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Haplodiploidy and the reproductive ecology of Arthropods

Andrés G de la Fila¹, Stevie A Bain¹ and Laura Ross



Approximately 15% of all arthropods reproduce through haplodiploidy. Yet it is unclear how this mode of reproduction affects other aspects of reproductive ecology. In this review we outline predictions on how haplodiploidy might affect mating system evolution, the evolution of traits under sexual or sexual antagonistic selection, sex allocation decisions and the evolution of parental care. We also give an overview of the phylogenetic distribution of haplodiploidy. Finally, we discuss how comparisons between different types of haplodiploidy (arrhenotoky, PGE with haploid vs *somatically* diploid males) might help to discriminate between the effects of virgin birth, haploid gene expression and those of haploid gene transmission.

Address

School of Biological Sciences, Institute of Evolutionary Biology, University of Edinburgh, Edinburgh EH9 3JT, UK

Corresponding author: Ross, Laura (laura.ross@ed.ac.uk)

¹ Authors contributed equally.

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Introduction

Behavioural ecology focuses on understanding how natural selection shapes the way organisms behave. Insects have featured prominently as model systems [1]. Despite providing important general insights, these studies fail to include the full diversity of reproductive systems in arthropods. Most assume that each parent is contributing an equal share of their genes to their offspring. Yet as many as 15% of arthropods are haplodiploids [2–4], where mothers monopolize the production of male offspring, either by the asexual production of sons (arrhenotoky) or by producing sons that eliminate their father's genome from their germline (paternal genome elimination, PGE) [4]. Haplodiploidy has received attention in the context of eusociality (though its importance has increasingly fallen out of favour [5]), yet how it affects other aspects of species' ecology has barely been addressed. Here we

consider its role in reproductive behaviour and mating system evolution. We summarize available theory (main text and [Table 1](#)) and empirical data (supplementary [Table S1](#)), provide verbal models when formal ones are lacking, and identify areas that need addressing in the future.

Most biologists are familiar with haplodiploidy in the Hymenoptera. The vast majority of hymenopterans reproduce through arrhenotoky [4], and most behavioural ecology studies on haplodiploid species involve members of this order. Yet, it constitutes just one of two-dozen independent origins of haplodiploidy [4]: arrhenotoky is also found among thrips, some hemipterans and several clades of beetles and mites. PGE, where males develop from fertilized eggs but subsequently eliminate the paternal chromosomes, is found in most scale insects (Hemiptera), some beetles, flies, springtails, lice and mites (in total about 20 000 species) [6] ([Figures 1 and 2](#)). Different PGE species vary in the timing of the elimination of the paternal genome, and in whether it becomes transcriptionally silenced or not [4,6]. As a result, male gene expression varies from haploid to diploid ([Figure 3](#)) with various intermediates. This variability is important as it might allow differentiation of the effects of haploid gene transmission and those of haploid gene expression, while comparisons between arrhenotokous and PGE taxa could provide insights into the importance of virgin birth (see [Table 1](#)).

Evolutionary genetics under haplodiploidy

Haplodiploidy affects the evolutionary genetics of species in a number of ways. Under arrhenotoky and some types of PGE, gene expression in males is haploid and maternal. Therefore, recessive mutations are exposed to selection in males, firstly, reducing genetic load, due to a lower effective mutation rate and the exposure of deleterious recessive alleles in haploid males [7] and secondly, increasing the rate at which rare recessive beneficial mutations can spread. As a result, these species are expected to adapt faster to changing environments. This is true only for non-sex specific traits. The evolution of male-limited traits is complex, as sons do not inherit them from their fathers ([Figure 3](#)). In addition, selection among females has a relatively greater impact on evolutionary change as each gene finds itself more frequently in females than males [8].

