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Dividing the Child

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Abstract

The evolution of genomic imprinting is viewed as a problem of economic optimization that is analyzed using the tools of evolutionary game theory. We specifically consider genetic conflicts over the allocation of maternal resources between present and future offspring. Five sets of genes, with the same interests within sets but distinct interests between sets, are considered as agents: maternal alleles (*Mater*), paternal alleles (*Pater*), unimprinted offspring alleles (*Filius*), and imprinted offspring alleles of maternal and paternal origin (*Matris* and *Patris*). Fitness functions are derived for each agent and the parameter space in which there is conflict defined. Three potential conflicts are considered: between mother and offspring (*Mater* v.s. *Filius*); between alleles of maternal and paternal origin within offspring (*Matris* v.s. *Patris*) and between mothers and the paternally derived alleles of offspring (*Mater* v.s. *Patris*).

They bought in a sword and the king gave the order:
'Cut the living child in two and give half to one and half to the other.'
First Book of Kings, New English Bible

The kinship theory of genomic imprinting

A gene that has a different pattern of expression depending on whether it is inherited via a sperm or an egg is said to be imprinted (Reik & Walter, 2001b). Haig and Westoby (1989) proposed that imprinting has evolved because what is 'best' for a gene when inherited via one kind of gamete may be different from what is 'best' for that gene when inherited via the other kind of gamete. Specifically, a conflict may arise when a gene's expression in one individual has fitness consequences for other individuals who have different probabilities of carrying a copy of the first individual's maternally and paternally derived alleles. Haig (1997, 2000b) argued that an imprinted gene's effects when it is maternally derived will evolve to maximize its carriers' matrilineal inclusive fitness (calculated using coefficients of matrilineal relatedness) whereas the gene's effects when paternally derived will evolve to maximize their patrilineal inclusive fitness (calculated using coefficients of patrilineal relatedness). This hypothesis has been called the kinship theory of genomic imprinting (Trivers & Burt, 1999).

The kinship theory has been developed mainly in the context of genes that are expressed in offspring and influence the level of resources extracted from mothers, but the theory's underlying logic applies to all interactions among kin (Haig, 2000a,b). This paper will focus on the simple case of parent–offspring relations. Haig and Graham (1991) argued that paternally derived alleles of offspring will be selected to favor a greater transfer of resources from mothers than will maternally derived alleles of the same offspring. Therefore, they proposed that imprinted genes that function to increase the allocation of resources from mother to offspring (hereafter *resource enhancer* or RE loci) will be silent when maternally derived, whereas imprinted genes that reduce the transfer of resources from the mother (hereafter *resource inhibitor* or RI loci) will be silent when paternally derived.

The spread of an RE allele that has increased expression when paternally derived makes possible the

spread of another RE allele with reduced expression when maternally derived or an RI allele with increased expression (Haig & Westoby, 1989; Wilkins & Haig, 2001). Thus, genomic imprinting fits Hurst, Atlan and Bengtsson's (1996) definition of a genetic conflict as occurring when 'the spread of one gene creates the context for the spread of another gene, expressed in the same individual, and having the opposite effect.' At an imprinted locus however, an allele that has high expression in one generation, because it is paternally derived, is the same allele that has low expression in another generation, because it is maternally derived. In what sense can an allele be in conflict with itself?

A useful way to think about this 'conflict' is to view the alleles as strategists in an evolutionary game. Each allele adopts a conditional strategy: do one thing when transmitted by an egg; do something else when transmitted by a sperm. In the game played by the two alleles at a diploid locus, the allele transmitted by the mother plays one role using its egg-transmitted strategy while the allele transmitted by the father plays the opponent's role using its sperm-transmitted strategy. An allele can swap roles in each generation playing the two roles with equal frequency. Such games belong to a class of games called *role games* by Hofbauer and Sigmund (1998). This game can be viewed from two perspectives: either as phenotypic 'conflict' between alleles playing maternal and paternal roles, or as genotypic 'competition' between strategies that are tested in both roles (Haig, 1997).

