RESEARCH ARTICLE

Influence of natal host and oviposition experience on sex allocation in a solitary egg parasitoid, *Anastatus disparis* (Hymenoptera, Eupelmidae)

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Abstract

Constraints on adaptation are a major topic in evolutionary biology. Sex allocation, in particular the ratio of the sexes, has often been used as a key process for studying constraints on adaptation. *Anastatus disparis* Ruschka (Hymenoptera: Eupelmidae) is a solitary egg parasitoid of gypsy moth, *Lymantria dispar* (L.) (Lepidoptera: Lymantriidae), and several other lepidopteran forest pests. Here, we compared two different sized substitute hosts, the smaller one *Dictyoploca japonica* Moore (Lepidoptera: Saturnidae) and the larger one *Antheraea pernyi* Guerin-Meneville (Lepidoptera: Saturnidae), and investigated the influence of natal host and oviposition experience on sex allocation by *A. disparis*. Results showed that natal host had almost no impact on sex allocation by *A. disparis*, but oviposition experience did influence sex allocation of *A. disparis* on *D. japonica* eggs. This suggests that information females obtain from the environment influences how they allocate sex in their offspring. However, the sex ratios of *A. disparis* emerging from *A. pernyi* eggs were consistent irrespective of oviposition experience of female *A. disparis*. This indicates that the eggs of *A. pernyi* are large enough to maximize female progeny of *A. disparis*.

Keywords

Parasitoid, substitute host, learning, gypsy moth

Introduction

Anastatus disparis Ruschka (Hymenoptera: Eupelmidae) is a solitary egg parasitoid of several noxious lepidopteran forest pests, including the gypsy moth, *Lymantria dispar* (L.) (Lepidoptera: Lymantriidae) (Crossman 1925, Kurir 1944, Yan et al. 1989, Li and Lou 1992, Alalouni et al. 2013, Liu et al, 2017). It can develop three to four generations on *L. dispar* eggs annually in Northern China (Yao and Yan 1994). In our previous research, we found that the offspring of *A. disparis* reared on egg masses of gypsy moth were male-biased and small-bodied (Liu et al. 2017). However, when they were reared on a larger host, *Antheraea pernyi* Guerin-Meneville (Lepidoptera: Saturnidae), the offspring were female-biased and had a larger body size compared with those reared from gypsy moth (Liu et al. 2017).

Sex allocation in haplodiploid arthropods has fitness-related implications and has received much attention with regard to insect parasitoids (West 2009). In particular, an important attribute of parasitoids is that they control the sex ratio of offspring in response to environmental variables (Godfray 1994). In parasitoid wasps, mated females can manipulate the sex-ratio of progeny by controlling fertilization during oviposition. Males develop from unfertilized eggs and are haploid, while females develop from fertilized eggs and are diploid (Heimpel and de Boer 2008). In the case of solitary parasitoids, for which only one individual develops in each host, the theory of host quality-dependent sex allocation has been proposed to explain the sex ratio variation in this group of parasitic Hymenoptera (Charnov 1979, Charnov et al. 1981). This theory states that the pattern of sex allocation is determined depending on male- and female-fitness relationships with host size; either female or male eggs could be allocated to higher quality hosts depending on which sex benefits more from being large (Charnov et al. 1981, Napoleon and King 1999, West and Sheldon 2002). Both theoretical predictions and empirical studies show that the sex (usually female) that benefits most from being larger, should be placed in a larger host for its development (Charnov et al. 1981, King and Lee 1994). The size of an emerging parasitoid is often positively correlated with the size of the natal host, as are other fitness components such as longevity, fecundity, dispersal and patch-finding ability in the field (King and Charnov 1988, King and Lee 1994, Visser 1994, Kazmer and Luck 1995, Bennett and Hoffmann 1998, Ellers et al. 1998, Jervis et al. 2003).

