

Female palm-seed borer beetles adjust their sex ratio according to relatedness of female neighbours

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ABSTRACT

Question: Can the sex ratio of the palm-seed borer beetle, *Coccotrypes dactyliperda* (Fabricius), be described by local mate competition? Does relatedness among neighbouring foundresses affect their offspring sex ratio in the context of local mate competition?

Hypothesis: According to Hamilton's local mate competition hypothesis, the optimal sex ratio (proportion of males out of the total clutch) should increase as the number of foundresses increases. We predict that when multiple foundresses can assess their relatedness, relatedness among foundresses will decrease the sex ratio.

Methods: We measured the effect of number of foundresses and relatedness among foundresses on offspring sex ratio in seven populations of *C. dactyliperda* in Israel.

Results: In line with local mate competition theory, offspring of related foundresses had a lower sex ratio than offspring of unrelated foundresses and the sex ratio among offspring of a single foundress was lower than that of several unrelated foundresses. However, when the multiple foundresses were related, the offspring sex ratio of one and of several foundresses did not differ. This result may be explained by a high expectation of the related females that their sons will encounter only related males.

Keywords: haplodiploid, local mate competition, sex allocation, sex ratio.

INTRODUCTION

Maternal sex allocation is a major component of the reproductive strategies of all sexual plants and animals (Godfray and Werren, 1996). Since Fisher (1958) predicted the predominance of an even sex allocation in panmictic populations with random matings, sex ratio studies have become one of the most productive research areas in evolutionary biology (Charnov, 1982; Leigh

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et al., 1985). Hamilton (1967) predicted that when offspring of one or a few mothers mate in their natal patch, a female-biased sex ratio is favoured. Hamilton suggested that local mate competition (LMC), i.e. competition for mates in a patch, among related male offspring, will become more severe as the average relatedness between foundresses increases, causing a selective response towards a more female-biased sex ratio (Hamilton, 1979; Frank, 1985; Herre, 1985). However, when the number of foundresses increases, the competition among unrelated males will escalate and selection will favour females that produce more male offspring (Hamilton, 1979; Frank, 1985; Herre, 1985). The basic LMC hypothesis, tested with parasitic insects, mites, and various other arthropods, confirmed that as the number of foundresses increases, the proportion of male offspring also increases, and the sex ratio becomes less female biased (Werren, 1987; Godfray, 1994; Herre *et al.*, 1997).

Based on Hamilton's (1967) LMC hypothesis, later models predicted that sex allocation bias will vary according to the relatedness among foundresses and assumed that foundresses can assess the level of their relatedness to other foundresses in the patch (Frank, 1986, 1987). While theoretical predictions of the effect of relatedness on local mate competition are straightforward, empirical tests are few. For example, Roeder *et al.* (1996) showed a significant effect of female relatedness on offspring sex ratio; their results, however, could be explained by factors other than female relatedness, such as differences in sex ratio between lines and high inbreeding levels in one line (Shuker *et al.*, 2004). A meta-analysis carried out on the sex ratio pattern of offspring in a patch (Shuker *et al.*, 2004) revealed that most studies do not support the effect of foundress relatedness on the offspring sex ratio. As an explanation, Shuker *et al.* (2004) suggested that females may cheat in signals of relatedness, thus leading to a reduction in the number of sons of competing females in a patch. Under this scenario, relatedness among foundresses is not expected to affect offspring sex ratio. Nevertheless, one would expect the evolution of reliable differentiation between related and non-related individuals when recognition of relatedness may lead to increased fitness through inbreeding avoidance. It is thus imperative to test the effect of relatedness among neighbouring foundresses in the context of local mate competition.

