Offspring sex ratio shifts of the solitary parasitoid wasp, *Trichopria drosophilae* (Hymenoptera: Diapriidae), under local mate competition

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Local mate competition (LMC) models predict a female-biased offspring sex ratio when a single foundress oviposits alone in a patch and an increasing proportion of sons with increasing foundress number. We tested whether the solitary pupal parasitoid, *Trichopria drosophilae* (Hymenoptera: Diapriidae), adjusted offspring sex ratio with foundress number when parasitizing *Drosophila melanogaster* pupae. Mean number of female offspring was higher than that of males, with a male proportion of 26 ± 16% when only one foundress oviposited. However, male proportion reached 58 ± 26%, 48 ± 22%, and 51 ± 19% in three-, five- and seven-foundress cohorts. That the male proportion of offspring increased with foundress number is consistent with LMC models.

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1. Introduction

Sex ratio theories are sometimes described as one of the most successful theories in evolutionary ecology (Fellowes *et al.* 1999, West *et al.* 2000, West 2009, Whitehorn *et al.* 2015). Sex ratio is adjustable in response to such biotic factors as interactions between relatives, out of which local mate competition (LMC) is one of the most famous. LMC implies that brothers would compete with each other for mating with their sisters in the strictly isolated patch founded by a single foundress (Hamilton 1967). In such a patch, a female-biased sex ratio adjustment would be adaptive, because the LMC among sons does not conform to the fitness interests of the foundress (Hamilton 1967, 1979). In such a highly structured population with inbreeding, where mating happens only between full siblings, relatedness differ between parents and offspring, so that female offspring are more related than male offspring to their mother (Hamilton 1964, Herre 1985). With this asymmetry in relatedness, a female-biased sex ratio is expected (Herre 1985). However, a less female-biased offspring sex ratio does bring interests to foundresses when more than one of them oviposit together, because the value of sons increases with the increase in the possibility to mate with the daughters of the other foundresses (Hamilton 1967, 1979, Herre 1985, 1987, Werren 1987, West 2009).

LMC models were formed for populations

that are subdivided into local mating groups, such as the pollinating fig wasps, and no male dispersal among groups is one of the key conditions of the original models (Hamilton 1967, 1979). "Strict LMC" then happens when mating always happens in the natal patch with relatives, e.g. the pollinating fig wasps, whose wingless males only mate in natal figs and females finish mating before dispersing (Hamilton 1967, 1979). *Ceratosolen solmsi* (Mayr), the pollinator of *Ficus hispida* L. f., has wingless males, which mate with females in the figs and then dig holes through the wall of the figs to allow females to disperse. Mating always happens between relatives, and a female-biased sex ratio evolved in the manner predicted by LMC models (Hu *et al.* 2013). Such a strict subpopulation is classic in theories, but is unusual in nature. But when mating does not occur entirely locally, the situation termed "partial LMC" happens, which seems more common in nature (Hardy 1994). For a large number of species with winged males, e.g. parasitoid wasps, "partial LMC" is more relevant, because some mating is also likely to occur away from the natal patch (Werren & Simbolotti 1989, Nadel & Luck 1992, Hardy 1994, West & Herre 1998, Fellowes *et al.* 1999, Martel *et al.* 2010). "Partial LMC" selects for a less female-biased sex ratio compared to "strict LMC" (Nadel & Luck 1992, Fellowes *et al.* 1999, West & Herre 1998).

