Rotten Kid Theorem. Becker appeals to the economic dominance of the household head, arguing that the head controls the relevant household budget decisions because his wealth is much greater than that of the other family members. Alexander relies on the physical primacy of the parent, asserting that "... the parent is bigger and stronger than the offspring, hence in a better position to pose its will."

The Becker-Alexander appeal to physical superiority and the parental ability to allocate resources has also come under attack by biologists. Dawkins [10] suggests that offspring may have private information about their own condition which parents can only guess. This puts offspring in a strong position to manipulate their parents by lying about their own condition. Amotz Zahavi [27] [28] proposed that a child might blackmail its parents into giving it more food than the parents would prefer to contribute by screaming until it is fed. Since the screaming is likely to attract predators, the parent must feed it or expect to lose the child. Both of these forms of manipulation of parents by offspring have received attention in the biological literature.

Alan Harper [21] and H. C. J. Godfray [15] [16] discuss models in which begging serves as a costly signal of an offspring's condition. Maynard Smith's [24] Sir Philip Sidney game is also frequently applied to scenarios involving parent-offspring communication and resource allocation.

Marcus Feldman and Ilan Eshel [14] constructed a model of family behavior that is strikingly similar to Gary Becker's scenario. Feldman and Eshel endowed parents with the power to redistribute wealth away from greedy children, where behavior of parents and of offspring is genetically coded. They found that parental ability to redistribute is not necessarily sufficient to induce offspring to behave as their parents would choose. In a later paper, Eshel and Feldman [12] present a detailed genetic model that incorporates Zahavi's idea that offspring might blackmail their parents by threatening to bring harm to themselves. They

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study a two-locus genetic model of interaction between parents and offspring in which individual offspring can advance their own reproductive interests by imposing "handicaps" on themselves; these handicaps increase the amount of resources needed to reach a given probability of survival. Eshel and Feldman find that under some conditions, this strategy of blackmail can indeed invade and resist invasion by non-blackmailing offspring. Thus they show that the fact that parents control resource allocation at the margin does not necessarily allow parents to enforce their will.

The Scope of This Paper

In the sections that follow, we address the question posed in this paper's title. That is, we ask whether evolutionary forces tend to support the Becker-Alexander position, that parent-offspring conflict will be resolved in favor of the parents' reproductive interests, or the Trivers-Dawkins position, that individual offspring can manipulate their parents to further its reproductive success at the expense of the parents' own reproductive success. In doing so, we address not only the extent of the genetic conflict between parents and offspring (the *battleground*, in

Godfray's [17] terms), but also the *resolution* of this conflict.

We have attempted to make this paper readily accessible to economists who have little or no background in evolutionary biology. Therefore we begin with a brief tutorial on two-locus genetics in Section 2. We then launch our attack on this problem by studying one of the simplest possible non-trivial examples of parent-offspring conflict, a model of weaning conflict between a mother and her first-born, in which resources can either be given to the first-born or reserved for a child who is not yet born. Because of its stark simplicity, this example is well-suited for illustrating fundamental principles of parent-offspring conflict that can be obscured in more complicated interactions among parents and their offspring.

In Section 3 we describe the model formally. We determine the weaning age that will be fixed by natural selection if first-born lambs control the weaning age unchallenged by their mothers, and the weaning age that will be fixed if mother have unchallenged control.

In Section 4 we consider a set of strategies in which mothers "offer" a certain weaning age, and offspring can either cease weaning at or before this age, or take drastic and costly action to express their dissatisfaction, bleating until they attract predators. Working within an explicit two-locus genetic framework, we consider the effects of these strategies on the survival probabilities of first-born and second-born offspring. We examine how the genetic conflict between parent and offspring will be resolved in such a system, and explore the characteristics of stable equilibrium.

Our work on this problem has been inspired by the two-locus models of parent-offspring conflict presented by Eshel and Feldman [12], and many of our results closely parallel findings in their paper. Eshel and Feldman address Zahavi's concept of the non-signalling "handicap," examining the evolution of

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strategies in which offspring actually reduce their own survival probability given any particular amount of resources. By contrast, we consider the evolution of strategies in which offspring reduce their own survival probability (to zero, in our model) if they do not get their way, but do not negatively affect their survival probability if they do get their way. Hence, at the equilibria which we consider, offspring will enjoy the maximum possible survival probability given the amount of resources received. This allows us to separate the persuasive potential of offspring "threats" from the handicap mechanism itself.

2   Elements of One-Locus and Two-Locus Genetics

In sexual diploids — all species of birds and mammals, for example — each individual has two copies of each "gene." More precisely, each individual has two (possibly identical) alleles at each genetic locus; one allele is inherited from its mother and one from its father. The allele inherited from each parent is a random draw from the parent's two alleles at the same locus. We will assume that the strategy that an offspring uses in dealing with its parents and siblings is determined by the pair of alleles at one genetic locus and that the strategy that it will pursue if it survives to adulthood is determined by the pair of alleles at another locus.

We introduce a number of definitions that will be useful in discussing evolution in populations of individuals with genetically encoded strategies.

Definition 1 *An individual is said to be* homozygous *at a given locus if its two allele copies at that locus are the same. An individual is* heterozygous *at a given locus if its two allele copies at that locus are different.*

Definition 2 *An allele is said to be* dominant *if a heterozygote with one copy of this allele expresses the same phenotype, strategy, or behavior as does a homozygote with two copies of the allele. An allele is said to be* recessive *if a heterozygote with one copy of this allele expresses the same phenotype, strategy, or behavior as does a homozygote with two copies of the* other *allele. That is, a dominant allele has its full effect even if heterozygous, whereas a recessive individual has no effect unless homozygous.*

Definition 3 *A genetic locus is said to be* monomorphic *when all individuals in the population — excepting the occasional rare mutant — have the same pair of identical alleles at this locus. A population is said to be monomorphic when it is monomorphic at all loci considered. For example, in the present model, a population will be considered monomorphic if both the locus controlling parental behavior and the locus controlling offspring behavior are monomorphic.*

Definition 4 *A dominant mutant allele will be said to* invade *a monomorphic population if it can increase in frequency when rare. More formally, a novel allele can invade if, when an arbitrarily small positive proportion of the novel*

allele is added to the original population, the average number of copies of the novel alleles that are passed on to surviving members of the adult population of the next generation exceeds the average number of copies of a normal allele that are passed on to surviving members of the adult population of the next generation.

Definition 5 *A* stable monomorphic equilibrium *is a monomorphic population that cannot be invaded by any possible rare dominant allele.*[5]

To determine the equilibrium strategies at the loci encoding juvenile and parental behavior, we will need to take into account the details of the transmission process for these alleles. Suppose an individual receives alleles A_1 and B_1, encoding parental and juvenile behavior respectively, from her mother, and alleles A_2 and B_2 from her father. What combinations of alleles A_i and B_i will she transmit to her offspring? Depending on the degree of *linkage* between the the A and B loci, she may transmit only the combinations received from her, parents, or she may — through the process of genetic recombination — transmit all possible combinations of the A_i and B_i alleles.

