Special Issue: Mark Jervis Memorial

Sex allocation and the evolution of insemination capacity under local mate competition

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Running title: *Sex allocation and insemination*

Key words: Hymenoptera, LMC, mating systems, parasitoids, sex ratio, sperm allocation, sperm competition, virginity

Accepted: 16 September 2015

Abstract

Local Mate Competition (LMC) theory has proved enormously successful in predicting sex ratios across a broad range of organisms when localised mating patches lead to mating competition amongst kin. As such, LMC is a key component of sex allocation theory. However, the mating systems that influence and promote LMC also shape other traits, as well as sex allocation. These aspects of LMC mating systems have received far less attention, including in species where LMC is common, such as parasitoid wasps. Here, we consider how LMC influences the evolution of insemination capacity in parasitoids, a key reproductive allocation decision for males that should be under both natural and sexual selection. Basic LMC theory predicts that a single female exploiting a patch should produce just enough sons to inseminate all her daughters, i.e., between them these sons should have sufficient insemination capacity to inseminate their sisters. However, the insemination capacity of males is generally higher than predicted and, in order to classify parasitoid species, we propose an Index of Insemination Strategy (IIS): the ratio between the insemination capacity of males on the emergence patch and the average number of females available per male at emergence on that patch. A survey of IIS for 25 species belonging to 10 hymenopteran families showed that IIS values ranged from 0.9 to 40.9, supporting the idea that males typically have more sperm than predicted. Several factors could explain these high IIS values, including non-local mating, temporal variation in emergence, variation in mate acquisition capacity, the intensity of sperm competition, and responses to host quality.

Introduction

Sex allocation theory describes how parents, typically females, allocate energy and resources to their offspring, including how they decide on the sex ratio of those offspring (Charnov, 1982; Hardy, 2002; West, 2009). Central to sex allocation theory is the notion of the net fitness benefits that parents obtain through the production of sons or daughters. One branch of sex allocation theory explores how the benefits of producing sons or daughters varies with the extent of competition amongst related males, including brothers, for mates: Local Mate Competition (LMC) theory (Hamilton, 1967). LMC theory assumes a localised mating structure with mating between siblings, as might occur in the body of a vertebrate host (e.g., *Plasmodium* parasites; Reece et al., 2008), within a fig fruit (fig wasps; Herre et al., 1997), or in the vicinity of arthropod hosts for numerous parasitioid wasps (Godfray, 1994). With such local mating, relatives, typically brothers, may compete for mates. Hamilton realised that under these conditions natural selection should favour a sex ratio that minimises this conflict, by reducing the number of sons relative to daughters. This will reduce LMC and also increase the number of females available for mating, maximising grand-offspring production by the mother (Hamilton, 1967, 1979; Taylor & Bulmer, 1980). The number of females contributing offspring to the local mating patch should then influence the optimal sex ratio for each of these females. If more unrelated females contribute offspring, so the level of LMC is reduced (even if mating competition per se is increased), favouring more equal investment in sons and daughters. If the number of females varies across patches, then LMC theory predicts the evolution of facultative sex allocation, with females varying their sex ratios depending on the predicted level of LMC their offspring will experience. Such facultative sex allocation under LMC has been shown in a wide variety of organisms, and LMC is a key component of adaptive sex allocation theory (Charnov, 1982; West, 2009).

The focus on the sex allocation consequences of localised mating patches, particularly in groups such as the parasitoid wasps, has perhaps taken attention away from the other consequences of mating systems in which LMC emerges. For instance, localised mating will shape patterns of sexual selection and sexual conflict, as well as sex allocation (for a review see Boulton et al., 2015). Here we consider one particular reproductive parameter influenced by LMC, namely male insemination capacity, focusing in particular on parasitoid wasps.

Female hymenopteran parasitoids adjust their offspring sex ratio (defined throughout as the proportion of offspring that are male) by controlling the fertilization of their eggs (Cook, 1993). As they are haplodiploid, unfertilized (haploid) eggs develop into males and fertilized (diploid) eggs develop into females. A female's fitness is thus determined in part by the way she distributes sons and daughters within host patches. As outlined above, basic LMC theory predicts that when a single female exploits a patch, she should produce just enough sons to inseminate all her daughters thus maximising daughter, and hence granddaughter, production. (Strictly speaking, classical LMC models predict a sex ratio of zero males when a single female, or 'foundress', lays eggs by herself; this is usually interpreted as laying the minimum number of males; Hamilton, 1967, Godfray, 1994). However, implicit in this interpretation is the assumption that between them all the brothers will have sufficient insemination capacity to inseminate all their sisters. The specific patterns of insemination across males are not explicitly considered. That said, LMC models that have treated clutch or brood size as integers do predict one male as the minimum number of males (Green et al., 1982; Nagelkerke, 1996).