Trichopria drosophilae (Perkins) (Hymenoptera: Diapriidae) is a solitary pupal parasitoid that attacks many species of Drosophilidae (Wang *et al.* 2016b). This species of parasitoid has become important in recent years in the fruit industry, because it may be a preferable candidate as an agent for the biological control of the spotted wing drosophila, *Drosophila suzukii* (Matsumura) (Diptera: Drosophilidae), which has brought disaster to soft and thinned fruits in Europe and North America (Lee *et al.* 2011, Hamby *et al.* 2013, Mazzetto *et al.* 2016, Wang *et al.* 2016a, b). *Trichopria drosophilae* seems to be a cosmopolitan parasitoid with a wide distribution. It is a solitary parasitoid parasitizing pupae of *D. suzukii* in France (Chabert *et al.* 2012), Italy (Miller *et al.* 2015, Rossi Stacconi *et al.* 2015, Mazzetto *et al.* 2016), Spain (Gabarra *et al.* 2015), South Korea (Daane *et al.* 2016, Wang *et al.* 2016b), Mexico (Cancino *et al.* 2015), and the USA (Kacsoh & Schlenke 2012, Wang *et al.* 2016a, b). *Trichopria drosophilae* has a female-biased sex ratio (Wang *et al.* 2016b). The distribution of the parasitoid can be expected to be consistent with that of their hosts. The drosophilid hosts breed in isolated patches such as orchards and dust heaps, and therefore it is possible that the parasitoid has also a structured population and sex ratio adjustment under LMC could be assumed. Given this, we predict that *T. drosophilae* females should adjust the offspring sex ratio with foundress number, and the sex ratio adjustment should be consistent with predictions of the "partial LMC" models.

2. Materials and methods

2.1. Study insects

Strains of *D. melanogaster* and *T. drosophilae* were initiated from field collections on May 2015 at the Huiwang blue berry orchard in Nanling, Anhui province, China (30.85° N, 118.40° E). *Drosophila melanogaster* were cultured with a standard medium (David & Clavel 1965) in an incubator with the 14:10 light:dark photoperiod at 25 ± 1 °C and the relative humidity of 60 ± 5%. Adult fruit flies were reared in a cube cage made of nylon mesh of 150-µm pore size, and 90 mm petri dishes with the medium put into the cage. Every 12 h, the dishes were taken out of the cage and placed in a plastic box, about 50 L in volume, sealed with nylon mesh around the rim. Four days later, the dishes were sprinkled with water and older *Drosophila* larvae crept into the box and pupated on the smooth box wall. *Drosophila* pupae were sprinkled and collected with a soft brush every day.

Trichopria drosophilae were maintained with pupae of *D. melanogaster* as hosts in the above-described incubator for about one year. Parasitoid wasps were reared in glass vials (25 mm in diameter, 50 mm in height) with *Drosophila* pupae and honey-soaked cotton wool as food. Before experiments, *Drosophila* pupae that were less than 2-d-old and similar in size were provided, in order to make the parasitoid wasps similar in size. Similar size was aimed at in order to produce parasitoids as similar in their life history traits as possible.

2.2. Offspring sex ratio shifts with foundress number

Parasitized *Drosophila* pupae were discernible before parasitoid offspring emergence, due to the dark pupae of the parasitoids inside. Preliminary studies showed that most *T. drosophilae* adults emerged 15 d after laid in host pupae. To obtain newly emerged virgin male and female parasitoid wasps, the parasitized host pupae were individually selected and laid into a transparent tube sealed with a fine nylon mesh, on the 14th day after having been exposed to parasitoid females. On the next day, the tubes were checked, and those with parasitoid adults inside were selected. Male and female parasitoids were identified by their antennae (Romani *et al.* 2008).

In order to test the effects of foundress number on offspring sex ratio adjustment, four treatments were designed, with 1, 3, 5, and 7 newly-emerged male-female pairs of the parasitoid, respectively. Clear plastic containers (6 cm diameter, 8 cm height) were used as oviposition patches, which were closed at the side with a fine nylon mesh for ventilation. A small cotton wick soaked in 10% honey solution was placed inside the container to provide a source of carbohydrate for adult feeding, and 30 laboratory-reared *Drosophila* pupae aged 1–3 d were provided as hosts in each treatment.

After every 24 h, the host pupae exposed to the parasitoids were changed to another set of 30 *Drosophila* pupae, together with the cotton wick. Experiments lasted five days. Ten replicate groups were finished for each of the above four treatments.

After each exposure, the host pupae were placed in transparent plastic tubes sealed with a fine nylon mesh. When adults of parasitoids or fruit flies had emerged from the exposed pupae (some had not been successfully parasitized), the number and sex of parasitoids, flies, and non-emerged host pupae were recorded. All of the experiments were conducted in an incubator under the photoperiod, temperature, and relative humidity conditions as described above. About one week after the emergence, all the remaining pupae were dissected and the parasitoid offspring that failed to emerge were recorded. As it is possible to determine the sex of parasitoids that failed to emerge, they were added up to the total male and female offspring.

