

Genomic Imprinting and Sex Allocation

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ABSTRACT: Genomic imprinting allows maternally and paternally derived alleles to have different patterns of expression (one allele is often silent). Kin selection provides an explanation of genomic imprinting because conflicts of interest can arise between paternally and maternally inherited alleles when they have different probabilities of being present in other individuals. Our aim here is to examine the extent to which conflicts between paternally and maternally inherited alleles could arise over the allocation of resources to male and female reproduction (sex allocation), for example, conflict over the offspring sex ratio. We examine the situations in which sex allocation is influenced by competitive or cooperative interactions between relatives: local resource competition, local mate competition, and local resource enhancement. We determine solutions for diploids and haplodiploids when either the mother or the offspring controls sex allocation. Our results suggest that the greatest conflict between paternally and maternally inherited alleles and therefore the strongest selection for genomic imprinting will occur in haplodiploid species where the offspring can control sex allocation, such as the social hymenoptera and the polyembryonic parasitoid wasps. Within the social hymenoptera, we expect especially strong selection for genomic imprinting in species subject to local resource competition, such as honeybees and army ants.

Keywords: conflict, direct fitness, kin selection, Hymenoptera, inclusive fitness, sex ratio.

Introduction

Genomic imprinting occurs when maternally and paternally derived alleles have different patterns of expression

(Burt and Trivers 2006). Usually one allele is silent and the other active, although the difference in levels of expression can be more subtle. The clearest examples of genomic imprinting were first described in insects, but this phenomenon has since been most studied in plants and mammals, especially mice and humans (Field et al. 2004; Burt and Trivers 2006).

Kin selection theory provides a possible explanation for the selective advantage of genomic imprinting. Very simply, kin-selected behaviors strike a balance among the competing interests of genetically related individuals (Hamilton 1964). In some cases, paternally and maternally inherited genes in one individual have different probabilities of also being present in other individuals, and so genetic relatedness differs depending on which point of view (paternally or maternally inherited genes) we adopt. In these same cases, maternally and paternally inherited genes naturally disagree over how a kin-selected balance among competing interests is to be struck (Haig 2000, 2002, 2004). This has been termed the kinship theory of imprinting.

The classic example of the kinship theory of genomic imprinting is overparental investment (Haig 2002; Burt and Trivers 2006). Assuming a large outbred population, a gene derived from the father will be unrelated to the mother and so will be selected to maximize the amount of resources obtained from the mother. In contrast, maternal genes have a kin-selected (indirect) interest in the mother's survival and production of further (related) offspring. Consistent with this prediction, a high proportion of the genes that are imprinted in the mammalian genome are involved in fetal growth, with paternal imprinting leading to greater growth and hence greater resource acquisition from the mother. Although the kinship theory of genomic imprinting has proved popular, other explanations have been suggested, and a potential limitation is that the theory has been developed to explain the data rather than data collected to test a priori predictions of theory (Wilson and Burley 1983; Hurst and McVean 1998; Wilkins and Haig 2003; Badcock and Crespi 2006; Wood and Oakley 2006).

Sex allocation has provided some of the clearest support for kin selection and social evolution theory (Charnov

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1982; Hamilton 1996; West et al. 2005; Meunier et al. 2008). Sex allocation theory predicts that under certain circumstances, the marginal fitness benefit of allocating resources to male or female reproduction differs, selecting for biased sex allocation. In particular, there is a huge theoretical literature predicting when sex allocation should be manipulated in response to environmental conditions and a rich empirical literature proving a wealth of qualitative and in some cases quantitative support for the predictions of theory (Charnov 1982). Indeed, it has been suggested that sex allocation theory is the area of evolutionary theory that best proves the power of the Neo-Darwinian paradigm and can have a predictive power almost comparable to that of the “hard” sciences such as physics or chemistry (Hamilton 1996).

Given these past successes of sex allocation theory, we suggest that it is useful to examine the extent to which sex allocation can provide testable predictions for genomic imprinting. The possibility of genomic imprinting influencing sex allocation has attracted only limited attention. It is well accepted that there are a number of cases in which we might expect conflict over sex allocation between mothers and their offspring (Trivers and Hare 1976; Werren and Hatcher 2000; Beukeboom et al. 2001; Werren et al. 2002; Gardner et al. 2007; Uller et al. 2007) or between parents (Trivers 1974; Charnov 1982; Pen and Weissing 2002; Wild and Taylor 2005; Pen 2006; Wild 2006). In situations where there are conflicts between parents, this opens the possibility for selection for genomic imprinting. The area in which this possibility has been most explicitly developed is in social insects, where the haplodiploid genetics means that fathers make a genetic contribution only to daughters. Consequently, if we consider the behaviors of the workers, paternally inherited alleles favor a more female-biased sex allocation (Haig 1992; Queller 2003). Conflicts between parents and the subsequent selection for genomic imprinting have also been suggested to be important in the evolution of sex determination systems, including the evolution of haplodiploidy (Werren and Beukeboom 1998; Normark 2003, 2006).

Our aim here is to examine when genomic imprinting in sex allocation is selectively advantageous. The kinship theory of genomic imprinting suggests that genomic imprinting can be favored when the genetic relatedness between social interactants differs from the point of view of maternal and paternal genes (Haig 2000, 2002, 2004). An area of sex allocation in which this could be important is that in which competitive or cooperative interactions between relatives drive the pattern of sex allocation: local resource competition (LRC) among related females (Clark 1978), local mate competition (LMC) among related males (Hamilton 1967), and local resource enhancement (LRE; Taylor 1981). Here, we investigate these three scenarios,

considering the influence of mating system (monogamy, polygyny, or polyandry), genetics (diploid or haplodiploid), and who has control of sex allocation (parents or offspring; e.g., Trivers and Hare 1976). In order to provide a treatment that is amenable to both empirical and theoretical workers, we describe our predictions conceptually and graphically, based on a formal theoretical analysis that is presented in appendixes A–E. In the majority of situations we shall discuss, there is a complete lack of data on whether genomic imprinting occurs in the relevant species, let alone whether it occurs in genes involved in sex allocation. However, we see this as an advantage because it allows us to make clear predictions before the data are available. The increasing interest in the genetic mechanisms underlying sex allocation and especially how these may be influenced by conflict will provide data that could be used to test our predictions qualitatively.

Where Could Conflict Occur?

