

## RESEARCH ARTICLES

### What Is a Marmoset?

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Callitrichid primates typically give birth to twin offspring that are somatic chimeras of cells derived from two products of conception. Each individual is thus the phenotype of two sibling genotypes, one of which may be more closely related to the germ line of the individual's parents than to the individual's own germ line. Chimerism could therefore help to explain the evolution of alloparental care and social suppression of reproduction in callitrichids. Placental chimerism may also have important implications for understanding kin interactions within the womb: on one side of the coin, the intimate juxtaposition of genotypes provides unique opportunities for antagonistic interactions between embryos; on the other side, chimerism could facilitate cooperation between sibling genotypes. *Am. J. Primatol.* 49:285–296, 1999. © 1999 Wiley-Liss, Inc.

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#### INTRODUCTION

Callitrichid primates (marmosets and tamarins) usually give birth to two (or more) offspring per pregnancy. For example, in a series of 39 term pregnancies, captive female *Callithrix jacchus* gave birth to five singletons, 19 pairs of twins, 13 sets of triplets, and two sets of quadruplets. Ultrasound revealed that all five singleton pregnancies began with twin products of conception, one of which was “lost” before term [Jaquish et al., 1996]. Single births appear to be the ancestral character for platyrrhine primates, with multiple births a derived feature of callitrichids [Hamlett & Wislocki, 1934; Ford, 1980; Martin, 1992]. As a consequence, callitrichid primates produce multiple embryos in a simplex uterus (an unusual combination of characters shared with some armadillos). Twinning is associated with another unusual feature: adult marmosets and tamarins are chimeras of cells derived from two (or more) products of conception. In the remainder of this paper, “marmoset” will be used as a generic term that includes tamarins.

Prenatal development has been best studied in *Callithrix jacchus*. Twin (or triplet) blastocysts implant about 12 days after ovulation. Chorionic fusion has begun by day 19 and is complete by day 29 when the embryos are still at an early presomite stage. After fusion, the embryos are located in a common exocoelom, delimited by a chimeric layer of trophoblast that almost completely

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lines the uterine surface [Moore et al., 1985]. Later in development, twin placental discs are formed, each of which is supplied, more or less equally, by vessels from both fetuses. In *Saguinus geoffroyi*, Wislocki [1939] observed that the placental arteries of the twins overlapped freely in their territories of distribution and he was unable to find any definite boundary within the placental discs that separated the cells of one twin from the other. Not only were the twin circulations intimately intermingled but they were also connected by vascular anastomoses that were clearly visible on the placental surface [also see Hill, 1926; Benirschke & Layton, 1969].

Cells from both products of conception colonize the bone marrow of both twins. As a result, blood samples from adult marmosets with a twin of the opposite sex contain lymphocytes with both XX and XY karyotypes [Benirschke et al., 1962; Gengozian et al., 1964]. In *Callithrix jacchus*, XY cells usually outnumber XX cells in the blood of both twins [Gengozian et al., 1969; Ardito et al., 1995]. Despite this chimerism, there is no evidence of intersexuality or subfertility in XX/XY chimeric marmosets [Benirschke et al., 1962; Abbott, 1984]. Like-sexed twins are presumably also chimeric, but this cannot be detected by studies of sex chromosomes. Systematic studies of which tissues are chimeric and which tissues are non-chimeric have not been reported. However, chimerism has been reported in blood, bone marrow, lymph nodes, spleen [Gengozian et al., 1964], and perhaps germ cells (next section) but is absent from lung and liver [Benirschke & Brownhill, 1962]. Overt chimerism is rare in humans, although a recent study detected low levels of chimerism in 8% of dizygotic twins and 21% of triplets [van Dijk et al., 1996].

Unlike marmosets, most human dizygotic twins have separate placentas without discernible anastomoses. On the other hand, human monozygotic twins usually have a shared chorion with vascular anastomoses connecting the two placental circulations [Benirschke & Kaufmann 1990; Baldwin, 1994]. Thus, chorionic fusion is not an inevitable outcome of dizygotic twinning in a simplex uterus, but vascular anastomoses appear to be an (almost) inevitable outcome of chorionic fusion. These data suggest that chorionic fusion (and the resulting chimerism) of marmosets is not merely an unselected side-effect of twinning but requires its own evolutionary explanation.