Whilst predicting and testing optimal sex ratios across multiple foundress situations (including superparasitism, when two females share a host patch, one after another) has proved very successful, it has been much harder to unpick how many males a single foundress female should produce. One key component has been the risk of male mortality, such that selection should favour a risk-averse, small over-production of males, to make sure enough males survive larval development and competition to emerge as adults (Green et al., 1982; Nagelkerke & Hardy, 1994; Heimpel, 1994). Integer effects in small broods also lead to more males than might otherwise be predicted. These risks of not producing enough males have been modelled in so-called 'fertilisation insurance' models (reviewed by West, 2009).

Generally, however, the number of males predicted to be allocated to a patch by LMC models rarely considers male mating capacity (for reviews of mating behaviour, mating systems, and sexual selection in parasitoids, see Hardy et al., 2005a,b; Boulton et al., 2015). This is a potential limitation as it has become clear that the number of females that a male can inseminate varies with several traits, including longevity, sperm production and management, capacity to acquire mates, and investment in offspring (Roitberg et al., 2001). Among these traits, sperm production and management, i.e. the pattern of gamete allocation among successive mates, has been studied in a number of parasitoid species (Wilkes, 1965; Gordh & DeBach, 1976; Nadel & Luck, 1985; Ramadan et al., 1991; Ode et al., 1996; King, 2000; Quimio & Walter, 2000; Damiens & Boivin, 2005; Burton-Chellew et al., 2007; Steiner et al., 2007; Bressac et al., 2008, 2009; King & Fischer, 2010; Boivin, 2013). However, the insemination capacity of males, including sperm depletion, has rarely been taken into account in studies looking at LMC. Most studies assume that natural selection acts against sperm depletion in males and simply verify whether males are able to inseminate all females available, as in *Megachile rotundata* (Fabricius) (Tepedino, 1993). Tagawa (2002) observed that in *Cotesia glomerata* L., the male's insemination capacity greatly exceeds the number of females available on the emergence site, whereas in *Goniozus legneri* Gordh no evidence of limited insemination has been observed (Hardy et al., 2000). In *Pachycrepoideus vindemmiae* (Rodani), on the other hand, males are unable to inseminate all their sisters if mated in rapid succession, but if emergence rate is taken into account, males could inseminate all their sisters (Nadel & Luck, 1985).

For species that allocate sex according to LMC, we should expect that the mating capacity of males reflects the number of females per male predicted to be present in a patch (Hartl, 1971; Tepedino, 1993). If males have a lower insemination capacity, some females will leave the patch without being inseminated, creating an evolutionary pressure to either increase the proportion of males or increase the insemination capacity of males. Conversely, if males have a higher insemination capacity than necessary, they will compete among themselves for mates and selection will favour females that invest in fewer sons on a patch (or that produce sons with a lower insemination capacity). However, no data are yet available to indicate whether females are able to adjust the insemination capacity of their sons in response to a change in the expected sex ratio in a host patch. Interactions between the sex ratio deposited by females and the insemination capacity of males exist in *Drosophila melanogaster* Meigen (Diptera: Drosophilidae) (Linklater et al., 2007), where lines that were maintained at a high sex ratio (i.e., an abundance of males) produced males that exhibited faster declines in fertility when mating in rapid succession, compared to males that had been reared under a lower sex ratio.

The purpose of this paper is to review the data on the insemination capacity of parasitoid males to assess whether or not it corresponds to what we might expect from mating systems prone to LMC. In addition, we also propose an index, the Index of Insemination Strategy (IIS), which is the ratio between the average insemination capacity of a male on the emergence patch and the average number of females available per male at emergence on that patch (for discussion on the use of quantitative indices in evolutionary ecology, see Boivin & Ellers, 2016). An IIS of 1 would correspond to a situation where females allocate sons that are collectively able to inseminate once all daughters present on the emergence patch. An IIS above 1 indicates that the sons have insemination capacities higher than needed to inseminate all the females on the emergence patch, whereas an IIS below 1 would indicate that the sons have insemination capacities lower than needed to inseminate the females on the emergence patch. We calculated the IIS for 25 species of parasitoid where data on the insemination or mating capacity of males and the number of females on the emergence patch are available in the literature, and use these values to discuss the various strategies in regards to the predictions of LMC. We go on to consider why these values may deviate from our expectations under LMC, and consider what ecological and environmental circumstances may result in the under- or over-production of sperm.

Materials and methods

We gathered from the literature, using Scopus and Google Scholar and the literature cited therein, papers referring to the insemination or mating capacity of parasitoid males from species exhibiting female-biased sex ratios, and where competition between males could occur at the emergence site, i.e., gregarious and quasi-gregarious species (solitary species in aggregated hosts; van den Assem et al., 1980). All the insemination or mating capacities presented in Table 1 were measured during the first day of life of the males and compared to the number of females present at the emergence site (either presented directly, or calculated from the sex ratio, i.e., proportion of male offspring, and the brood size at emergence, when available in the literature). This assumes that most of the mating events take place at the beginning of the male's life. For most of the species, it is estimated that males disperse from the emergence patch within 24 h (Myint & Walter, 1990; Nadel & Luck, 1992; Hardy et al., 1998; Leonard & Boake, 2006; Martel & Boivin, 2007), although for some species dispersal occurs within 48 h [e.g., *Spalangia endius* Walker (King, 2006), *Goniozus nephantidis* Muesebeck (Hardy et al., 1999), *G. legneri* (Hardy et al., 2000)], or not at all.