Learning and memory have been demonstrated in a large number of animal species. Hymenopteran parasitoids can learn to recognize particular visual and olfactory stimuli and use them to modify subsequent behaviours (Vet et al. 1995, Vinson 1998). Learning may occur at any phase of the host selection process (Dauphin et al. 2009). Therefore, learning includes 'pre-imaginal learning' at adult emergence (Cortesero and Monge 1994, Gandolfi et al. 2003), 'post-emergence learning' or 'early adult learning' immediately after emergence (Lentz and Kester 2008), and 'ovipositional learning' at oviposition (Turlings et al. 1995). Numerous studies have demonstrated the positive effects of learning on host selection (Vet and Groenewold 1990, Hastings and Godfray 1999, Morris and Fellowes 2002), optimizing foraging efficiency (Vet and Groenewold

1990, Vet et al. 1995, Vinson 1998) and encountering suitable hosts (Papaj and Vet 1990, Baaren and Boivin 1998, Dutton and Dorn 2000).

Trivers and Wilard (1973) suggest that females should adjust the sex of their offspring in response to environmental conditions, and there is considerable empirical evidence for such adjustments and deviations from optimal sex allocation strategies (West and Sheldon 2002, Lewis et al. 2010). As a parasitoid, *A. disparis* can parasitize small body-sized hosts through to large body-sized hosts, with females seeming to prefer larger hosts which produce more female offspring (Liu et al. 2017). However, we do not know whether natal host or oviposition experience influence the offspring sex allocation of adults. For this reason, we devised a series of experiments aiming firstly to determine whether natal host could influence sex allocation in female *A. disparis*, and secondly whether a learning experience, in this case oviposition experience on one host species, influences sex allocation by females during oviposition on a different host species. Two substitute host species of different sizes were evaluated: the smaller was *Dictyoploca japonica* Moore (Lepidoptera: Saturnidae) and the larger was *Antheraea pernyi* Guerin-Meneville (Lepidoptera: Saturnidae).

Material and methods

Insect cultures

Pupae of *Antheraea pernyi* were purchased from a farmer in Qinglong Manchu Autonomous County, Qinhuangdao City, Hebei Province, China; adults that emerged from those pupae were maintained at 25–30 °C for less than two days prior to egg extraction (see below); *Dictyoploca japonica* eggs were provided directly from the Forestry Academy of Liaoning Province, China. Eggs of the two lepidopteran host species for use in experiments were obtained by laparotomizing the adult females' abdomen and removing the eggs; these eggs were maintained at 0 °C prior to use, and for not longer than 60 days (Wang et al. 2014).

An *Anastatus disparis* colony was first established from a population developing in *L. dispar* egg masses collected in Longhua County, Hebei Province (41°31'N, 117°74'E) in March, 2012, and was subsequently maintained on *A. pernyi* eggs in several cylindrical rearing boxes (height: 5 cm, diameter: 5 cm) at 25±0.5°C, RH 60%, 14L:10D. Prior to experiments cohorts of *A. disparis* were also reared on *D. japonica* eggs for three generations to provide the different treatments for the experiments (see below). All adult female *A. disparis* had no experience of hosts or oviposition before experiments began and were fed with honey water (honey: water=4: 6) on cotton balls (Yan et al. 1989). The age of the females selected for the experiments ranged from 3 to 5 days because under standard conditions offspring sex ratio does not fluctuate widely during this period (Liu et al. 2015). All females were placed with males for 24 hours to ensure they were mated before each experiment.

Measurement of egg sizes of different lepidopteran host species

The host egg sizes were determined from their length (Morris and Fellowes 2002), which was measured using a light microscope (Leica M205A, Germany). Thirty replicate eggs were measured for each host species.

Sex allocation by *Anastatus disparis*

One large experiment with six treatments was conducted to answer two primary questions, the first concerning sex-allocation by females offered a choice of different sized hosts (treatments 1 and 2) and the second concerning females offered different sized host sequentially (treatments 3-6; in all cases, they gained oviposition experience when offered the first host which then had the potential to influence their behaviour in relation to the second host offered). All treatments were run at the same time but, to aid interpretation, we describe them below in relation to the question being asked.

