



Sex ratios in the haplodiploid herbivores, Aleyrodidae and Thysanoptera: A review and tools for study

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Abstract

Sex allocation studies in hymenopterans have been used to test adaptive predictions, to predict the quality of biological control agents, to theorize how eusociality is maintained, and to predict population dynamics. Almost all hymenopterans are haplodiploid, so mothers may have an ability to adaptively adjust sex allocation. The insect order Thysanoptera (thrips) and the Hemipteran family Aleyrodidae (whiteflies) are also haplodiploid and include important agricultural pests, but have been the subject of comparatively few sex allocation studies. This review summarizes studies of Aleyrodidae and Thysanoptera sex ratios as influenced by temperature, host plant, nutrition, conspecifics, competitors, endosymbionts, predators, parasitoids and other pathogens.

Sex ratio influences were reported in studies testing effects of temperature, host plant, conspecifics, competitors, bacterial endosymbionts and a fungal pathogen. Viruses, predators, and parasitoids were not found to affect sex ratios in Aleyrodidae and Thysanoptera, although not many studies have collected the data to assess these factors. Because sex ratio studies in Thysanoptera and Aleyrodidae have only recorded secondary, adult or operational sex ratios instead of primary sex ratios at oviposition, differential developmental mortality is a potential confounding variable for interpreting all of these records, and it is difficult to confirm whether sex ratios reflect sex allocation. To conclude whether sex allocation by mothers is taking place, primary sex ratios need to be recorded. Our review refers to a cytogenetic and survival assay to find primary sex ratios or confirm differential developmental mortality in these haplodiploid organisms.



1. Introduction

The study of sex allocation in arthropods has focused extensively on the insect order Hymenoptera, in part due to the flexible nature of the haplodiploid sex-determination system, which allows females to allocate reproduction towards female (diploid, fertilized eggs) or male (haploid, unfertilized eggs) offspring through selective fertilization. Rich theory in sex ratio has been solidified through empirical study using hymenopterans, including local mate competition (LMC; [Hamilton, 1967](#)), the Trivers–Willard hypothesis ([Charnov et al., 1981](#)), and theories on the origins of eusociality ([Gardner and Ross, 2013](#); [Schwarz, 1988](#) and see Sections “[Glossary](#)” and “[Relevant sex allocation theories](#)”). The hymenopteran species chosen for study have been primarily parasitoid wasps, fig wasps, and eusocial ants, bees and wasps. This research has served as a cornerstone in the field of behavioural ecology, as qualitative and even quantitative predictions of sex ratios have been developed and then tested in different environments based on adaptive hypotheses ([Bourke and Franks, 1995](#); [Charnov, 1982](#); [Godfray, 1994](#)). Sex ratios also are an important component of population dynamics. An understanding of factors that influence sex ratios have applications in the use of parasitoid wasps in biological control ([Chow and Heinz, 2005](#)), as even or female-biased sex ratios are considered beneficial for pest management and evidence of high-quality biological control agents ([Heimpel and Lundgren, 2000](#); [van Lenteren, 2003](#)).

Given the pressing need to predict dynamics of herbivorous pests, it is perhaps surprising that hypotheses regarding sex ratios have been hardly developed outside of Hymenoptera, especially since two groups of economically

important insect pests are haplodiploid and may exhibit labile sex ratios. These are the important hemipteran sap-feeding family of whiteflies, Aleyrodidae, and the entire order of thrips, Thysanoptera. Whiteflies are generally specialized, tree-feeding sap-feeders, but include a handful of notorious polyphagous forb-feeding species that have broad host ranges, attack many crop plants, and vector a hundred or more viruses (Gilbertson et al., 2015; Jones, 2003; Oliveira et al., 2013). Thrips are mostly herbivorous cell-feeders, with a few predacious exceptions, and some pest species can also vector viruses (Gilbertson et al., 2015; Jones, 2005; Mound, 2005). We might expect resource use (plants rather than other insects), life history, and other environmental pressures to affect the sex ratios of these insects differently than in parasitic or predatory Hymenoptera. However, while many life history studies have been performed on these taxa, often measuring adult sex ratios along with other demographic parameters such as development time and fecundity, there are relatively few studies that interpret sex ratios within a conceptual framework. Here, we will review what is known about sex ratios of herbivorous, haplodiploid taxa as they are influenced by host plants, conspecifics, competitors, predators, parasitoids, pathogens, endosymbionts, viruses, and temperature. Although selfish genetic elements may also play a role in altering sex ratio, there are few or no records of these in whiteflies and thrips, so they will not be discussed in this review.

Sex ratios in most studies of thrips and whiteflies to date have been limited by the data collected; investigators commonly record adult sex ratios, or occasionally operational sex ratios from field studies. However, comparing the influence of treatment effects on sex allocation is at best very approximate when adult or operational sex ratios are measured. Adult sex ratios may be hard to interpret because primary sex ratios and differential mortality of the sexes during development may vary simultaneously. Operational sex ratios are even farther from primary sex ratios and can include multiple confounding variables such as sex-specific differences in timing of emergence, longevity of the sexes, dispersal and microhabitat choices, all of which may influence what adults are collected in a sample. Nonetheless, tools for directly investigating or inferring the primary sex ratios of whiteflies are available. We argue that these techniques, borrowed from the study of hymenopteran parasitoids, can improve sex ratio data collection and ultimately our understanding of the cause of variable sex ratios of haplodiploid herbivores, and help to put the study of sex ratio of these groups on a more rigorous footing.



2. Effects of temperature on sex ratio

Temperature may differentially affect the sexes and adult sex ratios of both Aleyrodidae and Thysanoptera. In the species complex that is collectively known as *Bemisia tabaci*, short exposure to extremely high temperatures (37 °C and higher) increases the proportion of males in the *B. tabaci* species known as Mediterranean (MED) as well as in Middle East Asia Minor 1 (MEAM1) (Cui et al., 2008; Lü et al., 2014; Xiao et al., 2016). Researchers that reared *B. tabaci* MEAM1 from egg to adult at less extreme temperatures of 15–37 °C found no alterations in adult sex ratios that corresponded to temperature, but did observe female-biased offspring at all temperatures (Wagner, 1995; Wang and Tsai, 1996), or sex ratios that approximated 50% (Guo et al., 2013). To find effects of exposure to high temperatures, Cui et al. (2008) and Lü et al. (2014) heat-shocked parents for 1 h at temperatures ranging from 37 to 45 °C, and then reared offspring at 26 °C to record survival and sex. Cui et al. (2008) found that sex ratio became significantly more male-biased when MEAM1 parents were exposed to 43–45 °C, while Lü et al. (2014) also found even or male-biased sex ratios after exposing MEAM1 parents to 41–45 °C. In both cases, the offspring were female-biased at lower temperatures of parental heat-shock, including at the control temperature of 26 °C. Xiao et al. (2016) heat-shocked MED and MEAM1 parents at 41 °C for 2 h, and found male-biased offspring (38–46% female) in comparison to the control group exposed to 26 °C (55–62% female). In all cases, alterations of sex ratio corresponded to decreases in developmental survival, suggesting that differential mortality of females might explain these patterns. In contrast, Elbaz et al. (2011) heat-shocked MED and MEAM1 parents for 1.5 h at 42 °C and found no significant difference in adult sex ratios of the offspring compared with the 27 °C control. These authors did find declines in adult survival after 43 °C heat-shock in MEAM1 females or after 45 °C in MED females, suggesting that these higher temperatures approach lethal limits for these species. Cui et al. (2008) found declines in parental adult survival at or above 41 °C, in egg survival at or above 43 °C, and in egg to adult survival after 41 °C. Lü et al. (2014) did not track offspring survival, but in separate heat-shock experiments on adults, found significant declines in survival after 1 h of exposure to 43–45 °C. Xiao et al. (2016) found marginal to significant declines in egg survival and significant declines in egg to adult survival after a 2-h 41 °C parental heat shock.