Estimates of insemination capacity are difficult to obtain, and the data available vary across studies. For example, in several studies, only the number of copulations was reported, without indicating the proportion of these copulations that were successful (i.e., whether the female had actually been inseminated). To try and take some of this variation into account, we therefore split the studies into those in which insemination capacity was estimated under the following conditions: (1) experimental copulations were performed in succession, (2) all copulations occurred within 24 h, or (3) females were checked to see whether they were ‘fully’ inseminated (either from quantifying the amount of sperm transferred to females or from offspring sex ratios). These data are presented in Table 1A, and we refer to these data as ‘insemination capacity’ data. If these conditions were not fulfilled (e.g., insemination was checked in terms of presence/absence of sperm, rather than quantity of sperm, or only the number of copulations was assessed), then we refer to these data as ‘mating capacity’ data, and these data were treated separately (Table 1B; see also Figure1). Although the number of matings could overestimate the number of fully inseminated females, we kept these data as we expect the proportion of partially inseminated females to be low at the beginning of the male's life. The concern arises because, of course, in several species the quantity of sperm transferred per copulation decreases gradually over time, resulting in mated females that are not fully inseminated, or even that do not receive any sperm (Damiens & Boivin, 2005). For species in which most of the matings occur on the emergence patch, males are expected to continue to mate even after having depleted their sperm supply (Damiens & Boivin, 2006).

To compare these two ways of estimating insemination capacity, we first calculated the minimum insemination capacity (using the minimum estimate or the bottom of the range, thus being conservative in the estimate of insemination capacity). We then explored the relationship between minimum insemination capacity and brood sex ratio (using the median value if there was a range of sex ratios) and how this relationship varied for our two estimates of insemination capacity (numbers of observed matings vs. number of known inseminations; both ln-transformed) using analysis of covariance (ANCOVA, implemented in SPSS v. 21; IBM Corporation, Armonk, NY, USA).

Results

Across our survey of parasitoid wasps, the IIS was generally greater than 1 (Figure 1). Table 1 presents the insemination and mating capacity of males and the number of females on the emergence patch for 25 species belonging to 10 Hymenoptera families. Data from 11 species met our criteria for insemination capacity. For most of these species, the males had an insemination capacity greater than the number of females per male present on the patch leading to IIS values exceeding one. The IIS values ranged from 0.88 to 12.88 (Table 1A). For example, in *Dinarmus basalis* Rondani, when only one female exploits a patch, the sex ratio is approximately 0.25 (Gauthier et al., 1997). However, a male can fully inseminate eight females (Bressac et al., 2008) suggesting that a sex ratio of 0.11 (instead of 0.25) would be the expected sex ratio to ensure that all females are inseminated.

In addition to these species, 14 more provided mating capacity estimates (Table 1B). The IIS of these species ranged from 1.56 to 40.93. In *Dahlbominus fuscipennis* Zetterstedt, an ectoparasitoid of diprionid sawflies, the proportion of sons laid increases with the number of females exploiting a patch (Victorov & Kochetova, 1973), as predicted under LMC. When a female exploits a patch alone, a sex ratio of 0.09 is deposited, indicating that a male has to inseminate 10 females according to the assumption of LMC. In this species, males are able to mate at least 25 females (Baldwin et al., 1964).

Male insemination capacity is negatively associated with patch sex ratio (ANCOVA: $F_{1,21} = 4.60$, $P = 0.044$; Figure 1). This means that males from species with low sex ratios (i.e., relatively few males at mating patches) tend to have higher insemination capacities. The slope of the relationship does not significantly differ between species where insemination capacity was estimated as the number of fully inseminated females or the number of matings (denoted in black and white respectively in Figure 1; comparison of slopes: $F_{1,21} = 1.03$, $P = 0.32$). However, there was a significant difference in intercepts between the two types of data ($F_{1,21} = 4.62$, $P = 0.044$), perhaps confirming that estimates of insemination capacity from numbers of matings are indeed over-estimates (Figure 1), even though the slopes are similar. The full ANCOVA model has an R^2 of 59.9% of the variance.

