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ORIGINAL PAPER

Local mate competition in the solitary parasitoid wasp *Ooencyrtus kuvanae*

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Abstract Local mate competition (LMC) occurs when brothers compete with each other for mating opportunities, resulting in selection for a female-biased sex ratio within local groups. If multiple females oviposit in the same patch, their sons compete for mating opportunities with non-brothers. Females, in the presence of other females, should thus produce relatively more sons. Sex ratio theory also predicts a more female-biased sex ratio when ovipositing females are genetically related, and sex-ratio responses to foundress size if it differentially affects fitness gains from sons versus daughters. The mating system of the parasitoid wasp *Ooencyrtus kuvanae* meets assumptions of LMC. Females insert a single egg into each accessible egg of gypsy moth, *Lymantria dispar,* host egg masses. Wasps complete development inside host eggs and emerge en masse, as sexually mature adults, resulting in intense competition among brothers. We tested the hypothesis that *O. kuvanae* exhibits LMC by manipulating the number of wasp foundresses on egg masses with identical numbers of eggs. As predicted by LMC theory, with increasing numbers of wasp foundresses on an egg mass, the proportions of emerging sons increased. In contrast, the presence of a sibling compared to a non-sibling female during oviposition, or the size of a female, did not affect the number or sex ratio of offspring produced. The *O. kuvanae* system differs from others in that larvae do not compete for local resources and thus do not distort the sex ratio in favor of sons. With no resource competition among *O. kuvanae* larvae, the sex ratio of emergent son and daughter wasps is due entirely to the sex allocation by ovipositing wasp foundresses on host egg masses.

Keywords Local mate competition · *Ooencyrtus kuvanae* · Solitary egg parasitoid · Sex ratio · Local resource competition

Introduction

Fitness consequences associated with controlling the sex ratio of offspring have been considered since Darwin (1871). In randomly mating populations, the evolutionary stable strategy is to invest equally in sons and daughters (Fisher 1930). By contrast, in spatially structured populations with mating or competition among siblings, a strongly biased sex ratio can be selected for (Hamilton 1967).

Local mate competition (LMC) contributes to a female-biased sex ratio (Hamilton 1967). In species exhibiting LMC, brothers remain in their natal patch and compete with each other for mating access to females. In this context, a mother will maximize her fitness by producing relatively few sons so as to limit competition among them, resulting in a daughter-biased sex ratio (Taylor 1981). Inbreeding also affects sex ratio in a way independent of LMC. In haplodipoids, inbreeding causes mothers to share more genes with their daughters than with their sons, favoring the production of daughters

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(Boomsma and Grafen 1991). This prediction has been supported by a study of fig wasps (Herre 1985), revealing that in those species, where female wasps are more likely to mate with a relative, they adjust the sex ratio of their offspring towards daughters.

Many species exhibiting female-biased sex ratios are Hymenoptera with a haplodiploid sex-determination system, enabling females to control the sex of their offspring. By fertilizing an egg, females produce a daughter, and by not fertilizing it, they produce a son. Haploid sons derive their entire genome from their mother, whereas daughters are diploid and receive genes from both parents. This simple mechanism of controlling the sex ratio of offspring has facilitated studies that investigated how females adaptively adjust sex ratio based on various factors, including clutch size, number of foundresses, and host quality (Hardy et al. 1992; Kjellberg et al. 2005; Pereira and Prado 2006). Studies of sex ratio adjustment by parasitoid wasps have revealed some of the most conclusive examples of adaptive behavior in animals (Godfray 1994).