Although these studies in aggregate show mixed results, in general it appears that lethal temperature limits of *B. tabaci* are reached near 41 °C, with greater impacts on developmental survivorship of females, leading to increases in sex ratio.

Reports of lower temperature effects on *B. tabaci* sex ratio are inconsistent. Sharaf and Batta (1985) found an increase in the proportion of females by rearing *B. tabaci* (unknown species) from egg to adult at cold temperatures. Whiteflies reared at 14 °C were 76% female while those reared at 25 °C were 64% female. The developmental survivorship was not reported. In contrast, Xiao et al. (2016) cold-shocked *B. tabaci* MED and MEAM1 adults for 2 h at 4 °C, but did not find effects on offspring sex ratio. Egg survival also was unaffected by exposure of parents to a 4 °C cold shock (Xiao et al., 2016).

Temperature has not been reported to influence sex ratios in the greenhouse whitefly, *Trialeurodes vaporariorum*. In addition to *B. tabaci*, Cui et al. (2008) also heat-shocked *T. vaporariorum* parents from 37 to 45 °C for 1 h. Offspring sex ratios remained close to 50% for all treatments, with no offspring produced at 43–45 °C (Cui et al., 2008). The results suggest that *B. tabaci* and *T. vaporariorum* have two responses when lethal temperatures are approached: more male offspring will result in *B. tabaci* as developmental survivorship declines, while an even sex ratio in *T. vaporariorum* is maintained until their thermal lethal limit is reached.

In the thrips *Ceratothripoides claratris*, Premachandra et al. (2004) found a positive correlation between temperature and the proportion of females over a range of three temperatures. Male-biased offspring emerged at the rearing temperature of 25 °C, while female-biased offspring emerged at 30 and 35 °C (Premachandra et al., 2004). Interestingly, reproductive success, as judged by preadult survival, fecundity and sex ratio, peaked at 30 °C. Because developmental survivorship was high at this temperature, female-bias in this case may approximately represent the sex allocation strategy (Premachandra et al., 2004). In *Frankliniella occidentalis*, Kumm and Moritz (2010) found a similar pattern. Kumm and Moritz (2010) reared *F. occidentalis* at three temperatures (17, 23, and 32 °C), and found a linear decrease in adult sex ratio with temperature, ranging from 55% male at 17 °C to 33% male at 32 °C. The change in sex ratio in this study could be a result of mothers altering the primary sex ratio, or of higher male mortality (or lower female mortality) with higher temperatures, as survival was not measured. At the higher temperature of 41 °C, Wang et al. (2014)

found opposing results. Wang et al. (2014) heat-shocked *F. occidentalis* adults at 41 °C for five time-intervals of between 2 and 36 h and reared and sexed offspring at 25 °C. Although all treatments produced female-biased offspring, the adults that were heat-shocked for longer time periods produced a relatively higher proportion of male offspring.

Surprisingly, Kumm and Moritz (2010) also found that 0.5% of *F. occidentalis* offspring from virgin females were female, even though this thrips is known to be arrhenotokous. To test whether the apparent thelytoky was due to parthenogenesis-inducing bacteria, the authors surveyed the population for *Wolbachia*, but not other bacteria now known to also cause parthenogenesis (e.g. *Cardinium*, *Rickettsia*) (Giorgini et al., 2010; Hagimori et al., 2006; Zchori-Fein et al., 2004). The phenomenon remained unexplained after *Wolbachia* was not detected in the studied population (Kumm and Moritz, 2010).

In Kelly's citrus thrips, *Pezothrips kellyanus*, no clear pattern in sex ratio was associated with temperature (Varikou et al., 2012). At rearing temperatures of 15 and 25 °C, female-biased offspring were found, while male-biased offspring were found in the 20 °C and 30 °C treatments (Varikou et al., 2012).

Overall, there appears to be some association between high temperatures and increased proportions of male offspring in the few Aleyrodidae and Thysanoptera studied. These temperatures also correlated with declines in developmental as well as adult survival. The absence of any direct measure of primary sex ratios makes it impossible to determine the cause of the pattern of increasing sex ratio with temperature. High-temperature exposures of parents could reduce sperm viability or the ability of females to fertilize eggs, leading to a lower primary sex ratio. The reduced developmental survivorship observed in many studies could also explain changes in adult sex ratios if females were more susceptible to heat during development. These hypotheses should be confirmed with mechanistic studies that measure the primary sex ratio of newly laid eggs.



3. Other abiotic effects on sex ratio

Few studies have tested abiotic effects on Aleyrodidae and Thysanoptera sex ratios outside of temperature. To our knowledge, no studies have examined the influence of humidity on sex ratios of whiteflies or thrips, but this would be valuable to investigate.



4. Host plant and nutritional effects on sex ratio

More than any other environmental factor, host plants mediate the life history of herbivorous insects. Plants provide varying levels of nutrition and have evolved a wide array of physical and chemical defences against their herbivores (Bernays and Chapman, 1994; Price et al., 2011). For whiteflies and thrips, there have been several studies determining the relative host quality of crops and other plants as assessed by insect life history parameters, with high-quality host plants supporting shorter development times to adulthood, higher survival during development, increased adult longevity and greater fecundity. How does sex ratio fit into this collection of work? Can haplodiploid insects adjust offspring sex ratio according to host plant quality, and is there a certain strategy that enhances fitness? More fundamentally, what relationship is observed between host plant quality and sex ratios? In a high-quality environment, resources are less limited, so sexes may become equal in cost to produce, trending towards even sex ratios in accordance with Fisher's principle. On the other hand, the Trivers–Willard and Charnov hypotheses may come into play, in which females may benefit relatively more than males with better maternal or environmental condition, leading to female-biased sex ratios on high-quality host plants. This could occur if high-quality plants are a limited resource, while, when quality plants are not limiting, even sex ratios may be adaptive. Studies in some herbivorous insects such as sawflies and aphids suggest that females are favoured on higher quality host plants (Barker and Maczka, 1996; Craig et al., 1992; Purdy and Miller, 2013). For example, Barker and Maczka (1996) found that the dry mass of *Pachynematus clitellatus* sawfly females was significantly greater on preferred host plants, whereas there was no difference in male dry mass between host plants of differing quality. Relatively higher fitness gains may have led to the greater female-bias on the preferred host plant (Barker and Maczka, 1996).