The results reported in Table 1 and the analysis presented above must be interpreted with caution. With only 25 species distributed in four superfamilies (Table 1), it is difficult to generalize our findings to a great extent. Our analysis is also not controlled for phylogenetic relationships. In addition, the number of females available to males on the emergence patch was estimated based on the patch sex ratio. Ideally, the emergence rate of females and the duration of patch residence of both males and females should be taken into account (Hardy et al., 2005a,b; Shuker et al., 2005, 2006; Moynihan & Shuker, 2011). Moreover, reported mating capacities are often for matings in rapid succession that may not necessarily be representative of the mate encounter rate on a patch. For example, for the only species with an IIS under 1, *P. vindemmiae*, males appeared to become sperm depleted after mating 5× in rapid succession. Females that mated such males produced 60% fewer daughters than females mated to virgin males (Nadel & Luck, 1985). However, when the copulations were 30 min apart, males were able to replenish their sperm supply, suggesting that IIS could reach 1 if emergence rate is taken into account.

Discussion

Basic LMC theory predicts that females exploiting a patch alone should allocate just enough sons to inseminate all their daughters. The key issue to understanding and predicting the extent of investment into male progeny is what ‘just enough’ means. Previous extensions to LMC theory exploring sex allocation under low foundress numbers have considered male mortality and constraints on male fertility under the umbrella of ‘fertility insurance’ models (Green et al., 1982; Heimpel, 1994; Nagelkerke & Hardy, 1994; West et al., 1998; Hardy et al., 1998, 2000; reviewed by West, 2009). Our data suggest that males across a range of parasitoid wasps are in general not constrained by their insemination capacity, and instead females of several species produced surplus sons with a collective insemination capacity far exceeding the number of available daughters, even though doing so may lead to competition between brothers. Indeed, IIS values based on the number of inseminated females ranged from 0.88 to 12.88, suggesting that insemination capacities of males generally exceed what is expected. However, our data do suggest that insemination investment strategies of males are associated with patch sex ratios, with males that have more females available to mate generally having higher insemination capacities.

The IIS integrates several factors that influence the relationship between insemination capacity and the number of females present on the patch. Factors such as female virginity risk, occurrence of non-local mating (Hardy, 1994), temporal pattern of emergence, mate acquisition capacity of males (Abe et al., 2003a), intensity of sperm competition, and host quality could explain IIS higher than 1. Under certain conditions, females producing males with a large insemination capacity may therefore be expected to obtain higher fitness. Here we consider these possibilities in turn, generating further hypotheses for future comparative analyses.

Female virginity risk

Because binomial allocation of low sex ratios increases the risk of having no son deposited in a patch, females may deposit a higher sex ratio to prevent this (Green et al., 1982; Hardy & Cook, 1995; Hardy et al., 1998). A clutch without males results in unmated daughters who would either be constrained to produce only sons or would have to disperse to find mates. In highly inbred species, the use of precise sex ratios results in more inseminated females emerging from broods compared to binomial sex ratios (Green et al., 1982). Male immature mortality could also result in female-only broods and to decrease this risk, ovipositing females could also produce more males than predicted. Nagelkerke & Hardy (1994) have modelled the effects of developmental mortality on optimal sex allocation, finding that early mortality of males, but not females, results in the allocation of more males than otherwise predicted by LMC theory.

We thus expect species with very low sex ratios in small broods, or with high male mortality, to have a high IIS. In patches where few of the allocated males survive, males with a high insemination capacity could still mate with most or all females. This implies that the evolutionary cost of maintaining males with high insemination capacity is lower than the cost of producing a higher sex ratio, although recent models have begun to explore the coevolution of female mating rate and male ejaculate expenditure under female-biased sex ratios, and suggest that female mating rates should increase under female-biased sex ratios as male ejaculate sizes decrease (Abe & Kamimura, 2015). These results therefore emphasise the importance of female mating rate for IIS.

Occurrence of non-local mating

When mating does not occur entirely locally, a situation termed partial LMC, the predicted sex ratios will typically differ from the simplest LMC models (Nunney & Luck, 1988; Hardy, 1994). Put another way, non-local mating reduces the strength of LMC. For example, in fig wasps, the proportion of males in a clutch is higher in species with dispersing males than in species where mating is entirely local [tested from data of 17 New World non-pollinating fig wasps (West & Herre, 1998), and in 44 Old World non-pollinating fig wasps (Fellowes et al., 1999)]. In these species, females produce more males in order to increase the probability that their sons will inseminate females from outside the natal patch. In cases where there is not precise sex allocation and where differential mortality between the sexes is unlikely, females could still produce males with a high insemination capacity in order for them to be able to outbreed. This could explain cases such as *Trichogramma euproctidis* Girault, where males mate at emergence and disperse from the emergence patch still with sperm in their seminal vesicles (Martel & Boivin, 2007; Martel et al., 2010).