Evolutionary game theory has close conceptual parallels to economic game theory, and it is convenient to view the relation between alleles with divergent interests as an interaction between rational agents, each striving to maximize an economic pay-off. In evolutionary games, the economic pay-off is fitness and it is natural selection, rather than reason, that chooses among strategies.

Five genetic agents will be considered that group together genes with a common set of interests and that will take the place of *Homo economicus* in classical economics. These are *Mater economica* (genes expressed in mothers), *Pater economicus* (genes expressed in fathers), *Filius economicus* (unimprinted genes expressed in offspring), and two agents that result from 'dividing the child,' *Filius matris economicus* (imprinted genes of offspring in their maternal role) and *Filius patris economicus* (imprinted genes of offspring in their paternal role; Figure 1). These agents correspond to Haig's (1996) distinction between maternal, paternal, unimprinted offspring, madumnal, and padumnal alleles. For the sake of brevity, they will be referred to as *Mater*, *Pater*, *Filius*, *Matris*, and *Patris*.

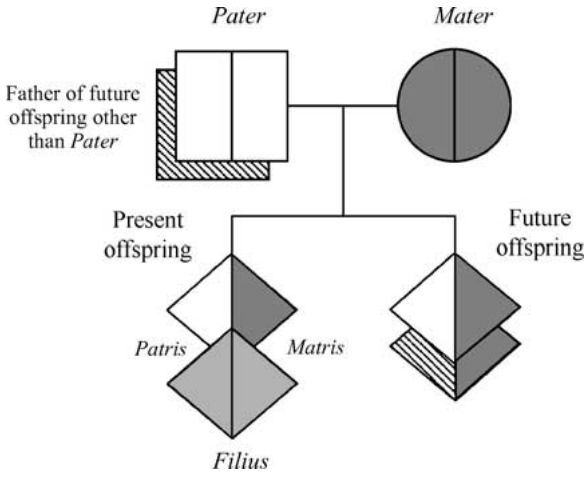


Figure 1. Identity of agents. *Mater*: genes expressed in the mother. *Pater*: genes expressed in the father of the present offspring and in the father of future offspring if the female does not change partner. Note that all offspring are maternal siblings. *Filius*: unimprinted gene expressed in the present offspring. *Matris*: imprinted allele inherited from the mother expressed in the present offspring. *Patris*: imprinted allele inherited from the father expressed in the present offspring.

Mater versus *Filius*

Conflict between *Mater* and *Filius* will be considered in the context of interbrood competition, that is, indirect competition between sequentially produced offspring mediated via demands made on the mother by current offspring (Parker & MacNair, 1978). This is an example of what Mock and Parker (1997) have called a *hierarchy* model of sibling rivalry: consumption by current offspring presents subsequent offspring with a *fait accompli*, but future offspring are unable to influence consumption of current offspring. Models of intrabrood (or scramble) competition (MacNair & Parker, 1979; Mock & Parker, 1997), in which simultaneous offspring compete for maternal resources, will have a different structure although similar conflicts arise (Haig, 1992; Haig & Wilkins, 2000).

Given a constrained resource budget, *Mater* is faced with the problem of how much to invest in the current offspring and how much to retain for future reproduction. *Filius* also has an interest in how these resources are divided between the current offspring and its future maternal sibs, but *Mater* and *Filius*

disagree on the appropriate weights to assign to returns on the two kinds of investment. Trivers (1974) was the first to describe their underlying conflict of interests. For *Mater*, expected returns from current and future offspring are assigned equal weight, because each allele at a maternal locus has an equal chance of being transmitted to each offspring. For *Filius*, returns from current offspring are given greater weight than returns from future offspring, because an allele of *Filius* is definitely present in the current offspring but has a lower probability, equal to the coefficient of relatedness among siblings r, of being present in future offspring.