Human monochorionic twins sometimes develop the so-called twin-to-twin transfusion syndrome; a condition that is associated with high mortality for both twins [Benirschke & Kaufmann 1990; Baldwin, 1994]. The symptoms of this syndrome are believed to be caused by uncompensated transfer of blood from one twin to the other. Twins with few placental anastomoses appear to be at greater risk than twins with many anastomoses because the probability of large asymmetries of exchange decreases as the number of anastomoses increases [Bajoria et al., 1995; van Gemert & Sterenborg, 1998]. Thus, twin-to-twin transfusion provides a selective factor that would have favored the more intimate merging of placental circulations given the regular occurrence of chorionic fusion in an ancestral marmoset, but does not in itself explain the reasons for the initial fusion.

## DO MARMOSETS HAVE CHIMERIC GERM LINES?

Fusion between neighboring clones of the colonial urochordate *Botryllus schlosseri* results in chimerism of the germ line as well as the blood [Pancer et al., 1995]. Could similar mixing of germ cells occur in marmosets? This question has important theoretical implications. If germ cells of two genotypes were present in the testes of twin brothers, both genotypes would have a direct (individual fitness) interest in both brothers' reproduction. If germ lines were well-mixed,

both genotypes would be evolutionarily indifferent about which brother copulated, although competition within the brothers' testes and ejaculates could be intense. If on the other hand chimerism were restricted to the soma, the somatic genotype that was not represented in a twin's germ line would be related to that twin's offspring as an "uncle" rather than a "parent."

The empirical evidence is equivocal. XX germ cells have been reported from the testes of male marmosets with a female twin [Benirschke & Brownhill, 1962; Egozcue et al., 1968, 1969; Hampton, 1973] but these reports have been questioned [Ford & Evans, 1977; Gengozian et al., 1980]. Anzenberger [1992] reported "preliminary results" that blood samples from same-sexed twins have identical DNA fingerprints, but that tissue samples (including gonadal samples) from the same animals have different fingerprints. This suggests an absence of germ-cell chimerism, but Anzenberger's report did not provide supporting data and I have found no subsequent publications. Although the balance of evidence seems to have shifted against germ-cell chimerism in marmosets, more studies are clearly needed. Moreover, what is true of one species need not be true of all.

Even if germ cells of two genotypes colonize a gonad, the ability of both genotypes to produce gametes would probably depend on the sexes of the twins. XX cells are unable to complete spermatogenesis in XX/XY testes of experimental mouse chimeras, and few (if any) XY cells complete oogenesis in XX/XY ovaries [McLaren, 1976; Solari, 1994]. By contrast, both genotypes of chimeric mice formed from the fusion of same-sex embryos can produce offspring [McLaren, 1976]. Therefore, if marmoset twins were germ-cell chimeras (and experimental results from mice could be extrapolated to primates), only cells whose chromosomal sex matched the sex of the gonad would be expected to produce gametes when the twins were different sexes. However, functional chimerism of the germ line would remain a possibility when the twins were the same sex.

## REPRODUCTIVE SUPPRESSION AND ALLOPARENTAL BEHAVIOR

Marmosets and tamarins are unusual primates in the degree to which reproduction is monopolized by a single female within social groups, and the degree to which other group members (of both sexes) help raise this female's offspring. The mechanisms of reproductive suppression vary among species. Non-breeding females of *Callithrix* and *Saguinus* do not ovulate in the presence of the dominant female but rapidly resume ovarian cycles if removed from the social group. By contrast, non-breeding females of *Leontopithecus* continue to cycle but do not solicit nor receive sexual attention from group males [for reviews, see Goldizen, 1987; Abbott et al., 1993; French, 1997; Tardif, 1997].

Group members who provide alloparental care are frequently the sons and daughters of the breeding couple, and thus may gain inclusive-fitness benefits from assisting a relative to raise offspring. However, helpers are not always relatives, and a number of individual-fitness benefits have been proposed. These include the chance of inheriting reproductive status by remaining within the group and the acquisition of valuable experience in infant care [Goldizen, 1987, 1990; Garber, 1997; Rylands, 1996; Dunbar, 1995]. Such benefits apply to all species and do not in themselves explain why alloparental behavior is more strongly developed in marmosets than other primates. Goldizen [1990] argued that alloparental care coevolved with twinning to meet the increased demands of caring for two infants. Others have suggested ecological factors such as predation pressure [Caine, 1993] and the restricted availability of suitable habitat for reproduction [Rylands, 1996].