The impact of partial LMC on IIS also depends on the capacity of males to produce sperm throughout their (short) lives, or whether they eclose as adult with their full sperm complement (i.e., whether males are synspermatogenic or prospermatogenic; Boivin et al., 2005). All other factors being equal, in prospermatogenic species, because the males cannot produce sperm after emergence, the IIS should be directly related to the probability of finding off-patch mates. When this probability is very low, males should emerge with just enough sperm to mate all females available locally and therefore have an IIS close to 1. In synspermatogenic species, the relation between IIS and off-patch mating depends on the trade-off between the production of sperm and the behaviours linked to mate finding and acquisition, both of which may be hard to measure in practice. If sperm production is costly and decreases the resources available for dispersal, males should emerge with just enough sperm to mate locally, then disperse and resume producing sperm when they have reached an area where females are available (Boivin & Martel, 2012). In this situation, a lower IIS would be predicted than if sperm production during immature development has little cost on subsequent mate finding behaviours, something that experimental studies could test with relevant species. (For an analogous argument in terms of egg loads see Luft, 1993; see also Humphries et al., 2006.)

Temporal pattern of emergence

In addition to mating opportunities in different places, males may also benefit from increased insemination capacity when they can gain extra matings at different times. One temporal pattern that could influence the IIS occurs when LMC is asymmetrical. Shuker et al. (2005) have extended LMC theory by considering asymmetrical mate competition between the offspring laid by different females on a patch. In asymmetrical LMC, multiple females visit and lay eggs sequentially on a single patch. Males that emerge from earlier broods can mate with their sisters and remain on the patch to mate with females of later broods. The resulting competition is asymmetrical because males from the later brood suffer greater total competition for mates but reduced LMC (amongst kin), as they have to compete with males from earlier broods without the possibility of copulating with females from these earlier broods. Males of *Nasonia vitripennis* (Walker) show such behaviour, and females allocate sex broadly in line with asymmetric LMC predictions (Shuker et al., 2005). In this case, the excess of male mating capacities could have been selected by the fact that males may have the opportunity to copulate with more females than those available from their own brood.

Another temporal pattern that could influence the IIS occurs when males and females themselves emerge asynchronously, as males that emerge at the appropriate time could acquire the most matings. These males would require an insemination capacity sufficient to fertilise all available sisters. In the quasi-gregarious species *Spalangia cameroni* Perkins, a large proportion of males emerge 1 day before the peak of female emergence, and leave the patch before any female has emerged. These males orient toward odours from suitable hosts or the hosts' environment (chicken manure) to find receptive virgin females (Myint & Walter, 1990). Only a few males emerge the same day that females begin to emerge (two males and 42 females; Myint & Walter, 1990). *Spalangia cameroni* males can successfully inseminate between 11 and 52 females during their reproductive lives (King, 2000), suggesting that the few males emerging synchronously with the females can inseminate all of them.

Again, all other factors being equal, we should predict a high IIS in species in which some of the males disperse before mating. However, in this case two evolutionary forces act on the IIS: the average number of females that dispersing males will find outside the emergence patch and the proportion of the male population that emerges synchronously with the females. Until some data are available to quantify these probabilities, one can only guess at what would be the resulting IIS. In the case of asymmetric LMC, we would expect a similar effect, the key difference being that subsequent mating occurs on the same patch and that there is likely to be little or no cost associated with dispersal and mate finding.

Differences in mate acquisition capacity between males

Under basic LMC theory, all males are assumed to have equal mate acquisition capacity (for an example where this is relaxed in terms of within-patch mating patterns, see above). However, although in some species males share more or less equally the available females in a patch, in many species high-quality males acquire the majority of females, whereas low-quality males mate with few, if any, females (van den Assem et al., 1989; Martel & Boivin, 2007). In species with a skewed distribution of mating opportunities among males, the IIS might be expected to be high and to reflect the level of the winning males. Such patterns have been demonstrated across a range of parasitoids. In *T. euproctidis* (= *T. evanescens*), when large males compete for mates with small males, they acquire 88% of all females (Boivin & Lagacé, 1999). With such patterns of mating, the average insemination capacity of males is expected to be higher because the high-quality males have enough sperm to mate with as many females as they acquire. Females can also use phenotypic traits to choose males of a higher quality or with a higher sperm complement, as in the pteromalid *N. vitripennis*, in which females use a male sex pheromone – positively correlated with sperm reserves – to discriminate male quality (Ruther et al., 2009; Blaul & Ruther, 2011).

The situation is similar in species with pugnacious males that fight to control access to the females on a patch (Browne, 1922). In *Melittobia digitata* Dahms, the sex ratio is about 0.05, suggesting that males are able to inseminate 20 females (Abe et al., 2003b). However, a male can in fact inseminate at least 50 females during the 1st day of his life and 163.5 females during his reproductive life (B.A. Wiltz & R.W. Matthews, unpubl.). Because these males spend their entire life inside the host cocoon in which they mature, their high insemination capacity cannot be a consequence of off-patch mating, and instead suggests that males winning the contest can inseminate most of the females present on that patch. Supporting this hypothesis, *Melittobia* satisfies all LMC assumptions but does not exhibit the expected change in sex ratio with an increase in foundress number (Cooperband et al., 2003, Matthews et al., 2009, Abe et al., 2014). Whatever the number of females exploiting the patch, sex ratio appears to be constant at around 0.05, reflecting the fact that in most cases only the winning male has the opportunity to mate on that patch. In *Trissolcus basalis* (Wollaston), sex ratios are female-biased and males also compete aggressively for control of the egg mass. The dominant male copulates with 82% of the females upon their emergence from the egg mass (Loch & Walter, 1999, 2002). As expected, these males have a high insemination capacity, being able to inseminate almost 50 females, which is about the number of females the dominant male can acquire (Loch & Walter, 1999).