Sexual selection

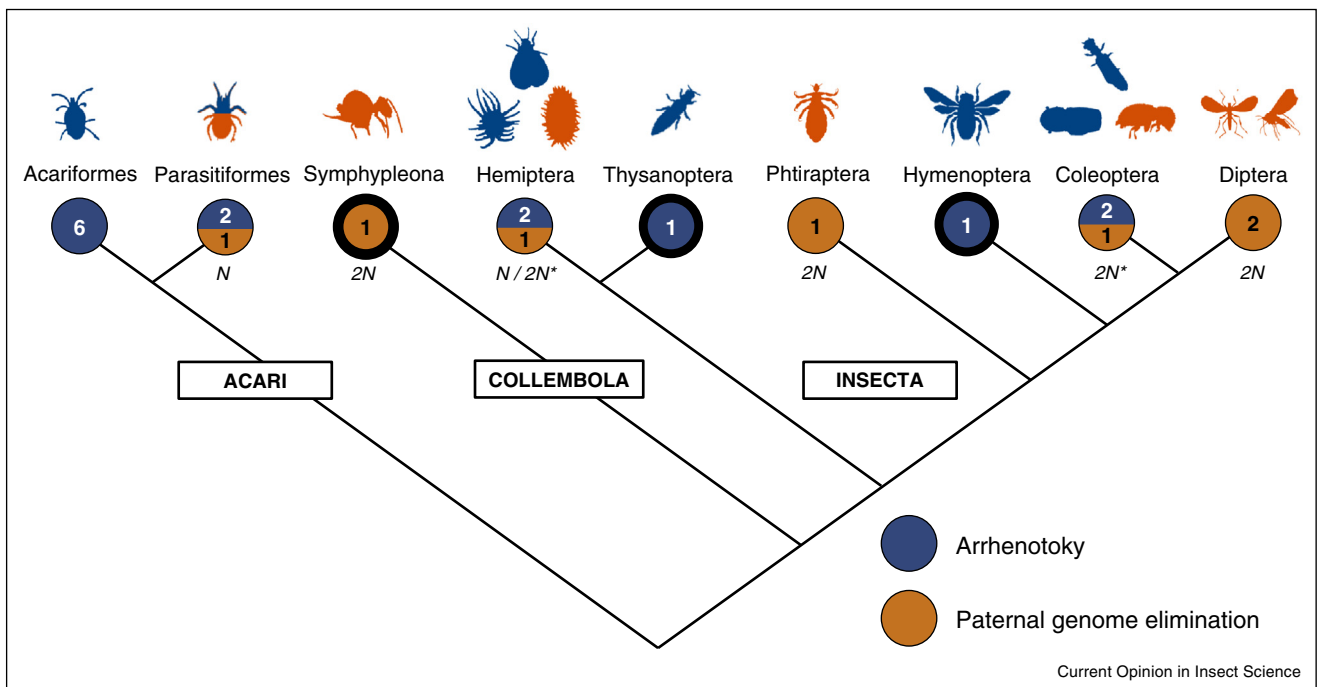
Sexual selection arises through competition within a sex (usually males) for access to mates (and their gametes) [9]

Table 1

An overview of the prediction for each of the reproductive ecology traits discussed in the manuscript. We summarize how we expect the three different types of haplodiploid organisms to differ with respect to diploid taxa. + indicates that trait is promoted relative to diploidy, – that the type of haplodiploidy inhibits the evolution of the trait, while = indicates that there is no expected difference between haplodiploids and diploids. Please note that most of these predictions, especially differences between the different types of haplodiploids, are based on verbal models and will need to be corroborated by formal theory in the future.