Following Wilkins and Haig (2001), let the amount of resources that an offspring gets from its mother, G, be an increasing function of X, the amount of RE produced by the offspring, where $G(X)$ is subject to diminishing returns: $\partial G/\partial X = G_X > 0$, $\partial^2 G/\partial X^2 < 0$. $G(X)$ is assumed to affect both the fitness of the current offspring, $U(G)$, but also the aggregate fitness of the mother's future offspring, $V(G)$. Specifically, an increase in G is assumed to have a marginal benefit for the present offspring ($U_G > 0$) but a marginal cost for the mother's residual reproductive value ($V_G < 0$). Thus, *Mater*'s and *Filius*' fitness functions are

$$W_{\mathrm{M}} = 1/2\, U(G(X)) + 1/2\, V(G(X)) \tag{1a}$$

$$W_{\mathrm{F}} = U(G(X)) + r V(G(X)) \tag{1b}$$

Mater does not directly control X, the production of RE by the current offspring, but she may be able to otherwise influence G, the amount of resources the offspring receives. If *Mater* were able to control the allocation of resources independently of X, that is, $G_X = 0$ for all X, she would be selected to follow the strategy that maximizes W_{M}. Such a strategy will satisfy the condition

$$U_G = -V_G \tag{2a}$$

That is, the marginal benefit of extra resources for the present offspring (U_G) will equal the marginal cost to future offspring ($-V_G$).

By contrast, if *Filius* were able to dictate the distribution of maternal resources by his own production of RE, he would be selected to follow a strategy that maximizes W_{F} and satisfies

$$U_G = -r V_G \tag{2b}$$

Whenever $r < |U_G/V_G| < 1$, *Mater* has incentives to reduce G, because her marginal fitness is negative ($\partial W_{\mathrm{M}}/\partial G < 0$), whereas *Filius* has incentives to increase G, because his marginal fitness is positive ($\partial W_{\mathrm{F}}/\partial G > 0$) (Figure 2).

Equations (2a) and (2b) specify what *Mater* and *Filius* would choose if they had complete control over the allocation of resources to current versus future offspring, and a comparison between their 'best' choices identifies a conflict of interests. However, the model has little to say about what allocation would actually be made given that *Mater* and *Filius* disagree. In the terminology of Godfray (1995), Trivers' (1974) model of parent–offspring conflict is a *battleground* model rather than a model of *conflict resolution*.

Matris versus *Patris*

Battleground model

Trivers' treatment of *Filius* as a unitary agent implicitly assumed that genes retain no information about their parental origin. If such information were available, alleles that made strategic decisions, contingent on their parental origin, would be able to outcompete alleles that did not use this information (Haig, 1992). *Filius* would split into opposing factions, *Matris* and *Patris*.

In Trivers' model, r was the probability that a randomly chosen allele of *Filius* would be present in a future offspring of *Mater*. This probability is a half for a maternally derived allele and $p/2$ for a paternally derived allele, where p is *Pater*'s probability of being the father of *Mater*'s future offspring ($0 \leq p \leq 1$). Since a randomly chosen allele is equally likely to be maternally derived or paternally derived, r is simply the average of these two probabilities. That is, $r = (1/2 + p/2)/2$, which is less than half whenever $p < 1$.

Filius is the appropriate agent when considering alleles at unimprinted loci but the separate interests of *Matris* and *Patris* must be considered at imprinted loci because their fitness functions differ in the weight attached to maternal residual reproductive value, $V(G)$. In this case, the parent-specific relatednesses – one half for *Matris*; $p/2$ for *Patris* – replace r in Equation (1b).

$$W_{\mathrm{m}} = U(G(X)) + 1/2\, V(G(X)) \tag{3a}$$

$$W_{\mathrm{p}} = U(G(X)) + p/2\, V(G(X)) \tag{3b}$$

The second term on the right-hand side of (3a) is the contribution to W_{m} from the mother's residual reproductive value. The corresponding term in (3b) is the