Consider a dioecious species, with separate sexes, where two parents produce offspring and the relevant sex allocation problem is the sex ratio of those offspring. Genomic imprinting could influence the sex ratio of those offspring in at least three ways (fig. 1). First, the maternally and paternally inherited alleles in the parents (derived from the grandparents) could favor a different sex ratio (fig. 1a). In this case, there could be imprinting on the genes that control offspring sex or genes involved in any parental behavior that differentially influences sex allocation. This could occur in any species where one or both of the parents are able to control the offspring sex ratio (primary or secondary).

The second and third cases both occur when the maternally inherited and paternally inherited genes in the offspring (derived from the parents) favor a different sex ratio. The second case is when sex determination occurs in the offspring, as with mechanisms such as environmental sex determination (fig. 1b). In this case, there could again be imprinting on the genes involved with sex determination. This could occur in species where the offspring control their own sex, such as environmental sex determination, sex change, or simultaneous hermaphrodites who can alter their relative allocation to male and female reproduction. The third possibility, when sex determination is not under the control of the offspring, is when the offspring has some mechanism to alter the sex ratio during development (Trivers and Hare 1976), for example, through influencing larval mortality. This would lead to a difference between the sex ratio at conception (primary sex ratio) and the sex ratio when reaching maturity (secondary sex ratio). In this case, there could be imprinting on the genes involved with interactions with

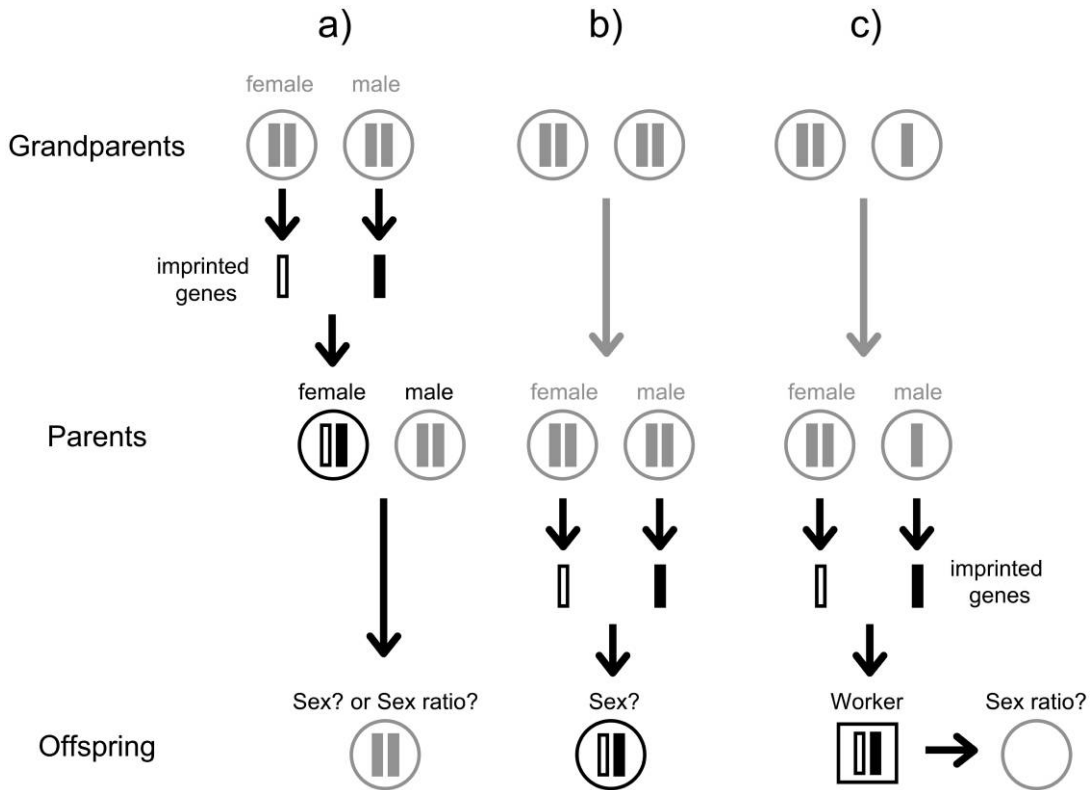


Figure 1: We will consider the effects of genomic imprinting under the assumption that there is either maternal control of the sex ratio or offspring control of the sex ratio. *a*, Under maternal control, imprinted alleles in the actor (*black*) influence the offspring sex and/or any behavior that affects sex allocation (diploid or haplodiploid). *b*, Under diploid offspring control, imprinted alleles in the actor (*black*) influence offspring sex. *c*, For haplodiploids, we consider the possibility that an offspring actor (e.g., a member of a worker caste; *black*) influences the sex ratio of a brood produced by its parents.

relatives. This could potentially occur in cooperative social species, where offspring help rear their siblings and other relatives (e.g., fig. 1c), in polyembryonic parasitoid wasps with a sterile soldier caste (Grbic et al. 1992), or when there is asymmetric larval competition for resources (Sykes et al. 2007).

The potential for genomic imprinting over sex allocation has been analyzed in the case of haplodiploid social species. Assuming that she has mated only once, a queen favors equal investment in the sexes because she is equally related to sons and daughters ($r = 0.5$ in both cases). In contrast, the workers are three times more related to sisters ($r = 0.75$) than to brothers ($r = 0.25$) and so are selected to invest three times as much resources in sisters, leading to a 0.75 allocation in females (Trivers and Hare 1976). Haig (1992) pointed out that conflict could occur over the sex allocation between paternal and maternal genes because the 0.75 investment was an average of the optimum from the point of view of a maternal gene ($r = 0.5$ to both brother and sisters, favoring an investment ratio of

0.5) and the paternal gene ($r = 1$ to sisters and $r = 0$ to brothers, favoring an investment ratio of 1.0 or a sex ratio of 0). A variety of factors such as queen mating frequency and the number of queens in the nest can alter the genetic relatedness structure of social insect populations, leading to more complicated patterns (Chapuisat and Keller 1999; Mehdiabadi et al. 2003; Meunier et al. 2008), but there has been a lack of further attention to the consequences of genomic imprinting (but see Queller 2003).

Local Resource Competition

We report results for a variety of different LRC models (see app. A). To help the reader, we summarize all LRC results in table 1.