Sex allocation by *Anastatus disparis* when offered a choice of eggs from two different lepidopteran host species presented at the same time

This question was answered by comparing between two treatments; specifically, between maternal females that were either reared on *Antheraea pernyi* (treatment 1) or *Dictyoploca japonica* (treatment 2) before being offered a choice of eggs from both lepidopteran species, for oviposition. One maternal adult (3–5 days) reared on either *A. pernyi* or *D. japonica* was introduced into a cylindrical rearing box (height: 5 cm, diameter: 5 cm) containing twenty *A. pernyi* eggs and twenty *D. japonica* eggs at 26±0.5 °C. After 24 hours, the eggs of both host species were collected and placed individually into polyethylene tubes (height: 7.5 cm; diameter: 1 cm) plugged with cotton and incubated at 28±0.5 °C until adult parasitoids emerged. The number and sex of offspring was recorded after eclosion. Since *A. disparis* is haplodiploid, virgin females lay 100% unfertilized eggs, which develop into males, while mated females lay a mixture of unfertilized and fertilized eggs, the latter of which develop into females. Therefore, any replicates resulting in 100% male offspring were assumed to be from unmated maternal adults and were excluded from subsequent statistical analysis. Thirty replicates of maternal adults were tested for each treatment (60 in total).

Sex allocation by *A. disparis* when eggs from two different lepidopteran host species are presented separately and in sequence

This question was answered by comparing amongst four treatments in which maternal females, reared either in *A. pernyi* or *D. japonica*, were offered eggs of one or other of the

Table 1. Number of maternal replicates for each experimental treatment.

Host species on which the maternal parasitoid had been reared	Sequence of parasitism	
	First *A. pernyi* eggs then *D. japonica* eggs	First *D. japonica* eggs then *A. pernyi* eggs
A. pernyi eggs	73 (treatment 3)	77 (treatment 4)
D. japonica eggs	66 (treatment 5)	64 (treatment 6)

lepidopteran species in sequence, i.e. first *A. pernyii* eggs and then *D. japonica* eggs or *vice versa*: all combinations (i.e. the four treatments, 3-6) and total replicates per treatment combination can be seen in Table 1. Specifically: One maternal adult reared either on *A. pernyi* or *D. japonica*, was introduced into a cylindrical rearing box (height: 5 cm, diameter: 5 cm) containing twenty *A. pernyi* or *D. japonica* eggs (depending on treatment) at 26±0.5 °C. Twenty-four hours later, all of the host eggs were collected and replaced by a new batch of twenty eggs of *A. pernyi* or *D. japonica* (depending on treatment) and incubated for a further 24 hours at 26±0.5 °C. Parasitised host eggs from each treatment were placed individually into polyethylene tubes (height: 7.5 cm; diameter: 1 cm) plugged with cotton and incubated at 28±0.5 °C until adult parasitoids emerged. The number and sex of offspring was recorded after eclosion. Results for maternal adults that had not mated were excluded from the subsequent statistical analysis as described previously.

Statistical analysis

The sex ratio of the parasitoid offspring was represented as the proportion of males (male divided by male+female). Sex ratios of offspring reared from the different host species (for each treatment), and the egg sizes of the two different host species, were compared using independent *T*-tests in the statistical package SPSS version 20, after arcsin (sqrt) transformation of the raw proportion data. For the whole experiment with simultaneous presentation of both host species in treatment 1 and 2, sex ratios and numbers of offspring reared from the different host species were compared by General Linear Model (GLM) with Univariate tests and Generalised Linear Mixed Models (GLMMs). For the effect of oviposition experience (hosts presented with different sequences), results from the whole experiment (treatment 3-6) were analyzed by GLM with Multivaritate tests. The confidence interval for all tests was set at 95%.

Results

Sizes of two host species

The eggs of *A. pernyi* (2.94±0.02 mm) were significantly larger than the eggs of *D. japonica* (2.31±0.02 mm; *t*=24.44, *df*=58, *p*<0.001).

