Genetic conflict within aphids clones

Joachim L. Dagg[1]

Abstract

A genetic conflict exists in aphids. The females of a clone are diploid for the autosomes and sex chromosomes. Parthenogenetic production of males includes the loss of one X chromosome, with no recombination between X chromosomes before the loss. Male offspring is diploid for the autosomes but haploid for the sex chromosomes (XO). Each clone can produce two brotherhoods of males. Those sharing the same X chromosome will be genetically identical. Relatedness between males of the same clone with different X chromosome will be less than 1. Sperm results from meiosis and is haploid, but the sperm cells that do not receive an X chromosome die. All surviving sperm cells share the male's X chromosome, which makes up the largest part of the genome. A clone's two brotherhoods of males produce two kinships of sperm. Sperm cells with the same X chromosome will share a part of the clone's genome that is larger than 0.5. Those carrying different X chromosomes will share less than 0.5.

This changes the default expectation for aphids from no to widespread sperm competition. The inconclusive evidence on adaptations towards sperm competition in aphids is, therefore, unexpected and needs an explanation.

The genetic conflict plays out at the level of genes, sperm, and behavior. Non-Mendelian inheritance of X chromosomes to male offspring can be a genetic resolution of the conflict. If genetic resolutions were widespread among aphids, this could explain the surprising scarcity of adaptations to the conflict at the level of male behavior or sperm.

Key words: negative relatedness, evolutionary spite, sperm competition, Aphidoidea

[1] *Eschborn 65760, Germany*

https://orcid.org/0000-0002-7310-5431

Email: jdagg@gmx.de

1 Introduction

When the default expectation is that aphids should have no sperm competition, then the inconclusive evidence requires no special explanation. But when sperm competition should be expected, then this evidence needs to be explained. The following genetic predisposition should change our expectation from no to widespread sperm competition in aphids.

1.1 Aphid sex determination

A clone is a set of cells or organisms asexually produced from a single progenitor. Disregarding mutations the individuals of a clone are usually taken to be genetically identical. Yet the asexually produced males of aphids are not genetically identical to their maternal clone nor to all the males produced by that clone. This is due to the sex determination mechanism in aphids. Aphids reproduce through cyclic parthenogenesis. Parthenogenetic females produce clonal offspring throughout the season, sexual females and males produce recombinant offspring at its end. The recombinant eggs overwinter, and the hatching animals reproduce through parthenogenesis, again.

Chromosomal sex determination happens during parthenogenesis in the mothers of the sexual animals. Sexual females receive two X chromosomes. Male offspring receive only one X chromosome, the other gets lost (Orlando, 1974; Spence & Blackman, 1998). Both X chromosomes can get lost at an equal risk during the production of males (Wilson et al., 1997; Caillaud et al., 2002), and no recombination between the X chromosomes occurs before (Hales et al., 2002). That is, males are diploid/clonal for the autosomes but haploid/hemizygous for the X chromosome (AA/XO). A balanced cell cycle requires sperm cells to be haploid for the autosomes as well, to form diploid zygotes by fusing with eggs. Meiosis in males reduces the autosomal part of their genome to produce sperm. That will only survive if it receives the male's X chromosome (A/X). Sperm that receive no X chromosome (A/O) degenerates. Recombinant eggs thus receive two X chromosomes and become (parthenogenetic) females.

1.2 Genomes of males and sperm from one clone

Ignoring new mutations, the females of an aphid clone are genetically identical. This includes parthenogenetic and sexual females. Since males receive only one of the two X chromosomes of their mothers/clone (hereinafter either X_1 or X_2), each clone produces two brotherhoods of males (carrying X_1O or X_2O). As sperm cells lacking an X chromosome die, these brotherhoods produce sperm of two kinships (carrying X_1 or X_2).[1]

Most aphid species have a small number of chromosomes (4-10 pairs is common), and the X chromosomes are the largest (Blackman, 1980). The following will consider the proportion, *p*, of a clone's genome carried by males and sperm of that clone.