Diploidy with Maternal Control of the Sex Ratio

Female Monogamy. We start by considering the simplest possible model of LRC among diploid females. We assume

Table 1: Summary of the equilibrium sex ratios for local resource competition models

Model, control, and mating system	Sex ratio		
	No imprinting	Paternally inherited	Maternally inherited
Diploidy:			
Maternal:			
Female monogamy	$\frac{N(3N+1)}{3N(2N-1)+1}$	$\frac{2N^2}{4N^2-3N+1}^a$	$\frac{2N^2(3N+1)}{(4N^2-N+1)(3N-1)}$
Polyandry	$\frac{MN(3N+1)}{6MN^2-2MN-N+1}$	$\frac{2MN^2}{2MN(2N-1)-N+1}^a$	$\frac{2MN^2(3N+1)}{2MN[3N(2N-1)+1]-(N-1)^2}$
Polygyny	$\frac{3N+1}{5N-1}$	$\frac{2N}{3N-1}$	$\frac{2N(3N+1)}{11N^2-4N+1}^a$
Offspring:			
Female monogamy	$\frac{3N+1}{6N}$	$\frac{2N}{4N-1}^a$	$\frac{2N(3N+1)}{12N^2-N+1}$
Polyandry	$\frac{M(3N+1)}{6MN+M-1}$	$\frac{2MN}{4MN-1}^a$	$\frac{2MN(3N+1)}{12MN^2-N+1}$
Polygyny	$\frac{3N+1}{5N+1}$	$\frac{2}{3}$	$\frac{2(3N+1)}{11N+1}^a$
Haplodiploidy:			
Maternal:			
Female monogamy	$\frac{N(3N+1)}{2(3N^2-2N+1)}$	$\frac{N^2}{2N^2-2N+1}$	$\frac{N^2(3N+1)}{6N^3-4N^2+3N-1}^a$
Polyandry	$\frac{MN(3N+1)}{2(3MN^2-MN-N+1)}$	$\frac{MN^2}{MN(2N-1)-N+1}^a$	$\frac{MN^2(3N+1)}{MN[3N(2N-1)+1]-(N-1)^2}$
Polygyny	$\frac{3N+1}{4N}$	1	$\frac{3N+1}{5N-1}^a$
Offspring:			
Female monogamy	$\frac{3N+1}{4(3N-2)}$	0	$\frac{N(3N+1)}{2(3N^2-2N+1)}^a$
Polyandry	$\frac{M(3N+1)}{2[M(3N-1)+3(N-1)]}$	0	$\frac{MN(3N+1)}{2(3MN^2-MN-N+1)}^a$
Polygyny	$\frac{3N+1}{4N}$...	$\frac{3N+1}{4N}$

Note: Recall that N refers to the number of females breeding on a patch and M refers to the number of mates chosen by each female in polyandrous systems.

^a The more moderate (i.e., less biased) allele-specific perspective.

nonoverlapping generations, and we assume that each generation proceeds as follows. (1) An amount N of singly mated (i.e., monogamous) females breed on a patch and produce a large number of offspring. On average, a fraction z of the offspring are sons (z is called the sex ratio). We assume that male and female offspring are equally costly to produce, and so z mirrors sex allocation decisions. (2) Following birth, males—and only males—disperse completely before the next round of mating occurs. We assume that males disperse infinitely far so that they do not compete against relatives. (3) After the dispersal phase, intrasexual competition occurs at random (among males, competition is for mates; among females, competition is for breeding sites) and the next generation begins.

If the sex ratio is under maternal control and if there is (for the moment) no genomic imprinting, then it is possible to show that the population is at an equilibrium with respect to the evolution of z when z itself is equal to no imprinting,

$$z^* = \frac{N(3N+1)}{3N(2N-1)+1}, \quad (1)$$

which is, in turn, greater than 1/2.

Under LRC, the production of daughters carries with it an inclusive fitness penalty (Clark 1978; Taylor 1981); hence, selection favors sex ratios—such as z^* in equation (1)—that are male biased. The extent of the bias depends on the severity of the inclusive fitness penalty, which, in turn, depends on \bar{R} , the average relatedness among competing females. When patch size is small, \bar{R} is quite large and equilibrium sex ratios become strongly biased toward males (the inclusive fitness penalty for production of daughters is relatively large). In contrast, when patch size is very large, \bar{R} becomes small and equilibrium sex ratios tend toward 1/2 (the inclusive fitness penalty for production of daughters is relatively small). As we shall see, thinking about how \bar{R} (or the appropriate analogue to \bar{R})