Sperm competition

For mating systems prone to LMC, most mating will occur on the emergence patch so that sperm competition is likely to arise if females exhibit any degree of polyandry (Boulton et al., 2015). The risk and intensity of sperm competition is well known to influence the patterns of sperm production and transfer across a broad range of species, including many insects (Simmons, 2001; Kelly & Jennions, 2011). When the costs of producing sperm are higher than the costs of finding mates, males should decrease their sperm expenditure per copulation as the number of male ejaculates increases and therefore when the probability of paternity decreases (Parker et al., 1996), as shown in *T. euproctidis* (= *T. turkestanica*; Martel et al., 2008). If intense sperm competition selects for a decrease in the quantity of sperm transferred per female, each male could inseminate a greater number of females. This would not affect the female’s sex allocation, which is influenced by the extent of LMC rather than the degree of polyandry per se (Hamilton 1967). The IIS should therefore reflect selection on sperm allocation per ejaculate in the context of the risk and intensity of sperm competition.

Host quality

The high insemination capacity observed in several species may also be linked to the influence of host quality. Indeed, both LMC (Hamilton, 1967) and host quality (Charnov, 1979, 1982; Charnov et al., 1981) are not mutually exclusive drivers of sex allocation and these processes can interact (Werren, 1983; Hardy, 1994). Host quality, determined mostly by host size but also by age, developmental stage, sex, species, and the presence of another immature parasitoid, will influence sex allocation by female parasitoids (Charnov, 1979; Charnov et al., 1981). The host quality model, directly analogous to condition-dependent sex allocation as envisioned by Trivers & Willard (1973), predicts that males will be preferentially laid in low-quality hosts, and females in high-quality hosts, with sex allocation being explained by sex-specific fitness-gain curves. Put simply, males lose less than females by developing in low-quality hosts and emerging as smaller adults. Therefore mothers will optimize their fitness by laying more males in low-quality hosts than in high-quality ones. Most, but not all, studies support this sex allocation prediction (van den Assem, 1971; Ueno, 1999; van Baaren et al., 1999; Ode & Heinz, 2002; Colinet et al., 2005; Lewis et al., 2010; Beltra et al., 2014).

Male size does not seem to have an impact on either male ability to mount a female or male insemination capacity in *Muscidifurax raptor* Girault & Sanders (Seidl & King, 1993), *S. cameroni* (King & King, 1994), *Bracon hebetor* (Say) (Ode et al., 1996), *Aphidius nigripes* Ashmead (Cloutier et al., 2000), and *C. glomerata* (Tagawa, 2002). In some species, smaller males are even advantaged by their ability to copulate with females of all sizes, as in *Itoplectis naranyae* (Ashmead) (Ueno, 1998), whereas large males are restricted to large females. In *N. vitripennis*, larger males do better in some components of mate competition (e.g., attracting females via sex pheromones: Blaul & Ruther, 2011) but the extent to which larger males overall outcompete smaller males appears to depend on access to females and whether there is also the opportunity for male-male scramble competition. For instance, when males have access to multiple females, Burton-Chellew et al. (2007) found no selection on male size. Larger males though did inseminate more females over a 2-h period in *Copidosoma floridanum* (Ashmead) (Ode & Strand, 1995, and see below).

However, there are many examples where small males that develop on low-quality hosts do have a reduced insemination capacity, as in *Lariophagus distinguendus* (Förster) (van den Assem, 1971; van den Assem et al., 1989), *I. naranyae* (Ueno, 1998), *Pimpla nipponica* Uchida (Ueno, 1999), and *Heterospilus prosopidis* Viereck (Jones, 1982). For such species, we could expect that even males developing in poor-quality hosts should be able to inseminate the females emerging in a patch. In *T. euproctidis* (= *evanescens*), males that emerge from *Ephestia kuehniella* Zeller eggs (0.28 mm^3; Bai et al., 1992) have 1 600 sperm (Damiens & Boivin, 2005) and can fully inseminate 12 females, and partially inseminate eight more. However, if they develop in the smaller *Plutella xylostella* L. eggs (0.13 mm^3; Pak et al., 1986), the emerging males are smaller (hind tibia length 77% of that of males developing in *E. kuehniella*) and have a sperm stock of 787 (Martel et al., 2011). However, this lower insemination capacity is still sufficient to inseminate the 2-6 females per male present on the emergence patch (Boivin & Lagagé, 1999; Jacob & Boivin, 2005). Small *L. distinguendus* males are able to inseminate five females, whereas large males can inseminate 10 females (van den Assem et al., 1989), but there is one male for three females on emergence patches. In *N. vitripennis*, the sex ratio is around 0.2-0.3 (Reece et al., 2004), so each male needs to inseminate an average of 2-4 females. As small males are able to inseminate 15 females and large ones around 30 females, each male is able to inseminate all females on the patch (van den Assem 1986). In the polyembryonic *C. floridanum*, the sex ratio at emergence from an optimal host is about 0.12 (Ode & Strand, 1995), which means that each male needs to inseminate 7-8 females and yet small males are able to inseminate about 100 females (more than 300 females for large males; Ode & Strand, 1995). In *D. basalis*, males emerging from small and large hosts inseminated 10 and 14 females, respectively, when confined with 20 females during 24 h (Lacoume et al., 2006). This suggests that small males could inseminate the three females per male found on the emergence patch. More data on the mating abilities of males developing in low-quality hosts are sorely needed, however.