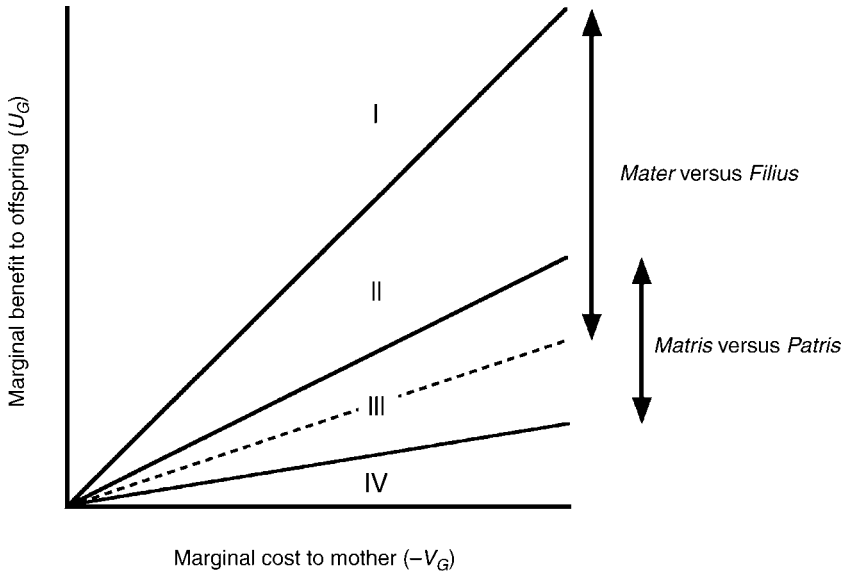


Figure 2. An agent's fitness is maximized ($\partial W/\partial G = 0$, $\partial^2 W/\partial G^2 < 0$) when $-U_G/V_G = k$. This will occur at some point on a line of slope k that passes through the origin on the $(U_G, -V_G)$-plane: for $-U_G/V_G > k$ (points to the left of the line), fitness would be enhanced by increased resources, whereas, for $-U_G/V_G < k$ (points to the right of the line), fitness would be enhanced by decreased resources. The value of k differs for different agents: for *Mater*, $k = 1$; for *Matris*, $k = 1/2$; and for *Patris*, $k = p/2$. Therefore, these values of k divide the plane into four regions. In region I ($-U_G/V_G > 1$), *Mater*, *Matris* and *Patris* would all benefit from increased resources, whereas, in region IV ($-U_G/V_G < p/2$), they would all benefit from decreased resources, Conflicts occur in regions II and III. In region II ($1 > -U_G/V_G > 1/2$), *Mater* would benefit from decreased resources but *Matris* and *Patris* would benefit from increased resources. In region III ($1/2 > -U_G/V_G > p/2$), *Mater* and *Matris* would benefit from decreased resources but *Patris* would benefit from increased resources. In the traditional theory of parent–offspring conflict, *Matris* and *Patris* are united in a single agent *Filius* whose k-value is the average of their respective values (represented by the dashed line).

contribution to W_p from the father's residual reproductive value (Lessells & Parker, 1999). These terms differ whenever $p < 1$, in which case *Matris* will favor smaller X and, consequently, greater allocation to future offspring.

Let x_m be the amount of RE produced by alleles of maternal origin and x_p be the amount produced by alleles of paternal origin. Then, the total production of RE by the current offspring will be $X = x_m + x_p$. *Matris* can control x_m but not x_p. If she were to have her own way, she would employ a strategy that maximizes W_m. Such a strategy would satisfy

$$U_G = -1/2\, V_G \tag{4a}$$

Patris can control x_p but not x_m. If he were to have his way, he would adopt a strategy that maximizes W_p and satisfies $\partial W_p/\partial x_p = 0$ which implies