Sex ratio theory predicts that if multiple females oviposit in the same patch, their sons will compete for mating opportunities not only among themselves but also among non-siblings. This makes it adaptive for females to produce relatively more sons in the presence of another ovipositing mated female. As the number of ovipositing females (n) in a patch increases, the optimal sex ratio (r % males) should increase according to the equation $r=(n-1)/2n$ (Hamilton 1967). This equation predicts a daughter-biased sex ratio for low numbers of foundresses, with increasing proportions of sons, as the number of foundresses in a patch increases, reaching an asymptote at a 1:1 sex ratio. Hamilton's (1967) original equation was later modified to incorporate effects of haplodiploidy $[r=(n-1)(2n-1)/n(4n-1)]$ (Hamilton 1979; Taylor and Bulmer 1980). For some parasitoid wasp species, notably *Nasonia vitripennis* (Werren 1983; King and Skinner 1991b), experimental manipulations of foundress numbers have confirmed predictions from theory regarding LMC.

Several additional selective forces are also predicted to affect optimal sex ratios. First, sex ratio theory predicts that if females can recognize sisters ovipositing on the same patch, they should produce a lower proportion of sons (Frank 1985; Taylor and Crespi 1994; Shuker et al. 2004a). Of five species tested to date for sex ratio adjustment in response to breeding with kin versus non-kin, none has demonstrated such abilities (Shuker et al. 2004a), for reasons that remain unclear.

Second, competition for host resources among developing larvae may also alter sex ratio. When several female *N. vitripennis* lay eggs in the same host, larval sons and daughters engage in local resource competition (LRC), often causing greater mortality of daughters (Godfray 1994; Santolamazza-Carbone and Rivera 2003; Suzuki et al. 1984). The effect of LRC among larvae is one of the most important confounding factors in experimental studies of LMC (Godfray 1994).

Third, the size of a female parasitoid may affect her clutch size and the sex ratio of her offspring. Larger females tend to hold more eggs and produce larger clutch sizes than smaller females (Visser 1994; Sagarra et al. 2001; Santolamazza-Carbone et al. 2007); larger clutch sizes engender a higher proportion of daughters in fig wasps (Kjellberg et al. 2005), apparently due to stronger effects from LMC. Similarly, smaller *N. vitripennis* foundresses, which contribute a relatively low proportion of offspring to a patch, produce proportionally more sons, because their sons are not likely to compete among themselves for mates and thus they are less affected by LMC (Werren 1980).

With the sex ratio of haplodiploid wasps affected by inbreeding, LMC, LRC, foundress relatedness, and/or the size of females, we have searched for a study organism that would allow us to isolate the effect of each one of these factors. The solitary parasitoid wasp *Ooencyrtus kuvanae* appeared to be a useful model organism for such studies. This 2-mm long haplodiploid egg parasitoid wasp oviposits singly into eggs of its host (gypsy moth, *Lymantria dispar*), which are found in large, discrete patches. A gypsy moth egg mass measures 2–3 cm across and contains several hundred eggs. Those in the uppermost layer (15–20%) are parasitized by one to multiple female wasps that each inserts a single egg into each accessible host egg. A second egg that is inserted into a parasitized host egg is not likely to develop; superparasitism is uncommon and invariably yields smaller-than-normal offspring (Hofstetter 1996). Within 4 weeks, son and daughter wasps complete development inside the host eggs and emerge en masse as sexually mature adults, females slightly later and about twice as numerous as males (Brown 1984), resulting in intense competition among males (Ablard et al., unpubl. data). There is no LRC among *O. kuvanae* larvae because a single larva completes development to a sexually mature adult wasp within each host egg (Hofstetter 1996). Moreover, the number, size, and relatedness of females on a gypsy moth egg mass can readily be experimentally controlled.

Working with *O. kuvanae* females, our objectives were to test whether: (1) increasing numbers of wasp foundresses on a gypsy moth egg mass produce proportionately more sons, as predicted by LMC (Hamilton 1967); (2) two sibling foundresses produce relatively fewer sons than the two non-sibling foundresses; and (3) the size of a single female affects her absolute clutch size and/or the sex ratio of her offspring.