It thus appears that the insemination capacity of males has been selected so that even males developing from low-quality hosts can inseminate the mean number of females present in a patch. Even small males have enough sperm to inseminate most of the females present, and large males are likely to have a higher than necessary insemination capacity given the mating system and our expectations under basic LMC.

Conclusion

Under mating systems characterised by local mate competition, parasitoid wasps tend to have an IIS greater than one. Rarely are males incapable of inseminating less than the mean number of females available per male on an emergence patch, and in the vast majority of cases males are capable of inseminating more females than required based on the predictions of LMC theory alone. As we have discussed, there are several factors that could select for a high IIS and still bring indirect fitness gains for females. In these situations, females following strictly the LMC prediction and producing sons with just enough sperm to inseminate all potential mates would be disadvantaged. Importantly, the number of factors acting on IIS, and the importance of each factor, will change depending on the ecology of each species, and currently we need many more data from a wider range of species to begin to test more formally the predictions we have generated here. To fully understand the influence of ecological factors (such as the pattern of dispersal of males and females from the emergence patch) and physiological factors (such as the pattern of sperm production) on the IIS, more studies on mating structure and insemination capacity of males are needed. We suspect that non-local mating and the response to host quality may be more frequently involved than the temporal pattern of emergence or asymmetrical LMC, but again for some species the latter factors may be important. Perhaps equally important is the need for new theory that teases apart selection on mothers and sons over sex allocation, and reproductive allocation by sons, which will interact through their effects on (local) mating competition and fertility insurance. There is scope for parent-offspring conflict over the patterns and control of both suites of traits.

Acknowledgements

We are very grateful to Ian Hardy and Eric Wajnberg for the opportunity to contribute to this special issue celebrating the research of our friend and colleague Mark Jervis, and for their editorship of the special issue. We are also very grateful to Ian Hardy, Paul Ode, and two anonymous referees whose generous and thorough comments helped us improve the manuscript enormously. RAB is supported by a NERC DTG studentship. DMS is also grateful to Leigh Simmons and members of the Centre for Evolutionary Biology at the University of Western Australia for their generous hosting whilst this manuscript was completed.

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Figure caption

Figure 1 Male insemination capacity is negatively associated with patch sex ratio (proportion of offspring that are male). Estimates of male insemination capacity are from direct measurement of the number of fully inseminated females (black dots) or less direct, including numbers of matings without full quantification of insemination (white dots). The dashed line represents the predicted male insemination capacity if the Index of Insemination Strategy (IIS) = 1. Insemination capacity is presented as its natural logarithm for clarity.

Fig 1

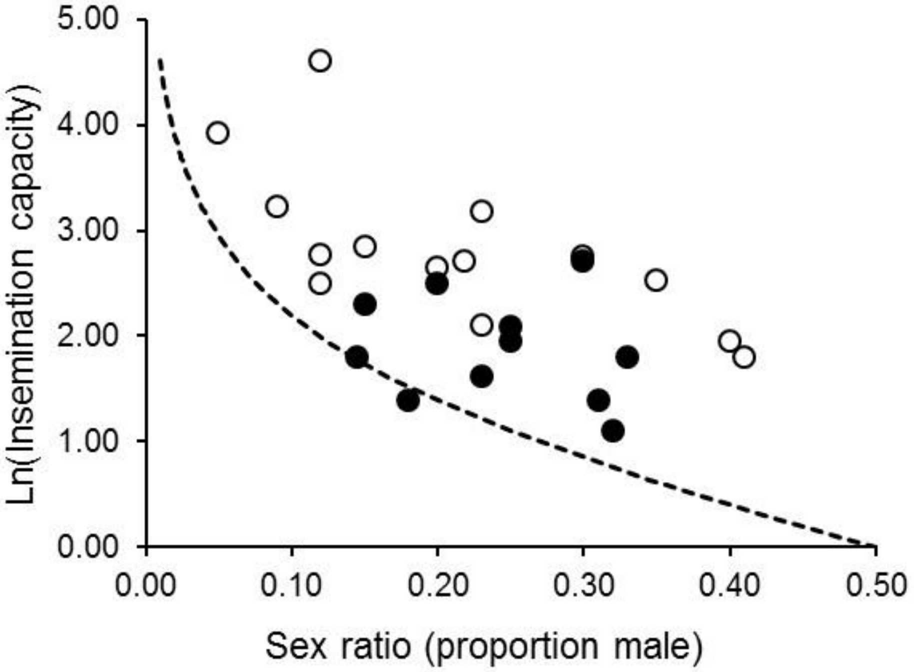
5.00
4.00
3.00
2.00
1.00
0.00
Ln(Insemination capacity)
0.00
0.10
0.20
0.30
0.40
0.50
Sex ratio (proportion male)