Previous discussions have not considered the possible implications of chimerism for the evolution of callitrichid social systems. Each marmoset contains cells of two sibling genotypes, and behaviors that increase the inclusive fitness of one genotype need not increase the inclusive fitness of the other. The next section presents a simple model of the selective forces acting on the different cell populations in chimeric twins. It will be argued that a chimeric twin contains a cell population that will often value reproduction by a parent more highly than reproduction by the twin itself. Subsequent sections then explore the possible relevance of the model for understanding callitrichid social systems, immunology, and pregnancy.

### THE DIOSCURI

In Greek myth, Leda was the mother of twin brothers, Castor and Pollux. In the present retelling, Leda conceived twin embryos, Heads and Tails, but cells of these embryos became mixed during early development so that the somatic tissues of Castor and Pollux were aggregates of cells (chimeras) derived from both products of conception. Germ cells however remained unmixed, with Castor's germ line composed solely of Heads' cells and Pollux's germ line composed solely of Tails' cells (or, what amounts to the same thing, with Heads' germ line located in Castor's soma and Tails' germ line located in Pollux's soma). Thus, Castor and Pollux (the phenotypic twins) could each be considered part of the *extended phenotype* of the genes of both Heads and Tails (the genotypic twins), with Castor a vehicle for transmitting the genes of Heads, and Pollux a vehicle for transmitting the genes of Tails [Dawkins 1982]. How then would natural selection acting on genes expressed in Heads and Tails weigh the fitness consequences of Castor producing an extra child of his own versus Castor helping his mother raise an additional child?

A maternal allele in Heads would have probability one half of being present in one of Leda's gametes and probability one half of being present in one of Castor's gametes. By contrast, a maternal allele in Tails would have probability one half of being present in Leda's gametes, but probability one quarter of being present in Castor's gametes. Therefore, a maternal allele that was expressed in Heads and caused a benefit  $B$  to Leda at cost  $C$  to Castor would be favored by natural selection if

$$\frac{B}{C} > 1, \quad (1)$$

whereas a maternal allele with the same effect but expressed in Tails would be favored if

$$\frac{B}{C} > \frac{1}{2}. \quad (2)$$

In other words, maternal alleles expressed in Heads would be indifferent between an extra offspring for Leda and an extra offspring for Castor, whereas maternal alleles expressed in Tails would be indifferent between an extra offspring for Leda and two extra offspring for Castor. Therefore, if Castor were contemplating the decision whether to help his mother raise an extra sibling or whether to put the same effort into raising an offspring of his own, the compo-

ment of Tails' cells in Castor's body would place an extra weight in the balance on the side of helping his mother. The selective interests of the genes of Heads and Tails differ because Leda's progeny are siblings of Heads and Tails, whereas Castor's progeny are offspring of Heads but nieces and nephews of Tails.

As a corollary, a maternal allele that was expressed in Heads (or Tails) and caused a benefit  $B$  to Leda at cost  $C$  to Castor, but which lacked information about whether Heads' cells were present in Castor's germ line and Tails' cells in Pollux's germ line, or the reverse, would be favored by natural selection if

$$\frac{B}{C} > \frac{3}{4}. \quad (3)$$

Thus, the strategic interests of genes expressed in Heads and Tails converge i) if there is uncertainty about whether Heads or Tails is present in Castor's germ line, ii) if there is uncertainty about whether a benefit or cost will be experienced by Castor or Pollux, or iii) if germ lines are functionally chimeric.

So far, only maternal alleles have been considered because the additional complications introduced by uncertain paternity would distract from (but not qualitatively alter) the major conclusion that the genes of Tails have a stronger tendency than the genes of Heads to promote helping behavior by Castor directed towards his parents. Calculations for paternal alleles are presented in the Appendix. Coefficients of relatedness are calculated separately for maternal and paternal alleles because of the possibility that behavior is influenced by genomic imprinting [Haig, 1997a]. In the special case where Leda produces all of her offspring with a single father, coefficients of relatedness are identical for maternal and paternal alleles. All probabilities used in this section and the Appendix have been calculated as probabilities of identity by recent common descent (under the assumption that sexual partners are unrelated and germ lines are non-chimeric). Thus, the probability that a maternal allele of Heads (or Tails) is present in a gamete of a specified individual can be interpreted as Heads' (or Tails') coefficient of maternal relatedness to the offspring of that individual, and likewise for paternal alleles.