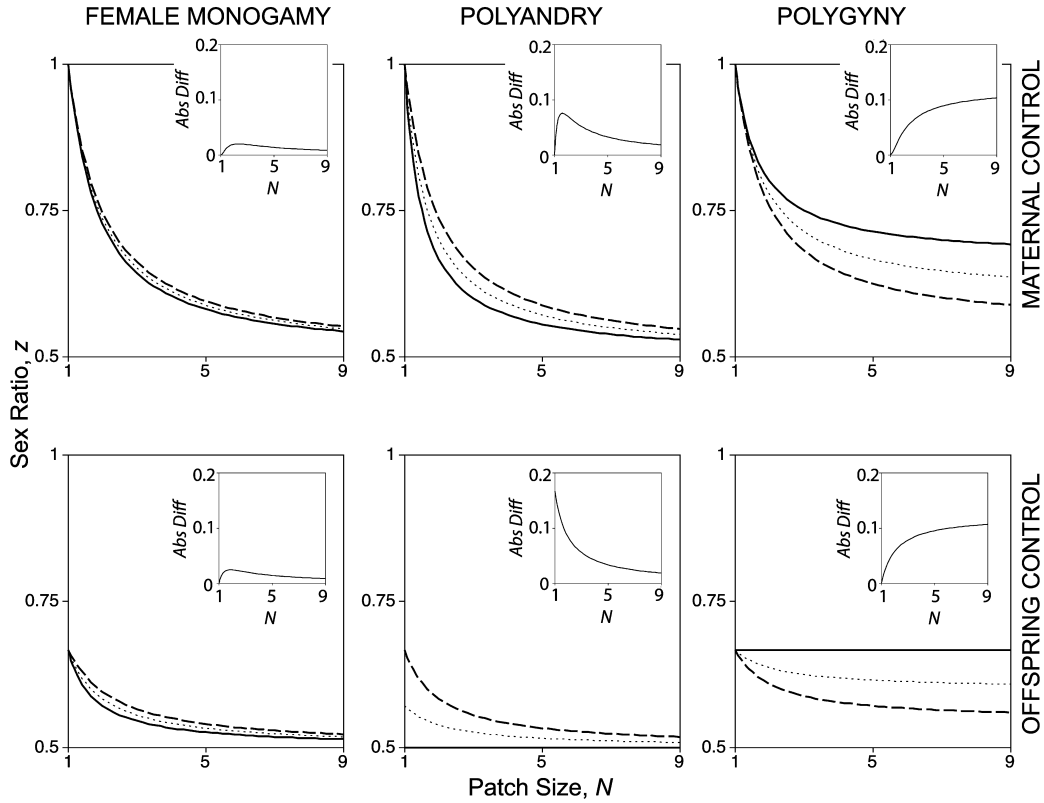


Figure 2: Graphical depiction of the relationship between the stable sex ratio and patch size for diploid local resource competition models. We show results for both maternal and offspring control and for each of the three different mating systems (in the polyandry case, the large M approximation is given). Solid curves refer to sex ratios “preferred” by paternally inherited alleles (i.e., grandpaternal alleles in mother or paternal alleles in offspring), dashed curves refer to sex ratios “preferred” by maternally inherited alleles (i.e., grandmaternal alleles in mother or maternal alleles in offspring), and dotted curves refer to standard “no imprinting” results. Insets depict how the absolute difference (*Abs Diff*) between sex ratios favored by paternally inherited and maternally inherited alleles changes with patch size.

changes as we vary model assumptions can effectively guide our intuition about z^* .

We now shift focus and consider the point of view of a maternally or paternally inherited allele in a breeding female. In this case, we are therefore considering the effect of which grandparent the allele in a parent comes from (fig. 1). Clearly, the LRC inclusive fitness penalty (as measured by the appropriate analogue of \bar{R}) will be judged to be less severe by the paternally inherited allele (from the grandfather of fig. 1). Imprinting acts as a cue that “reminds” paternally inherited alleles that they are relative newcomers to the patch and much less likely than their maternally inherited counterparts (from the grandmother of fig. 1) to randomly encounter genetically identical copies of themselves during competition.

Using information presented in appendixes A–E, it can be shown that the population is at evolutionary equilibrium from the perspective of the paternally inherited allele when

$$z^* = \frac{2N^2}{4N^2 - 3N + 1}, \quad (2)$$

and at evolutionary equilibrium from the perspective of the maternally inherited allele when

$$z^* = \frac{2N^2(3N + 1)}{(4N^2 - N + 1)(3N - 1)}. \quad (3)$$

For simplicity, we refer to equations (2) and (3) as the sex ratios “preferred” or “favored” by the paternally and maternally inherited alleles, respectively.

Equations (2) and (3) show that both alleles favor male-biased sex ratios ($z^* > 1/2$; fig. 2). However, in keeping with our intuition, maternally inherited alleles prefer sex ratios that are more strongly male biased than those favored by paternally inherited alleles—although the difference in the preferred sex ratios from the perspective of

paternally and maternally inherited alleles is relatively minor (fig. 2). The “no imprinting” result reported in equation (1) lies between the allele-specific preferences (in fact, eq. [1] is the harmonic mean of eqq. [2], [3]).

Polyandry. The size of the LRC inclusive fitness penalty (i.e., the size of the relevant \bar{R}) can also be adjusted by changing the assumptions one makes about the mating system (Pen 2006). We assumed that each female mates with exactly one male. Relaxing this assumption and allowing females to mate with exactly M males (polyandry) increases the genetic diversity of a brood and decreases \bar{R} . Polyandry, then, promotes the evolution of more even sex ratios in the absence of imprinting (table 1).

As was the case with female monogamy, both maternally and paternally inherited genes favor male-biased sex ratio, but the bias preferred by the maternally inherited gene (from the grandmother of fig. 1) is stronger than that preferred by the paternally inherited one (from the grandfather of fig. 1). A plot of the absolute difference between sex ratios preferred by paternal alleles and those preferred by maternal alleles (a variable we call “Abs Diff”) shows that polyandry exacerbates the conflict between paternally and maternally inherited alleles (fig. 2). Multiple matings reduce the likelihood that sisters (i.e., female parents of fig. 1 who compete for the same patch) share the same father (i.e., the same grandfather of fig. 1). This leads to a reduction in the relatedness between paternally inherited alleles of broodmates and hence a greater difference in relatedness between the maternally and the paternally inherited alleles.

Polygyny. If we now assume that one male monopolizes all matings on the patch (polygyny), then \bar{R} increases (a consequence of the fact that all female patchmates in this scenario are at least half-sibs). A larger \bar{R} means larger LRC inclusive fitness penalties. Larger penalties are reflected in equilibrium sex ratios that are more strongly male biased than those found with other model mating systems (fig. 2).

Interestingly, we find that in a polygynous mating system, it is the paternally inherited allele that prefers the more strongly biased sex ratio. Although this result provides a stark contrast to the results obtained under assumptions of monogamy and polyandry, it is hardly surprising. All female patchmates have the same father but may not have the same mother. As a result, females are more closely related to one another through patriline than through matriline. A high degree of relatedness through patriline means that—relative to maternally inherited alleles—paternally inherited alleles incur larger penalties for producing daughters. To avoid the more substantial pen-

alties, then, paternally inherited alleles favor greater investment in sons.

Diploidy with Offspring Control of the Sex Ratio

Under maternal control of the sex ratio, inclusive fitness penalties are balanced against fitness gains made by the actor’s own offspring. When we give control of the sex ratio to offspring (in this case, an offspring determines its own sex), penalties become balanced against fitness gains made by the actor itself. Because actors, in this case, are always more closely related to themselves than they are to the offspring produced by their parent, the scales tip more heavily away from sex ratio bias. In short, all else being equal, handing control of the sex ratio to offspring acts as an “effective” reduction in \bar{R} . In addition to an effective reduction, we see in appendix D that there is an “actual” reduction in \bar{R} brought about by the arrival of foreign paternal genes.