2.3. Statistical analyses

Count data as number of parasitoid offspring and proportion data as sex ratio (male proportion) have often non-normally distributed errors. Therefore, we used generalized linear model (GLM) analysis of deviance to those data, assuming Poisson errors and a log link function to the count data, and binomial errors and a logit link function to the proportion data. We assessed the appropriateness of the assumptions of the Poisson or binomial errors by comparing the residual deviance with the residual degrees of freedom after fitting the explanatory variables. Large relative values of the residual deviance indicated over-dispersion, which may result in an overestimation of significance levels, and therefore we replaced Poisson or binomial errors with quasipoisson or quasibinomial ones in the analyses. When more than one explanatory variable was considered, a full model was initially fitted to the data, including explanatory variables and their interactions. Terms were then removed from the full models by stepwise deletion. Whether the removal of a term caused a significant increase in the deviance was assessed with a χ^2 test, and the final models were tested by an *F*-test (Crawley 2007). All of the above analyses were conducted in R2.13.0 (R Development Core Team 2011). In comparisons of the numbers of male and female offspring, we used Wilcoxon test in SPSS 11.5 (SPSS Inc., Chicago, IL, USA).

The values of the degree of infestation (DI) and the success rate of parasitism (SP) among different foundress numbers were calculated and analyzed (Gibert *et al.* 2010, Chabert *et al.* 2012). Numbers of adult *Drosophila* (di) and parasitoids (pi) emerging from each group were counted. The DI measures the proportion of *Drosophila* killed by the parasitoid and was calculated as $(T-di)/T$, with T being the average number of emerging flies in the absence of the parasitoid. The SP measures the probability that an infested host will give rise to an adult parasitoid, and this was calculated as $pi/(T-di)$ (if $pi > (T-di)$, we set $SP = 1$). Data of DI and SP were also analyzed with GLM

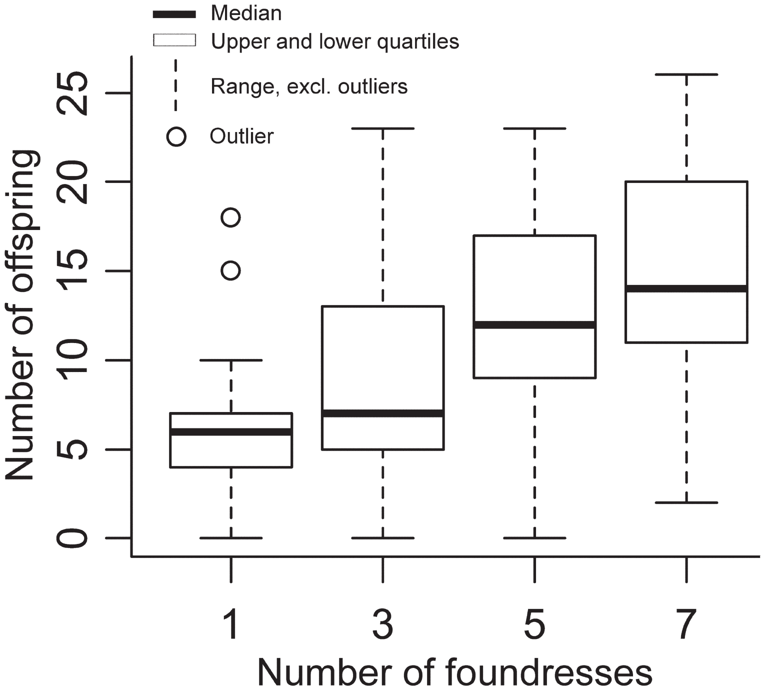

Fig. 1. Offspring numbers of the solitary parasitoid, *Trichopria drosophilae,* in treatments of different numbers of foundresses with the five days of oviposition pooled. Outliers as defined by Crawley (2007).

models assuming binomial errors as described above.