Two features in the biology of the palm-seed borer beetle, *Coccotrypes dactyliperda* (Coleoptera: Scolytidae), coincide with the basic life cycle underlying Hamilton's (1967) LMC hypothesis, making this species ideally suited to test theories of local mate competition. First, mated females of variable group sizes are confined inside a seed of a palm tree, and second, daughters disperse after mating inside the seed (Herfs, 1950). In addition, female *C. dactyliperda* have the ability to distinguish between individuals originating from their own and different populations (Gottlieb *et al.*, 2009). These characteristics encouraged us to test the effects of relatedness among foundresses on offspring sex ratio in *C. dactyliperda*. Based on the LMC hypothesis, we predicted that related foundresses would produce a lower offspring sex ratio than non-related foundresses.

METHODS

Study organism

The palm-seed borer beetle, *Coccotrypes dactyliperda* (Fabricius), develops in seeds of date palm, *Phoenix dactylifera*, and other palm species. Colonization usually takes place by a single female, but in high beetle densities several females (i.e. foundresses) may colonize a single seed (Herfs, 1950; Bar-Shalom and Mendel, 2003). In natural conditions, ovipositing

C. dactyliperda females may experience varying numbers of conspecific foundresses in a seed (D. Gottlieb, unpublished data), which can be from the same or different populations (Gottlieb *et al.*, 2009). Before entering the seed, females walk on it and examine it (D. Gottlieb and A.R. Harari, personal observations), potentially assessing the presence of entrance holes of other foundresses.

The foundresses excavate brood chambers where both foundresses and emerged offspring feed. Galleries excavated in the seed by different foundresses and their offspring eventually merge and all individuals within a seed can interact. *Coccotrypes dactyliperda* is a haplodiploid species (Normark *et al.*, 1999), thus offspring sex ratio can be determined by whether females fertilize the eggs (producing diploid females or haploid males). Mature offspring usually mate in the seed, defined in this study as a patch. Following mating, most ovipositions occur in a new seed and more rarely females oviposit in the natal seed (where oviposition can occur over several generations), while males generally remain in the natal seed (Sitkov-Sharon, 2010).

Natural populations of *C. dactyliperda* beetles exhibit inbreeding levels higher than expected from random mating (Hardy-Weinberg equilibrium), low estimated migration rate ($N_m = 0.869$ per generation), and high inbreeding coefficients (Gottlieb *et al.*, 2009). These characteristics indicate that relatedness is higher within a population than between populations (Gottlieb *et al.*, 2009; Holzman *et al.*, 2009).

We measured the effect of relatedness among foundresses on offspring sex ratio in seven populations of *C. dactyliperda* in Israel, collected from Haon (On), Ashdot Ya'akov (Ash), Nir David (ND), Beit Dagan (BD), Chatsor (Ch), Ein Habsor (Be), and Sede Boker (SB) (Fig. 1).

Experiments and observations

In a previous study, we demonstrated that *C. dactyliperda* females can distinguish between individuals originating from the same or a different population, i.e. related and unrelated individuals (Gottlieb *et al.*, 2009). This allowed us to study the maternal sex allocation when females encounter related or unrelated additional foundresses in the seed.

Females from the above populations were brought to the laboratory, reared individually in a small Petri dish (6×1 cm), with a seed for oviposition, at $25 \pm 0.5^\circ\text{C}$ and a controlled light/dark cycle of 14:10 h. A month later, when females (future foundresses) were expected to be mated with their brothers within the natal seed, the seed was opened and from each clutch one adult female offspring was randomly taken. The foundresses were randomly allocated to one of three treatments:

1. *Control*: One female was placed alone in a Petri dish (sample size, N : On = 46, Ash = 48, ND = 12, BD = 106, Ch = 32, Be = 8, and SB = 46).
2. *Related females*: Groups of three ($N = 33$) or seven ($N = 38$) females originating from the BD population were placed in a Petri dish.
3. *Unrelated females*: Groups of three ($N = 83$) or seven females ($N = 34$), each female representing one of the seven populations, were placed in a Petri dish.