Given that \bar{R} is both “actually” and “effectively” smaller, we expect equilibrium sex ratios under offspring control to be less biased than those found with maternal control. Indeed, this is what we observe (fig. 2). Note that a shift toward less biased strategies is the only substantive difference between maternal and offspring control. The qualitative effects of changing mating system remain unchanged (fig. 2). However, in this case, the conflict between paternally and maternally inherited alleles is now played out in the offspring between alleles that came from the mother and father, as opposed to in the parent between alleles that came from the grandfather and grandmother (fig. 1).

Haplodiploidy

The main qualitative differences between haploid and diploid models occur in cases with offspring control of the sex ratio (in this case, “offspring” are assumed to be sterile female workers). First, equilibrium sex ratios are not always male biased. If there is no imprinting, then offspring-controlled equilibrium sex ratios tend toward the well-known value $z^* = 1/4$ (i.e., the 3 : 1 female : male ratio predicted by Trivers and Hare 1976) as patch size N becomes large. Of course, in haplodiploids, paternally inherited alleles in worker-offspring have no genetic interest in workers’ brothers, and so these alleles prefer extreme female bias (fig. 3). The “extreme” point of view of paternally inherited alleles also means that the conflict with maternally inherited homologues can be substantial (fig. 3, *insets*). In addition, we find that under offspring control with polygyny, the paternally inherited allele has no preferred sex ratio strategy. From the point of view of the paternally inherited allele in this case, LRC exactly cancels any fitness gained through the production of daughters.

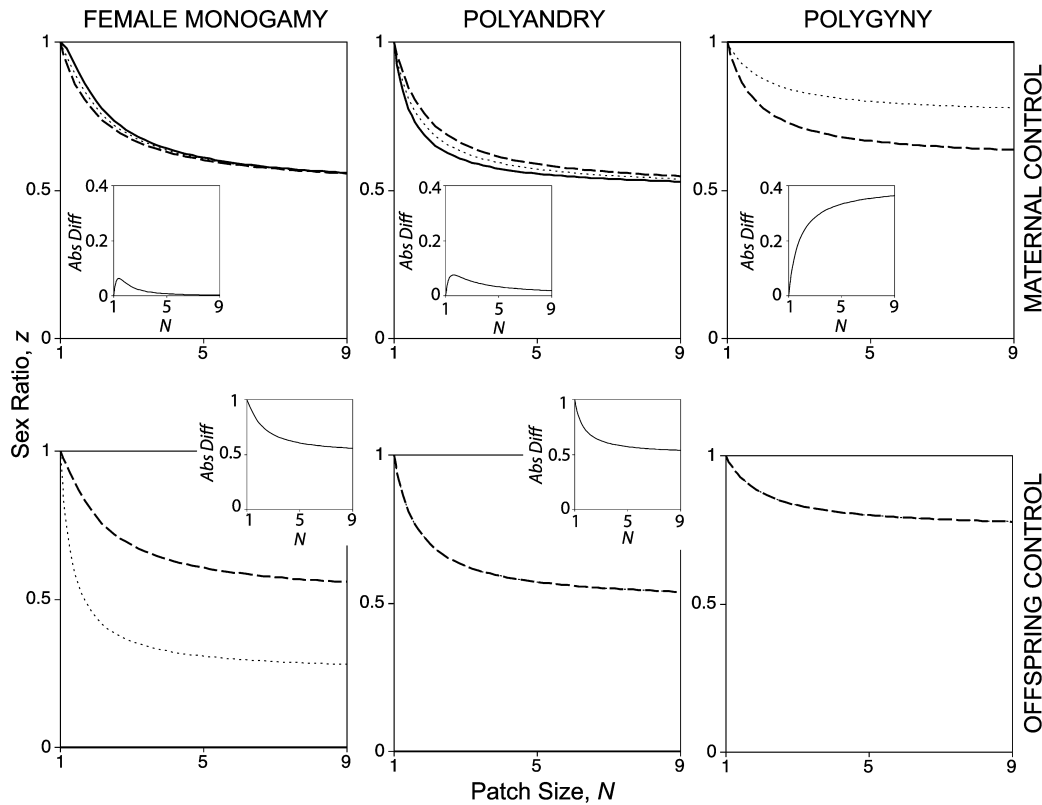


Figure 3: Graphical depiction of the relationship between the stable sex ratio and patch size for haplodiploid local resource competition models. We show results for both maternal and offspring control and for each of the three different mating systems (in the polyandry case, the large M approximation is given). Solid curves refer to sex ratios “preferred” by paternally inherited alleles (i.e., grandpaternal alleles in mother, or paternal alleles in offspring), dashed curves refer to sex ratios “preferred” by maternally inherited alleles (i.e., grandmaternal alleles in mother or maternal alleles in offspring), and dotted curves refer to standard “no imprinting” results. Where appropriate, insets depict how the absolute difference (*Abs Diff*) between sex ratios favored by paternally inherited and maternally inherited alleles changes with patch size. Note that the dotted and dashed curves of the bottom middle panel coincide and that there is only a dashed curve in the bottom right panel.

The paternally inherited allele is equally indifferent to workers’ brothers because these brothers are not, from the perspective of the allele, relatives.

Local Mate Competition

We report results for a variety of different LMC models (app. B). To help the reader, we summarize all results in table 2.

Diploidy with Maternal Control of the Sex Ratio

We first consider the classic LMC model constructed by Hamilton (1967): (1) N singly mated females lay eggs on a patch. (2) The offspring develop and mate. Males die. (3) Following mating, fertilized daughters disperse.

Under these conditions, Hamilton showed that the equilibrium sex ratio from the perspective of a mother (i.e.,

under maternal control) is given by $z^* = (N - 1)/2N < 1/2$, a result that holds for all mating systems we consider here (table 2). Taylor (1981) emphasized that the female bias in Hamilton’s z^* occurs because there are both inclusive fitness penalties for production of sons (sons compete for mates against related males) and inclusive fitness bonuses for producing daughters (daughters provide new mating opportunities for related males).

In diploids, LMC does not lead to a conflict that favors genomic imprinting over the sex ratio, simply because male and female genes disperse together (unlike LRC) and are transmitted to offspring in a symmetric manner (unlike haplodiploidy). Therefore, grandpaternal and grandmaternal genes are equally likely to be in grandoffspring of either sex, and so the genes suffer inclusive fitness penalties or enjoy inclusive fitness bonuses to the same extent.