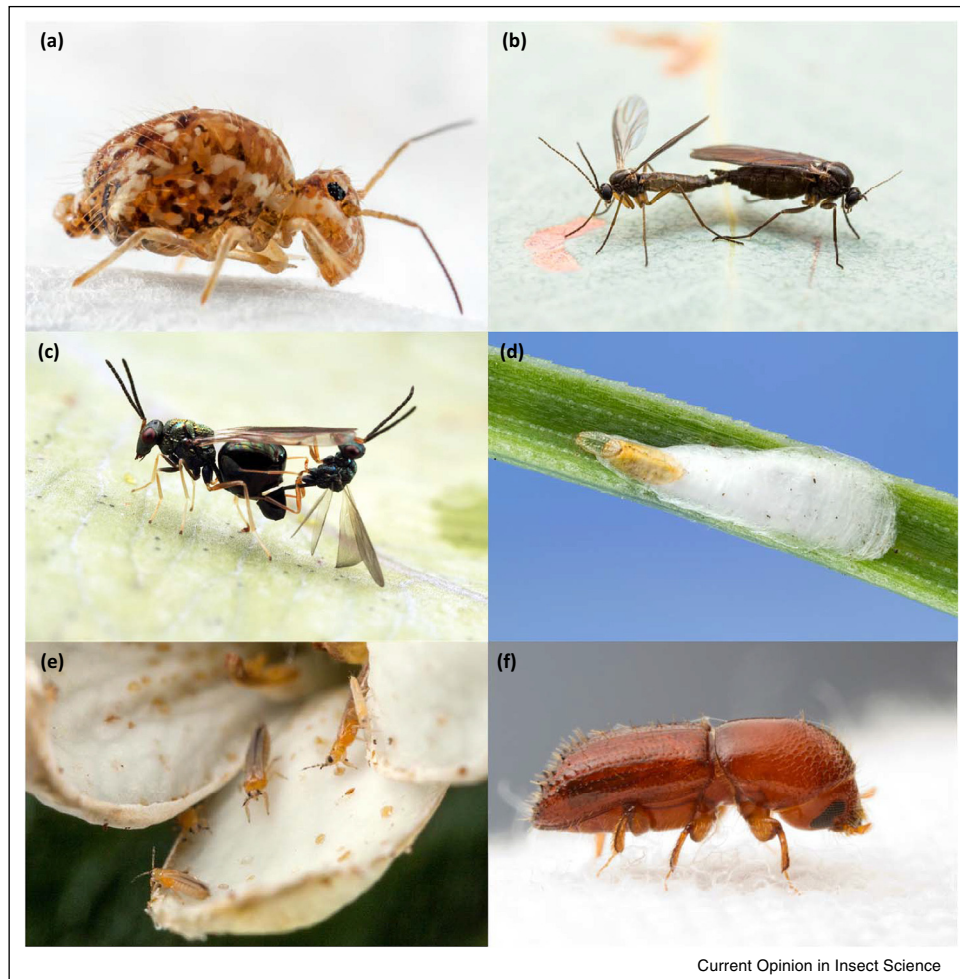
	Arrhenotoky	PGE (haploid soma)	PGE (diploid soma)
Inbreeding depression	– [24]	–	=
Exaggerated sexual selected traits (under Fisherian runaway selection)	– [12]	–	–/= Sons might express their fathers' ornament, increasing their reproductive success, yet are unable to pass it on to their offspring
Exaggerated sexual selected traits (handicap principle)	+ [13]	+	+
Intra-locus conflicts	Resolved in favour of females (dominant traits), polymorphism (recessive traits) [16]	Resolved in favour of females (dominant traits), polymorphism (recessive traits)	Resolved in favour of females (both dominant and recessive traits).
Inter-locus conflicts	Females are more likely to evolve resistance to male trait [16]	Females are more likely to evolve resistance to male trait	= (?) Mothers equally likely to evolve resistance as sons might express their fathers' trait, benefitting the mother through their increased reproductive success
Sperm cooperation	+ [52]	+ [52]	+ [52]
Fertility assurance	+	– Virgin females unable to produce offspring	– Virgin females unable to produce offspring
Facultative sex ratio control	+ [33,53]	+/= [54,55]	+/= [56**]
Polyandry	–/= [11**]	+	+
Maternal care	= [49]	=	=
Paternal care	+ [50**]	+	+

Figure 1



Schematic cladogram of arrhenotokous (blue) and PGE (orange) groups in Arthropoda. The number of independent origins of haplodiploidy is indicated within the circles. Clades in which all members are haplodiploid are indicated with a black ring around the circle. The type of PGE is indicated below the circle with $2N$ for germline PGE, $2N^*$ for germline PGE, where the paternal genome is transcriptionally silenced in somatic cells and N for embryonic PGE. Origins outside the Arthropoda (rotifers and nematodes) are not shown.

Figure 2



A number of examples of PGE species: **(a)** a globular springtail (Symphyleona), **(b)** a pair of mating fungus gnats (Sciaridae), **(d)** the armoured scale insect *Chionaspis pinifoliae*. And a number of arrhenotokous species: **(c)** Eucharitid wasps mating, **(e)** flower thrips, **(f)** *Xyleborus* sp. ambrosia beetle.