In all treatments, a single seed was placed in each Petri dish. When three females were placed with a seed, various combinations of populations were formed involving females from all populations. Treatment 1 served as a control for differences in mortality rates and sex ratios

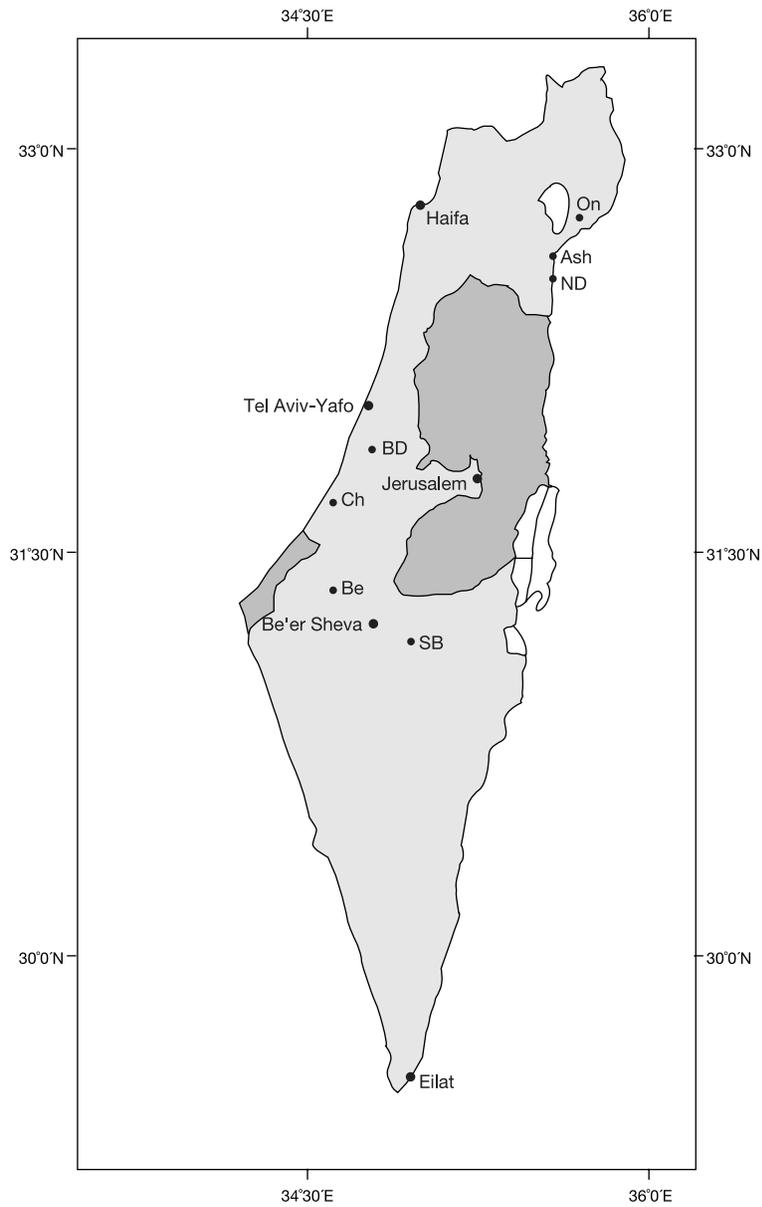


Fig. 1. Locations of *C. dactyliperda* populations that were sampled in the study: On = Haon, Ash = Ashdot Ya'akov, ND = Nir David, BD = Beit Dagan, Ch = Chatsor, Be = Ein Habsor, SB = Sede Boker.

among the tested populations. In all treatments, the females received a fresh seed as food and oviposition site. After one month, when full development of offspring from egg to adult was expected, we cut open the seeds and checked for offspring number and sex ratio.

Statistical analysis

For the analyses, the unit of replication was a seed. We defined sex ratio as the proportion of male offspring out of the total clutch size. When galleries in a seed are merged, it is impossible to tell apart siblings from non-siblings, therefore sex ratios and number of offspring were calculated for the combined broods of all three or seven foundresses, accordingly.