$$U_G = -p/2\, V_G \tag{4b}$$

Clearly *Matris* and *Patris* cannot both get their way, except when $p = 1$. Whenever $p/2 < |U_G/V_G| < 1/2$, *Patris* has an incentive to increase his contribution to X, and hence increase G, because $\partial W_p/\partial G > 0$, whereas *Matris* has an incentive to reduce her contribution to X, and reduce G, because $\partial W_m/\partial G < 0$. The smaller the value of p (e.g., the more frequently females change partners) the greater the range of $|U_G/V_G|$ over which *Matris* and *Patris* disagree. How this conflict is likely to be resolved is discussed in the next section.

Figure 2 divides the space of $|U_G/V_G|$ for different values of p into four regions. Within region I ($|U_G/V_G| > 1$), *Matris*, *Patris*, and *Mater* would all agree to allocate more resources to future offspring. Within region II ($1/2 < |U_G/V_G| < 1$), *Matris* and *Patris* would both favor greater allocation in the current offspring but *Mater* would favor less. Within region III ($p/2 < |U_G/V_G| < 1/2$), *Patris* would favor greater allocation to the current offspring but *Mater* and *Matris* would favor less. Finally, within region IV ($|U_G/V_G| < p/2$), all three agents would agree to allocate more resources to the current offspring.

Resolution model

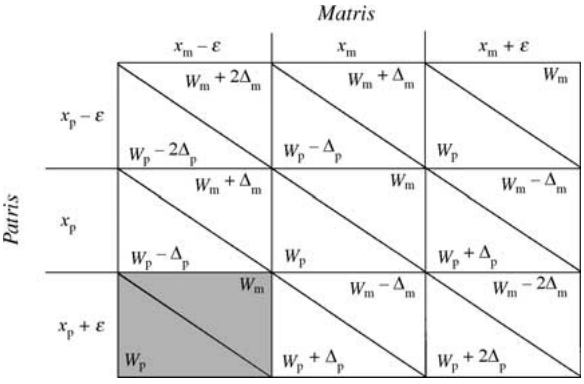
Battleground models identify conflicts of interest but do not predict outcomes; this task is left to

resolution models (Godfray, 1995). When conflict between *Matris* and *Patris* is restricted to expression levels at a single locus, Haig (1996) identified a simple principle for the resolution of their conflict: the *loudest voice prevails*. Consider the conflict between *Matris* and *Patris* over the level of expression at an RE locus. *Matris* favors a lower level of gene product than *Patris*. The conflict is resolved when *Matris* is silent and *Patris* produces his optimal amount $\hat{X}_p$ (Haig, 1996; Mochizuki, Takeda & Iwasa, 1996), because neither agent then has an incentive to change his or her level of expression. That is, $x_m = 0$ in the maternal role and $x_p = \hat{X}_p$ in the paternal role constitute an evolutionary stable strategy (ESS).

Let $\{x_m, x_p\}$ represent an allele's level of expression when transmitted through egg and sperm, respectively. Assume that mutation introduces a set of rare strategies $\{x_m \pm \varepsilon, x_p \pm \varepsilon\}$ into a population in which most alleles employ strategy $\{x_m, x_p\}$. If $X = x_m + x_p$ lies within the zone of conflict (region III of Figure 2), then the payoffs for all pairwise interactions between maternally and paternally derived alleles are summarized in Table 1. Alleles that play $x_m - \varepsilon$ when having a maternal origin will do better than alleles that play x_m in the same circumstance. Conversely, alleles that play $x_p + \varepsilon$ when having a paternal origin will do better than alleles that play x_p. Therefore, $\{x_m - \varepsilon, x_p + \varepsilon\}$ is the best strategy within the neighborhood of $\{x_m, x_p\}$ and will displace the latter strategy from the population. In other words, within the zone of conflict, *Matris* benefits from reducing her level of expression but *Patris* benefits from increasing his.