Sex allocation by *A. disparis* when offered a choice of eggs from two different lepidopteran host species presented at the same time

When maternal *A. disparis* that had been reared on *A. pernyi* eggs encountered *A. pernyi* and *D. japonica* eggs simultaneously (treatment 1), the proportion of male offspring emerging from *A. pernyi* eggs was 9.35±1.87% and the proportion emerging from *D. japonica* eggs was 44.53±8.34% (Fig. 1). When maternal *A. disparis* that had been reared on *D. japonica* eggs encountered *A. pernyi* and *D. japonica* eggs simultaneously (treatment 2), the results were similar: the proportion of male offspring emerging from *A. pernyi* eggs was 10.60±2.66% and the proportion emerging from *D. japonica* eggs was 30.60±7.02%. GLM with univariate analysis showed that offspring sex ratios of maternal adults from the two host species varied little (F=1.558; df=1, 116; P=0.215), but when females made a choice between the two host species, the sex ratios of offspring from *A. pernyi* eggs and *D. japonica* was significantly different (F=15.233; df=1, 116; p<0.001) (Fig. 1). Analysis by GLMMs also showed that offspring sex ratios of females from the two host species (natal influence) were not significantly different (p>0.05), but their offspring differed when emerging from different host eggs (Estimate=0.237, Wald Z=7.616, p<0.001).
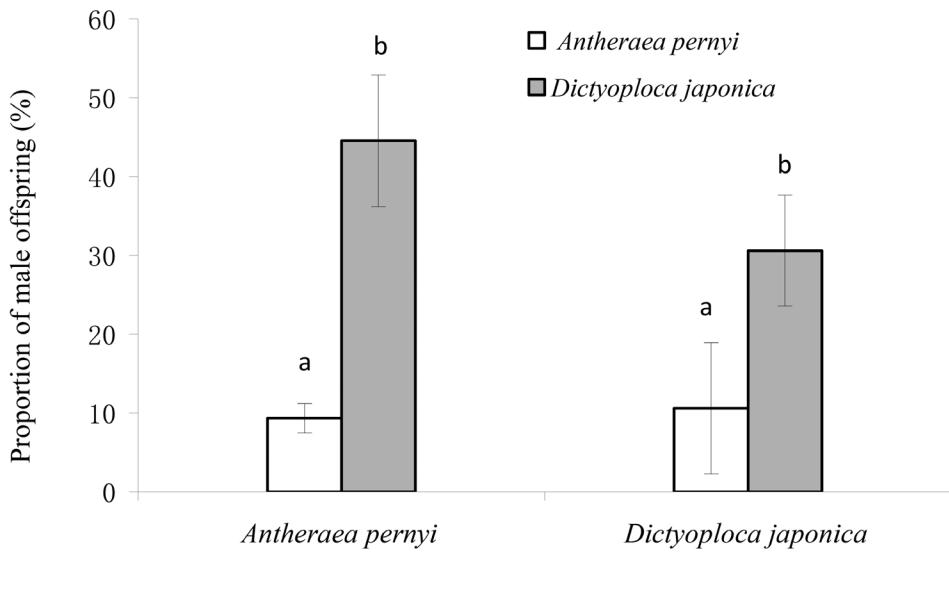
The total number of offspring emerging from *A. pernyi* eggs parasitized by maternal *A. disparis* from host *A. pernyi* or *D. japonica* were 7.27±0.62 and 7.00±0.79, respectively. The total number of offspring emerging from *D. japonica* eggs parasitized by maternal *A. disparis* from host *A. pernyi* or *D. japonica* were 3.53±0.69 and 2.97±0.55, respectively. Analysis showed that the total offspring number laid by the two kinds of females varied little (F=0.387, df=1, 116, p=0.535), This was consistent in the treatments where eggs of the two hosts were presented sequentially and so we only report total numbers here. However, there was a significant difference between the two parasitized host species (F=33.634, df=1, 116, p<0.001).

Sex allocation by *A. disparis* when the eggs of two different lepidopteran host species were presented separately and in sequence

When maternal *A. disparis* reared on *A. pernyi* eggs were first offered *A. pernyi* eggs and then *D. japonica* eggs (treatment 3) a significantly higher proportion of male offspring emerged from *D. japonica* eggs (28.02±3.20%) than *A. pernyi* eggs (7.65±0.65%; t=-6.640, df=72, p<0.001) (Fig. 2).

When maternal *A. disparis* reared on *D. japonica* eggs were first offered *A. pernyi* eggs and then *D. japonica* eggs (treatment 5) a significantly higher proportion of male offspring emerged from *D. japonica* eggs (34.37±3.42%) than from *A. pernyi* eggs (7.57±1.09%; t=-8.570, df=65, p<0.001).