Definition 6 *The* recombination distance r *is a common measure of the degree of linkage between two loci; r is defined as the probability that recombination occurs between the two loci in one generation. If the alleles at the two loci are transmitted only in the combinations received from an individual's parents — A_1B_1 and A_2B_2, in the example above — the loci are said to* perfectly linked, *with a recombination distance $r = 0$. When alleles at the A and B loci assort independently — i.e., when an individual is equally likely to transmit all possible combinations A_1B_1, A_1B_2, A_2B_1, and A_2B_2 — the A and B loci are said to be* unlinked, *with a recombination distance of $r = 1/2$. When the alleles are more likely to be transmitted in the combinations received from the parents, but are not necessary transmitted only in those combinations, the loci are said to be* partially linked *with $0 < r < 1/2$. Recombination distances greater than $1/2$ are almost never observed in nature.*

The coefficient of relationship between siblings

In general, natural selection will not result in a population of individuals who simply maximize their own survival probability without
regard to the survival probabilities of their relatives. The key to understanding the evolution of behavior in games between relatives is to notice the following: a rare allele that affects the behavior of one individual is more likely

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[5]Because we define invasion to occur only when invading gene reproduces *faster* than the normals, this is weaker notion of a stable equilibrium than one which excludes "drift" among alleles that reproduce equally rapidly. It is also a weaker concept than Maynard Smith's notion of evolutionarily stable strategies since we do not impose restrictions on the case in which a mutant gene reproduces exactly as rapidly as the normal genes. Thus the equilibria studied here may not be resistant to the possibility of novel alleles reaching high frequency by drift.

to be found in close kin than it is to be found in an average member of the population. In games played among siblings, or between parents and offspring, the expected payoff to an individual with a rare allele will be influenced not only by the way that this allele changes its *own* behavior, but also by the probability that its relatives carry the same allele and behave accordingly.

Definition 7 *The* coefficient of relationship *between two relatives, which we will denote by k, is the probability that a rare allele carried by one of them will also be carried by the other.* [6]

It is instructive to work through a calculation of the coefficient of relationship between two lambs born to the same mother. Assuming that this allele is not sex-linked and does not have differential effects on survival of the two sexes, copies of the rare allele in the population are equally likely to be present in males and females. When this allele is rare and mating is random, carriers of the rare allele will almost always mate with an individual who is homozygous for the normal allele. Since offspring receive one allele from each parent, almost all carriers of the rare allele will be heterozygotes with one copy of the rare allele and one copy of the normal allele; moreover, the rare allele is equally likely to be inherited from the offspring's father or its mother.

If an offspring has inherited the rare allele from its mother, its mother's other offspring will almost certainly inherit a normal allele from its father, and this sibling is equally likely to inherit its mother's rare allele as her normal allele. Therefore the probability is $1/2$ that a copy of a maternally inherited rare allele will also be found in the mother's other offspring. If an offspring inherits the rare allele from its father and its mother's other offspring does not have the same father, then since the allele is rare, almost certainly the other offspring's father and mother both lack the rare allele and hence the sibling will not have the rare allele. If the offspring inherits the rare allele from its father and if the mother's other offspring has the same father, then the probability that the other sibling has the rare allele will be $1/2$. Let s be the probability that two offspring of the same mother also have the same father. Thus the probability that a copy of a paternally inherited rare allele will also be found in the mother's other offspring must be $s/2$. Since an offspring is equally likely to inherit the rare allele from its father or its mother, it follows that for two offspring of the same mother, the coefficient of relationship is $k = 1/2(1/2 + s/2) = (1 + s)/4$. If mating is perfectly monogamous, then $s = 1$ and $k = 1/2$. If females never mate twice with the same individual, then $s = 0$ and $k = 1/4$.

A Simplifying Assumption about Fertility

In the long run, the alleles that are found in the population will be those that mandate strategies that lead to success in reproduction. In general, the long run

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[6]A more commonly-used definition (as applied to sexual diploids) is "The coefficient of relationship between two individuals is the proportion of genes in one that are 'identical by descent' to genes present in the other." For the study of invasion of a monomorphic population by rare mutant alleles, our definition operationalizes the standard definition.

reproductive success of a gene may depend on more than the expected number of copies that it produces in the next generation. For example, an individual may be able to produce a greater number of surviving grandchildren by having fewer, but healthier and/or more cooperative children. Similarly, in the case of primogeniture, a parent may maximize the number of descendants by treating some offspring differently from others. In the models considered in this paper, we will avoid these complications by assuming the following:

Assumption 1 *The probability that an individual reaches adulthood depends only on its own actions and the actions of its parents and siblings. All individuals who survive to adulthood have the same expected number of offspring.*

The reproduction rate of an allele can be measured as the expected number of copies of each allele of its kind that are passed from a surviving adult in one generation to a surviving adult in the next generation. Since we have assumed that all individuals that survive to adulthood are equally fertile, the only variation in the reproduction rates of alleles comes from variation in the probabilities that offspring who carry these alleles will survive to adulthood. Assumption 1 allows us to determine the reproductive success of a rare allele simply by comparing the average survival probabilities of offspring that carry the rare allele with the average survival probabilities of homozygous normal offspring.

Remark 1 *Given Assumption 1, a rare dominant allele can invade a monomorphic population if and only if the average survival probability of lambs born with a single copy of the rare allele exceeds the average survival probability of lambs born with two copies of the normal allele.*

3   The Case of the Bleating Lamb

Imagine a breed of sheep in which adult females have one lamb per year and survive as adults for at most two years. A more realistic model of ovine reproduction would permit ewes to have more than two fertile seasons, in which case the analysis here would apply to the lambs born in the last two years of their mother's life.[7] These simple two-year sheep will, however, be adequate for illustrating the ideas to be discussed here.

As the first-born lamb matures, it is able to forage for itself, but it still benefits from feeding on its mother's milk. The longer that it continues to nurse, the stronger it will be when winter arrives and the more likely it will survive to adulthood. But a long period of nursing is costly to the mother. The sooner the first-born lamb is weaned, the healthier its mother will be when she

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[7]Unless female sheep have been secretly cloning themselves for some time, we would not expect to find surviving real breeds in which ewes on average have fewer than two surviving lambs per lifetime. Economists, of course, are accustomed to dealing with abstract sheep–the traditional economists' sheep, unlike a real sheep, produces wool and mutton in fixed, unalterable proportions.

gives birth to her second lamb, and the more likely the second-born will survive. In evolutionary terms, this conflict of interest between mother and lamb takes the form of a tradeoff between the survival probability of the first-born and that of the second-born lamb[8].