Let $x'_m = x_m - \varepsilon$ and $x'_p = x_p + \varepsilon$. A consequence of the pay-off matrix of Table 1 is the strategy $\{x'_m, x'_p\}$ will increase to fixation in a population in which most alleles initially adopted $\{x_m, x_p\}$. As long as $\{x'_m, x'_p\}$ remains within the zone of conflict, the game can be redefined with $\{x'_m, x'_p\}$ replacing $\{x_m, x_p\}$ as the central cell of Table 1 and mutation introducing a new set of variant strategies $\{x'_m \pm \varepsilon, x'_p \pm \varepsilon\}$. Natural selection will favor further decreases in maternal production and matching increases in paternal production. However, once x_m is reduced to zero, the only alternative strategies available to *Matris* involve an increase in x_m and decreased pay-off, whereas *Patris* can still benefit from increments in his expression until he achieves his optimum $\hat{X}_p$. When it is adopted by most individuals in a population, $\{0, \hat{X}_p\}$ is an unbeatable strategy that has higher fitness pay-off than any rare alternative strategy.

Table 1. The production of a resource enhancer is considered as a game among *Matris* and *Patris*[a]



[a] Originally $1 > p > 0$, $x_m > 0$, $x_p > 0$ and $X = x_m + x_p$ belongs to the interval $1/2 < -U_G/V_G < p/2$. $\varepsilon > 0$ is small. *Patris* payoffs appear in the lower-left corner of each cell while *Matris* payoffs appear in the upper-right corner. W_p and W_m are the fitness of *Patris* and *Matris* corresponding to production x_m and x_p. Δ_m and Δ_p are the absolute value of changes in matrilineal and patrilineal fitness associated with the change in expression ε. The shadowed region corresponds to the evolutionary stable strategy.

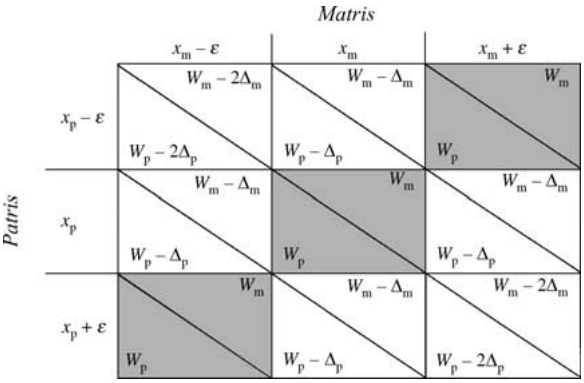
Strict life-time monandry

If $p = 1$, *Matris* and *Patris* have identical fitness functions with an optimal level of RE, X^*, that verifies $|U_G/V_G| = 1/2$. Under this circumstance, any strategy $\{x_m, x_p\}$ for which $x_m + x_p = X^*$ is an ESS. This condition defines a set of potential ESSs that is bounded by $\{X^*, 0\}$ and $\{0, X^*\}$ and corresponds to a line of neutral equilibria that is represented by the shaded diagonal of the pay-off matrix in Table 2.

Suppose that a population initially had a mating system in which $p < 1$, and had attained an ESS at which *Matris* was silent, $\{0, \hat{X}_p\}$, but that the mating system changed so that $p = 1$. Now *Matris* and *Patris* would both favor X^* (less than $\hat{X}_p$) and both would benefit from mutations that reduce x_p, but neither would benefit from mutations that increase either x_m or x_p. Thus, natural selection would tend to shift the population from $\{0, \hat{X}_p\}$ toward $\{0, X^*\}$, but would not favor reactivation of the silent maternal allele (Moore & Mills, 1999).