Changing the mating system has no effect on our basic conclusion: in diploid LMC models with polygynous or

Table 2: Summary of the equilibrium sex ratios for local mate competition models

Model, control, and mating system	Sex ratio		
	No imprinting	Paternally inherited	Maternally inherited
Diploidy:			
Maternal:			
All mating systems	$\frac{N-1}{2N}$	$\frac{N-1}{2N}$	$\frac{N-1}{2N}$
Offspring:			
Monogamy/polygyny	$\frac{N-1}{2N-1}$	$\frac{N-1}{2N-1}$	$\frac{N-1}{2N-1}$
Polyandry	$\frac{2M(N-1)}{(4N-3)M+1}$	$\frac{(N-1)[4MN+(M-1)]_a}{2N[(4N-3)M+1]}$	$\frac{(N-1)[4MN-(M-1)]}{2N[(4N-3)M+1]}$
Haplodiploidy:			
Maternal:			
All mating systems	$\frac{(2N-1)(N-1)}{N(4N-1)}$	$\frac{(2N-1)(N-1)_a}{2N(2N-1)+1}$	$\frac{N-1}{2N+1}$
Offspring:			
Monogamy/polygyny	$\frac{N-1}{4N-1}$	$\frac{N-1}{N(4N-1)}$	$\frac{(2N-1)(N-1)_a}{N(4N-1)}$
Polyandry	$\frac{2MN(N-1)}{(4N-1)[N(M+1)+M-1]}$	$\frac{M(N-1)}{(4N-1)(N+M-1)}$	$\frac{(2N-1)(N-1)_a}{N(4N-1)}$

Note: Recall that N refers to the number of females breeding on a patch, and M refers to the number of mates chosen by each female in polyandrous systems.

^a The more moderate (i.e., less biased) allele-specific perspective.

polyandrous mating systems, imprinting continues to have no consequences for equilibrium sex ratios when these are under maternal control. As we will see, however, imprinting does introduce some complications when offspring have control.

Diploidy with Offspring Control of the Sex Ratio

Female Monogamy or Polygyny. In monogamous or polygynous mating systems, when control of the sex ratio is given to offspring, we calculate the equilibrium value to be $z^* = (N-1)/(2N-1)$. Just like LRC, the LMC equilibrium sex ratios become less biased when control is taken away from parents and given to offspring (Werren and Hatcher 2000; Beukeboom et al. 2001). Furthermore, because both maternally and paternally inherited alleles (1) have arrived together on a foreign patch and (2) are equally likely to be transmitted to offspring of either sex, there is no conflict between parental genes in offspring. Consequently, imprinting has no effect on z^* .

Polyandry. When we assume that each female mates with exactly M males, bias in the offspring-controlled equilibrium sex ratio changes. Specifically, in the absence of bias, z^* is reduced as M increases (table 2).

Because males and females now have unequal genetic shares in broods, we expect imprinting to have an effect on equilibrium sex ratios. Indeed, this is what we observe (table 2). While both paternally and maternally inherited

alleles favor a female-biased sex ratio, that favored by the maternally inherited allele (the allele that stands to lose more through inclusive fitness penalties and that stands to gain more from inclusive fitness bonuses) prefers the stronger bias (fig. 4a). However, this difference is not substantial.

Haplodiploidy with Maternal Control of the Sex Ratio

With LMC and maternal control of the sex ratio, the equilibrium trait values are the same for all mating systems considered (table 2). If we allow imprinting, we find that paternally and maternally inherited genes come into conflict: paternally inherited genes favor a more even sex ratio (table 2; fig. 4b). The effect of imprinting here is counterintuitive at first glance. Both alleles in the mother have an equal chance of being transmitted to sons and daughters, and both alleles find themselves on a nonnative patch—so why do they have different perspectives?

To answer this question, we must consider what happens over three generations, beginning with the parents of the focal actor (i.e., the grandparents of fig. 1). Fixing attention on a single grandmaternal allele, it becomes clear that there are two ways that this allele can possibly find its way into granddaughters: (1) through daughters or (2) through sons. The same cannot be said for the grandpaternal allele. The only way that the grandpaternal allele finds its way into a granddaughter is through daughters. Overall, the “echo” of the asymmetric modes of transmission in hap-