When maternal *A. disparis* reared on *A. pernyi* eggs were first offered *D. japonica* eggs and then *A. pernyi* eggs (treatment 4) there was no significant difference in the proportion of male offspring emerging from *D. japonica* eggs (10.33±0.93%) com-

Figure 1. Proportion of male offspring from maternal *A. disparis* when simultaneously presented with eggs of two host species. Bars with different lowercase letters are significantly different from each other from the General Linear Models with Univariate test analysis (*p*<0.001).
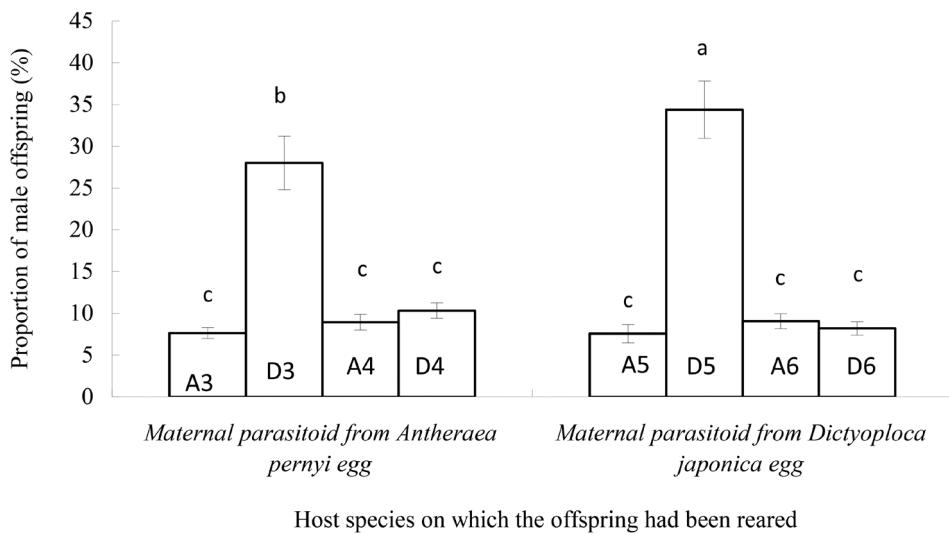
Figure 2. Proportion of male offspring from female *A. disparis* with different prior oviposition experience. Bars with different lowercase letters are significantly different from each other from the General Linear Models with Multivariate tests analysis (*p*<0.001). A3 and D3 represent host *A. pernyi* eggs and *D. japonica* eggs in treatment 3, respectively; A4 and D4 represent two hosts in treatment 4; A5 and D5 represent two hosts in treatment 5; A6 and D6 represent two hosts in treatment 6.

pared with the proportion emerging from *A. pernyi* eggs (8.93±0.93%; *t*=1.137, *df*=76, *p*>0.05).

When maternal *A. disparis* reared on *D. japonica* eggs were first offered *D. japonica* eggs and then *A. pernyi* eggs (treatment 6) there was no significant difference in the proportion of male offspring emerging from *A. pernyi* eggs (9.07±0.92%) compared with the proportion emerging from *D. japonica* eggs (8.19±0.80%; *t*=-0.754, *df*=63, *p*>0.05).

In both treatments in which the maternal adults had been reared on *A. pernyi* eggs (treatments 3 and 4), the proportion of *A. disparis* male offspring emerging from *D. japonica* eggs was significantly higher when the female had previous oviposition experience on *A. pernyi* eggs (28.02±3.20%; treatment 3), than when they had no previous oviposition experience (10.33±0.93%; *t*=5.02, *df*=148, *p*<0.001; treatment 4) (Fig. 2). The results were similar for the maternal adults that had been reared on *D. japonica* eggs: a significantly higher percentage of male offspring emerged from *D. japonica* eggs parasitized by females with oviposition experience on *A. pernyi* eggs (34.37±3.42%; treatment 5), than when they had no previous oviposition experience (8.19±0.80%; *t*=7.46, *df*=128, *p*<0.001; treatment 6) (Fig. 2).