Offspring number was tested using nested analysis of variance (ANOVA), with the different origins of foundresses nested within the number of foundresses and their relatedness. Offspring sex ratio was tested using nested analysis of covariance (ANCOVA), with the different origins of foundresses nested within the number of foundresses and their relatedness, and number of offspring as covariate. We analysed the data with SPSS v.14.0 (SPSS, Chicago, IL). Differences in foundress mortality rate among populations were tested by comparing the proportion of dead single foundresses among populations. We used the chi-square distribution of the proportion of dead females in contingency tables (Glenn *et al.*, 1995). The results are presented as means and standard errors of the mean.

RESULTS

Control: one foundress beetle

Some of the populations suffered high mortality when transferred to the laboratory, resulting in different sample sizes among the populations in the experiment. Once the beetles penetrated into the seed, no significant difference in the proportion of dead beetles was observed (On = 0.31, Ash = 0.27, ND = 0.5, BD = 0.23, Ch = 0.33, Be = 0.38, SB = 0.24; $\chi^2 = 9.005$, d.f. = 6, $P = 0.173$). The total number of offspring differed significantly among populations (On = 11.15 ± 0.60 , Ash = 13.04 ± 0.79 , ND = 8.75 ± 0.82 , BD = 18.1 ± 1.07 , Ch = 13.06 ± 0.94 , Be = 16.87 ± 1.23 , SB = 11.84 ± 0.65 ; ANOVA: $F_{6,297} = 8.04$, $P < 0.0001$). Thus, when testing for the effect of population on the sex ratios, number of offspring was treated as a covariate ($F_{1,296} = 10.24$, $P = 0.02$). No significant differences were observed in offspring sex ratio of beetles from the various populations (sex ratios: On = 0.097 ± 0.078 , Ash = 0.090 ± 0.099 , ND = 0.051 ± 0.077 , BD = 0.075 ± 0.085 , Ch = 0.123 ± 0.190 , Be = 0.070 ± 0.014 , SB = 0.086 ± 0.067 ; ANOVA: $F_{6,296} = 1.875$, $P = 0.085$) (Fig. 2).

Number of offspring per patch

We checked the effects of the treatments, namely, foundress relatedness and number of foundresses, on the number of offspring per patch (i.e. seed). As the galleries in most date seeds merged, it was not possible to distinguish between offspring belonging to an individual foundress. There was a significant effect of relatedness ($F_{2,486} = 116.42$, $P < 0.0001$) and of number of foundresses ($F_{2,486} = 92.42$, $P < 0.0001$) on the number of offspring per patch, with a significant interaction between relatedness and number of foundresses ($F_{4,486} = 17.98$, $P = 0.007$; Fig. 3). Tukey's HSD *post-hoc* test indicated that unrelated foundresses in groups of three and seven produced fewer offspring than the related foundresses in the respective groups (Fig. 3).

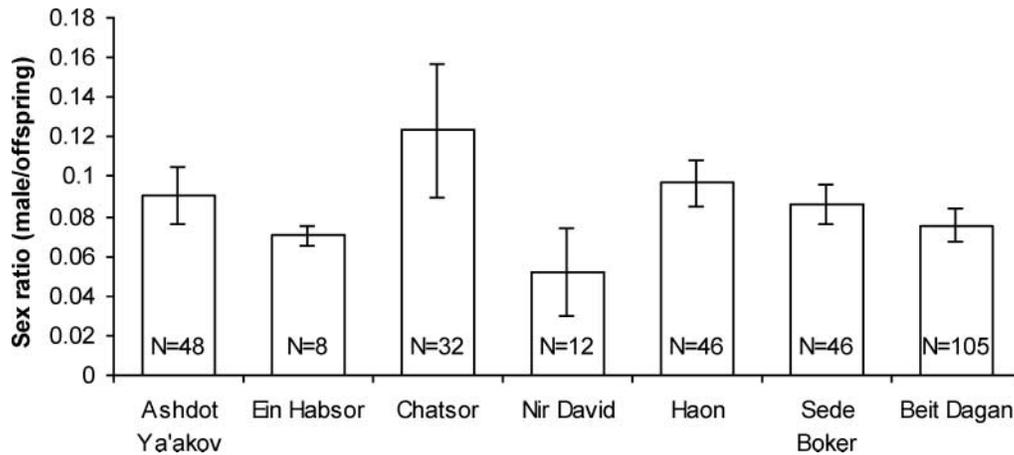


Fig. 2. Sex ratio of a single foundress originating from different populations. Sex ratio is defined as the proportion of males out of the total clutch. The figure shows sample size (N = number of seeds) and mean \pm 1 standard error.