Let x denote the weaning age of the first-born lamb, where possible weaning ages range from a minimum of $\underline{x}$ to a maximum of $\bar{x}$. We assume that the survival probabilities of the first-born and the second-born lambs are twice-differentiable functions of x and that the survival probability of the first-born is an increasing function of x whereas the survival probability of the second-born is a decreasing function of the x. We further assume that as x increases, the first-born's marginal gain from a longer nursing period diminishes while the second-born's marginal cost from delayed weaning of the first-born increases. We assume that for a first-born who is weaned at the earliest possible age $\underline{x}$, the marginal gain in survival probability from increasing the nursing period exceeds the marginal cost of this extended weaning to its younger sibling. Finally we assume that the expected number of surviving offspring will be lower if the mother does not nurse her first-born at all, letting it die, than if she nurses it for some positive length of time. We summarize these conditions as follows.

Assumption 2 *Where x is the weaning age and $\Pi_1(x)$ and $\Pi_2(x)$ are the survival probabilities of the first-born and second-born lambs:*

i.) $\Pi_1'(x) > 0$ and $\Pi_2'(x) < 0$ for all $x \in [\underline{x}, \bar{x}]$.

ii.) $\Pi_1''(x) < 0$, and $\Pi_2''(x) < 0$ for all $x \in [\underline{x}, \bar{x}]$.

iii.) $\Pi_1'(\underline{x}) > -\Pi_2'(\underline{x})$.

iv.) $\Pi_2(\underline{x}) < \Pi_1(x) + \Pi_2(x)$ for all $x \in [\underline{x}, \bar{x}]$.

We can trace out the parametrically-generated curve which we will call the *survival probability frontier*.[9]

Definition 8 *The* survival probability frontier *is the locus of points $(\Pi_1(x), \Pi_2(x))$ where x is between $\underline{x}$ to $\bar{x}$.*

The curve AB in Figure 1 is an example of a survival probability frontier. Taking derivatives, we find that the survival probability has the following properties.

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[8]David Haig [19] describes the situation with a colorful analogy:

> "Suppose that a mother buys a milkshake to be shared among her children, but the milkshake has only a single straw. If the first
> child takes a drink and passes the remainder on to the second, and so on down the line, then the greater the consumption of each child, the fewer children receive a drink."

[9]This curve is conceptually the same as the "utility possibility frontier" that is commonly used in the theory of welfare economics.

Remark 2 *The slope of the survival probability frontier at the point $(\Pi_1(x), \Pi_2(x))$ is $\Pi_2'(x)/\Pi_1'(x)$. Assumption 2 implies that $\Pi_2'(x)/\Pi_1'(x)$ is a decreasing function of x and hence that the survival probability frontier bulges away from the origin, as in Figure 1.*

Figure 1: Survival Probability Frontier
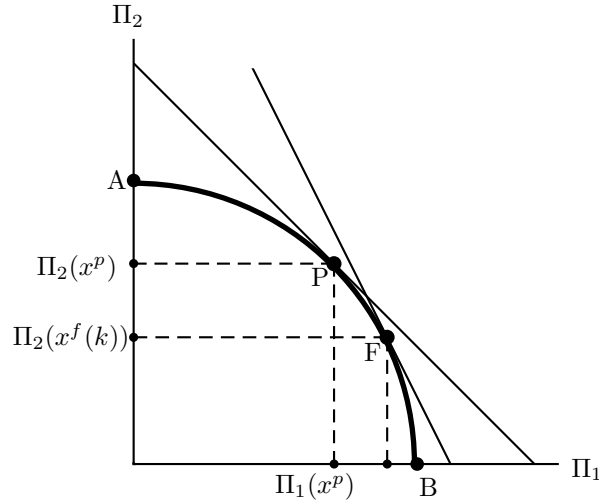
What would the first-born choose?

What age of weaning would we expect to find in a population where first-born lambs could freely dictate the age at which they will stop nursing? In this case, natural selection would operate on the genetically transmitted instructions determining the demands made by first-born lambs. We will assume that the age at which a first-born lamb allows itself to be weaned is controlled by a single genetic locus.

It will be useful to define a function H such that $H(x, v)$ is a weighted sum of the survival probabilities of the first-born and second-born lambs when the first-born is weaned at age x. Specifically, we define:

Definition 9 *For all $x \in [\underline{x}, \bar{x}]$ and $v \in [0, 1]$,*

$$H(x, v) = \Pi_1(x) + v\Pi_2(x). \tag{1}$$

It turns out that if the first-born lambs can dictate their age of weaning, the equilibrium age of weaning will be governed by a proposition that is similar to Hamilton's Rule. First-borns would act as if they valued the survival probability of their younger siblings at the fraction k of their own, where k is the coefficient or relationship between two offspring of the same mother.

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Proposition 1 *If first-born lambs are able to dictate whether they are weaned at age x or at age x' and if a single genetic locus determines the lambs' demands, then a monomorphic population in which first-born lambs demand to be weaned at x will be invaded by a dominant mutant allele which causes lambs to demand to be weaned at x', if and only if $H(x', k) > H(x, k)$ where k is the coefficient of relationship between the two offspring.*

Proof: Consider a monomorphic population in which first-born lambs who are homozygous normal will demand to be nursed until age x and suppose that there is a rare dominant allele such that the first-born who are heterozygous for this alternative allele will demand to be nursed until age $x' \neq x$. Almost every individual born with the rare allele will have one parent who is heterozygous for this allele and one who is homozygous normal. Half of the offspring who carry the rare allele will be first-born and half will be second-born lambs. All first-born carriers of the rare allele will demand to be nursed until age x' and will have survival probability $\Pi_1(x')$.

The survival probability of a second-born lamb who carries the rare allele will be $\Pi_2(x')$ if its older sibling also carries this allele and $\Pi_2(x)$ if its sibling is homozygous for the normal allele. The probability that a second-born who carries the rare allele has an older sibling who also carries this allele is (by definition) k. The survival probability of a second-born lamb who carries the rare allele is therefore $k\Pi_2(x') + (1-k)\Pi_2(x)$.