Once the population attained the neutral line, any deviation by either *Matris* or *Patris* would be associated with lower payoffs. At this stage the game played by *Matris* and *Patris* corresponds to an asymmetric coordination game with separate populations of players (Fudenberg & Levine, 1998). If players agree (increasing or decreasing their combined expression)

Table 2. In this case $p = 1$; any pair of strategies corresponding to the diagonal of the payoff matrix is an ESS



they get a smaller payoff. If players disagree (neutralizing changes in their combined expression) they get a higher payoff. The payoff matrix for *Matris* is equal to the payoff matrix for *Patris*. The replicator equation for such games converge to the asymmetric equilibria (Fudenberg & Levine, 1998), the resulting equilibrium depends on the initial conditions. In our particular case, given the initial state $\{0, X^*\}$ there is no reason for the system to abandon it unless there is a positive selection in favor of reactivation of the maternal allele. Such selective force should be able to compensate for the adverse selection against deviation from the ESS.

Hurst (1998) claims that such selective force corresponds to deleterious recessive mutations. A deleterious mutation in *Patris* for an imprinted locus would result in the unviability of the corresponding genotype but the same mutation for an unimprinted locus would result in a viable genotype as long as the mutation is recessive. Note, however, that the strength of selection in favor of reactivation will be given by the frequency of mutation and will be effective only when inherited through the patriline; on the other hand, it will be counterbalanced not only by the force that stabilizes $\{0, X^*\}$ but also by opposing selection whenever monogamy is not perfect.

Reciprocally imprinted antagonists

At $\{0, \hat{X}_p\}$, $\partial W_m/\partial X$ is negative. *Matris* has an incentive to reduce X, but is unable to reduce x_m below zero. However, *Matris* may have other options that reduce the effective level of RE. These might include the production of a resource inhibitor (RI) that acts as an antagonist of RE. Total expression at an RI locus Y is the sum of y_m (expression of the maternally derived allele) and y_p (expression of the paternally derived allele). Kondoh and Higashi (2000) and Wilkins and Haig (2001) have modeled the coevolution of expression at an RE locus ($G_X > 0$) and an RI locus ($G_Y < 0$). In their models, *Patris* favors more RE than *Matris* ($\partial W_m/\partial X < \partial W_p/\partial X$) but *Matris* favors more RI than *Patris* ($\partial W_m/\partial Y > \partial W_p/\partial Y$). At the joint ESS, the loudest voice prevails at each locus: *Matris* produces all RI ($y_p = 0$) and *Patris* produces all RE ($x_m = 0$).

Given that $x_m = y_p = 0$, the payoff matrix for the zone of conflict can be obtained by substituting y_m for x_m, $y_m + \varepsilon$ for $x_m - \varepsilon$, and $y_m - \varepsilon$ for $x_m + \varepsilon$ in Table 1. If production of RE and RI were cost-free, every increase in production of RE by *Patris* could be matched by an increase in production of RI by *Matris*, and so on *ad infinitum*. Kondoh and Higashi (2000) and Wilkins and Haig (2001) avoided such an endless escalation by including costs of production in their models. Such costs can be represented in the fitness functions of *Matris* and *Patris* by the addition of a term $I(X, Y)$ where ($I_X, I_Y > 0$):

$$W_m = U(G(X, Y)) - I(X, Y) + \\ +1/2\, V(G(X, Y)) \tag{5a}$$

$$W_p = U(G(X, Y)) - I(X, Y) + \\ +p/2\, V(G(X, Y)) \tag{5b}$$

A joint ESS must satisfy $\partial W_m/\partial Y = 0$ and $\partial W_p/\partial X = 0$ simultaneously. Differentiating (5a) with respect to y_m and (5b) with respect to x_p gives the ESS conditions:

$$U_G - I_Y/G_Y = -1/2\, V_G \tag{6a}$$

$$U_G - I_X/G_X = -p/2\, V_G G_X \tag{6b}$$

From (6a) and (6b) the following condition is obtained:

$$\frac{1-p}{2} V_G = \frac{I_Y}{G_Y} - \frac{I_X}{G_X} \tag{7}$$

If there were no biochemical costs associated with production of RE and RI, or these costs were fixed (i.e., $I_X = I_Y = 0$), then the right-hand side of (7) would be zero. In that case a joint equilibrium would exist only when there was no conflict between *Patris* and *Matris*, either because $p = 1$, or because changes in the allocation of resources to the present offspring are without consequence for future offspring ($V_G = 0$).