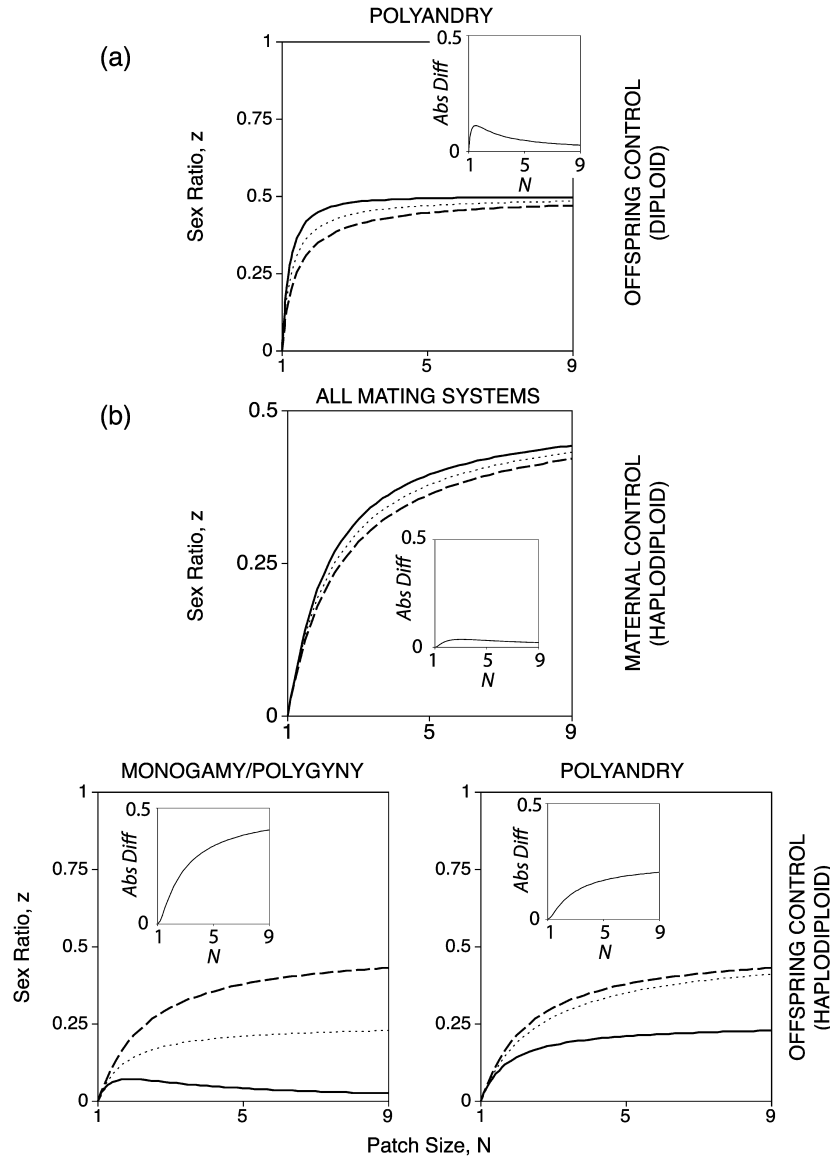


Figure 4: Graphical depiction of the relationship between the stable sex ratio and patch size for diploid local mate competition models. *a*, We show results for diploid offspring control with polyandry (large M approximation) only because conflict does not occur with diploid maternal control or other diploid offspring control models. *b*, We show the results for haplodiploid models (again, large M approximation is given polyandry models). In both *a* and *b*, solid curves refer to sex ratios “preferred” by paternally inherited alleles (i.e., grandpaternal alleles in mother or paternal alleles in offspring), dashed curves refer to sex ratios “preferred” by maternally inherited alleles (i.e., grandmaternal alleles in mother or maternal alleles in offspring), and dotted curves refer to standard “no imprinting” results. Insets depict how the absolute difference (*Abs Diff*) between sex ratios favored by paternally inherited and maternally inherited alleles changes with patch size.

lodiploids means that, in LMC models, the maternally inherited allele is more closely related to daughters than is the paternally inherited allele. The fact that the maternally inherited allele places greater genetic value on daughters is reflected in its preference for a stronger female bias.

Haplodiploidy with Offspring Control of the Sex Ratio

Female Monogamy or Polygyny. Now we give control of the sex ratio to female offspring (e.g., members of a worker caste). In the absence of imprinting, we find that, relative

to maternal control, there is a stronger female bias to the equilibrium sex ratio under offspring control, provided that $N > 1$ (table 2). The stronger bias is due to the fact that the paternally inherited allele in female offspring has less genetic interest than the maternally inherited alleles in that offspring's brothers. In fact, when we allow imprinting, we find that the sex ratio preferred by the paternally inherited allele is more strongly biased than that favored by the maternally inherited allele (table 2; fig. 4b). Note that previous models (Haig 1992; Queller 2003) consider one queen, singly mated (Queller's table 3), and correspond to the case in which there is no LMC (i.e., $N \rightarrow \infty$). In these models, the paternally inherited allele favors $z^* = 0$, and the maternally inherited allele favors $z^* = 0.5$ (fig. 4b). Note also that the sex ratio conflict that exists between the parental alleles also increases with increasing patch size (fig. 4b, *inset*).

Polyandry. The relatedness between a worker female and her reproductive sister decreases with increasing M . However, because males arise from unfertilized eggs, changing M does not change the relatedness between a worker female and her brother. Intuitively, there is a reduced inclusive fitness incentive in a polyandrous system for workers to invest in sisters. We therefore expect less biased sex ratios at equilibrium with increasing M , an expectation that is supported by analytical results for the "no imprinting" case (table 2; fig. 4b).

When imprinting is allowed, we find that, from the perspective of the maternally inherited allele, polyandry has changed nothing (cf. final two entries in the rightmost column of table 2). As suggested, though, polyandry means that paternally inherited alleles have less interest in daughters. We still see that the sex ratio preferred by the paternally inherited allele is the one that is more strongly biased toward daughters (fig. 4b).

Local Resource Enhancement

Sometimes the production of one sex increases the overall productivity of a breeding pair (LRE), for example, in a range of cooperatively breeding vertebrates and bees (Griffin et al. 2005; West et al. 2005). In species that exhibit sex-specific helping behavior, sex ratios are often predicted to favor the more helpful sex (Emlen et al. 1986; Pen and Weissing 2002). However, in diploids, LRE alone will not promote conflict over the sex ratio, unless we build in additional assumptions. There is a wide variety of additional assumptions available and an equally wide variety of ways in which they can be added to LRE models (e.g., Pen and Weissing 2002; Wild 2006). Our goal then is to stimulate future work with a brief introduction of how

intragenomic conflict might arise when LRE models incorporate assumptions of the LRC models.

We modify the basic LRC model by adding the assumption that the brood size of a given female, K , increases with the number of daughters produced on its natal patch. To be clear, we posit a maximum brood size that decreases at a rate proportional to the patch-average sex ratio, y . Mathematically, $dK/dy = -\alpha K$, where $\alpha > 0$ describes the strength of the LRE effect (larger α indicates stronger effect of LRE). In this very simple model, we find that LRC and LRE exert opposing pressure on the sex ratio (app. C). As we outlined, LRC favors male-biased sex ratios, and LRE favors (in this case) the "more helpful" sex, females. Although an analytical expression for the equilibrium sex ratio is not available, we do find that there is a threshold value of $\alpha = 4$ below which equilibrium sex ratios are male biased (LRC dominates). Of course, above the threshold value, the reverse is true (LRE dominates).

When we allow imprinting, we find that (1) both maternally and paternally inherited alleles agree on the direction of sex ratio bias (again the direction of bias depends on α) and (2) the paternally inherited allele never favors a sex ratio bias that is more extreme than that favored by the maternally inherited allele. Of course, these results depend on the assumption that the nondispersing sex (females) is also the more helpful sex. In many species with juvenile helpers, the nondispersive sex is indeed more helpful (Griffin et al. 2005). When, instead, the dispersive sex is more helpful, biased investment in this sex is promoted by both LRE and LRC. In these cases, we expect the conflict between maternally inherited alleles found in models with LRC alone to be maintained.