Since half of the carriers of the rare allele are first-born and half are second-born, the average survival probability of offspring who carry the rare allele will be

$$\frac{1}{2}\Pi_1(x') + \frac{1}{2}\left(k\Pi_2(x') + (1-k)\Pi_2(x)\right). \tag{2}$$

Since the alternative allele is rare, almost all copies of the normal allele are carried by homozygous normal individuals who have homozygous normal siblings. Half of them are older siblings and half are younger siblings, so the average survival probability of carriers of the normal allele is just $\frac{1}{2}\Pi_1(x') + \frac{1}{2}\Pi_2(x)$. Therefore the alternative allele for a weaning age of x' can invade the population only if

$$\frac{1}{2}\Pi_1(x') + \frac{1}{2}\left(k\Pi_2(x') + (1-k)\Pi_2(x)\right) > \frac{1}{2}\Pi_1(x) + \frac{1}{2}\Pi_2(x). \tag{3}$$

The expression in Equation 3 is equivalent to

$$\Pi_1(x') + k\Pi_2(x') > \Pi_1(x) + k\Pi_2(x). \tag{4}$$

which in turn is equivalent to $H(x', k) > H(x, k)$.
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Using Assumption 2 it is a matter of straightforward calculus to verify that for all $v \in [0, 1]$ the derivative $H_x(0, v)$ is positive and for all $x \in [\underline{x}, \bar{x}]$, the second derivative $H_{xx}(x, v)$ is negative. From simple calculus it follows that there is a unique x that maximizes $H(\cdot, v)$ on the interval $[\underline{x}, \bar{x}]$. With these facts in mind, we are entitled to make the following definition and remark.

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Definition 10 *For all $v \in [0,1]$, define $x^f(v)$ to be the age of weaning that maximizes $H(x,v)$ over all x in the interval $[\underline{x}, \bar{x}]$.*

Remark 3 *For all $v \in [0,1]$, the function $H(\cdot, v)$ is "single-peaked" in x with its peak at $x^f(v)$. That is, $H(x,v)$ is maximized at $x = x^f(v)$ and $H(x,v)$ is strictly increasing in x for $x < x^f(v)$ and strictly decreasing in x for $x > x^f(v)$.*

From Proposition 1 and Remark 3 it follows that if $x \neq x^f(k)$ a monomorphic population of lambs who demand a weaning age of x can be invaded by a dominant mutant allele that causes lambs to demand a weaning age of $x^f(k)$. Thus we conclude the following.

Proposition 2 *If first-born lambs are able to dictate the age at which they are weaned and if a lamb's choice of weaning age is determined by a single genetic locus, then in a stable monomorphic equilibrium it must be that first-born lambs demand a weaning age of $x^f(k)$ where k is the coefficient of relationship between two lambs born to the same mother.*

We can also demonstrate that if first-born lambs can dictate the age of weaning, then in equilibrium the higher the coefficient of relationship between a mother's two lambs, the earlier the first-born will choose to be weaned.

Remark 4 *Where $x^f(k)$ maximizes $H(x,k)$ on the interval $[\underline{x}, \bar{x}]$, it must be that $x^f(k)$ is a decreasing function of k.*

Proof: The first-order calculus condition for finding $x^f(k)$ is

$$H_x(x,k) = \Pi_1'(x^f(k)) + k\Pi_2'(x^f(k)) = 0 \tag{5}$$

Differentiating both sides of Equation 5 with respect to k and rearranging terms, we find that

$$\frac{d}{dk}x^f(k) = -\frac{\Pi_2'(x^f(k))}{\Pi_1''(x^f(k)) + k\Pi_2''(x^f(k))} < 0 \tag{6}$$

where the inequality follows from Assumption 2 which requires that $\Pi_2'(x) < 0$, $\Pi_1''(x^f(k)) < 0$ and $\Pi_2''(x^f(k)) < 0$.
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It is instructive to look at a geometric representation of these results. Since the point $x^f(k)$ maximizes $H(x,k) = \Pi_1(x) + k\Pi_2(x)$ on the survival possibility frontier, the first-order conditions for maximization require that the slope of the survival possibility frontier, which is

$$\frac{\Pi_2'(x^f(k))}{\Pi_1'(x^f(k))}$$

is equal to $-1/k$. This means that in Figure 1 we can find the point $F = \left(\Pi_1(x^f(k)), \Pi_2\left(x^f(k)\right)\right)$, by finding the point at which the survival possibility

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frontier is tangent to a line with slope $-1/k$. In Figure 1, we have drawn a tangent line through the point F with slope -2. This depicts the case of a monogamous species where $k = 1/2$ and $-1/k = -2$. For higher values of k, it must be that $-1/k$ is smaller in absolute value and the tangency will lie further to the left, which corresponds to lower values of x.

What Would Mothers Choose?

What age of weaning would we expect to find in a population where tough-minded ewes are able to dictate the age of weaning to their docile lambs?

The answer to this question is quite simple. Any monomorphic population in which mothers do not wean their first-born at an age that maximizes their expected number of surviving offspring can be invaded by any dominant allele for a weaning age that facilitates a higher number of surviving offspring. In particular, the following propositions are true.

Proposition 3 *If ewes are able to dictate whether their lambs are weaned at age x or at age x' and if a single genetic locus determines a ewe's weaning strategy, then a monomorphic population in which first-born lambs are weaned at x can be invaded by a dominant mutant allele for weaning at age x' if and only if $\Pi_1(x') + \Pi_2(x') > \Pi_1(x) + \Pi_2(x)$.*

From Proposition 3, it is immediate that if mother sheep can unilaterally choose the weaning age of their first-born, then the only stable monomorphic equilibrium is an outcome in which a mother weans her first-born at an age that maximizes the expected number of her own surviving offspring. That is:

Proposition 4 *If ewes are able to dictate the age at which they wean their first-born and if this action is determined by a single genetic locus, then in a stable monomorphic equilibrium it must be that mothers will wean their first-born at the age x^p where x^p maximizes $\Pi_1(x) + \Pi_2(x)$ on the interval $[\underline{x}, \bar{x}]$.*

Despite the simplicity of the answers stated in Propositions 3 and 4, we believe it is important to understand exactly why they are true. Thus we prove Proposition 3 in what may seem to be excruciating detail. The importance of proving, rather than simply asserting this result will become more apparent later when we show that if the loci for juvenile and parental behavior are tightly linked, monomorphic populations can sometimes be invaded by alleles that mandate weaning at an age that gives them a smaller expected number of surviving offspring than that enjoyed by normal mothers.

Proof of Proposition 3:

Here we assume that the ewe is able to dictate the age of weaning absolutely, without resistance from her offspring. Consequently, we need to concern ourselves only with a single genetic locus controlling the age at which mothers wean their first-born. Consider a monomorphic population in which mothers wean their offspring at age x. Suppose that to this population is added a small

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proportion of an alternative dominant allele, such that mothers heterozygous for this alternative allele wean their offspring at age x'.

As we noted in Remark 1, Assumption 1 enables us to determine whether the alternative allele can invade the population by comparing the average survival probability of lambs born with a single copy of the rare allele to that of lambs born with two copies of the normal allele.

Since the alternative allele is rare and mating is random, almost all individuals with this allele will be heterozygotes, with one copy of the alternative allele and one copy of the normal allele. A lamb who inherits the rare allele is equally likely to be a first-born or a second-born and (independently of whether it is first-born or second-born) is equally likely to inherit the allele from its mother or from its father. Thus 1/4 of all lambs fall into each of these four categories.