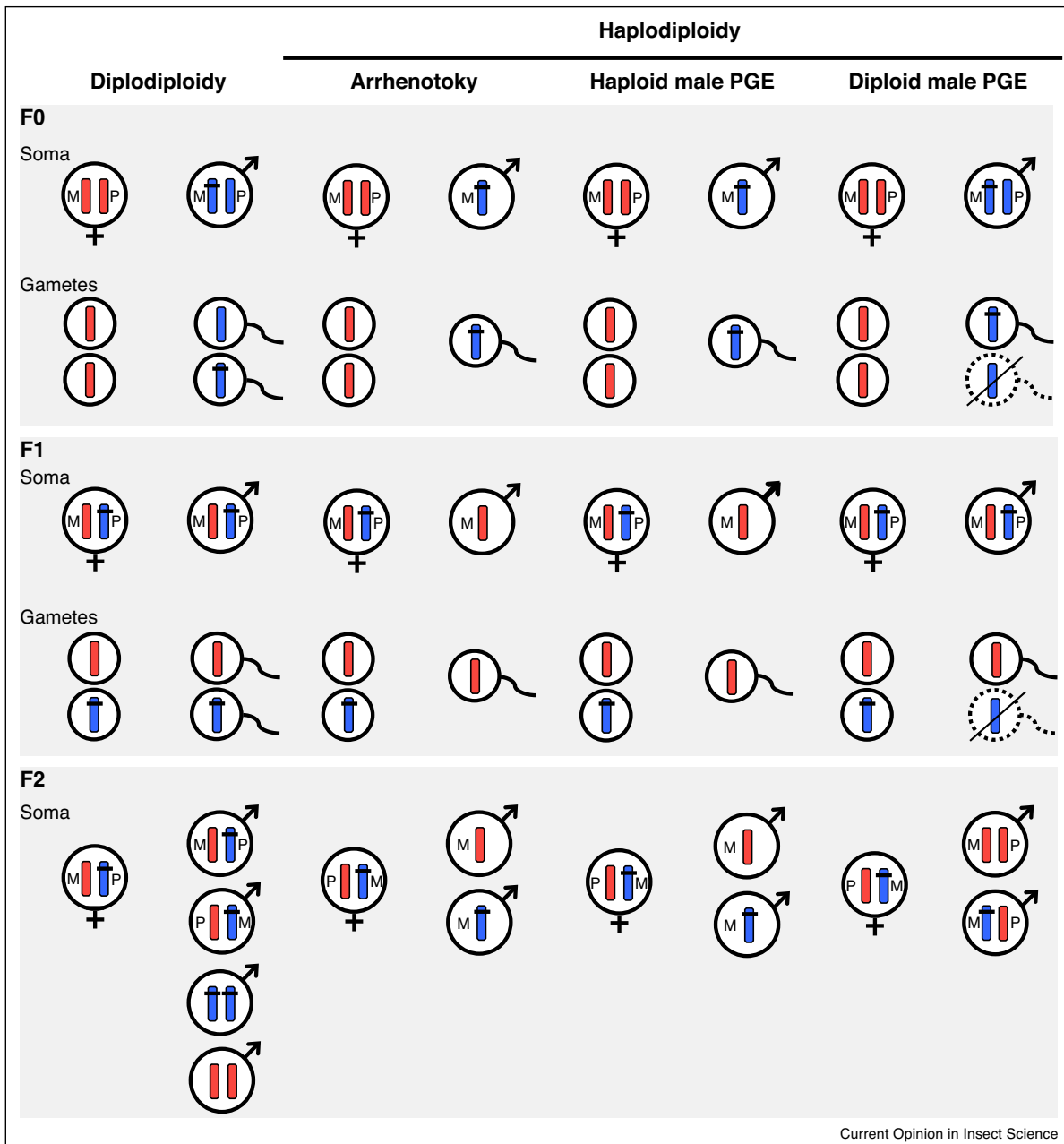
Source: Images b-f © Alex Wild and image a © Gil Wizen, used with permission.

and can result in the evolution of exaggerated traits. Such traits evolve if females chose to mate with males carrying them, either because the trait signals genetic quality (the handicap principle) [10], or because their sons will inherit it and therefore be attractive to other females (Fisherian runaway selection) [9].