Similar results have been found in the castor whitefly, *Trialeurodes ricini* (Shishehbor and Brennan, 1996). Shishehbor and Brennan (1996) determined eggplant and cotton to be the better hosts for *T. ricini* due to higher fecundity, shorter development time and higher survivorship to adulthood. On these host plants, sex ratios were even, whereas sex ratios on poorer host plants were male-biased. The data for this species is inconsistent, however. Huang et al. (2014) also found that the best host plant resulted in even sex ratios for *T. ricini*. However, poorer host plants (including cotton and

eggplant, in contrast to [Shishehbor and Brennan, 1996](#)) had sex ratios that varied from 43% to 73% female. The difference in results could have been due to many environmental variables as well as to the specific plant or *T. ricini* population. Overall, sex ratios in *T. ricini* appear to be even and conform to Fisher's principle on high-quality host plants, but are more variable on host plants of lower quality.

In the greenhouse whitefly, *T. vaporariorum*, [Hosseini et al. \(2015\)](#) artificially created host plants of varying quality by providing different amounts of nitrogen to tomato plants. Nitrogen is a common limiting nutrient for phloem-feeding insects. Increases of nitrogen levels in tomato plants increased the growth rate of *T. vaporariorum*, but did not alter sex ratio, which was close to 50% in all treatments ([Hosseini et al., 2015](#)).

Other studies also do not find any clear association between host plant quality and sex ratio. [Greenberg et al. \(2009\)](#) found no relationship for species of *B. tabaci* MEAM1, *Trialeurodes abutiloneus*, and *T. vaporariorum*, while [Fekrat and Shishehbor \(2007\)](#) found no associations in *B. tabaci* MEAM1. Studies of Thysanoptera have also been unable to associate host plant quality with predictable changes in sex ratio ([Cao et al., 2018](#); [Tang et al., 2015](#); [Zhang et al., 2007](#)).

Currently then, published studies do not show any consistent relationship between sex ratios and host plant quality in Aleyrodidae and Thysanoptera. This is clearly an area that would benefit from a more rigorous examination of the sex allocation patterns that lead to adult sex ratios. Given potentially large differences in host plant quality, do females allocate sex similarly on hosts of a given quality? And does host quality differentially influence male and female developmental success?

Although mycophagous insects have different life histories than herbivorous ones, varying levels of resource quality may prompt sex allocation in the same way. Sex ratios in one mycophagous thrips, *Elaphrothrips tuberculatus*, appear to conform to the Trivers–Willard hypothesis. [Crespi \(1988\)](#) did not need to rule out differential mortality to determine sex allocation, because mothers are flexible in producing all-male broods viviparously, or all-female broods oviparously. Therefore, one may only need to look at the reproductive mode of mothers to verify sex allocation ([Crespi, 1988](#)). [Crespi \(1988\)](#) found a strong relationship between viviparity (male production) and maternal condition, the latter measured by either a larger body size in early summer, or when mothers had access to denser fungal fruiting bodies on leaves in spring. [Crespi \(1988\)](#) quantitatively confirmed the Trivers–Willard hypothesis; he found greater gains for male

fitness with body size increases relative to those for females. In this case, larger males gained fitness by their better ability to mate-guard, and the relationship showed a steeper slope than for female size and fecundity (Crespi, 1988). A mother should therefore become viviparous (male-producing) during times when she can produce larger offspring, and oviparous (female-producing) at all other times.



5. Effects of conspecifics on sex allocation

Among Hymenoptera, conspecific strategies largely drive sex allocation. The responses in sex allocation to LMC, LRC, and LRE (see Section “[Relevant sex allocation theories](#)”) have been documented across multiple taxa and sex determination systems, and these responses have generally been larger in effect size in comparison with the influence of other environmental cues (West et al., 2005).

In Thysanoptera, LMC is expected to affect gall-inducing thrips, especially in cases where galls are closed, males do not disperse, and there is one founding female, or the founders are sisters (Crespi, 1993). Fisherian sex ratios are expected for free-living thrips under random mating, as they are not constrained to mate on their natal patches (Crespi, 1993; Higgins and Myers, 1992). As expected, most gall-inducing thrips comply to LMC, or partial LMC (Crespi et al., 1997; Tree and Walter, 2009; Tsuchida and Ohguchi, 1998; Willis et al., 2004). *Akainothrips francisi*, a thrips species that resides in the nest of domicile-building thrips as an inquiline, may also have female-biased sex ratios due to LMC (Gilbert et al., 2012). Surprisingly, female-biased sex ratios have been recorded in free-living thrips as well (Crespi, 1993; Gerin et al., 1994; Higgins and Myers, 1992; Kanara and Acharya, 2014; Rugman-Jones et al., 2012; van Rijn, 1995). Researchers have suggested that this may be due to inbreeding of brothers and sisters before dispersal, as chances of finding a mate are very small considering the size of the thrips and uncertainty of where the wind will take them, but this needs confirmation (Higgins and Myers, 1992; Kranz et al., 2001). Crespi (1993) suggested that the female-biased sex ratios may be due to a systematic sampling error, because mostly adult or operational sex ratios have been recorded. Male thrips have been shown to have higher nymphal mortality (Higgins and Myers, 1992), shorter adult lifespans (Higgins and Myers, 1992; Kranz et al., 2001), and differential dispersal and distribution compared to females (Terry and Kelly, 1993), making it difficult to determine if the common female-bias is due to differential

mortality during development, differential longevity, incomplete sampling or to female sex allocation.

LMC is expected to be reduced or absent for most whiteflies. Feeding sites are not generally patchily distributed for whiteflies as they are for gall-enclosed thrips or parasitoid wasps, and male whiteflies are winged and can disperse. Perhaps unusually, then, [Hu et al. \(2010\)](#) invoked partial LMC in the spiralling whitefly *Aleurodicus dispersus*. Strongly female-biased adult sex ratios were recorded from single egg spirals laid by isolated females, and sex ratios increased linearly to 50% on leaves with many egg spirals, evidence of multiple females ([Hu et al., 2010](#)).