Since mothers who carry the alternative allele wean their offspring at age x', a first-born who inherits this allele from its mother is weaned at age x' and has survival probability of $\Pi_1(x')$. If a second-born inherits this allele from its mother, the mother will have weaned the first-born at age x' and the survival probability of the second-born must be $\Pi_2(x')$

If a lamb inherits the alternative allele from its father , then since mating is random and the alternative allele is rare, the lamb will almost certainly have a homozygous normal mother, who will wean her first-born at age x. Therefore a first-born who inherits the alternative allele from its father will have survival probability $\Pi_1(x)$ and a second-born who inherits the alternative allele from its father will have survival probability $\Pi_2(x)$.

It follows that the average survival probability of lambs born with the mutant allele is

$$\frac{1}{4}\left(\Pi_1(x') + \Pi_2(x') + \Pi_1(x) + \Pi_2(x)\right). \tag{7}$$

Since the alternative allele is rare, almost all homozygous normal offspring have homozygous normal mothers who wean their first-born at age x. These offspring are equally likely to be first-born or second-born so their average survival probability is

$$\left(\Pi_1(x) + \Pi_2(x)\right)/2 \tag{8}$$

The alternative allele for weaning at age x' will be able to invade a monomorphic population of mothers who wean at age x if and only if Expression 7 exceeds Expression 8. Subtracting Expression 8 from Expression 7 and multiplying the result by 4, we see that the rare allele will invade if and only if

$$\Pi_1(x') + \Pi_2(x') > \Pi_1(x) + \Pi_2(x). \tag{9}$$

∎

The distribution of survival probability between first-born and second-born that corresponds to a weaning age of x^p is shown on Figure 1 by the point $P = (\Pi_1(x^p), \Pi_2(x^p))$, which is the point where the slope of the survival probability frontier at P is -1.

From the definition of $H(x, v)$, we see that

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$\Pi_1(x) + \Pi_2(x) = H(x, 1)$. Therefore $x^p = x^f(1)$, and since $k < 1$, it is immediate from Remark 4 that $x^p < x^f(k)$. Therefore we can assert the following.

Proposition 5 *If mothers are able to dictate the age at which their first-born are weaned, then in stable monomorphic equilibrium, they will be weaned at an earlier age than would be the case in stable monomorphic equilibrium if first-born were able to dictate the age at which they are weaned.*

4 Resolving the Genetic Conflict

The Lamb Who Would Call Wolves

We have shown that in an equilibrium where first-born lambs could choose their age of weaning, they would choose a later date than that which would maximize the number of surviving offspring produced by their mothers. We now might follow Alexander and ask, "So what?

Mother sheep are bigger, stronger, and can run faster than their lambs. Surely the mother has the physical ability to enforce her own choice of weaning age." But, as Eshel and Feldman pointed out, the lamb is not limited to physical coercion as a means of enforcing its will and the resolution of parent-offspring conflict may not always coincide with the parent's will.

Let us explore one strategy by which first-born lambs may be able to blackmail their mothers into letting them nurse to an age $x > x^p$ where x^p is the age of weaning that mothers would dictate if they had full control of the behavior of their lambs. Suppose that first-born lambs are genetically programmed to use the following

decision rule: "Demand to be nursed until you reach age x. If you are younger than x and your mother does not let you nurse, then bleat so loudly that you will attract predators." This is by no means the only sort of strategy an offspring might use to influence its mother (for example, Eshel and Feldman [12] consider a different class of strategies that serve a similar purpose).

If a first-born lamb uses this strategy and if its mother weans it before age x, the lamb will make an awful ruckus, attract a predator, and get eaten; the mother will lose her first-born. The lamb's extortionary strategy changes the shape of the survival probability frontier in such a way that with the altered survival probability frontier, the mother will maximize her number of descendants by yielding to her first-born's demand. In Figure 2, we sketch the survival probability frontier $ABCD$ for the offspring of a sheep whose first-born lamb adopts the extortionary strategy demanding x. If the mother allows the lamb to nurse until it reaches age x (the lamb's preferred age) it will behave normally, but if the mother attempts to wean it before age x, it will bleat suicidally. The point C represents the distribution of survival probabilities $(\Pi_1(x), \Pi_2(x))$ between her two offspring if the mother accedes to the lamb's demand to be nursed until age x.

When the first-born pursues this extortionary strategy, the distribution of survival probability the mother would have chosen to maximize her expected

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Figure 2: Survival Probability Frontier with a First-born Extortionist
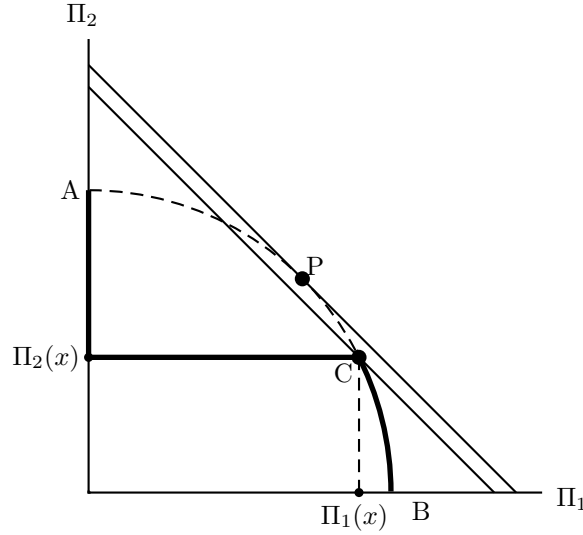
number of surviving offspring (point P in Figure 2) is longer accessible to her. Given the restricted survival probability frontier imposed by the first-born's threat, the the expected number of surviving offspring is maximized at the point $C = (\Pi_1(x), \Pi_2(x))$. We might naively generalize from our previous results to predict that this point will correspond to the only stable monomorphic equilibrium when such strategies are available

to lambs. However, we will find in the subsequent analysis that for certain degrees of linkage, this combination of offspring threat and parental acquiescence will not be a stable equilibrium.

Equilibrating Behavior of Parents and Offspring

Readers familiar with the notion of subgame perfection in game theory are likely to be skeptical that a first-born lamb's threat "Feed me or I will bleat until a wolf eats me," would be respected in equilibrium. Certainly this threat is not credible in the sense that if a rational lamb who made this threat was ignored by its mother, it would not find it in its interest to commit suicide by bleating. Rational mother sheep, in appraising this situation would realize that their rational progeny would not carry out this incredible threat and would ignore it.[10]. But even economists are likely to quail at attributing such powers of ratiocination to a sheep. Instead of making *a priori* assumptions on the mental abilities of sheep, we will posit that they are genetically programmed to

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[10]Arthur Robson relates that as a child, he once threatened to hold his breath until his mother bought him an ice cream cone. His mother, ever sensible, refused to capitulate. Given that Arthur himself now tells this story, we can infer that his threat was not particularly credible.

use strategies as lambs and adults that lead to successful reproduction of the genes that program their behaviors and we will investigate possible equilibrium outcomes. In fact, we will see that genetically programmed strategies allow players to commit to playing subgame-imperfect strategies in a manner which would not be possible for rational players.