### INTERESTS, POWER, AND INFORMATION

The simple model of the previous section suggests that chimerism may have predisposed marmosets to delay reproduction and help their mother raise siblings because one of the genotypes present in a marmoset's body devalues the marmoset's own reproduction relative to reproduction by its mother. However, showing that a class of genes has an interest in the decision whether to be a parent or an alloparent does not prove that genes of that class will influence the decision. Genes are neither omniscient nor omnipotent. A gene's influence on any given decision will be determined not only by its *interests*, but also by its *power* to influence the outcome and by the *information* it has about prevailing circumstances.

The two genotypes (Heads and Tails) within a marmoset's body may have very different power and information. If Tails' cells are limited to Castor's bone marrow and blood, Heads might have greater power than Tails to influence Castor's behavior. On the other hand, ripe oocytes are heavily outnumbered by lymphocytes, and a cell population that is a minority within the body could still exercise an effective veto [Haig 1992] on the decision whether to ovulate.

Given that a gene has an interest and the power to influence a decision, how

the gene will exert its influence will depend on what *information* is available to guide its actions. For example, a gene's interests might depend on whether the dominant female is a mother or a non-relative but, if the gene has no way to tell the difference, the best it can do is base its actions on the frequency with which mothers and non-mothers have been dominant females in the past. In this manner, information on long-term averages is substituted for direct information about current circumstances. If the cells of Heads and Tails have different information about whether the dominant female is a mother, one set of genes could base its response on direct information about the current composition of the social group, whereas the other set of genes could base its response on long-term averages. (The information available to a gene about long-term averages comes from past natural selection, as does the gene's ability to "interpret" information about current circumstances.)

Heads' and Tails' coefficients of relatedness to individual germ lines are generally identical, except for their different relatedness to the gametes of Castor and Pollux. If Tails' cells are excluded from Castor's sense organs and nervous system, the genes of Tails-in-Castor might have very limited information about the relatedness of individuals in any particular social interaction and would either have to rely on long-term averages or delegate decision-making to Heads. In most situations, delegation of authority to the set of genes with better information would be favored because Heads and Tails have similar interests, but delegation need not be favored in interactions with fitness consequences for Pollux (because Pollux carries Tails' germ line). If the genes of Tails-in-Castor lack information about the identity of the other individual in an agonistic interaction, these genes might adopt the "general principle" of reducing Castor's level of aggression in all interactions because of the possibility that some of Castor's aggression is directed towards Pollux.

Questions about phenotypic power and information are primarily empirical questions about proximate mechanisms. If so, the role of the theory presented above is to widen the scope of alternative mechanisms that are considered. For example, in a study of ovarian morphology in *Saguinus fuscicollis*, 58% of antral follicles were intact in breeding females, but only 2% of antral follicles were intact in non-breeding daughters, with the remainder showing signs of atretic degeneration [Mansdotter et al., 1992]. Previous attempts to understand the mechanism of ovarian suppression have concentrated on the roles of the hypothalamus and anterior pituitary because this is where ovulation is controlled in other primates, but the evolutionary arguments of this paper suggest that it might also be worth looking at factors produced by the engrafted cell populations of bone marrow and blood.

## IMMUNOLOGICAL CONSIDERATIONS

Bone-marrow chimerism has probably been a powerful selective force against the cells of one genotypic twin being recognized as foreign by the lymphocytes of the other, and this may explain why the major histocompatibility complex (MHC) class I antigens of marmosets are less diverse than the class I antigens of other primates. The lack of class I diversity limits the variety of peptides that can be presented to T cells for immune surveillance and may, in turn, explain why marmosets are particularly susceptible to viral infections [Watkins et al., 1990]. Callitrichid class I antigens show a high ratio of non-synonymous to synonymous substitutions in their peptide-binding region. Thus, sequence analysis provides evidence for ongoing diversifying selection to present a greater range of peptides,

but diversity remains limited because of periodic turnovers that cause the descendants of one sequence to replace all others [Cadavid et al., 1997].