Examples of LRC have not been reported in Aleyrodidae, possibly because both sexes can disperse, and whiteflies such as *B. tabaci* are extremely polyphagous, providing more opportunities to switch host plants when the current host plants are exhausted. [Kranz et al. \(1999, 2001\)](#) studied potential LRC and LMC adjustments to sex ratios in eusocial galling thrips. Eusocial galling thrips have alternating generations; after a queen establishes a gall, she rears a generation of wingless male and female soldiers that protect the nest from invaders. The soldiers and the queen will then lay eggs to produce a second generation of winged dispersers. LMC and LRC may both occur in these tight quarters, with single foundresses, sib mating, and limited dispersal of soldiers (LMC) as well as food limitation and the potential differential use of gall tissue by the sexes, especially in the second generation (LRC). Perhaps unsurprisingly, given the complexity, [Kranz et al. \(1999, 2001\)](#) found results in *Kladothrips hamiltoni*, *Oncothrips waterhousei* and *O. habrus* that were difficult to interpret. Even sex ratios were found in *K. hamiltoni* soldiers, and dispersers of *O. waterhousei* and *O. habrus*. Meanwhile, female-biased sex ratios were found in *K. hamiltoni* dispersers, and soldiers of *O. waterhousei* and *O. habrus*. Although LMC and LRC could have played roles in these thrips species, it is difficult to conclude whether sex allocation played any role in the observed adult sex ratios.

Studies have not shown clear LRE in Aleyrodidae or Thysanoptera, but it may possibly contribute to the high female-bias found in *Dunatothrips aneurae*, a social thrips in which females have more-armed forelegs than males and thus may be more helpful in defence of the colony ([Bono and Crespi, 2008](#)). Overall, the studies above support the possibility of sex allocation by Aleyrodidae and Thysanoptera in response to conspecific behaviour, but measurement of primary sex ratios would help confirm these patterns.



6. Effects of interspecific mating interference on sex ratio

While complexes of sibling species may be a relatively common phenomenon, the global swarm of dozens of whitefly species known collectively as *B. tabaci* is perhaps an extreme example (De Barro et al., 2011; Liu et al., 2012). In these species, mating interference may influence the outcome of interspecific competition (De Barro et al., 2011; Liu et al., 2012). In haplodiploid organisms, interspecific copulations can result in unsuccessful fertilization and male-biased offspring. Male-biased offspring of one but not the other species may thus signify the loser, and tilt competitive interactions to the species less influenced by interference. The Middle East Asia Minor 1 (MEAM1) and Mediterranean (MED) species are the two most invasive *B. tabaci* whiteflies worldwide, and interactions between the two have been well documented. The MED species is more tolerant to pesticides, so the MED species may outcompete the MEAM1 species in locations of widespread pesticide use (Sun et al., 2014; Tsueda and Tsuchida, 2011). In the absence of heavy pesticide use, MEAM1 can eventually exclude the MED population after a starting population frequency higher than 10% (Sun et al., 2014). There is evidence that the MEAM1 takeover is partly due to asymmetrical mating interference; in comparison to MEAM1 or MED populations by themselves, MED whiteflies show male-biased sex ratios in mixed populations, whereas MEAM1 whiteflies in mixed populations showed the same sex ratios as the control group (Crowder et al., 2010b; Pascal and Callejas, 2004; Sun et al., 2014; Tsueda and Tsuchida, 2011). In mating behaviour studies, MEAM1 males were more successful at interrupting mating events of a MED pair than vice versa (Sun et al., 2014). Further, MEAM1 females increased copulation events with MEAM1 males in the presence of MED males, in contrast to when MEAM1 females were only exposed to MEAM1 males (Crowder et al., 2010b). Overall, MEAM1 males and females can discriminate more effectively than MED males and females (Crowder et al., 2010a).

Behavioural asymmetries were also found between MED and native Asia II-1 (formally known as ZHJ2 biotype) whiteflies in China (Wang et al., 2012) and between MEAM1 whiteflies and native Australian or Asia II-3 (formally known as ZHJ1 biotype) whiteflies (Liu et al., 2007). In both studies, the MED or MEAM1 females increased copulation events in the

presence of more males, regardless of the male species identity (Liu et al., 2007; Wang et al., 2012). MED and MEAM1 females also showed greater proportions of female offspring in mixed species cohorts, in comparison to single species cohorts (Liu et al., 2007; Wang et al., 2012). Native females, on the other hand, decreased copulation events in the presence of MED or MEAM1 males, and produced male-biased offspring (Liu et al., 2007; Wang et al., 2012). In general, MED or MEAM1 males had a greater capacity to interfere in mating events than native whiteflies. These studies provide evidence for asymmetrical mating interference helping to drive displacement of native *B. tabaci* by *B. tabaci* MED and MEAM1.

T. vaporariorum may also be asymmetrically affected by *B. tabaci*, but not through significant changes in sex ratio (Zhang et al., 2013). When a tomato leaf was previously occupied by *T. vaporariorum* conspecific eggs or *B. tabaci* eggs, *T. vaporariorum* eggs laid subsequently suffered reduced immature survival (Zhang et al., 2013). On the other hand, the previous occupation of *B. tabaci* conspecific eggs or of *T. vaporariorum* eggs had little or marginal consequences on the fitness of *B. tabaci* nymphs hatched from eggs laid subsequently (Zhang et al., 2013).



7. Effect of symbionts on host sex ratio

7.1 Bacterial endosymbionts

Intracellular endosymbionts that are strictly vertically transmitted can generally spread only through egg cytoplasm, as sperm is usually too small to transfer bacteria to the next generation of hosts. Therefore, transmission of endosymbionts depends on host females, and spread either by increasing the overall fitness of infected mothers (relative to uninfected females), or by manipulating the reproduction of the host to produce more, or higher quality females, often at the expense of males (Bull, 1983; O'Neill et al., 1997). Many bacterial endosymbionts metabolize essential nutrients for their hosts (Douglas, 2009, 2015; Moran et al., 2008) or defend hosts against pathogens and parasitism (Douglas, 2015; Oliver et al., 2003; Scarborough et al., 2005). There are also four well-known reproductive manipulations. Parthenogenesis inducing (PI) endosymbionts act on haplodiploid organisms to convert haploid males into diploid females (Cordaux et al., 2011; Ma et al., 2014; Ma and Schwander, 2017; Stouthamer, 1997). Feminizing endosymbionts transform genetic males into fully functional females (Cordaux et al., 2011; Ma et al., 2014). Male-killing endosymbionts cause death to male embryos or later larval/pupal stages. Male-killing may result in

enhanced fitness of females by decreasing resource competition among female survivors, providing more resources to cannibalistic females, and decreasing inbreeding (Hurst and Majerus, 1993). Cytoplasmic incompatibility (CI) is a mating incompatibility observed, at its simplest, between bacteria-infected males and uninfected females. In this cross, many if not all of the fertilized eggs are inviable, or behave as if unfertilized. In haplodiploid systems, since unfertilized, uninfected eggs are incipient males, uninfected females that mate with infected males may have only male offspring. In haplodiploid organisms then, we expect a short-term sex ratio skew towards males as the CI-causing symbiont sweeps through the population. Only strains of *Wolbachia* have been found to induce all four reproductive manipulations.