An evolutionary model of the resolution of conflicting reproductive interests of parents and offspring requires that we specify the genetic basis of childhood behavior, and its relation to adults behavior. In this discussion, we will assume that the alleles at one genetic locus control an individual's behavior towards its parents and siblings when it is a child, and that the alleles at a second locus control its behavior as a mother. As we will show, the extent of linkage between these two loci will be crucial in determining the resolution of this conflict.

It will be useful to spell out more detailed "rules of the game" that apply in encounters between a first-born lamb and its mother. Let us assume that each day after the lamb reaches the first possible age of weaning, its mother either offers to nurse the lamb or she refuses to nurse it. If the mother offers to nurse the lamb, the lamb can either accept nursing or refuse to be nursed. If the mother refuses to nurse the lamb, it can either submit to its mother's refusal or loudly demand to be fed despite its mother's refusal.

We will simplify our task by confining our attention to a restricted class of strategies. We assume that mothers must use a strategy from a class of strategies that we call *x-offer strategies* and that lambs must use a strategy from a class of strategies that we call
x-demand strategies.

A ewe who follows an *x-offer strategy* will act according to the rule: "Offer to nurse your first-born if it is younger than x. Refuse to allow it to nurse if it is older than x ."

We consider two kinds of x-demand strategies, which differ in the action that a lamb takes if its mother offers to let it nurse beyond the age x. A lamb that uses either type of x-demand strategy will bleat and demand to be fed if its mother refuses to nurse it before it reaches age x. A lamb who follows the *greedy x-demand strategy* will continue to nurse beyond age x if its mother permits it to do so. A lamb who follows the *temperate x-demand strategy* will reject nursing after it reaches age x even if its mother would permit it to nurse.

Invasion by Separate Mutations

In this section we consider mutations that enter the population one locus at a time. We investigate in turn whether a monomorphic population can be invaded by a dominant mutant allele that alters offspring behavior, and whether a monomorphic population can be invaded by a dominant mutant allele that alters parental behavior. We do not consider the possibility that some individuals might have mutant alleles at both of these loci.

We will show that if mutations only arise in this single-locus fashion, the conflict between the genetic interests of mothers and first-born could be resolved

in many different ways. In fact any weaning age between the age x^p that maximizes $H(x, 1)$ and the age $x^f(k)$ that maximizes $H(x, k)$ could be maintained by a population that cannot be invaded by any single mutation at either locus.

Proposition 6 *For any x such that $x^p \leq x \leq x^f(k)$, a monomorphic population in which all first-born lamb use x-demand strategies and all mothers use x-offer strategies cannot be invaded by a dominant allele that mandates that first-borns use an x'-demand strategy for $x' \neq x$.*

Proof:

Let us first show that the normal population cannot be invaded by an allele that causes lambs to demand nursing until an age greater than x. Suppose that a rare allele at the locus controlling first-born behavior causes first-born lambs to use an x'-demand strategy, where $x' > x$. Since mothers all use the x-offer strategy, a first-born lamb that uses x'-strategy will be confronted with a mother who refuses to let it nurse after age x. A first-born carrying this rare allele will not be able to nurse any longer than a normal lamb, but will reduce its survival probability by bleating when its demand is refused. Whether or not its older sibling carries the rare allele, a second-born lamb who carries the rare allele will have survival probability $\Pi_2(x)$ since its mother will nurse the first-born only until age x. Thus first-born carriers of the mutant allele have lower survival probability than first-borns with two normal alleles and second-born carriers of the mutant allele will have the same survival probability as normals. It follows that on average, carriers of the mutant allele will have lower survival probability than normals and hence this mutant allele cannot invade.

Next we show that the normal population cannot be invaded by an allele that causes first-born lambs to accept weaning before age x. Suppose that such an allele causes lambs to use an x'-demand strategy where $x' < x$. We will show that neither a greedy x'-demand strategy nor a temperate x'-demand strategy can invade. Since its mother would offer to nurse it until age x, a first-born lamb carrying a dominant allele for the greedy x'-demand strategy would be offered — and would accept — the opportunity to nurse until the normal age x. Therefore both first-born and second-born carriers of this allele would have exactly the same survival probability as first-borns and second-borns in the normal population and could not invade.[11] A first-born lamb with a dominant allele for the temperate x'-demand strategy would be offered the chance to nurse until age x but would stop nursing at age x'. Since $x' < x < x^f(k)$, it follows from Remark 3 that $H(x', k) < H(x, k)$ and therefore Proposition 1 implies that the allele for a temperate x'-demand strategy cannot invade the original population. ∎

Proposition 7 *For any x such that $x^p \leq x \leq x^f(k)$, a monomorphic population in which all first-born lambs use x-demand strategies and in which all*

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[11]Recall that by our definition, a mutant allele can invade only if it reproduces *faster* than normal alleles.

mothers use x-offer strategies, cannot be invaded by a dominant allele that mandates that mothers use an x'-offer strategy for $x' \neq x$.

Proof: We first show that the normal population cannot be invaded by an allele that causes mothers to refuse nursing to their first-born before they reach age x. Suppose that a rare allele at the locus controlling maternal behavior causes mothers to use an x'-offer strategy where $x' < x$. If a lamb inherits the rare allele from its father, it will almost surely have a normal mother and hence will have the same survival probability as normal lambs. But suppose

that a lamb inherits the mutant allele from its mother. Since all lambs use x-demand strategies, a first-born lamb that carries the rare allele for maternal behavior will surely die. Since whether or not her first-born inherits the rare allele, the mother nurses the first-born until age x', it must be that any second-born lamb who inherits the rare allele from its mother has survival probability $\Pi_2(x')$. Therefore the average survival probability of lambs who inherit the rare allele from their mother is $\Pi_2(x')/2$. But Assumption 2 implies $\Pi_2(x')/2 < \Pi_1(x) + \Pi_2(x)$. Since half of the lambs who carry the rare allele receive it from their fathers and half receive it from their mothers, the average survival probability of lambs who inherit the rare allele must be lower than that of lambs born to two normal parents.