Suppose a clone is completely heterozygous (A'A"/X_1X_2), where A' and A" denote the heterozygous autosomal parts of the genome and X_1 and X_2 the different X chromosomes. One half of its males will share one of its X chromosomes, and the remaining half will share the other. The two X chromosomes take the largest part of a clone's genome. According to Wilson et al. (1997, p. 235), it amounts to 28% in an Tasmanian descendant of the Holarctic *Sitobion fragariae* (Walker). This clone produces a sexual generation under temperate autumn conditions and can serve as a model. Since males lack one X chromosome (14%), they carry only 0.86 of their clone's diploid genome. Those males of a clone that receive different X chromosomes will only share the autosomal part, $p = 0.72$. Although producing males involves no meiosis, they can differ in their X chromosomes (fig. 1, male A'A"/X0 genomes).

Sperm cells are haploid through meiosis, but those that do not get an X chromosome degenerate. Surviving sperm cells of a male share half of their autosomal genome, but the whole of their X chromosome. Furthermore, males of the same clone that carry different X chromosomes share only the autosomal part of the clone's genome 0.72. These autosomal parts go through independent meioses, leaving only 0.18 of the clone's

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[1] Autosome behaviour during spermatogenesis can differ between aphids: crossing-over recombination between homologues does not occur in every species (Manicardi et al., 2015). I ignore this for simplicity.

genome to be shared by sperm cells of the same clone with different X chromosomes (fig. 1, sperm: A/X genomes). This is less than the 0.25 share after two meioses of a full genome.

The shared portions, p, considered above are not the same as estimates of evolutionary relatedness considered below.

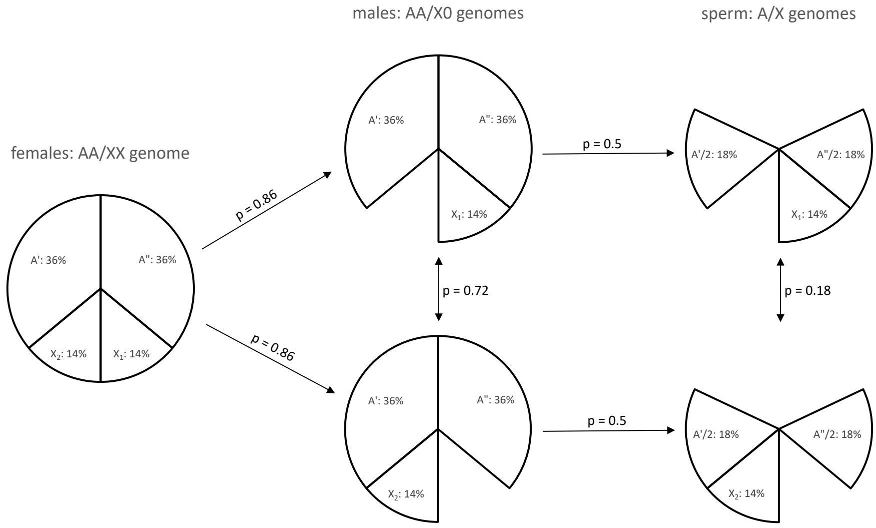


Figure 1: Female, male, and sperm genomes of an aphid clone. Shared portions, p, of a diploid clone's genome in Tasmanian *S. fragariae*. Two X chromosomes of diploid females constitute 28% of their AA/XX genome. Males get a diploid set of autosomes but lack one X chromosome. Hence, their AA/XO genomes carry 0.86 of the diploid AA/XX genomes. Meiosis during spermiogenesis reduces the autosomal part of the male genomes to yield a haploid A/X genome. This is 0.5 of the clone's genome, as would also result from one direct meiosis. Spermatozoa with different X chromosomes share 0.18 of the clone's genome with each other. This is less than would result from two meiosis of the clone's genome (0.25).