In whiteflies, there is not yet any evidence that symbionts cause parthenogenesis, feminization, male-killing or CI, although female-bias has been associated with facultative symbionts in a few instances. All whiteflies examined to date, including *B. tabaci*, contain *Portiera*, an obligate nutritional bacterial endosymbiont not shown to alter sex ratio. Cryptic species in the *B. tabaci* complex also contain different combinations of facultative bacterial endosymbionts: *Wolbachia*, *Cardinium*, *Rickettsia*, *Hamiltonella*, *Arsenophonus*, *Fritschea* and *Hemipteriphilus*. Intracellular symbionts are difficult to study in this host family, as they cannot be cultured outside of their hosts, and antibiotic curing or heat shock treatments can lower titers of the primary symbiont *Portiera* or incompletely remove the desired bacteria.

The most comprehensive studies on the effects of facultative symbionts in *B. tabaci* to date have been on *Rickettsia* and *Cardinium*. Himler et al. (2011) found a rapid spread of *Rickettsia* in *B. tabaci* MEAM1 populations in the Southwestern USA in a 6-year period. After introgression of naturally infected and uninfected lines to homogenize nuclear genetic differences, they found that *Rickettsia*-infected whiteflies developed faster, had higher survival from egg to adult, higher fecundity, and 70–85% female offspring compared to ~40–60% female offspring in the uninfected line (Himler et al., 2011). Other studies showed the phenotype of *Rickettsia* association varied among host genotypes (Cass et al., 2016), and that host nuclear genotype was more influential than cytological genetic lineages (including mitochondrial and symbiont genes) in affecting the *Rickettsia* phenotype (Hunter et al., 2017). The importance of host genotype may explain why Chiel et al. (2009), examining the same whitefly and a highly similar if not identical *Rickettsia* in Israel (Cass et al., 2015), found that *Rickettsia* decreased development time but did not affect any other fitness parameters.

Parrella et al. (2013) also showed an association between *Rickettsia* and female-biased sex ratios in *B. tabaci* MED in Italy. One mitochondrial type of the whitefly, Q1, contained no *Rickettsia* and exhibited even sex ratios, whereas the mitochondrial type Q2 was nearly fixed for *Rickettsia* and had a strong female-bias (71% female). One cannot separate *Rickettsia* effects and host genetic effects in this study, but they are suggestive of a possible symbiont effect.

In another study of whitefly symbionts, Fang et al. (2014) observed that only 7.6–17.3% of *B. tabaci* MED whiteflies were infected with *Cardinium* in Shandong, China. After establishing *Cardinium*-infected and uninfected lines in the laboratory (all fixed for *Portiera* and *Hamiltonella*), Fang et al. (2014) found that uninfected whiteflies greatly outnumbered infected individuals after a few generations, and had higher growth rates, indicating that *Cardinium* might have been detrimental to its host. However, the authors did not control for host genotype, which makes it difficult to distinguish how much of the difference seen is due to *Cardinium* relative to host differences coincidentally associated with *Cardinium* infection. *Cardinium* was not shown to manipulate reproduction or sex ratios in this study (Fang et al., 2014).

Laboratory manipulations have also been conducted to study the effects of *Arsenophonus*, *Wolbachia*, and *Hamiltonella*. *Arsenophonus* was cured via tetracycline in the *B. tabaci* Asia II-1 species, and no changes in sex ratio were observed, but the cured whiteflies had increases in fecundity, longevity, and egg to adult survival (Raina et al., 2015), suggesting that *Arsenophonus* is costly to *B. tabaci*, at least in the laboratory environment (Raina et al., 2015). However, *Rickettsia* and *Wolbachia* were also found to infect 55–60% of the tested population, and maintenance of *Portiera* was only verified through diagnostic PCR, leaving the possibility that partial curing of other symbionts, at least, may have confounded these results.

Wolbachia has not been shown to skew *B. tabaci* sex ratios. In a survey in China, Ji et al. (2015) found that MED and MEAM1 invasive species appeared to be female-biased (the operational sex ratio in the field for each was 74% female). When Ji et al. (2015) reared *Wolbachia*-infected and uninfected populations in the lab, the *Wolbachia*-infection was associated with reduced female-bias compared to uninfected females, suggesting that *Wolbachia* was not the cause. As for *Hamiltonella*, Ruan et al. (2006) cured *B. tabaci* MEAM1 of *Hamiltonella* in three treatments using different antibiotics, and found the offspring were male-biased; however, the sample sizes were too small for analysis of the sex ratio results. Due to the small sample

size and lack of qPCR to verify if titers of *Portiera* fully recovered, these results should be interpreted as preliminary.

More studies on the roles of bacterial endosymbionts on reproduction and performance of *B. tabaci* would be valuable. The endosymbiont complex and the species limits of the *B. tabaci* complex itself are still being determined, and methods to manipulate the symbiont complex (via antibiotic treatment, heat, or introgression) are still in progress. Outside of *B. tabaci*, studies of endosymbionts of Aleyrodidae are rare, but it would be interesting to know if endosymbionts are involved with the thelytokous parthenogenesis recorded in *Parabemisia myricae* (Rose et al., 1981) or *Aleurotrachelus atratus* (Borowiec et al., 2010).

In Thysanoptera, *Wolbachia* PI has been shown in *Frankliniopsis vespiiformis* (Arakaki et al., 2001) and *Hercinothrips femoralis* (Kumm and Moritz, 2008), where male offspring appear after antibiotic and/or heat treatment. In many other cases, *Wolbachia* was not found in parthenogenetic thrips, or is found in arrhenotokous thrips (Kumm and Moritz, 2008; Nault et al., 2006; Nguyen et al., 2015; van der Kooi and Schwander, 2014). van der Kooi and Schwander (2014) warn that the presence of male offspring after antibiotic treatment should not be conclusive evidence for *Wolbachia* PI. After treating *Aptinothrips rufus* with antibiotics, van der Kooi and Schwander (2014) observed male offspring, but then pointed out that less than 70% of their sampled, parthenogenetic *A. rufus* populations were infected with *Wolbachia*. The thrips may be parthenogenetic due to another unidentified bacterium (van der Kooi and Schwander, 2014); both *Cardinium* and *Rickettsia* have been shown to cause PI (Giorgini et al., 2010; Hagimori et al., 2006; Zchori-Fein et al., 2004), and there may well be others.

Recently, Nguyen et al. (2017) found the first-recorded CI in Thysanoptera, caused by *Wolbachia* and *Cardinium* coinfections in *Pezothrips kellyanus*. In haplodiploid organisms, CI can cause female mortality (FM) or a male development (MD) phenotype (Nguyen et al., 2017; Vavre et al., 2001). In FM, all fertilized eggs in a CI cross fail to develop, resulting in few or no females and similar numbers of males compared to control crosses, while in MD, fertilized eggs survive but as haploid males, resulting in greater numbers of males compared to control crosses (Nguyen et al., 2017; Vavre et al., 2001). Uninfected females do not lose as many offspring in a CI cross of the MD phenotype, but will still suffer fitness costs by a sex ratio skew up to 100% male. To differentiate between the phenotypes, Nguyen et al. (2017) counted male offspring of CI crosses and compared it with the

number of males in a control cross of uninfected thrips. Because the number of males was significantly greater in the CI cross compared to the control cross, [Nguyen et al. \(2017\)](#) concluded that *Cardinium* causes a CI phenotype intermediate between FM and MD. In contrast, *Wolbachia* CI causes FM ([Nguyen et al., 2017](#)).