We next show that the normal population cannot be invaded by an allele that causes mothers to offer nursing to lambs older than age x. Suppose that such an allele mandates x'-offer strategies by mothers where $x' > x > x^p$. If a lamb inherits the rare allele from its father it will almost surely have a normal mother and hence will have the same survival probability as normal lambs. First-born lambs using temperate x-demand strategies will refuse to nurse after age x and hence they and their second-born siblings will have the same survival probabilities as the offspring of normal mothers. First-born lambs who use greedy x-demand will have survival probability $\Pi_1(x')$, while their younger siblings will have survival probabilities $\Pi_2(x')$. The average survival probability of offspring who use the greedy x'-demand strategy and who inherit an allele for the maternal x'-offer strategy from their mothers is therefore $(\Pi_1(x') + \Pi_2(x'))/2$. Since $x' > x > x^p$, it follows from Assumption 3 that $(\Pi_1(x') + \Pi_2(x'))/2 < (\Pi_1(x) + \Pi_2(x))/2$. Therefore it must be that the average survival probability of lambs who carry the rare allele for maternal behavior is lower than that of lambs who have two normal parents.

∎

In this section, we have shown that if the loci controlling parental and offspring behavior are unlinked and if mutations occur only in one locus at a time, there will be equilibria that sustain any weaning age x such that $x^p < x < x^f(k)$. Thus the range of possible genetic resolutions to the conflict of interest between parent and offspring is no narrower than the extent of the conflict itself. In the following sections, we will show that when the loci are linked, tighter bounds are placed on the resolution of this parent-offspring conflict and the more closely the loci are linked, the more closely the possible genetic resolutions coincide

with the outcome that maximizes the mother's expected number of surviving offspring.

Perfectly Linked Loci

Suppose that the genetic locus controlling the nursing demands of first-born lambs and the locus controlling the nursing offers of mothers are perfectly linked. In this case the genetics of parent-offspring interaction can be modeled as if a single locus controls a sheep's behavior both when it finds itself cast in the role of a first-born lamb, and when it finds itself cast in the role of a mother.

Let us define an allele that would lead sheep to behave in accord with Alexander's view that, in equilibrium, offspring will act in their parents' reproductive interests. We will call this allele an *Alexandrian allele*, a sheep who carries this allele an *Alexandrian sheep* and a lamb who carries this allele an *Alexandrian lamb*. Formally, an Alexandrian allele instructs lambs to use the greedy $\underline{x}$ strategy and mothers to offer to nurse their first-born only until they reach the maternal optimal age x^p. Notice that an Alexandrian lamb never demands to nurse unless its mother offers, and it always accepts nursing if offered. In a monomorphic population of Alexandrian sheep, all lambs would be weaned at age x^p.

Where linkage is perfect, we have a striking result. Any monomorphic population in which lambs are not weaned at age x^p can be invaded by the Alexandrian allele. Conversely, in a monomorphic population of Alexandrian sheep, all lambs are weaned at age x^p, and this population cannot be invaded by alleles for alternative strategies by lambs and/or ewes.

Proposition 8 *With perfect linkage, any monomorphic population in which lambs use x-demand strategies and ewes use x-offer strategies where $x \neq x^p$ can be invaded by a dominant Alexandrian allele. Conversely, a monomorphic population of Alexandrian sheep cannot be invaded by mutants using x^l-demand strategies as lambs and x^e-offer strategies as ewes.*

Proof:

Suppose that a mutant Alexandrian allele arises in a monomorphic population in which lambs use x-demand strategies and ewes use x-offer strategies.

If a first-born lamb inherits the Alexandrian allele from its mother, then the mother will be using an x^p-offer strategy and so the lamb will be weaned at age x^p and have survival probability $\Pi_1(x^p)$. If a second-born lamb inherits the Alexandrian allele from its mother, then the mother will wean its older sibling no later than x^p (possibly earlier, if in the original population the older sibling is a temperate x demander and $x < x^p$) and so the survival probability of the younger sibling will be at least $\Pi_2(x^p)$. Since a lamb inheriting the rare allele from its mother is equally likely to be first-born or second-born, the average survival probability of lambs that inherit the rare Alexandrian allele from their mothers is at least $(\Pi_1(x^p) + \Pi_2(x^p))/2$.

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If a first-born lamb inherits the rare Alexandrian allele from its father, then its mother almost certainly will be homozygous normal and will use an x-offer strategy. A first-born lamb who inherits the Alexandrian allele from its father will be offered nursing until age x by its normal mother. Since an Alexandrian lamb accepts exactly what its mother offers, a first-born who inherits the rare allele from its father will be weaned at age x and have survival probability $\Pi_1(x)$. Since the first-born is weaned at age x, regardless of whether it carries an Alexandrian allele or two normal alleles, the second-born will have survival probability $\Pi_2(x)$. Therefore the average survival probability of lambs that inherit the rare Alexandrian allele from their fathers is $(\Pi_1(x) + \Pi_2(x))/2$.

A lamb that is born with the rare Alexandrian allele is equally likely to have inherited this allele from its mother or from its father. Therefore the average survival probability of lambs that carry the rare allele is:

$$\frac{1}{4}\left(\Pi_1(x^p) + \Pi_2(x^p) + \Pi_1(x) + \Pi_2(x)\right) \tag{10}$$

Since the average survival probability of normal first-born lambs is

$$\left(\Pi_1(x) + \Pi_2(x)\right)/2, \tag{11}$$

the Alexandrian allele will be able to invade the normal population if Expression 10 exceeds Expression 11. Subtracting the latter expression from the former and multiplying by 4, we see that this is equivalent to

$$\Pi_1(x^p) + \Pi_2(x^p) > \Pi_1(x) + \Pi_2(x) \tag{12}$$

which is always true since x^p strictly maximizes $\Pi_1(x^p) + \Pi_2(x^p)$. It follows that the Alexandrian allele can always invade the original population

Verifying the converse statement is straightforward.

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Partially Linked Loci

Suppose that behavior of first-born lambs and behavior of mothers are controlled by two partially linked loci separated by a recombination distance of r, where $0 < r \leq 1/2$. Consider a monomorphic population of sheep in which all first-borns are weaned at age $x^p < x < x^f(r)$. As we have demonstrated, if the two loci are perfectly linked, this population can be invaded by an Alexandrian allele. Even if the two loci are not perfectly linked, it is still possible in principle that the original monomorphic population can be invaded by a pair of offspring-strategy and parent-strategy alleles which encode Alexandrian behavior. In the presence of recombination, however, not all of the double-mutants — we call them *double heterozygotes* — will breed true. When genetic variation is found at only one locus, half of the offspring of an individual who carries a rare allele will inherit the rare allele. When variation is found at two loci and the recombination distance is r, only the fraction $(1-r)/2$ of the offspring of a

double heterozygote parent will inherit both rare alleles. Even if those offspring who have a mutation in a single locus are less likely to survive than homozygous normal offspring, the proportion of double heterozygotes in the population can increase if $(1 - r)$ times the average survival probability of double heterozygote offspring exceeds survival probability of normal individuals.[12] In the case of unlinked loci, where $r = 1/2$, this would mean that the double heterozygote could invade if the survival probability of double heterozygote offspring was more than twice as large as that of normal individuals.