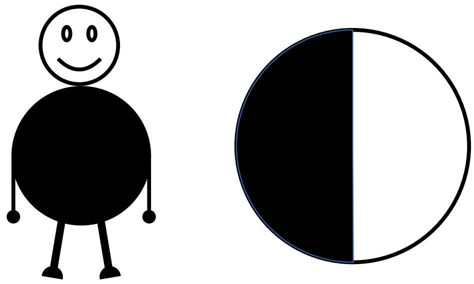
1.3 Evolutionary relatedness

The evolutionarily relevant relatedness depends on the size and genetic composition of the background population of actual interactors (Gardner & West, 2004). If the recipient carries the actor's genes at a frequency greater than the average in this arena of competitors ($r > \bar{r}$) then its reproductive success will increase the frequency of the actor's genes in the competitive arena. The actor's inclusive fitness benefit will be positive, $RB > 0$. If the recipient carries the actor's genes at a frequency lower than the average in the social arena ($r < \bar{r}$) then its reproductive success will decrease the frequency of the actor's genes in it. The actor's inclusive fitness benefit will be negative, $RB < 0$.

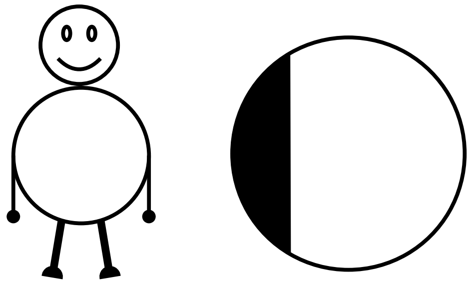
Focusing on X-linked genes in male aphids, their X-relatedness depends on the question whether they compete within or between clones. Yet the X-relatedness of clonal males with different X chromosomes will always be negative and that sharing X chromosomes will always be positive (fig. 2). The same holds for sperm cells on a haploid level. That is, the X-relatedness of sperm cells sharing an X chromosome will be positive and that of sperm cells carrying different X chromosomes will be negative.

Altruism entails a fitness cost (C) to the actor and a benefit (B) accruing to the recipient. Natural selection can favor it if the relatedness (R) of the recipient to the actor is sufficiently positive, $RB > C$ (Hamilton's rule). Spiteful behavior entails a fitness loss for the recipient ($B < 0$) and a fitness cost for the actor ($C > 0$). Natural selection can favor it, if the R is sufficiently negative ($R < 0$) to satisfy Hamilton's rule, $RB > C$. While an actor will always be negatively related with its average social background (fig. 2c, d), the absolute value is inversely proportional to the size of its social arena or deme (Gardner & West, 2004; Lehmann et al., 2006). The smaller this scale of competition, the more can negative R differ nontrivially from zero. With two male aphids competing in a patch of females R could become -1. Male aphids therefore have a genetic predisposition for both types of traits, when competition is local and the scale of the competitive arena small.

Figure 2: An actor's genes linked to its chromosome X_1 (shaded) are present in a recipient at frequency r and in the competitive arena at frequency $\bar{r}$. **a)** For a recipient male sharing X_1, r will be 1. **b)** For a recipient carrying chromosome X_2, r will be zero. **c)** If the clone is the arena of competition, $\bar{r}$ will be 0.5. **d)** If males from several clones form the social arena of competition, $\bar{r}$ will be < 0.5. In either case, recipients sharing chromosome X_1 will be positively related, while those carrying X_2 will be negatively related to the actor.



a) recipient male (with X_1) **c)** clone (social arena)



b) recipient male (with X_2) **d)** population (social arena)

2. Gene level

Aphid X chromosomes accumulated genes that biasedly express in males (Jaquiéry et al., 2012, 2013, 2022; Li et al., 2020). This should facilitate the selection of mutations in male traits adaptive to the genetic conflict between males of the same clone. Yet this potential for genetic conflict can also be resolved at the gene level. Non-Mendelian inheritance of X chromosomes to males could remedy the sperm competition between males of a clone. If all males of a clone receive the same X chromosome, they will be genetically identical. Their sperm will vary in the haploid autosomal portion, but this variation within males will not differ from that between males of the same clone.

Evidence of non-Mendelian X-inheritance in aphids exists: The loss of one X chromosome in male production is random in some taxa of *Acyrthosiphon pisum*, *Myzus persicae*, and *Sitobion spp.*, but non-random in others (Wilson et al., 1997; Caillaud et al., 2002; Wilson & Sunnucks, 2006; Wilson et al., 2014). Furthermore, it is nonrandom in some taxa of *Macrosiphum euphorbiae* and *Rhopalosipum padi* (Frantz et al., 2005; Monti et al., 2011; see also Manicardi et al., 2015).