7.2 Viral endosymbionts

Few studies have shown a viral influence on arthropod sex ratios (exceptions include [Juchault et al., 1991](#); [Nakanishi et al., 2008](#); [Wang et al., 2017](#)). Few viruses of Aleyrodidae or Thysanoptera have been described. [Báo et al. \(1996\)](#), [Costa et al. \(1996\)](#), and [Hunter et al. \(2001\)](#) provided morphological evidence of one or more *B. tabaci* viruses, but there is no evidence that this/these viruses influence sex ratios. In comparison, there are many studies of plant virus effects on whitefly and thrips vectors. Plant viruses appear to have relationships with insect vectors that span mutualism to parasitism ([Colvin et al., 2006](#); [Jiu et al., 2007](#); [Nogia et al., 2014](#)), likely dependent on rates of viral replication in the vector ([Sinisterra et al., 2005](#)) and whether the relationship is general or special ([Colvin et al., 2006](#)). Two studies formally tracked how plant viruses affected the adult sex ratios of their Aleyrodidae vectors, both directly, when infected vectors fed on clean plants, and indirectly when uninfected vectors fed on virus-infected plants. [Thompson \(2002\)](#) found that the *East Africa cassava mosaic virus* (Ugandan variant) did not affect the sex ratio of *B. tabaci* collected in Uganda in either instance. [Maluta et al. \(2014\)](#) also did not find any changes in sex ratio for *B. tabaci* MED infected with *Tomato yellow leaf curl virus* (TYLCV). [Zheng et al. \(2014\)](#) tested the indirect effects of *Tomato zonate spot virus* (TZSV) on *F. occidentalis* feeding on tomato or pepper, and also did not find significant viral effects on sex ratio, although there was a trend towards more female offspring from TZSV-infected plants.

Although there are no current studies in Aleyrodidae or Thysanoptera that show viruses affecting sex ratio, *Tomato spotted wilt virus* (TSWV) has been shown to differentially change the behaviour and other fitness parameters of female and male *F. occidentalis* thrips ([Stafford-Banks et al., 2011](#)). TSWV-infected males increased both feeding and probing events up to threefold, while TSWV-infected females increased predation ([Stafford-Banks, 2013](#); [Stafford-Banks et al., 2011](#)). These changes are most likely a vector response to the virus' propagative nature, replicating within its vector

(Stafford-Banks, 2013). *Franklinella occidentalis* males appear to be better transmitters of TSWV because the virus needs viable plant cells to replicate, and male probing is innocuous relative to female probing that will often lead to greater plant cell death (Stafford-Banks, 2013). Indeed, Rotenberg et al. (2009) found that male *F. occidentalis* were better than females at transmitting TSWV multiple times. If a virus depends disproportionately on one sex to be transmitted from vector to plant, it would be in the evolutionary interest of the virus to alter not only the behaviour but also the sex ratio of its vector, altering the host plant to produce an environment more favourable to the sex that is more reliable for transmission. For example, when *F. occidentalis* fed on TSWV-infected foliage at 18.3°C, one of two tested strains of TSWV significantly decreased the development time of males but not of females (Stumpf and Kennedy, 2007).



8. Sex ratio effects from biological control: Interactions with predators, parasitoids, and pathogens

The literature is replete with documentation of predator and parasitoid sex ratios on different hosts, in part because of the goal of determining whether certain predators or parasitoids are potential biological control agents (Heimpel and Lundgren, 2000; van Lenteren, 2003). Unfortunately, we know little about whether these natural enemies influence the sex ratio of their prey or hosts. This missing data may be an overlooked factor in determining effective biological control agent effectiveness, especially for those agents that cause high parasitism/predation rates: biological control agents that induce a male-bias in their host/prey will be more effective at decreasing population growth. A male-bias in pests may also decrease crop damage absolutely if females cause more feeding damage as adults, such as in the western flower thrips *F. occidentalis* (Higgins and Myers, 1992; Stafford-Banks, 2013).

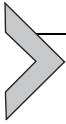
Although there is a lack of study in this area, it would be interesting to determine if biological control agents of Aleyrodidae cause male-bias in their hosts. In whiteflies, female nymphs, especially at later instar stages, are significantly larger than male nymphs (Baig et al., 2015, 2016; Hora et al., 1995). Parasitoids targeting late stage nymphs could consistently prefer larger, female hosts, especially when only female eggs are laid in whiteflies, such as in parthenogenetic wasps such as *Encarsia formosa*, or autoparasitoid *Encarsia* in which males are hyperparasitoids and eggs are not laid in

whiteflies but in developing wasp pupae (Hunter and Woolley, 2001). One laboratory study, however, has shown that *E. formosa* does not exhibit a preference for larger, female nymphal whiteflies. The authors suggest that the wasp may not be very discriminatory because it is generally more time-limited than egg-limited (Hora et al., 1995). Alternatively, parasitoid wasps could selectively oviposit female offspring in relatively larger hosts and males in smaller hosts (Charnov et al., 1981; Clausen, 1939; Werren, 1984), and larger hosts might be differentially targeted when wasp sex allocation is female-biased. Similarly, if a whitefly predator preferentially consumes larger whitefly instars, a male-bias in the whiteflies could emerge. Whether preference for larger hosts occurs is, however, unknown, and complicating the picture is the fact that cohorts of whitefly immatures are rarely synchronous, so parasitoids and predators may be most often presented with a range of stages and sizes, such that the relationship between relative size at a particular time and whitefly sex may not be very strong.

Many insect prey, including thrips and whiteflies, alter their behaviour in the presence of predators and parasitoids. Through nonconsumptive effects, natural enemies cause changes in prey feeding behaviour (Jandricic et al., 2016; Schmitz, 2003), landing and settling behaviour (Lee et al., 2014; Meng et al., 2006), oviposition behaviour and in some cases reproductive allocation (Deas and Hunter, 2012). For example, Jandricic et al. (2016) found that second instars of *F. occidentalis* are too large to be eaten by the predatory mite *Neoseiulus cucumeris*, but can still be attacked. Second instar thrips exposed to the mites decreased feeding activity, most likely to avoid attacks, and had significantly decreased survival to adulthood in comparison to thrips raised without mites. *Bemisia tabaci* will also exhibit avoidance behaviour, increasing settling time on enclosed leaf discs or moving to upper leaves of a cucumber plant in the presence of the predatory beetle *Delphastus catalinae* (Lee et al., 2014). If insects alter behaviour when enemies are present, it would not be far-fetched to imagine that these herbivores may alter the sex ratio of their offspring as well, perhaps biasing offspring sex towards the sex that disperses the greatest distance.