Materials and methods

Study insects

In July 2009 and May 2010, we collected gypsy moth egg masses parasitized by *O. kuvanae* from central Pennsylvania and from Maryland (USA), respectively. These field sites were ~266 km apart and consisted of *Quercus* hardwood forests lightly populated with *L. dispar*. The resulting laboratory populations A and B each originated from ~10 egg masses. Populations were kept in the Global Forest Quarantine Facility at Simon Fraser University. They were reared under a 16-L: 8D photoperiod at 22–25°C and 50–70% RH (Hoffstetter and Raffa 1998). Females of each population were provided with gypsy moth eggs supplied by the US Forest Service (Hamden, Connecticut, U.S.A.). Fourteen days later, 120 parasitized eggs from each population were isolated. Emergent wasps were provisioned with a honey–water-imbued cotton wick (1×1.3 cm), identified by sex based on the translucent antennae of males and opaque antennae of females (Brown 1984), and allowed to mate with a wasp from the same polulation. All matings were observed under a Petri dish lid (30 mm diameter). Mated females were immediately separated and introduced to ca. 65 gypsy moth eggs. Each parasitized egg was then transferred to, and kept in a separate translucent Solo plastic cup (104 ml) until the adult wasps emerged and could be used in experiments.

General protocols

Within 3 days of emergence, virgin females were paired with a non-sibling male from the same population under a Petri-dish (30 mm diameter) where mating was observed. Mated females were assigned to specific treatment groups (see experiments 1–3), placed in a glass jar with 100 gypsy moth eggs, and allowed 14 days to parasitize them, after which they were removed, and offspring were allowed to emerge. Every day for 14 days, each jar was checked to ensure parent females were alive, and every 3 days, the honey-imbued cotton wick (1×1.3 cm), which sustained the female(s) was replaced. Jars (7%) that contained a dead parent female were excluded from data analyses. In total, 96% of females survived for the duration of the experiments, and all females assigned a ‘large’ or ‘small’ body size in experiment 3 remained alive for the duration of that experiment. After 14 days, parent females were removed, and emergent sons and daughters were counted. To ensure all offspring were accounted for, eggs were kept for an additional 4 weeks after the parent females had been removed.

Experimental methods

Experiment 1: Effect of number of foundresses on sex ratio and number of offspring

Mated females were assigned to one of five treatment groups: (1) 1 female (n=5); (2) 2 females (n=6); (3) 3 females (n=5); (4) 4 females (n=5); and (5) 10 females (n=5). In each replicate, the treatment group was then placed in a glass jar with 100 gypsy moth eggs and allowed 14 days to parasitize them. Emergent offspring in each jar were counted and identified by sex.

Experiment 2: Effect of presence of a sibling or non-sibling female on sex ratio and number of offspring

Mated females were divided into three groups; (1) single female (n=11) [A=6, B=5], (2) two female siblings (n=10) [A=6, B=4], and (3) two female non-siblings (n=10) [A=4, B=6]. Each group of females was then placed in a glass jar with 100 gypsy moth eggs and allowed 14 days to parasitize them. Emergent offspring in each jar were counted and identified by sex.

Experiment 3: Effect of female size on number and sex ratio of her offspring

Within 3 days of emergence, virgin females were classed as ‘small’ (n=10) or ‘large’ (n=9). Each mated female was then placed into a glass jar with 100 gypsy moth eggs and allowed 14 days to parasitize them, after which she was removed. Emergent offspring in each jar were counted and identified by sex. Post mortem, the head width and left hind tibia length of the parent female were measured under a microscope using a micrometer (Joyce et al. 2009).

Statistical analyses

In experiment 1, the statistical relationship between the number of foundresses in a patch and the proportion of sons emerging from it was analyzed by the Pearson's correlation coefficient. To test the proportion of males recorded in our study versus the proportion predicted by Hamilton's theory, a generalized linear mixed model (GLMM) and an omnibus test were applied. The GLMM tested the estimated probability of the proportion of sons (logit scale) in each foundress class compared to the predicted probability, assuming that the actual numbers of sons recorded followed a binomial distribution and incorporating overdispersion among the replicate trials within each foundress class. The omnibus test then determined whether all five mean proportions matched with the predicted proportions. Total numbers of offspring per foundress class were analyzed by One-way ANOVA followed by Tukey's HSD test. The mean per foundress number of offspring among foundress classes was analyzed by One-way ANOVA.