Adaptations to the genetic conflict at the level of sperm or male behavior should not be expected in taxa with nonrandom transmission of X chromosomes to males. If this genetic resolution of the conflict was widespread in aphids, this would explain the heterogeneous evidence on adaptations at the level of male behavior or sperm.

3. Behavior

3.1 The scale of competition in male aphids

Migration is a major factor affecting the scale of competition between aphid males. Particularly relevant is winged migration occurring shortly before or during the lifetime of the sexual generation (usually in autumn). Two different modes of autumn migration will affect the males' scales of competition contrarily. If the parthenogenetic mothers of the sexual females and males (*sexuparae*, S) fly to the overwintering sites, sibling males will migrate together inside them (fig 3, upper panel). That will shrink their scale of competition regardless of walking occurring on the target site. If the sexual females migrate inside their winged mothers (*gynoparae*, G), winged males will fly independently of each other (fig 3, lower panel). That will expand their scale of competition.

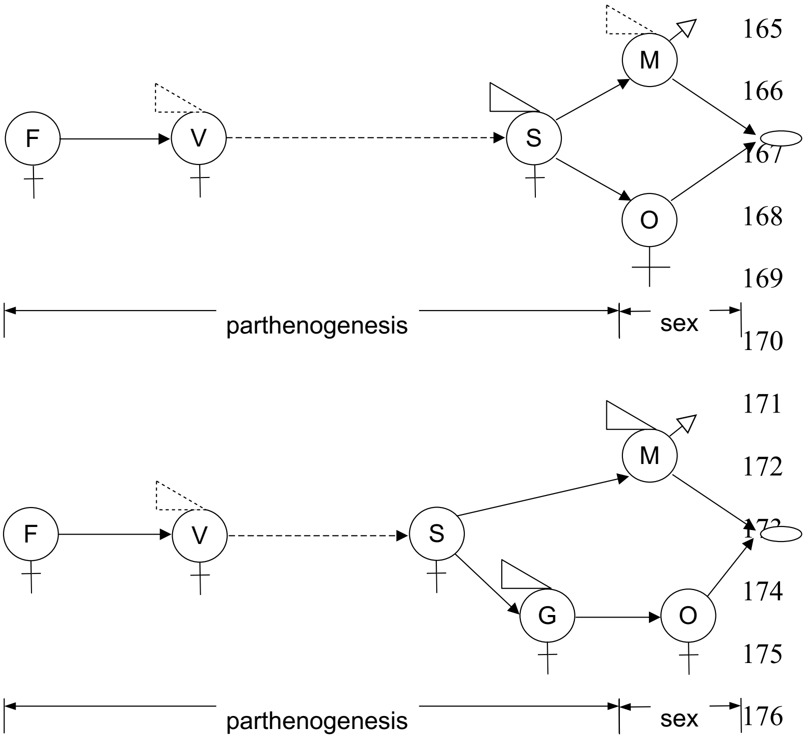


Figure 3: Migration in aphids. Triangles: wings; dashed triangles: possible polymorphism of winged and wingless morphs; dashed arrows: variable number of generations; axis: mode of reproduction. Founding mothers (F) hatch from eggs after overwintering. They give birth to larvae through parthenogenesis. These and a varying number of following generations reproduce in the same way (*viviparae*, V). Some V migrate to the summer sites. At the season's end viviparous females produces sexual morphs (*sexuparae*, S) parthenogenetically. In the simpler case [upper panel], S migrate to the overwintering site and produce *males* (M) and sexual females that lay eggs after fertilization (*oviparae*, O). The eggs (ellipse) are recombinant. In the complex case [lower panel], S produce winged males and mothers of sexual females (*gynoparae*, G). M and G migrate independently to the winter site, where G produce sexual females (O).

3.2 Male behavior under different scales of competition

Migration in the willow-carrot aphid, *Cavariella aegopodii* (Scopoli) expands the males' scale of competition (fig. 3, lower panel). Winged males fly individually from carrots to willows. Sexual females migrate inside their gynoparous mothers (G). Studying this aphid species, Dixon and Kundu (2013, 108) stated "male aphids are not known to fight for access to females and mating appears to be a very simple affair" (cf. Dhatwalia, 2024).