As for pathogens, the exposure of *F. occidentalis* to an entomopathogenic fungus, *Beauveria bassiana*, resulted in male-biased offspring, compared to an even sex ratio found in unexposed thrips (Zhang et al., 2015). No significant differences in fecundity or survival to adulthood were recorded, suggesting perhaps that exposed thrips fertilized fewer eggs, possibly due to *B. bassiana* interfering with sperm production in males, egg fertilization by females

(Zhang et al., 2015), or sex allocation. Overall, the ability of potential biological control agents to skew host/prey sex ratio should be considered in the assessment of their quality.



9. Tools for connecting sex ratios to sex allocation

Many have studied the life histories of Aleyrodidae and Thysanoptera, including the measurement of adult sex ratios. However, it has been difficult to interpret the results in light of sex allocation. To determine if a mother allocates more resources to a certain sex, it is best to observe the primary sex ratio, or the sex of the eggs. All studies to date of Thysanoptera and Aleyrodidae have recorded changes in sex ratios of later stages, which may be a result of changes in sex allocation, but this remains to be clarified. Knowledge of sex allocation in these taxa may be helpful in predicting future pest population dynamics. For instance, global climate change or higher pest densities may initiate unforeseen sex allocation patterns. For this reason, we (Bondy and Hunter, 2019) developed a cytogenetic protocol for determining egg fertilization rates in *B. tabaci*. We also recommend an old but reliable method to determine differential mortality during development, borrowed from the parasitoid sex allocation literature. This second technique is a quicker, albeit indirect method of determining whether adult sex ratios are equivalent to primary sex ratios, i.e., sex allocation by the female.

The primary sex ratio of *B. tabaci* can be found after a simple decoloration of eggs with bleach, a series of fixation steps, and application of the general DNA fluorescent stain, DAPI, to bind to female and male pronuclei as shown in Fig. 1 (Bondy and Hunter, 2019; modified from Vavre et al., 2004).

If there are no protocols to directly find the primary sex ratio, and the cytogenetics approach is infeasible, one can determine the extent of differential developmental mortality in haplodiploid organisms through survival assays. Haplodiploid virgin mothers only produce male offspring, whereas mated females produce both male and female offspring. Therefore, comparing the developmental mortality between offspring of virgin and mated females can determine whether differential mortality among males and females is occurring. If offspring mortality is different between virgin and mated females, then we can infer that females either have a lower or higher developmental mortality than males. This method has been practiced with

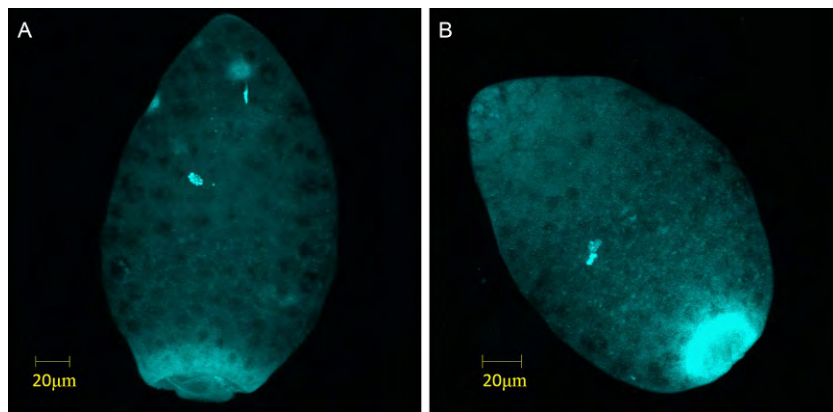


Fig. 1 *Bemisia tabaci* MEAM1 fertilized, incipient female (A) and unfertilized, incipient male (B) eggs. The eggs were fixed less than 1 h after oviposition and stained with DAPI (4',6-diamidino-2-phenylindole), a general DNA stain, using the techniques described in [Bondy and Hunter \(2019\)](#). The base of each egg is bright because it contains a bacteriocyte cell with bacterial endosymbiont DNA (*Portiera*, *Hamiltonella*), which is included in the laid egg ([Luan et al., 2018](#)). In each egg, the female pronucleus is near the centre of the egg, and in the female egg only, the sperm is visible as a bright streak near the apex of the egg near what is presumably the autofluorescent micropyle.

many parasitoid wasps ([King, 1988](#); [Pandey and Singh, 1999](#); [Sandlan, 1979](#); [Seidl and King, 1993](#); [West, 2009](#)), but to our knowledge has not been applied to haplodiploid herbivores.



10. Conclusions and future directions

Sex ratios of some species of Aleyrodidae and Thysanoptera are influenced by temperature, host plant, conspecifics, competitors, bacterial endosymbionts and fungal pathogens. Extremely high temperatures appear to cause male-biased offspring in the whitefly *B. tabaci* ([Cui et al., 2008](#); [Lü et al., 2014](#); [Xiao et al., 2016](#)) and in the thrips *F. occidentalis* ([Wang et al., 2014](#)), while at less extreme temperatures, a positive correlation between temperature and the proportion of female offspring is found in both the thrips *C. claratris* ([Premachandra et al., 2004](#)) and *F. occidentalis* ([Kumm and Moritz, 2010](#)). Higher quality host plants may be associated with even sex ratios in the castor whitefly, *T. ricini* ([Huang et al., 2014](#); [Shishehbor and Brennan, 1996](#)), but the results in the current literature appear inconsistent. LMC has been invoked in a convincing manner to explain the sex ratios of certain galling thrips ([Crespi, 1993](#); [Tree and Walter, 2009](#); [Tsuchida and](#)

Ohguchi, 1998; Willis et al., 2004), inquiline thrips (Gilbert et al., 2012) and the spiralling whitefly, *A. dispersus* (Hu et al., 2010). Otherwise, LMC has not been found in pest species such as *B. tabaci* and *F. occidentalis*, and there are no clear examples of LRC or LRE in these taxa. The Trivers–Willard hypothesis most likely explains reproductive allocation towards male broods in times of greater fungal-resources in the fungus-feeding *E. tuberculatus* (Crespi, 1988).

There is evidence that the *B. tabaci* species complex undergoes interspecific mating interference, in which *B. tabaci* MEAM1 causes a male-bias in *B. tabaci* MED through asymmetric mating interference (Crowder et al., 2010b; Pascal and Callejas, 2004; Sun et al., 2014; Tsueda and Tsuchida, 2011). The addition of either *B. tabaci* MED and MEAM1 to endemic *B. tabaci* species may simultaneously cause male-biased offspring in the endemic species, and female-biased offspring in MED or MEAM1 (Liu et al., 2007; Wang et al., 2012). Bacterial endosymbionts may also influence sex ratios. *Rickettsia* may cause a female-bias in *B. tabaci* (Cass et al., 2016; Himler et al., 2011; Parrella et al., 2013), *Wolbachia* causes parthenogenesis in the thrips *F. vespiformis* (Arakaki et al., 2001) and *H. femoralis* (Kumm and Moritz, 2008), and *Wolbachia* and *Cardinium* simultaneously cause male-bias as result of cytoplasmic incompatibility in *P. kellyanus* (Nguyen et al., 2017). Finally, a *B. bassiana* fungus causes male-biased offspring in exposed *F. occidentalis* (Zhang et al., 2015). No effects of sex ratio by viruses, predators or parasitoids have yet been recorded.