The deleterious fitness effects of reduced class I diversity pose two questions. Why did chimerism initially become established in an ancestral callitrichid and why are there periodic purges of class I diversity, despite strong balancing selection to preserve polymorphism? Both questions may be answered by the existence of potent selective forces within the uterus. For most polytocous mammals, long uterine horns with separate implantation chambers for each embryo provide an effective means of keeping offspring apart *in utero* [for a dramatic exception, see O'Gara, 1969]. In this manner, uterine architecture minimizes opportunities for prenatal sibling rivalry. However, no such architectural barriers exist in the marmoset uterus. Thus, marmosets may be particularly vulnerable to the maladaptive consequences of genetic conflicts within the womb.

One possible scenario is that vascular anastomoses initially provided a means for an embryo to mount an immunological assault on its twin. A short-term evolutionary equilibrium of this process can be imagined at which both twins colonize each other's bone marrow, neither twin expresses polymorphic target molecules, and both suffer the costs of increased vulnerability to pathogens. Over the longer term, new class I variants would arise that increase the diversity of peptides presented to T cells without themselves being recognized as foreign by the chimeric immune system. However, this slow accumulation of polymorphism would be periodically set to zero by the origin of new immune effectors that could discriminate among the new variants. If so, different species would be expected to have accumulated different amounts of polymorphism since the last purge. Because the possession of particular antigens rather than degree of kinship is being assessed, the evolutionary interactions between immune effectors and their target molecules may be best explained as a green-beard effect (rather than in terms of classic kin selection) if effector and target genes are closely linked [Haig 1996a, 1997b].

### IN UTERO COOPERATION

In the absence of chimerism, some interactions between twin genotypes will take the form of a Prisoner's Dilemma: the genes of both twins could do better by mutual "cooperation" than mutual "defection," but the genes of either twin could do better still by defecting if the genes of the other cooperate. Standard game theory predicts that both sets of genes will defect in a Prisoner's Dilemma and the benefits of mutual cooperation will not be achieved. An example might be the placental expression of a gene for a cell-surface receptor that removes nutrients from the mother's blood. In the absence of cooperative restraint, the twins might overexploit their mother because the marginal benefit of extra resources is experienced in full by the twin with the higher level of gene expression, but the marginal costs (associated with maternal depletion) are shared. In this case, the inability of the twins to cooperate increases the total demands on the mother. A somewhat different example is provided by the production of a placental hormone that is secreted into the mother's circulation. Higher levels of gene expression increase nutrient levels for both twins, but each twin does better if the other bears the full marginal cost of increased expression. In this case, the inability of the twins to cooperate reduces the total demands on the mother [Haig, 1996b]. Thus, increased cooperation between the twins could either increase or decrease maternal costs.

Chimerism may allow marmoset twins to avoid some of the maladaptive con-

sequences of intrauterine competition. In a Prisoner's Dilemma, mutual cooperation is predicted if the two sets of genes could make a binding agreement to share all pay-offs (strictly, the game ceases to be a Prisoner's Dilemma). Placental chimerism may have an analogous effect: all regions of the placenta supply both twins with the result that the marginal costs and benefits of placental gene expression are shared equally by Castor and Pollux. If costs and benefits are shared, the twins can be considered a unit that extracts resources from the mother at the expense of future siblings. The average relatedness of a maternal allele in Heads (or Tails) to the germ lines of Castor and Pollux is three-quarters, whereas the average relatedness to the germ lines of future siblings is one half. Therefore, if the expression of a maternal allele in the placenta confers a benefit  $B$  on the current twins at cost  $C$  to the mother's future offspring, the action will be favored if

$$\frac{3}{4}B - \frac{1}{2}C > 0 \Rightarrow \frac{B}{C} > \frac{2}{3}. \quad (4)$$

Thus, parent-offspring conflict exists when the benefit-to-cost ratio is less than one but greater than two-thirds [Lazarus & Inglis, 1986]. The zone of conflict is reduced relative to mothers giving birth to singletons [in which case conflict is predicted for benefit-to-cost ratios less than one but greater than half; Trivers, 1974].

## CONCLUSIONS

Inclusive-fitness calculations differ for the two genotypes resident in a marmoset's body. Therefore, the genotypes may have conflicting interests in interactions involving kin. However, showing that the extra genotype has an interest in modifying a marmoset's behavior does not prove that this interest will be exercised. A genotype cannot exert an influence unless it possesses the appropriate phenotypic power and the appropriate information to distinguish one situation from another. Put in other words, the models indicate when the extra genotype has a motive to influence a decision, but are silent on whether it has the means.