In experiment 2, proportion of sons and the total number of offspring by females in the presence of a sibling or non-sibling were analyzed by One-way ANOVA, followed by Tukey's HSD test. In experiment 3, sizes of ‘large’ and ‘small’ females were compared by a two-sample *t*-test. SPSS version 18.0 was used for all data analyses. The confidence interval for all tests was set at 95%.

Results

In experiment 1, with increasing numbers of foundresses in a patch, the proportion of sons emerging from it significantly increased [Pearson's correlation $r=0.650$, $n=26$, $P<0.0001$] (Fig. 1, top). For each foundress class, and for all classes combined, there was a significantly greater mean proportion of sons recorded than predicted by Hamilton's theory [$F_{5,21}=12.55$, $P<0.001$] (Table 1). Both the mean total number and the mean per foundress number of offspring varied significantly among foundress classes [$F_{4,21}=6.733$, $P=0.001$; $F_{4,21}=108.218$, $P<0.0001$] (Fig. 1, bottom).

In experiment 2, there was a significant difference in the proportion of sons between treatments [$F_{2,28}=3.135$, $P=0.05$]. Single females produced a significantly lower proportion of sons than females paired with a sibling foundress ($P=0.013$) or a non-sibling foundress ($P=0.002$) (Fig. 2, top). The proportion of sons produced by paired sibling and non-sibling females did not significantly differ [$F_{1,18}=0.744$, $P=0.400$]. There was also no significant difference in the number of total offspring produced by single or paired sibling or non-sibling females [$F_{2,28}=0.890$, $P=0.422$](Fig. 2, bottom) and by paired sibling and non-sibling females [$F_{1,18}=0.806$, $P=0.381$].

In experiment 3, pre-mated females that were assigned to groups considered ‘large’ or ‘small’ in body size, and that were measured post-oviposition and post mortem, significantly differed in body size [df=18, $t=0.6990$, $P=<0.001$] (Fig. 3, top). There were no significant differences in the proportion of sons [$F_{1,18}=2.623$, $P=0.123$] (Fig. 3, middle) and in the total number of offspring [$F_{1,18}=0.003$, $P=0.958$) (Fig. 3, bottom) produced by large or small females.

Discussion

Our findings that two female *O. kuvanae* foundresses on a gypsy moth egg mass produce a higher proportion of sons