As haplodiploid sons do not inherit traits from their fathers their maternal grandfathers are their closest male progenitors, so that selection on male traits skips generations (Figure 3) [11^{••}]. A simulation study [12] showed that, due to this delay, rare alleles encoding male ornaments are particularly likely to be lost through genetic drift. The same might be true for alleles underlying traits that increase a male's reproductive success without being a direct target of female choice, such as combat ability.

Subsequent deterministic models showed that haplodiploid transmission genetics also affects the genetic correlation between male traits and female preference, thereby promoting sexual selection through the handicap principle, but impeding Fisherian runaway selection [13]. Together, these models suggest that haplodiploidy should affect the evolution of exaggerated male traits. Comparative efforts to identify the prevalence of such traits and the degree of sexual dimorphism between haplodiploid and diplodiploid species might therefore, in principle, provide insight into the relative importance of runaway versus handicap selection. However these predictions are based on a number of simplifying assumptions, and there is an urgent need for more formal theory considering finite population sizes, costs of female preference, sex-specific mutation rates and allelic dominance.

Figure 3



Genetic inheritance of a paternal allele under diploidy and the three different types of haplodiploidy. Somatic genotypes are represented for three generations (F0, F1 and F2) and gamete genotypes for F0 and F1. (For simplicity, assume that there is no meiotic recombination and that offspring mate to produce the next generation.) Maternal chromosomes in F0 are shown in pink and paternal chromosomes in F0 are shown in blue. Black lines in the upper half of some chromosomes represent a given male trait (e.g., an advantageous trait in inter-locus conflict or sexual selection), whose inheritance we follow across three generations. M, inherited from the mother P, inherited from the father. Colours refer to maternal (red) and paternal (blue) genomes in F0. In F1 and F2, only one out of four possible female soma genotypes are shown, while all possible male soma genotypes carrying the original paternal allele are indicated for both generations. The figure shows how transmission of the male trait is affected by the different genetic systems. Paternal line inheritance is possible under diploidy only. Due to the fact that arrhenotokous males develop from unfertilized eggs, they do not inherit paternal chromosomes. In haploid male PGE, the situation is similar because paternal chromosomes are eliminated in the early developmental stages of the zygote. Also, in certain groups with diploid male PGE, such as in Neococcidae, the paternal genome is transcriptionally repressed and F1 males will not express the male trait. In these three scenarios, selection does not act upon this trait in F1 males.

Sexual conflict

Sexual conflicts result from the discordance of genetic interests between the sexes; males and females might differ in their optimal allele state or expression level at the same gene (intra-locus conflict) [14] or different loci (inter-locus conflict) [15^{••}]. Specific theory on the role of haplodiploidy is scarce, but analogies to X-chromosome inheritance allow us to utilize theory of sexual conflict under sex linkage [16]. As haplodiploid males obtain reproductive success only through daughters, male-beneficial traits that reduce female fitness are particularly unlikely to spread [16]. Intra-locus conflicts, in particular, will tend to be resolved in favour of females. Only if the trait is recessive and its effects are masked in females, could a polymorphism with a female advantageous allele arise [14], though not under PGE with somatically diploid males. By contrast, inter-locus conflict, especially over sex-limited traits, will not necessarily be resolved in favour of females. For example, a trait that reduces female fecundity but increases sperm competitive ability is as likely to spread under haplodiploidy as under diplodiploidy [15^{••}], yet, while diplodiploid females could benefit indirectly, through sons inheriting it, haplodiploid mothers cannot. As a result haplodiploid females are more likely to evolve resistance mechanisms [16]. Unfortunately there are few empirical studies on either intra-locus or inter-locus sexual conflicts and the predictions outlined here remain to be corroborated.