3. Results

The total number of *T. drosophilae* offspring summed across the four treatments and the five oviposition days increased with increasing number of foundresses ($F_{1, 198} = 92.72, p < 0.001$) (Fig. 1). The number of female and male offspring both increased with foundress number on all but the third day (Table 1). When only one foundress oviposited, the mean number of female offspring (3.96 ± 2.08, mean ± SD) was higher than that of male (1.68 ± 1.72) (Wilcoxon test, $z = -5.53$, $p<0.001$, $N = 50$). In contrast, when three foundresses oviposited together, the mean number of male offspring (5.42 ± 4.55) was higher than that of female (3.34 ± 2.71) (Wilcoxon test, $z = -2.12$, $p = 0.034$, $N = 50$). The mean number of female and male offspring was similar in the five-foundress cohort (6.32 ± 3.35 and 6.22 ± 4.00)

Table 1. Mean (SD) number of female and male offspring of *Trichopria drosophilae* on different oviposition days.

Number of foundresses	1st day		2nd day		3rd day		4th day		5th day	
	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂
1	4.80	2.40	4.50	1.30	4.60	3.00	3.00	1.00	2.90	0.70
	(1.93)	(1.90)	(2.01)	(1.06)	(2.27)	(2.36)	(1.89)	(0.82)	(1.79)	(0.95)
3	3.60	11.40	2.50	3.20	2.40	2.90	2.80	3.70	5.40	5.90
	(2.01)	(4.43)	(1.84)	(1.62)	(1.84)	(2.81)	(2.82)	(3.97)	(3.78)	(3.31)
5	7.30	7.80	6.60	5.60	4.70	4.60	4.30	4.80	8.70	8.30
	(2.87)	(4.13)	(2.46)	(4.17)	(3.33)	(3.41)	(2.67)	(3.12)	(3.71)	(4.27)
7	7.50	10.60	9.10	5.80	6.50	7.00	6.20	5.90	7.00	9.00
	(2.76)	(3.75)	(4.18)	(3.16)	(4.22)	(4.69)	(3.39)	(3.38)	(4.22)	(4.03)
$F_{1, 38}$	10.63*	9.59*	18.50*	17.92*	3.31^{NS}	8.83*	8.59*	12.77*	9.36*	25.87*

* = $P < 0.01$
NS = Not significant. The tests are for differences among the classes of foundress numbers.

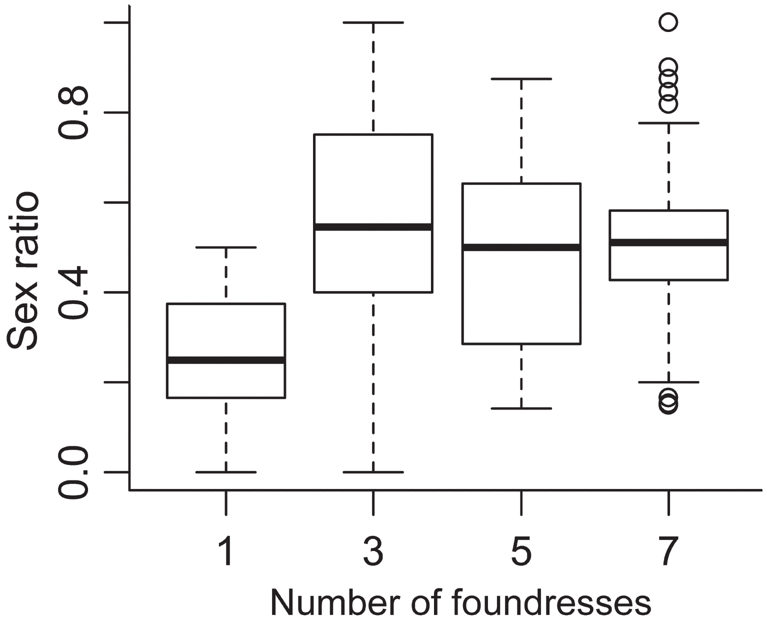

Fig. 2. Proportion of male offspring produced by *Trichopria drosophilae* in treatments of different numbers of foundresses with the five days of oviposition pooled. Boxes as in Fig. 1.