When treatments 3-6 were put into a 2×2 GLM analysis, ie, the first factor being mother (emerged from *A. pernyi* or *D. japonica*) and the second factor being 'when experienced' (first or second order), and the offspring sex ratios of *A. disparis* from *A. pernyi* eggs and *D. japonica* eggs were regarded as two dependent variables, respectively, several interesting results were observed. The first was that the offspring sex ratios were not different across the first and second broods, regardless of host species (*F*=0.494, *df*=2, 275 *p*=0.61), i.e., mothers (natal experience) either from *A. pernyi* or *D. japonica* had little influence on offspring sex ratios. The second was that the offspring sex ratios differed for the *D. japonica* between different orders (*F*=6.944, *df*=1, 276, *p*<0.01), but were similar for the *A. pernyi* regardless of the oviposition experience of the maternal adult (*F*=1.480, *df*=1, 276, *p*=0.225). Moreover, host species (natal) and order (oviposition experience) interacted in above treatments (*F*=34.835, *df*=2, 275, *p*<0.001), and the main contributor was *D. japonica* (*F*=62.773, *df*=1, 276 *p*<0.001).

Discussion

Natal host can influence parasitoid host preference, handling time and sex allocation behaviour. Morris and Fellowes (2002) speculated that, in part, host size may be judged by self-reference by the ovipositing female comparing host size with a component of her own size, such as the time it takes to walk over the surface of the host. However, we found that despite the fact that females emerging from *A. pernyi* were significantly larger than those emerging from *D. japonica* this had no significant effect of their subsequent sex allocation. We suggest that *A. disparis* may, therefore, have no self-reference ability, i.e. it does not judge potential host size by comparing it with its own size.

In theory, the sex (usually female) that benefits most from larger size should be placed in larger hosts (host quality-dependent sex allocation theory) (Charnov and Stephens 1988, King and Lee 1994). We found strong support for this hypothesis as, regardless of whether maternal *A. disparis* had themselves been reared on *A. pernyi* or *D. japonica*, they all preferred to lay more female offspring in relatively larger host species and more male offspring in relatively smaller host species when both host species were supplied simultaneously. The difference in host size could be judged by direct comparison using visual and tactile cues.

We also found that sex allocation in *A. disparis* was affected by oviposition experience. For instance, the proportion of male offspring emerging from *D. japonica* eggs parasitized by females with oviposition experience of *A. pernyi* eggs, was significantly higher than the proportion of males emerging from *D. japonica* eggs parasitized by females that had no oviposition experience. We speculate that females can judge current host size from oviposition experience of previously parasitized hosts. If females have laid eggs in *A. pernyi* eggs, then when they subsequently encounter *D. japonica* eggs, the female would compare the host quality (host size) of the *D. japonica* eggs with its stored oviposition memory of *A. pernyi* eggs (Goubault et al. 2004, Papaj and Prokopy 1989), and determine that the *D. japonica* egg is smaller. If this is the case, then more male offspring would be laid in the *D. japonica* eggs if the host quality-dependent sex allocation theory is correct (Charnov and Stephens 1988, King and Lee 1994). However, we did not find evidence for this when female parasitoids were first offered *D. japonica* eggs and then *A. pernyi* eggs, when the proportion of male offspring emerging from the *A. pernyi* eggs was not significantly different from the proportion of males emerging from *A. pernyi* eggs that had been parasitized by females that had no oviposition experience. Therefore, we supposed that *A. pernyi* eggs were large enough for the parasitoid to achieve maximum female progeny in nature.

In conclusion, sex allocation in *A. disparis* females fitted with the predictions of condition-dependent sex allocation theory in parasitoids (Trivers and Willard 1973, West and Sheldon 2002, Lewis et al. 2010). It also provided a nice test of experience (i.e. context-dependence) in terms of sex allocation: when first presented with eggs of the larger host, females produced a more male-biased clutch on a patch of the second, smaller host eggs; however, when females experienced the small eggs first, the sex ratios did not shift when they moved to larger hosts. This suggests that information females obtain from the environment influences their sex allocation. The asymmetry in response suggests that female-biased sex ratios on the larger host were optimal come what may, whilst if only presented with the smaller host, female biased sex ratios are optimal, but in the presence of (or experience of) larger hosts, then more males are produced in the smaller hosts (Lewis et al. 2010).

Further studies with longer intervals between oviposition on different host species should be performed to evaluate the effects of learning and memory in this species.

Acknowledgements

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