Discussion

Theoretical Predictions

We have shown that in a variety of sex allocation scenarios where relatives can interact, the favored sex allocation can differ between paternally and maternally inherited alleles. This conflict, which could select for genomic imprinting, can occur either when parents control the sex of their offspring (though we have considered only mothers) or when offspring control sex allocation. Specifically, genomic imprinting can be selected for when (1) there are competitive interactions between relatives (LRC or LMC; figs. 2–4; tables 1, 2), (2) there are cooperative interactions between relatives (LRE), or (3) sex allocation is determined by offspring (siblings) in haplodiploid species (as occurs in the social hymenoptera and polyembryonic wasps with soldier castes; Haig 1992; Queller 2003).

Intuitively, the extent of the conflict between allele-specific perspectives reflects the strength of selection for

imprinting. To be precise, increasing the distance between the population-average sex ratio (i) and the equilibrium value (z^*) favored by a particular allele will increase the selective pressure on that allele to regulate its activity when information about the sex of the parent from which it originated is available. Having said this, we predict that the greatest selection for genomic imprinting will occur when sex allocation is controlled by offspring in haplodiploid species (case 3). If we consider cases involving diploid species with parental or offspring control of sex allocation and haplodiploids with parental control of sex allocation (cases 1 and 2), LRC and LRE can lead to noteworthy conflict between maternally and paternally inherited genes (figs. 2, 3), but there seems to be relatively minimal scope for such conflict under LMC (fig. 4). In contrast, in haplodiploids with offspring control (case 3), there can be considerable conflict with both LRC and LMC. In these cases, LRC increases the extent of conflict, and LMC decreases the extent of conflict (cf. insets on bottom panels of figs. 3, 4b).

Genomic imprinting at a sex allocation locus could also be selected for in the absence of kin interactions such as LRC, LMC, or LRE. If females mate with different males in different years and the survival cost (to the female) of producing a son or daughter differ, then females will be selected to produce a lower proportion of the costly sex than their mates (Trivers 1974; Charnov 1982; Leigh et al. 1985; Pen and Weissing 2002). We expect that this conflict will promote the evolution of genomic imprinting when offspring have control of parental sex allocation decisions. However, the importance of such conflicts is not clear. In particular, in species where sex differential survival effects may occur, such as vertebrates, sex allocation appears to be controlled by parents. In addition, in species where interactions between relatives are unimportant, the primary reason for conditional adjustment of sex allocation is when the environment has different effects on the fitness of male and female offspring (Trivers and Willard 1973), which would tend to align the strategies favored by males and females and hence reduce selection for genomic imprinting. Explicit theory is needed to examine these issues.

Application to the Real World

One way to test our predictions would be to look for genomic imprinting at the level of the genes involved in sex allocation. This could be done with either molecular or quantitative genetic approaches (Burt and Trivers 2006). As discussed in "Introduction," an advantage of this study is that the data to test it do not yet exist. We are therefore in a position to make *a priori* predictions over what situations and species are most likely to involve imprinting on genes that influence sex allocation (see also Queller

and Strassman 2002; Queller 2003). The greatest candidates are clearly haplodiploid species in which offspring can control sex allocation. The most obvious group here is the social hymenoptera (ants, bees, and wasps), where workers have been shown to manipulate sex allocation (of their reproductive siblings) in the nest, through mechanisms such as male killing or biasing the final caste (queen or worker) of developing females (Sundstrom et al. 1996; Hammond et al. 2002). In this case, we would expect imprinting on genes that influenced these behaviors, such as paternally inherited alleles leading to higher levels of male killing or a higher queen : worker caste ratio (Queller 2003). Similar conflicts could potentially occur in the haplodiploid eusocial thrips (Kranz et al. 1999).

Within the social hymenoptera, our models suggest that selection for genomic imprinting would be increased in species where there is LRC (fig. 3; table 1) and reduced in species where there is LMC (fig. 4). LRC can occur as a result of colony fission, colony budding, or when nests recruit their own daughters as reproductive queens (Trivers and Hare 1976; Bourke and Franks 1995; West et al. 2005). Another complication in the social hymenoptera that we have not considered is that there is often selection for split sex ratios, where some colonies produce predominantly male sexuals and others produce predominantly female sexuals. This can be selected for in response to variation in relatedness asymmetry, arising from factors such as variation in mating frequency and queen number (Boomsma and Grafen 1990, 1991; Boomsma 1991) or variation in the extent of LRC (Ward 1983; Brown and Keller 2000; Kummerli et al. 2005). Further theory is required to determine the consequences of split sex ratios for selection on genomic imprinting.

The other haplodiploid taxa where offspring can have a large influence on sex allocation are the polyembryonic wasps (Strand and Grbic 1997). In these species, the offspring have control over sex allocation, both because they control the proliferation of embryos and because, in some species, some larvae develop as sterile soldier larvae. These sterile soldiers are predominantly females, who preferentially kill the males (brothers; Grbic et al. 1992; Giron et al. 2004). The production of these soldiers appears to result from sex ratio conflict under LMC because the females would prefer a more female-biased sex ratio than would the males (Gardner et al. 2007). Consequently, genomic imprinting could be selected for in genes that influence the relative proliferation rate of the two sexes or the development and behavior of the sterile soldier caste.

In species where sex allocation is controlled by parents, selection for genomic imprinting is weaker but can still occur with LRC between females and LRE (figs. 2, 3; table 1). LRC and LRE have been suggested to occur in a range of organisms where parents appear to control offspring

sex ratios, including cooperative breeding birds and mammals (Komdeur et al. 1997; Griffin et al. 2005), cooperative breeding bees (Schwarz 1988; Stark 1992; Martins et al. 1999), rodents (Lambin 1994), lions (Packer and Pusey 1987), mealybugs (Varndell and Godfray 1996), primates (Clark 1978), marsupials (Cockburn 1990; Johnson et al. 2001), ungulates (Clutton-Brock et al. 1982), aphids (Dagg and Vidal 2004), thrips (Kranz et al. 1999), and plants (de Jong et al. 2002). Even when there is relatively little sex allocation conflict, this could lead to substantial differences in gene activity, leaving evolutionary footprints in sex-determining mechanisms (Pen 2006; Uller et al. 2007). A general issue here is that the ability to test our models will depend on the taxonomic distribution of genomic imprinting, about which relatively little is known (Burt and Trivers 2006). Particularly exciting from this perspective are recent molecular and genetic advances suggesting the possibility for genomic imprinting in both the social (honeybee; Wang et al. 2006) and the parasitic hymenoptera (*Nasonia vitripennis*; Beukeboom and van den Assem 2001, 2002; Beukeboom et al. 2007).

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