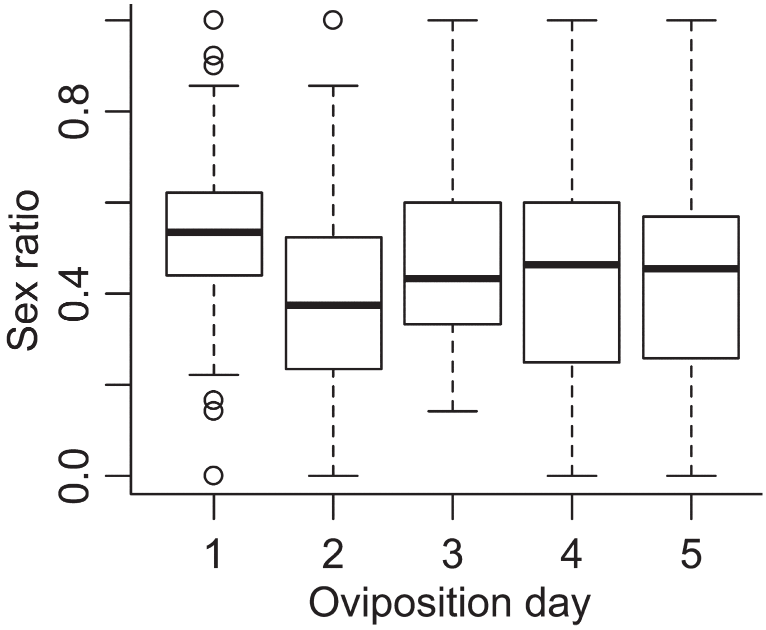

Fig. 3. Proportion of male offspring of *Trichopria drosophilae* on different oviposition days with treatments of different numbers of foundresses pooled. Boxes as in Fig. 1.

(Wilcoxon test, $z = -0.32$, $p = 0.750$, $N = 50$) and in the seven-foundress cohort (7.26 ± 3.78 and 7.66 ± 4.13) (Wilcoxon test, $z = -0.36$, $p = 0.719$, $N = 50$).

Male proportion increased with increasing foundress number (Fig. 2; $F_{1,190} = 4.74$, $p = 0.031$). The final generalized linear model (GLM) did not include the interaction between foundress number and oviposition days, meaning that such sex ratio adjustment of offspring also existed on the different oviposition days. Compared with the proportion in the one-foundress cohort, male proportions in the three-, five- and seven-foundresses cohorts were each significantly higher (GLM, $F_{1,\ 91} = 61.74$, $p < 0.001$; $F_{1,93} = 22.73$, $p < 0.001$; $F_{1,94} = 29.28$, $p < 0.001$; respectively). There was a fe-

Table 2. Mean (SD) degree of infestation (DI) and success rate of parasitism (SP) of *Trichopria drosophilae* on different oviposition days.

Number of foundresses	1st day		2nd day		3rd day		4th day		5th day	
	DI	SP	DI	SP	DI	SP	DI	SP	DI	SP
1	0.56 (0.09)	0.52 (0.19)	0.51 (0.16)	0.48 (0.20)	0.56 (0.14)	0.54 (0.29)	0.42 (0.14)	0.41 (0.28)	0.45 (0.18)	0.33 (0.23)
3	0.63 (0.15)	0.95 (0.10)	0.35 (0.22)	0.73 (0.31)	0.33 (0.15)	0.70 (0.32)	0.28 (0.21)	0.80 (0.33)	0.47 (0.22)	0.90 (0.17)
5	0.82 (0.13)	0.75 (0.18)	0.59 (0.18)	0.80 (0.21)	0.50 (0.18)	0.73 (0.31)	0.41 (0.13)	0.88 (0.13)	0.68 (0.20)	0.96 (0.07)
7	0.79 (0.13)	0.89 (0.20)	0.65 (0.16)	0.90 (0.17)	0.67 (0.13)	0.78 (0.23)	0.54 (0.22)	0.92 (0.12)	0.68 (0.22)	0.88 (0.14)

male-biased sex ratio when only one foundress oviposited (one sample t-test, $t_{45} = -10.18$, $p<0.001$), but a male-biased sex ratio when three foundresses oviposited (one sample t-test, $t_{46} = 2.20$, $p = 0.033$). Sex ratio was not significantly different from 50% with five or seven foundresses (one sample t-test, $t_{48} = -0.63, p = 0.534$; $t_{49} = 0.53$, $p = 0.603$, respectively).