Sperm cooperation

In diploids, each individual sperm carries a unique haploid genome, different from the diploid genome of the male [17, 18^{••},19]. Under haplodiploidy sperm are produced mitotically, so individual sperm are genetically identical (barring mutations). As a result, there might be more scope for sperm cooperation, especially under post-copulatory sexual selection [18^{••}]. Empirical data on sperm behaviour under haplodiploidy are limited. However, a peculiar type of sperm cooperation has been found among scale insects with PGE. In this group, individual sperm cells have lost their motility, which they regain by assembling into motile sperm bundles, consisting of tens or even hundreds of sperm cells [20].

Mating systems and inbreeding

There is a strong empirical association between the occurrence of haplodiploidy and certain mating systems, especially those in which inbreeding is systematic (Table S1). Examples include arrhenotokous species such as many parasitoid wasps or bark and ambrosia beetles [21,22], and PGE species such as the coffee-borer beetle [23]. Haplodiploids are more resistant to inbreeding depression due to their reduced genetic load [24,25^{••},26,27]. However, inbreeding can be detrimental under some conditions: hymenopterans with complementary sex determination (CSD) are greatly affected, as inbreeding produces sterile diploid homozygous males [28]. In PGE species in which the paternal genome is transcriptionally

active [29] (diploid male PGE, Figure 3) deleterious recessive alleles are not exposed to selection, so such species are expected to suffer from substantial inbreeding depression. Some of them might have evolved monogamy (where all offspring of each individual female are either exclusively male or exclusively female) as an elaborate mechanism to avoid inbreeding [30]. Finally we expect substantial inbreeding depression in females under all types of haplodiploidy when inbreeding depression is caused by genes with female-limited expression [27].

Another aspect that could have strong implications on mating systems of arrhenotokous, but not PGE, species is that unmated females can still reproduce by producing all-son broods, which could result in relaxed selection for mate-finding traits compared to diploid/PGE females [31], or allow females to be more choosy. The capacity for virgin birth might also make arrhenotokous females good colonizers: a single arrhenotokous female could theoretically establish a population by producing sons and mating with them. Sex ratio control under arrhenotoky allows for the female-biased sex ratios favoured under such conditions [32,33]. Empirical support comes from ambrosia beetles, where incestuous arrhenotokous species are predominant over diploid outbreeding species with similar ecology on remote islands [34].

Finally, haplodiploidy might affect female mating rates. Monogamy has received considerable attention in the Hymenoptera as an important pre-requisite for the evolution of eusociality. Yet, although there is a huge literature on the link between haplodiploidy and eusociality, few authors have discussed whether monogamy is more or less prevalent among haplodiploids (although see [11^{••},31,35]). Females are thought to mate multiply to obtain either direct (nuptial gifts, replenishment of sperm supplies) or indirect benefits (promote genetic diversity, increase probability of genetic compatibility) [11^{••}]. In theory, haplodiploidy could affect both. Arrhenotokous females use sperm only to fertilize their female eggs and are able to produce sons without sperm. As a result they might both be less likely to become sperm depleted, and to suffer low reproductive success [22,31,36]. In addition, because the cost of remaining unmated is less severe, females can afford to be choosier about whom to mate with. This is not expected under PGE, as females require sperm to fertilize zygotes of both sexes. In terms of indirect genetic effects, both PGE and arrhenotokous females produce broods that are less genetically diverse on average than diplodiploid females do. They might, therefore, be selected to compensate for this by multiple mating. This is supported by various studies on haplodiploid obligately eusocial species [37,38]. To summarize, female remating rates might vary substantially among haplodiploids, but the relative balance between direct and indirect benefits suggests that, on average, they

would be lowest for arrhenotokous female and highest for those with PGE.