Migration in poplar spiral gall aphid, *Pemphigus spyrothecae* Passerini, decreases the males' scale of competition (fig. 3, upper panel). Sexuparous mothers (S) fly to the overwintering sites, crevices on poplar bark. They always produce two wingless sons and a variable number of wingless sexual females (O) depending on their condition. If the loss of one X chromosome is random in the production of these sons, their chance to carry the same X chromosome will be 0.5.

Sexuparae (S) of *P. spyrothecae* tend to aggregate a little, so that the average number of S in a crevice is 2.49 ± 0.18 and the median 1.61 (Foster & Benton, 1992). The males (M) mature before the females (O) and guard them before their adult molt. There is a considerable amount of interference between males on the females both before and during copulation. Even when there were only two sibling males in a patch, "the two brothers were on the same female simultaneously, constantly scrabbling and pushing at each other [reference to figure omitted]. On three occasions, one male clearly pushed the other off the female." (Foster & Benton, 1992, p. 302). Interference seemed equally intense between two brothers as between two non-sib males (Foster and Benton 1992, 302).

The fighting of males could be an ancestral or a derived behavioral trait of *P. spyrothecae*. In the first case, evolving mechanisms for discriminating males could have been constrained. Indiscriminate fighting would be a vestige that is maladaptive if it occurred between positively related males (with the same X chromosome). In the second case, male fighting would be a derived trait of *P. spyrothecae* and should be adaptive. It could then be selfish or spiteful, depending on the cost and benefit resulting for the actor, recipient, and third parties.

If the actor manages to push the recipient off a tended female, it will be selfish. If the actor only reduces the fitness of a negatively related recipient, while a positively related third male benefits from this, it will be direct spite or indirect altruism to the third male (West & Gardner, 2010; Krupp, 2013). Since the chance for siblings to be positively related is only 0.5, the chance of negative relatedness between any two males should be >0.5 in patches founded by more than one S mother. Even indiscriminate fighting may, on average, be adaptive in such a competitive arena.

4. Sperm

For sperm competition to occur, sperm from at least two genetically different males must compete for fertilization within a female. The hitherto ignored split kinship of sperm from the same clone increases the chance for sperm competition to occur in aphids. Yet aphid sex ratios are usually female biased (Foster, 2002), and this reduces the chance for sperm competition to occur. Complex adaptations to sperm competition (see Pitnick et al. 2009) should therefore not be expected in aphids.

The relatedness of sperm cells of the same male will be ≫0.5, because they receive the male's single X chromosome without having been recombined in meiosis. They will be positively related in comparison to the average spermatid from its competitive arena. Cystic spermatogenesis in insects results in the formation of sperm bundles within the male genital tract before they usually disband (Virkki, 1969; Phillips, 1970; Wieczorek & Swiątek, 2008; Vitale et al., 2009, 2011). Therefore, sperm bundles found in male genital tracts only prove cystic spermatogenesis. A mere delay of the disbanding of sperm bundles would allow sperm cooperation within the female genital tract. This seems to be the simplest possible adaptation to sperm competition.

Thomas Henry Huxley studied aphids found on an oak tree in the London Zoological Gardens. His description (Huxley, 1858, p. 203) fits that of a *Myzocallis* species. Upon dissecting females, he found 'a multitude of large filiform spermatozoa bent upon themselves' in the spermatheca (Huxley, 1858, p. 205). The phrase 'bent upon themselves' is unfortunately ambiguous.

Balbiani observed sperm within the spermathecae of mated females (*U. jaceae*). ‘They appear, sometimes in the form of isolated filaments, entangled in each other, sometimes in the form of small bundles variously wound on themselves’ (Balbiani, 1870, art. no. 2, p. 19, translated). He had earlier observed sperm bundles disbanding inside the males (Balbiani, 1869, p. 79).