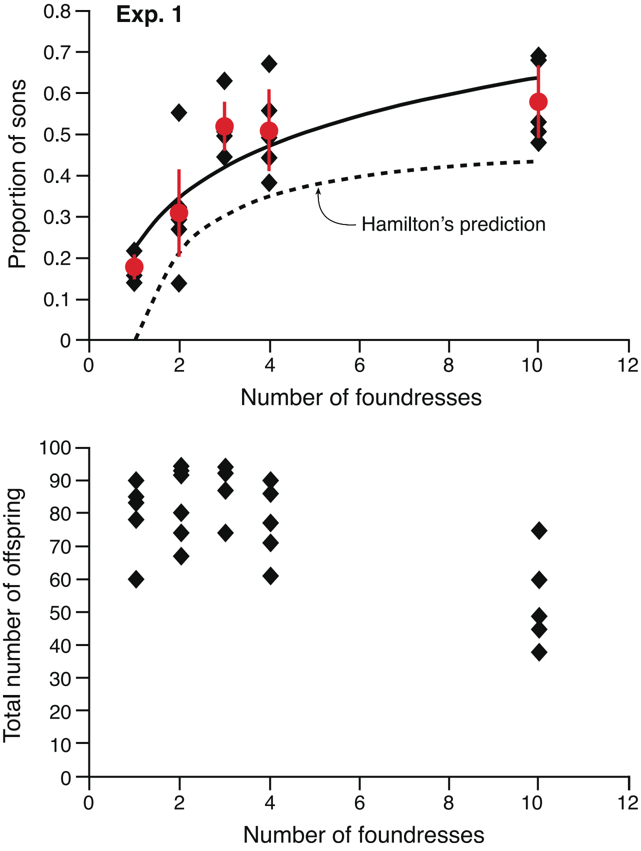

Fig. 1 Correlation between the number of female *Ooencyrtus kuvanae* foundresses on a gypsy moth egg mass and the proportion of sons (*top*; Pearson's $r=0.650$, $n=26$, $P<0.001$) and the total number of offspring (*bottom*) produced. The confidence intervals for the mean proportion of sons are depicted in *red*. Hamilton's (1979) theoretical prediction is drawn for comparison. For each foundress class, and for all classes combined, there was a greater mean proportion of sons recorded in our study than predicted by Hamilton's theory [$F_{5,21}=12.55$, $P<0.0001$] (Table 1). The mean total number of offspring of ten foundresses was significantly smaller than that of any other number of foundresses; One-way ANOVA followed by Tukey's HSD test, $P<0.05$

Table 1 Statistical analyses of the mean proportions of sons recorded in our study and predicted by Hamilton's theory for each foundress class and for all five classes combined

Number of foundresses	Recorded [sons]	Predicted [sons]	GLMM: *P* (SE)
1	0.18	0.10	0.0044 (0.2083)
2	0.31	0.21	0.0086 (0.1771)
3	0.52	0.30	<0.0001 (0.1874)
4	0.51	0.35	0.0028 (0.1913)
10	0.58	0.44	0.011 (0.2049)
Omnibus test:			<0.0001

[*sons*] Proportion of sons; *Predicted* Proportion of sons predicted by Hamilton's model; *GLMM* Generalized linear mixed model

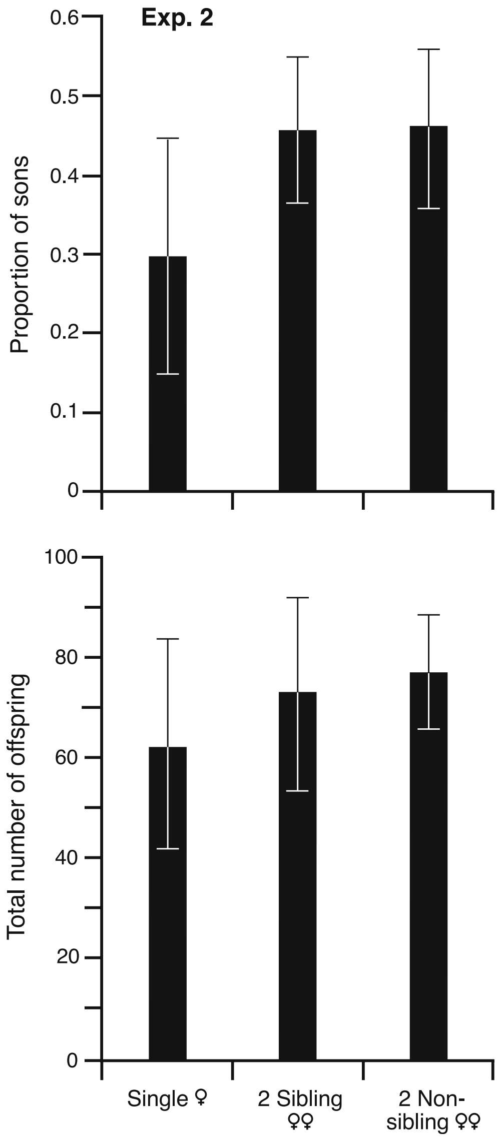

Fig. 2 Proportion of sons (*top*) and the total number of offspring (*bottom*) produced by females of the parasitoid wasp *Ooencyrtus kuvanae* when they oviposited singly ($n=11$) or in the presence of a sibling foundress ($n=10$) or a non-sibling foundress ($n=10$). The proportion of sons was significantly lower for single females but was nearly identical between sibling and non-sibling pairs; One-way ANOVA followed by Tukey's HSD test, $P<0.05$. There was no difference in the total number of offspring produced by females of all treatment groups; One-way ANOVA, $P>0.05$