In the presence of conflict, costs of production prevent endless escalation.

So far, we have assumed that the strategic options of *Matris* and *Patris* are limited to quantitative variation in the expression of invariant gene products (RE and RI), but this is a very limited repertoire when compared to the manifold evolutionary possibilities. Options that might be available for *Matris* could include changes in the RI that increase its efficiency as an antagonist without increasing its metabolic cost of production, perhaps by increasing its affinity for RE or extending its half-life. Conversely, options that might be available for *Patris* could be the production of a variant RE that fails to be antagonized by RI, perhaps, by subtle changes in the conformation of a binding site (McVean & Hurst, 1997). The molecular details of a particular system will probably determine whether conflict between *Matris* and *Patris* is ongoing or settles to some stable resolution.

Mater versus *Matris* and *Patris*

Section 2 considered conflict between *Mater* and *Filius* when the latter was considered as a unitary agent. Section 3 considered conflict between *Matris* and *Patris* and implicitly assumed that the production of RE and RI was controlled by these agents and not by *Mater* (or *Pater*). Comparison of (1a), (3a) and (3b) shows that *Mater*'s fitness function (W_{M}) differs from those of *Matris* (W_{m}) and *Patris* (W_{p}). *Mater* has an incentive to reduce the allocation to the current offspring (at her optimum $|U_G/V_G| = 1$) below the level that is optimal for *Matris* ($|U_G/V_G| = 1/2$), and the even higher optimum of *Patris* ($|U_G/V_G| = p/2$; Figure 2). She thus has an interest in controlling the production of RE and RI by her offspring, but does she have the means?

Mater may have considerable power to influence how and when genes are expressed in her offspring because the imprints of the maternally derived alleles of her offspring are established in her germ line, and because *Mater* provides the egg cytoplasm in which imprints are initially interpreted. Similarly, *Pater* has an incentive to reduce the allocation to current offspring (at his optimum $|U_G/V_G| = p$) below the level favored by *Patris* ($|U_G/V_G| = p/2$) whenever $p > 0$. Although *Pater* may be able to influence the expression of paternally derived genes in his offspring, he is likely to have limited ability to control the expression of the offspring's maternally derived alleles.

The beneficial modification for *Mater* would be to erase the imprint of *Patris*. Demethylation of *Patris* by *Mater* results in an increase of expression of RI genes only, genes in which the ESS of *Patris* is to become silent. If *Mater* is able to demethylate *Patris* but not *Matris* she would increase her fitness; *Patris* however has incentives to prevent such action. Recent evidence suggests that this happened during eutherian evolutionary history. Out of the three mechanisms described for repression of allele transcription – methylation of promoter, antisense transcript and chromatin boundaries (Reik & Walter, 2001b) – methylation of promoter (epigenetic silencing) is used for the repression of expression in *Matris* while antisense transcript (genetic silencing) is the most frequent method for the repression of expression in *Patris* (Reik & Walter, 2001a). Note that genetic silencing is not sensitive to demethylation but epigenetic silencing is susceptible. Reik and Walter (2001a) proposed that given a primordial mechanism of imprinting in which silencing is achieved through methylation, genetic mechanisms of silencing evolve as a response to genome-wide demethylation of *Patris*.

A critical issue, therefore, is the extent to which *Mater* and *Pater* control the imprinted expression of genes in offspring and the extent to which this is controlled by *Matris* and *Patris*. From an evolutionary perspective, the question is whether parent-specific expression is a property of the *imprinted* genes themselves or of *imprinting* genes that apply the imprints in parents (Mochizuki, Takeda & Iwasa, 1996; Burt & Trivers, 1998).

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