Table 1 Insemination capacity of males, sex ratio (proportion male), number of females per male, and Index of Insemination Strategy (IIS) in hymenopteran parasitoid species. Male insemination capacity is based on (A) direct estimates of the number of fully inseminated females, or (B) less direct estimates of insemination capacity, including numbers of matings (see main text for details). The data are for a male's first exposure to females and include all matings that occurred in the first 24 h. All numbers of females per male have been calculated from sex ratio values found in literature

	Species			Male insemination capacity	Sex ratio	No. females/ male	IIS	References
A	Chalcidoidea	Pteromalidae	*Anisopteromalus calandrae*	6	0.145	5.90	1.02	Do Thi Khanh, pers. comm.; Nishimura & Jahn, 1996
			Dinarmus basalis	8	0.25	3.00	2.67	Gauthier at al., 1997 ; Bressac et al., 2008
			Lariophagus distinguendus	7	0.25	3.00	2.33	van den Assem et al., 1989; Steiner et al., 2007
			Nasonia vitripennis	15-30	0.3	2.33	6.44-12.88	van den Assem, 1986; Werren, 1983
			Pachycrepoideus vindemmiae	4	0.18	4.56	0.88	Nadel & Luck, 1985, 1992; Nadel, 1985
			Pteromalus venustus	At least 6	0.33	2.03	>2.96	Tepedino, 1988, 1993
			Spalangia cameroni	At least 4	0.31	2.23	>1.79	King, 1989, 2000; Myint & Walter, 1990
			Spalangia endius	3	0.25-0.39	3.00-1.56	1.00-1.92	King & Fisher, 2010; Donaldson & Walter, 1984; King, 1991
		Trichogrammatidae	*Trichogramma euproctidis*	12	0.2	4.00	3.00	Damiens & Boivin, 2005; Boivin & Lagacé, 1999
	Ichneumonoidea	Braconidae	*Lysiphlebus delhiensis*	At least 5	0.23	3.35	1.49	Mishra & Singh, 1993; Srivastava & Singh, 1995
	Platygastroidea	Scelionidae	*Trissolcus basalis*	10	0.15	5.67	1.76	Loch & Walter, 1999
B	Chalcidoidea	Eulophidae	*Colpoclypeus florus*	At least 15	0.218	3.59	>4.18	Dijkstra, 1986; Hardy et al., 1998
			Dahlbominus fuscipennis	At least 25	0.09	10.11	>2.47	Baldwin et al., 1964; Wilkes, 1965
			Melittobia digitata	At least 50	0.05	19.00	>2.63	Abe et al., 2003b; B.A. Wiltz & R.W. Matthews, unpubl.
		Aphelinidae	*Aphytis lingnanensis*	12.4	0.35	1.86	6.67	Gordh & DeBach, 1976

	Trichogrammatidae	*Trichogramma minutum*	8.2	0.23	3.35	2.45	Nagarkatti, 1973; Martel & Boivin, 2004
	Encyrtidae	*Copidosoma floridanum*	100-300	0.12	7.33	13.64-40.93	Ode & Strand, 1995
	Torymidae	*Philotrypesis* spec.	At least 7	0.40	1.50	>4.67	West et al., 1997, 1998
	Agaonidae	*Sycoscapter* spec.	At least 6	0.41	1.44	>4.17	West et al., 1997, 1998
Ichneumonoidea	Braconidae	*Cotesia glomerata*	14	0.1-0.3	9.00-2.33	1.56-6.01	Tagawa, 2000, 2002
		Aphidius testaceipes	15.75	0.3	2.33	6.76	Sekhar, 1957
		Praon aguti	17.25	0.15	5.67	3.04	Sekhar, 1957
		Lysiphlebus delhiensis	24	0.23	3.35	7.16	Mishra & Singh, 1992, 1993; Srivastava & Singh, 1995
Chrysidoidea	Bethylidae	*Goniozus nephantidis*	At least 12	0.12	7.33	>1.64	Hardy & Cook, 1995; Hardy et al., 1998
		Goniozus legneri	At least 16	0.12	7.33	>2.18	Hardy et al., 1998, 2000