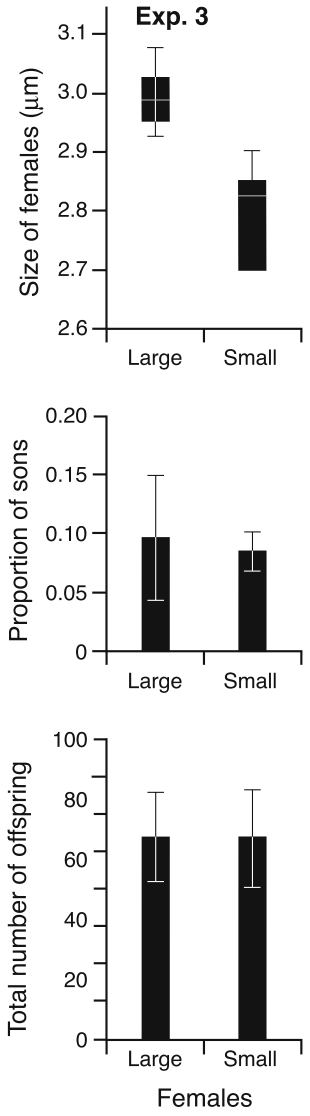

Fig. 3 (*top*) Size (presented as mean between head width and hind tibia length) of female *Ooencyrtus kuvanae* classed as ‘large’ ($n=9$) or ‘small’ ($n=10$) prior to the experiment and in post mortem measurements; (*middle* and *bottom*) proportion of sons and the total number of offspring produced by large or small females ($n=10$ each) of *O. kuvanae*. The size of large and small females differed significantly (indepent sample *t*-test, $P<0.05$), but the total number and proportion of sons did not (One-way ANOVA, $P>0.05$)

than a single female (Fig. 2, top), and that the proportion of sons increases with increasing numbers of foundresses present on the egg mass (Fig. 1, top), fit with the pattern of sex ratio adjustment predicted by Hamilton (1967), and suggest that *O. kuvanae* exhibits sex ratio effects from LMC. Similar proportions of sons produced by females ovipositing in the presence of a sibling or a non-sibling female (Fig. 2, top), indicate that females either do not recognize, or do not respond to the presence of kin. Finally, similar numbers of offspring and proportions of sons produced by small or large females that oviposit in isolation (Fig. 3) indicate that the size of a female does not affect her absolute reproductive output and the sex ratio of her offspring.

While our data are in general agreement with the LMC theory, the proportion of sons in our study exceeded that predicted by Hamilton's (1967) theory. This deviation could not be attributed to competition among larvae, or the size or relatedness of female foundresses. Instead, the higher than predicted proportion of sons indicates that there may be some deviation from the strict assumptions of the LMC theory, and that some sons may disperse and mate away from their natal patch with non-sibling females. This hypothesis is supported by observations that host egg masses can be within centimeters of each other, particularly during *L. dispar* population outbreaks (PWS and GG, personal observations). Close proximity of host egg masses and dispersal of sons would decrease LMC on an egg mass and select for foundresses to produce a higher proportion of sons than predicted by Hamilton's model, which assumes complete male philopatry (Debout et al. 2002; West and Herre 1998).

Equal clutch size laid by foundresses, and simultaneous oviposition, are additional assumptions implicit in Hamilton's original model (Hamilton 1967). We could not follow focal individuals and control for potential differences in clutch size, or the order in which foundresses sampled the patch and oviposited. These factors could have modulated the sex ratio of offspring, as previously shown in *N. vitripennis* (Shuker et al. 2006), but they would not be expected to generate the direction of deviations from theory that we observed.