The various life histories of Aleyrodidae and Thysanoptera have been thoroughly documented, especially from the “supervectors” *B. tabaci* and *F. occidentalis* (Gilbertson et al., 2015). Although changes in adult sex ratio may be sufficient to predict future populations of Aleyrodidae and Thysanoptera, discovering sex allocation in haplodiploid herbivores would further enhance our fundamental understanding and our ability to make predictions about these important and interesting insects. If sex allocation that departs from even sex ratios occurs in these taxa, it may also elucidate patterns in other herbivorous insects with less labile sex allocation. Tools already present in the sex ratio literature of parasitic Hymenoptera are available to find primary sex ratios in Aleyrodidae or differential developmental mortality in whiteflies and thrips.

Glossary

Sex allocation reproductive investment in male and female offspring

Sex ratio The proportion of all offspring that are males

Primary sex ratio The proportion of males after egg fertilization (Majerus, 2003), when sex allocation by haplodiploid parents may occur via selective fertilization

Secondary sex ratio The proportion of males after egg eclosion (Majerus, 2003; Terry and Kelly, 1993)

Adult sex ratio The proportion of males after pupal eclosion or sexual maturity. It also may be referred to as the tertiary sex ratio (Majerus, 2003; Terry and Kelly, 1993) or secondary sex ratio (if there is no way to identify the proportion of males after egg eclosion). Here we use “adult sex ratio” exclusively

Operational sex ratio The proportion of sexually active/receptive males (relative to all adults) in a population (Emlen, 1976; Shuster, 2016)

Even/Fisherian sex ratio 50% male

Female/male-bias Statistically significantly greater or less than 50% male

Thelytoky A form of parthenogenesis in which diploid females are produced from unfertilized haploid eggs after doubling of the chromosome complement

Arrhenotoky synonymous with the haplodiploid genetic system: males are produced from unfertilized, haploid eggs, while females are produced from fertilized, diploid eggs

Relevant sex allocation theories

Fisher’s principle First proposed by Darwin (Darwin, 1871; Edwards, 1998) but clearly articulated, and largely attributed to Fisher (1930). In a randomly mating population with equal costs to producing males and females, the sex ratio should converge on 50%. This is because, if a bias exists, then the rarer sex will have more mating opportunities and selection will favour individuals that produce the rarer sex and the bias will then decrease. A Fisherian sex ratio of 50% is most commonly found in sexually reproducing species, and is considered an evolutionarily stable strategy (ESS, Maynard-Smith and Price, 1973)

Local mate competition (LMC) predicts female-bias when resources are patchy, males mate on the natal patch and do not disperse, and females typically mate once (Hamilton, 1967). Under these conditions, a female-bias will reduce competition among males that may be brothers. In the extreme case of a single foundress, a mother’s best strategy would be to produce a single male, given that he is able to mate with all of his sisters. More male offspring will occur with a greater number of female foundresses. The inbreeding that may result from LMC also favours female-biased sex ratios in haplodiploid organisms since it increases the average relatedness between mothers and their diploid daughters (Frank, 1986; Keller et al., 2011). Although Hamilton referred to a study on the thrips *Limothrips denticornis* as a candidate for LMC (Hamilton, 1967; Pussard-Radulesco, 1930), studies of LMC have mostly been supported by empirical study in mites and parasitoid wasp species that sib-mate and attack patchily distributed hosts (Charnov, 1982; Godfray, 1994; Werren, 1980)

Partial local mate competition When males disperse and have mating opportunities beyond the natal patch, their reproductive value is increased, and the expected sex ratio is less female-biased than in full LMC (Werren and Simbolotti, 1989)

Local resource competition (LRC) is similar to local mate competition in that it predicts mothers will bias offspring sex ratio towards the sex that will compete less with each other or with their mothers, but is focused on competition for limited resources (other than mates) such as food or territory (Clark, 1978). Under these conditions, mothers should produce more of the sex that disperses from the natal patch. In many insect species, a male-bias is expected in sexually dimorphic insects where males are winged and disperse

but females do not. In addition, female insects are usually larger than males and will therefore compete more with each other for resources for development, especially in depleted environments. LRC has been investigated in mealybugs, which have large females and dispersing males (Ross et al., 2010; Varndell and Godfray, 1996)

Local resource enhancement (LRE) occurs when a particular sex increases the fitness of its mother, for example by helping the mother care for offspring (Clark, 1978). Mothers are expected to bias production to the beneficial sex, but once the benefit has been optimized, the bias may decrease as the mother starts to produce the other sex. Researchers argue that sex ratios in primitively social or eusocial Hymenoptera are guided by LRE (Gardner and Ross, 2013; Schwarz, 1988)

Trivers–Willard hypothesis (TWH) depends on three conditions: (1) An individual's physiological condition correlates with that of its mother; (2) this endures into adulthood; (3) the reproductive success of one sex relies relatively more on its individual physiological condition. The original Trivers–Willard assumption stated that males will benefit relatively more with a better maternal physiological condition, especially in environments with dominance hierarchies (Trivers and Willard, 1973). Mothers with better health should invest more in the sex that will benefit more from her condition. A common example of a test of the Trivers–Willard hypothesis is found in red deer; high ranking females invest more in sons than daughters (Clutton-Brock et al., 1984)

Host quality sex ratio hypothesis focuses on the third condition of the Trivers–Willard hypothesis: that the sexes may not benefit equally from greater physiological condition (health or size) (Charnov et al., 1981). Charnov reasoned that when resource quality predicts offspring quality, mothers will lay eggs of the sex that benefits the most from a greater physiological condition in the richest resource. For instance, if a parasitoid wasp is exposed to hosts of different sizes, she will oviposit female eggs in relatively large hosts and male eggs in relatively small hosts. Wasps that develop in larger hosts will have a larger body size, and generally, the relationship between female size and number of offspring is strongly positive, while for males, the relationship between size and reproductive value is not as steep. For instance, large female parasitoid wasps of *Itopectis naranyae* (Ueno, 1998) and *Pimpla nipponica* (Ueno, 1999) lived longer than smaller females, but large males did not live longer than smaller males. In fact, smaller males of both species mated successfully with all females, whereas larger males only mated successfully with larger females (Ueno, 1998, 1999). In general, a mother should allocate each sex to the environments that benefit them the most

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Cover Image: A burying beetle parent feeding its young larvae.
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