Buckton described sperm cells squeezed out of males: ‘If a gentle pressure on the abdominal rings of the male Aphis be continued after the protrusion of the penis, a copious escape of minute bodies from the ejaculatory tube will be noted, and these will scatter themselves throughout the weak solution of sugar or albumen used during dissection. […] These spermatozoids have a tendency also to gather into knots.’ (Buckton 1883, 127f). While this suggests that sperm cells might be able to from secondary aggregates inside the females, Buckton concluded: ‘When the sperm-cells are mature the cysts break up or burst, and the filamented cells disentangle, and are then free to move down the vessels into the suitable vesicles’ (Buckton, 1883, p. 128).

Dagg (2002, 12) observed lengthy conjugates in the spermathecal duct and spherical ones in the spermatheca of female *Uroleucon cirsii* (Linnaeus) (see also Dagg 2003, 202). Hales (2005) rejected this for *M. persicae*, observing that the sperm cells within testes of adult males ‘were not joined at the head, though they were during the last nymphal stage’ (Hales, 2005, p. 645), and concluding that the ‘round objects in the spermatheca are likely to be an optical artefact’ (Hales, 2005, p. 643).

Huang and Caillaud (2012, fig. 1C) found spherical sperm bundles inside the spermathecae of *Acyrthosiphon pisum* (Harris), where, after successful sperm transfer, ‘the spermatheca was well inflated and included a small bundle of opaque white material.’ Staining confirmed that it was a bundle of spermatozoa (Huang & Caillaud, 2012, p. 5). Vitale and Viscuso (2015, 88) reported material inside the spermatheca of *E. betulae* that seemed to be a degenerating cap of a sperm bundle.

Wieczorek et al. (2019) reported ‘chaotically oriented bunches of spermatozoa’ in the testes and ‘a dense substance in which spermatozoa are embedded’ in the spermathecae of *A. pisum*. Finally, the testes of the arctic species *Acyrthosiphon svalbardicum* Heikinheimo were seen to contain ‘bunches of ripe spermatozoa,’ while the spermathecae contained ‘dense aggregations of spermatozoa and male accessory gland secretions’ (Wieczorek et al., 2020).

In the above-mentioned taxa, the males of *Myzus persicae* migrate independently. Winged males and the winged mothers of the sexual females (G) fly to the winter host. Species of the genera *Myzocallis* and *Uroleucon* do not alternate hosts, but their males have wings. The same is true for *Euceraphis betulae*. Males of *Acyrthosiphon pisum* can be either winged or wingless. Huang and Caillaud (2012) had a clone with wingless males, whereas Wieczorek et al. (2019) had winged males.

A. svalbardicum is also monoecious but has an extremely short life cycle. The founding mothers (F) directly produce sexual morphs that are both wingless. Founding mothers can also produce some viviparous daughters under favourable conditions (winged or wingless), but this has only rarely been observed (Wieczorek et al., 2020). Sperm competition between clones can still result, if more than one winter egg of a patch survives, and the recombinant founding mothers produce their offspring in the same patch.

5. Conclusion

The chromosomal sex determination system in aphids (XX/XO) creates a predisposition for genetic conflict between males of the same clone with different X chromosomes (section 1). In some taxa inheritance of X chromosomes to males is nonrandom (Caillaud et al., 2002; Frantz et al., 2005; Wilson & Sunnucks, 2006; Monti et al., 2011; Wilson et al., 2014). This will reduce the incidence of a clone’s males carrying different X chromosomes. The genetic conflict would be resolved at the gene level (section 2).

In other taxa the random loss of one X chromosome in males has been documented (Wilson et al., 1997; Caillaud et al., 2002; Wilson & Sunnucks, 2006). Here, the bias of X-linked genes to express in males (Jaquiéry et al., 2012, 2013, 2022; Li et al., 2020) could ease the selection of mutations adaptive to sperm competition between males. This basic situation fits the heterogeneous evidence for sperm cooperation in aphids (section 4).

The conditions for evolving behavioral adaptations to genetic conflict among a clone's males seem even more restrictive. The males' relatedness must be negative and the scale of competition small (section 3). The existence of only one well documented case of fighting in sibling aphid males also fits this basic situation. Conversely, the infrequence of evidence for sperm competition adaptations at the level of behavior or sperm suggests that gene level resolutions of the genetic predisposition should be widespread.

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