The effect of larval LRC on sex ratio has been an important complicating factor in previous studies on LMC (Godfray 1994; King and Skinner 1991a; Werren 1983). While (asymmetrical) larval competition in *N. vitripennis* was predicted to have a minimal effect on LMC (Sykes et al. 2007), we provide the first experimental evidence for LMC in a system entirely decoupled from LRC among larvae.

A suite of studies has demonstrated that female parasitoids adjust the sex ratio of their offspring in relation to foundress number (Werren 1983; Frank 1985; Burton-Chellew et al. 2008; King 1987; King and Skinner 1991a, b) but the mechanisms mediating such adjustments are little understood. Female *N. vitripennis* apparently adjust the sex ratio of their offspring not only in response to the presence of another female but also in response to her size, possibly as a proxy for fecundity (Flanagan et al. 1998). In other parasitoid wasps with potentially multiple foundresses on a patch, each foundress laid proportionally fewer eggs than she would on her own, and thus more male eggs are laid first (Green et al. 1982; Griffiths and Godfray 1988), resulting in a higher proportion of sons (Debout et al. 2002; Kjellberg et al. 2005; Raja et al. 2008; van Welzen and Waage 1987). Our study shows that the number of offspring per foundress decreases with an increasing number of co-foundresses, as also found by Hoffstetter and Raffa (1998). In these studies, the question remains whether females adjusted the sex ratio in response to other females on a patch or simply as a result of laying fewer and thus more male eggs. As the *O. kuvanae* reproductive system exhibits LMC without larval LRC, it is well suited for testing mechanisms of adaptive sex ratio adjustment.

The size of female *O. kuvanae* affected neither the clutch size nor the proportion of sons (Fig. 3). These results contrast those of other studies showing that large female parasitoids produce larger clutch sizes and relatively more daughters than do small female parasitoids (Hardy et al. 1992; Kjellberg et al. 2005; Sagarra et al. 2001). The effect of female size on reproductive output may vary between species and may depend upon their reproductive strategy or life history traits; for example, wasp size may be constrained by host egg size in egg parasitoids such as *O. kuvanae*. Within the context of LMC, the size of a female may also affect the sex ratio of her offspring. A foundress may compare her size to that of others and adjust the number and sex ratio of her offspring accordingly (Flanagan et al. 1998). Whether this also applies to *O. kuvanae* cannot be inferred from our data. In experiment 1, the multiple females present on the same gypsy moth egg mass were similar in size, and in experiment 3 large and small females oviposited in isolation.

The relatedness of ovipositing *O. kuvanae* foundresses did not affect the number or sex ratio of their offspring (Fig. 2). These results parallel those of experimental studies, and meta-analysis, of parasitoid wasps, ants, fig wasps, and spider mites which show that species exhibiting LMC fail to recognize, or respond to, foundress kin (Shuker et al. 2004a, b). This conclusion, however, does not apply to the thrips *H. pedicularius* which adjusts sex ratio in accordance with whether or not a female has dispersed (and breeds with non-relatives), as opposed to breeding with relatives in her natal colony (Taylor and Crespi 1994); this form of sex ratio adaptation thus need not involve kin recognition per se. More generally, the apparent lack of foundress kin recognition in *O. kuvanae*, and in other species (Shuker et al. 2004a, b), may be due to some combination of a lack of suitable kin-recognition cues, a general absence of interactions between related females after dispersal, or weak selection compared to other factors (Shuker et al. 2004a). These possible interpretations would need to be addressed in further studies.

In conclusion, the *O. kuvanae* mating system allowed us to isolate and study the effect of various factors that engender changes in the sex ratio of offspring. It differs from others in that larvae do not compete for local resources, and thus, do not distort the sex ratio in favor of sons. With no resource competition among larvae, the sex ratio of emergent son and daughter wasps is due entirely to the sex allocation by ovipositing wasp foundresses on host egg masses. With increasing numbers of wasp foundresses, the proportions of emerging sons increased as predicted by the LMC theory (Hamilton 1967).

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