Male proportion across all the foundress-number treatments differed among the five oviposition bouts (Fig. 3). Compared to the proportion on the first oviposition day, the proportion of male offspring on the 2nd day was significantly lower ($F_{1,\,77} = 13.30$, $p<0.001$), but similar with that on the 3rd, 4th, and 5th day ($F_{1,\,76} = 3.65$, $p = 0.060$; $F_{1,\,74} = 3.74$, $p = 0.057$; $F_{1,\,77} = 3.44$, $p = 0.071$; respectively). More males were laid on the first oviposition day.

Trichopria drosophilae foundresses increased the degree of infestation (DI) with increasing number of foundresses ($F_{1,\,198} = 28.91$, $p < 0.001$) (Table 2). Less adult flies emerged with increasing number of foundresses. The means of DI lowered with the progress of the oviposition days ($F_{1,\,197} = 14.14, p < 0.001$). The final GLM model showed that only foundress number affected significantly the success rate of parasitism (SP) ($F_{1,\,198} = 5.47, p = 0.019$). The means of SP were higher when more foundresses oviposited.

4. Discussion

Partial LMC has been observed in many parasitoids, e.g. *Pachycrepoideus vindemmiae* (Rondani) (Pteromalidae) (Nadel & Luck 1992, Li *et al.* 2014), *Leptopilina heterotoma* (Thompson) (Eucoilidae) (Debout *et al.* 2002), and *Trichogramma euproctidis* (Girault) (Trichogrammatidae) (Martel *et al.* 2010). Males' ability to mate in an off-natal patch has also been studied (Nadel & Luck 1992, Martel *et al.* 2010). For example, males of *T. euproctidis* disperse, and the overall off-patch mating proportion reaches 40.5% (Martel *et al.* 2010). Wings of *T. drosophilae* males are almost as long as those of females (Romani *et al.* 2008), suggesting that off-patch mating is likely. Our results showed that this solitary pupal parasitoid shifted its offspring sex ratio with different numbers of foundresses when ovipositing in a patch. A female-biased sex ratio was produced by lone *T. drosophilae* females, but offspring number of both sexes tended to be equal with the increasing number of foundresses. The sex ratio adjustment of *T. drosophilae* is consistent with the partial LMC models.

Sex ratio theories attract attention in evolutionary biology in explaining adaptation, but also as bases of methods to obtain a highly female-biased mass of parasitoids for the purposes of pest control. As mentioned above, *T. drosophilae* is a preferable candidate for the biological control of the invasive spotted wing drosophila, *D. suzukii*. Rearing and releasing of this parasitoid in fields may be important in controlling *D. suzukii* (Mazzetto *et al.* 2016) and then a female-biased sex ratio would be useful. Our results suggest that reducing crowding of foundresses and avoidance of their interaction would increase the efficiency of *T. drosophilae* as a biological control agent. On the other hand, degree of infestation (DI) and success rate of parasitism (SP) decreased when fewer foundresses oviposited, meaning less efficient host utilization.

Trichopria drosophilae produced a greater proportion of sons on the first day of oviposition than on the second to fifth day. This may result from a male-first strategy (Bayram *et al.* 2004, Hu *et al.* 2012); that is, in some species, male offspring tend to be produced at the start of oviposition bouts, followed by mostly females, as seen for some pollinating fig wasps (Kjellberg *et al.* 2005, Moore *et al.* 2005, Raja *et al.* 2008, Hu *et al.* 2013). An egg parasitoid wasp, *Telenomus busseolae* Gahan (Scelionidae), also has a higher proportion of females with increasing egg mass size (Bayram *et al.* 2004). As LMC models predict, a female-biased sex ratio would conform to the interests of a single parasitoid. Such a parasitoid should produce the minimum number of males required to inseminate all her daughters. Laying more male offspring at the beginning of oviposition may result in males that have emerged and are ready to mate by the time that females emerge.

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