Using essentially the same argument used to prove Proposition 8, we can prove the following.

Proposition 9 *Suppose that the nursing demand strategies of first-born lambs and the nursing offer strategies of ewes are controlled by two genetic loci which have a recombination fraction r. Then if $(1 - r)\left(\Pi_1(x^p) + \Pi_2(x^p)\right) > \Pi_1(x) + \Pi_2(x)$, a monomorphic population where first-borns use x-demand strategies and mothers use x-offer strategies can be invaded by a double*

heterozygote with a dominant pair of mutations encoding Alexandrian behavior.

Mothers Don't Always Seek to Maximize Expected Number of Surviving Offspring

In our discussion of "What would mothers choose?", we promised to show that when the genetic locus that controls juvenile behavior is linked to the locus that controls maternal behavior, it cannot automatically be assumed that selection will favor maternal behavior that maximizes the number of the mother's surviving offspring. Where a single locus controls the behavior of first-born lambs and of ewes, as in the previous section, consider a monomorphic population in which normal first-born lambs pursue x-demand strategies and normal mothers pursue x-offer strategies, where $x > x^p$. The expected number of surviving offspring that a normal mother will have is $\Pi_1(x) + \Pi_2(x)$. Now consider a rare dominant allele that mandates that first-born lambs use the greedy x^p-demand strategy and that mothers use the x^p-offer strategy. If a mother carries a copy of the rare allele, then the probability is $1/2$ that her first-born will inherit the rare allele and the probability is $1/2$ that it will inherit the normal allele. If her first-born inherits the rare allele, it will use the x^p strategy and its survival probability will be $\Pi_1(x^p)$, but if the lamb does not inherit the rare allele, it uses the x strategy and since its mother will refuse to nurse it beyond age x^p, the lamb will not survive. In either case, the mother weans her first-born at age x^p and so the survival probability of the second-born is $\Pi_2(x^p)$. It follows that

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[12]While it is true that some double heterozygotes are formed by from single heterozygotes by recombination when $r > 0$,

it turns out that when both single and double heterozygotes are rare and when selection acts against the all single heterozygotes, such recombination events have a negligible effect on the growth rate of the proportion of double heterozygotes.

the expected number of surviving offspring that this mother produces will be

$$\frac{1}{2}\Pi_1(x^p) + \Pi_2(x^p).$$

As we know from Proposition 8, the allele for x^p-demand and x^p-supply strategies will invade the original monomorphic population. But while they are rare, mothers who carry the mutant allele will have a smaller expected number of surviving offspring than normals (at least if x is sufficiently close to x^p). We can see this as follows. The difference between the expected number of surviving offspring of a normal mother and a mother with the mutant allele is

$$\Pi_1(x) + \Pi_2(x) - \left(\frac{\Pi_1(x^p)}{2} + \Pi_2(x^p)\right) \tag{13}$$

Since $x > x^p$, the Expression 13 will have the same sign as

$$\frac{\Pi_1(x) - \Pi_1(x^p)}{x - x^p} + \frac{\Pi_2(x) - \Pi_2(x^p)}{x - x^p} - \frac{\Pi_1(x^p)}{2(x - x^p)} \tag{14}$$

In the limit as $x \to x^p$, the first two terms of Expression 14 approach respectively $\Pi_1'(x^p)$ and $\Pi_2'(x^p)$, both of which are finite, while the third term approaches minus infinity. This implies that for x sufficiently close to x^p, the expected number of surviving offspring of mothers with the rare allele is lower than that of normal mothers.

How can the rare allele invade, even though mothers who carry this allele have fewer expected surviving offspring than normal mothers? The answer is simple and instructive. Although mothers who carry the rare allele, unlike normal mothers, lose half of their first-born to wolves, the offspring that are lost to wolves do not carry the mutant allele. In fact the number of her surviving offspring who carry the rare allele is $(\Pi_1(x^p) + \Pi_2(x^p))/2$. Hence the expected number of copies of her rare allele which are passed to surviving adults in the next generation is also $(\Pi_1(x^p) + \Pi_2(x^p))/2$. This exceeds the number of copies $(\Pi_1(x) + \Pi_2(x))/2$ of a normal allele that are passed from one generation to the next.

5   Conclusions

There is much to be learned from our simple pastoral fable of weaning conflict. We began by posing a pair of hypothetical questions. At one extreme, at what age will first-born lambs be weaned if mothers have no control of the weaning age and natural selection operates exclusively on the age at which first-borns choose to wean themselves? At the other, at what age will first-born lambs be weaned if mothers have unchallenged control over weaning age and natural selection acts exclusively on the weaning age that mothers choose?

In this model, the answers to both questions turn out to be answers that would be predicted by users of Hamilton's rule. If first-born lambs could choose,

they would pick the age of weaning that maximizes a weighted average of their own survival probability and that of their younger siblings. Here, the relative weight placed on the younger sibling is simply the coefficient of relationship between a mother's two lambs. If mothers could choose, they would pick the age of weaning that maximizes an equally weighted average of survival

probabilities of first and second born. The weaning age $x^f(k)$ that the first-born would choose is always greater than the age x^p that ewes would choose.

The answers to these questions define the extent of the genetic conflict over weaning age. How will this conflict be resolved? We find that the answer to *this* question depends on the strategies available to mother and offspring, and on the details of the process by which these strategies are inherited. We first considered the possibility of unilateral change in offspring strategies or maternal strategies. We found that there is a large class of monomorphic equilibria that cannot be invaded unilaterally by mutant alleles at the locus that controls the behavior of lambs, or by mutants at the locus controlling the behavior of mothers. Such equilibria support any age of weaning x between the parental optimum x^p and the offspring optimum $x^f(k)$. Thus if single-locus mutations were the only kind observed, there would be little theoretical support for the Alexander view that natural selection would inevitably result in the outcome x^p that maximizes the reproductive interests of the mother.

Two-locus genetic models, however, allow the possibility that novel pairs of maternal and offspring strategies can invade in association with one another. We found that this possibility gives more support to the Alexander-Becker viewpoint. If the genetic loci that control behavior of first-born and behavior of mothers are perfectly linked, then the Alexander-Becker view is dramatically vindicated. The

only outcome that can be a monomorphic equilibrium is the one in which mothers are able to enforce their will, i.e., in which first-born are weaned at their mothers' preferred outcome x^p. In intermediate cases, where linkage is not perfect, we have intermediate results. The greater the probability that genetic recombination will break up allele combinations at maternal and offspring strategy loci, the further the equilibria can stray from the mothers' preferred outcome. For sufficiently loose linkage, the Alexander-Becker position again collapses and we find that every weaning age between x^p and $x^f(r)$ can be an equilibrium.

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