Lymphocytes are versatile cells that have access to most parts of the body, and that have had ample time to evolve novel functions since the origin of chimerism. Therefore, the "graft" may have considerable phenotypic power even if its cells are restricted to bone marrow and blood. Information, however, is probably a major limitation on the engrafted cells' freedom to influence social interactions (another is counter-selection on the host to avoid manipulation). The graft obtains most of its information about the outside world indirectly, filtered through the sense organs and nervous system of the host. Therefore, the host genotype has an (evolutionary) incentive to withhold relevant information or provide misleading information in situations in which the two genotypes have conflicting interests. If the graft has an interest to block ovulation when the twin's mother is the reproductive female in a group, and has the phenotypic power to do so, but lacks reliable information as to whether the reproductive female is a mother or a non-relative, then its optimal response may be to block ovulation in all situations where the reproductive female is *probably* a mother. If, on the other hand, the genotypes lack information about which is graft and which is host (that is, which genotype is represented in a marmoset's germ line), this uncertainty is predicted to promote cooperation between the genotypes and reduce overt phenotypic conflict between the twins.

The question whether there are functional differences between graft and host cells could be addressed experimentally by studying non-chimeric marmosets. Gengozian & Batson [1975] were able to obtain a high proportion of non-chimeric singletons in *Saguinus fuscicollis* by ligation of one Fallopian tube. It should be straightforward to test if non-chimeric marmosets are subject to reproductive suppression. Other questions could be addressed by field studies. Behavioral interactions between siblings of the same sex often differ from interactions between siblings of different sex but, in callitrichid primates, interactions between “siblings” may be expressed within, as well as between, individuals. Are there systematic differences in the behavior of male (or female) marmosets with a twin of the same or opposite sex? Are there subtle differences in morphology? Dixson [1993] and Garber et al. [1996] both report large variation in testis volume within species. Is this variation correlated or uncorrelated with the sex of a male’s co-twin?

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**APPENDIX**

According to some classical accounts, Castor was the son of Leda’s husband Tyndareus, but Pollux was the son of Zeus. Maternal coefficients of relatedness among Leda’s offspring are unaffected by changes of paternity, but paternal coefficients depend on her marital fidelity. If  $x$  is the probability that a paternal allele in Heads is present in one of Leda’s future offspring and  $y$  the probability that a paternal allele of Heads is also present in Tails (or vice versa), then  $x = y$  if all of Leda’s future offspring are fathered from the same sperm pool as Heads and Tails;  $x < y$  if there is some probability of turnover in Leda’s sexual partners; and  $y = 1/2$  if Heads and Tails have the same father. Therefore, a paternal allele that was expressed in Heads with benefit  $B$  to Leda and cost  $C$  to Castor would be favored by natural selection if

$$\frac{B}{C} > \frac{1}{2x}. \tag{A1}$$

Conditions (1) and (A1) are identical in the special case of strict monandry ( $x = 1/2$ ), otherwise Heads’ paternal alleles are less likely than Heads’ maternal alleles to favor Castor helping his mother. Specifically, the interests of Heads’ maternal and paternal genomes conflict when

$$\frac{1}{2x} > \frac{B}{C} > 1. \tag{A2}$$

Similarly, a paternal allele that was expressed in Tails with benefit  $B$  to Leda and cost  $C$  to Castor would be favored by natural selection if

$$\frac{B}{C} > \frac{y}{2x}. \tag{A3}$$

Conditions (2) and (A3) are identical if Leda’s future offspring are fathered from the same sperm pool as Heads and Tails ( $x = y$ ); otherwise Tails’ paternal alleles are less likely than Tails’ maternal alleles to favor Castor helping his mother. Specifically, the interests of Tails’ maternal and paternal genomes conflict when

$$\frac{y}{2x} > \frac{B}{C} > \frac{1}{2}. \tag{A4}$$

Thus, Castor’s body contains multiple genetic parties with distinct interests that might attempt to influence his decision whether to help his mother. The differ-

ent strategic interests are defined by both zygotic origin (genes expressed in Heads may have different interests from genes expressed in Tails) and parental origin (maternally-derived genes may have different interests from paternally-derived alleles). Castor's decision can be viewed as a social choice made by aggregating the preferences of these different agents [Haig, 1997c].