Sex allocation

Sex allocation is perhaps the only aspect of insect reproductive behaviour where studies on haplodiploid species are over-represented. The ability of haplodiploids to precisely alter the sex ratio of their offspring is well documented [39]. Increased control over sex allocation is obvious in haplodiploid taxa, where, unlike under genetic sex determination in diploids, there is no default sex ratio of 50:50. Sex ratio control might have allowed haplodiploid species to evolve a wide range of mating systems and promote alloparental brood care, as mothers are able to bias their sex ratio towards the more helpful sex [40]. However, this flexibility might come at the cost of increased conflicts over sex allocation: First of all, sexual conflict arises between parents over the sex ratio of their offspring [41,42]. Haplodiploid mothers generally favour an equal investment into each sex [43]. Yet fathers, who are not related to male offspring, favour a strongly female biased sex ratio and may evolve ways to persuade their partner to increase fertilization rates (under arrhenotoky) or manipulate the sex determining mechanism (under PGE). Support for the possibility that arrhenotokous males can, under some conditions, manipulate sex allocation decisions of their partners comes from parasitoid wasps [44,45], and spider mites [46**]. Although no studies have yet considered male influence on sex allocation under PGE, it might be more likely to occur as fathers' genes are present in sons [41].

Haplodiploidy might also lead to conflicts among siblings over sex allocation, and between parents and offspring, in those species where siblings interact. Under haplodiploidy, a female is more closely related to her sisters than to her brothers, and should favour a more female-biased sex ratio. The occurrence of these conflicts and how they are resolved has been studied extensively in the eusocial Hymenoptera [47] but have received less attention in other taxa where they are expected to occur, such as social thrips and mites.

Parental care

Another aspect of insect reproduction that varies dramatically between species is the presence of parental care and the relative energy expenditure males and females devote to caring for their young. A number of studies have investigated how haplodiploidy affects the evolution of paternal versus maternal care. A population genetic model by Wade [48] suggested that haplodiploidy facilitates the evolution of maternal care, but assumed that the cost of maternal care rests on both parents, not just on the mother. A subsequent model [49] included the latter possibility as well as effects of inbreeding and alternative assumptions about the genetic underpinning of the

maternal care. The result of this model suggests that haplodiploidy does not generally promote maternal care.

What about paternal care? Intuitively, haplodiploidy might be expected to inhibit paternal care as males are selected to care only for their female offspring. However, although fathers value their sons less than under diploidy, they value their daughters more, and these two effects exactly cancel [50**]. So under outbreeding, haplodiploidy neither promotes nor inhibits paternal care. By contrast, under inbreeding haplodiploidy may promote paternal care, as it inflates a male's relatedness to his offspring more than under diploidy [50**]. This suggests that paternal care might be overrepresented in haplodiploids, although empirical support is ambiguous (Table S1). Exclusively paternal care is rare among insects (probably for reasons unrelated to ploidy). The only clear examples are found in three (sub)families of diploid Hemipterans and one family of haplodiploid and strong inbreeding thrips [51], which seem to fit the model well.

One important assumption of these models [48–50**] is that parents are unable to preferentially care for the offspring to which sex they are most related. Under outbreeding, haplodiploid females are equally related to both offspring sexes, but fathers are related only to daughters. Therefore, if males are able to preferentially care for their daughters, paternal care might be promoted. The same might be true for maternal care under inbreeding, as mothers become more related to their daughters than to their sons.

Conclusion

Haplodiploid reproduction is widespread among arthropods. Males either do not inherit any genes from their fathers or, if they do, they fail to pass them on to their offspring. Here we discussed how haplodiploidy can profoundly alter mating system evolution, sex allocation and the evolution of traits under sexual selection or sexual antagonism. These predictions are not just significant to understanding the evolution of haplodiploid taxa, but, in comparison, with diploid taxa, could provide more general insights into these phenomena. Unfortunately, predictions are overwhelmingly based on verbal or very simplistic models, and much of the formal theory that is available was developed for other purposes: either extrapolated from models of X-linkage or motivated by a presumed link with eusociality and therefore tailored specifically to hymenopterans. It is clear that more formal theoretical effort is needed. A particular challenge will be to address how the different types of haplodiploidy (arrhenotoky and PGE with haploid or somatically diploid males) could help dissect the relative importance of the ability of virgin birth and effects of haploid gene expression or transmission. In Table 1, we present how we expect them to affect each of the traits discussed in

the manuscript. As each of the three types of haplodiploidy has evolved repeatedly, these predictions lend themselves well to a formal phylogenetic comparative approach. Data presented in Table S1 could serve as an excellent starting point. Finally, there is scope for a multitude of empirical tests to test predictions.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.cois.2015.04.018](https://doi.org/10.1016/j.cois.2015.04.018).

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