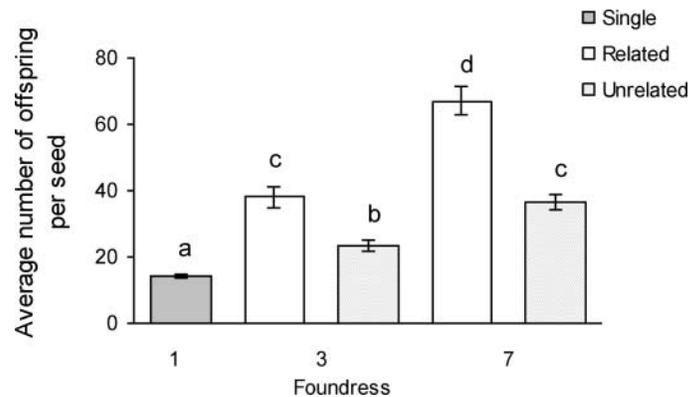


Fig. 3. Number of offspring per foundress. The figure shows mean \pm 1 standard error. Letters represent Tukey *post-hoc* analysis results and indicate significant differences among the means ($P < 0.05$).

Sex ratio per patch

We tested the effects of relatedness among foundresses and number of foundresses on offspring sex ratio, with number of offspring per patch as the covariate ($F_{1,486} = 34.68$, $P < 0.0001$). There was a significant effect of relatedness among foundresses ($F_{2,486} = 3.22$, $P = 0.02$) and of the number of foundresses ($F_{2,486} = 10.20$, $P < 0.001$) on the sex ratio. No interaction was detected between relatedness and number of foundresses ($F_{4,486} = 1.23$, $P = 0.155$). Tukey's HSD *post-hoc* test indicated that the sex ratio of offspring of unrelated foundresses ($N = 117$, 0.168 ± 0.021) was significantly less female-biased than that of offspring of related foundresses ($N = 71$, 0.061 ± 0.009) and less than the sex ratio of a single female ($N = 298$, 0.084 ± 0.005) (Fig. 4).

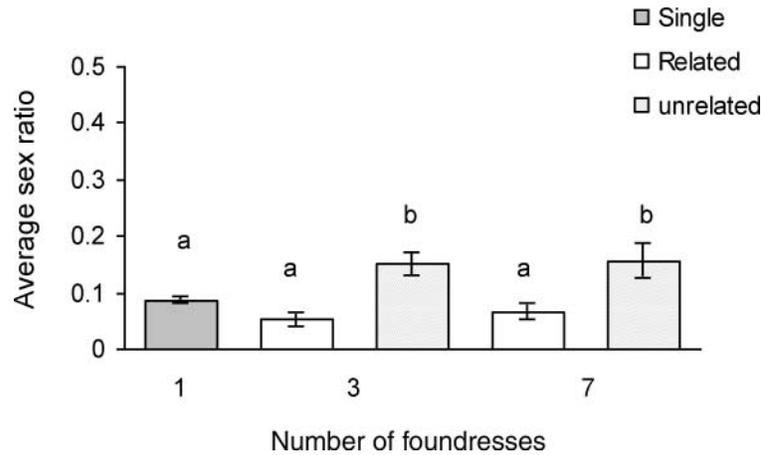


Fig. 4. Sex ratio of offspring belonging to single, related or unrelated females. The figure shows mean \pm 1 standard error. Letters represent Tukey *post-hoc* analysis results and indicate significant differences among the means ($P < 0.05$).

DISCUSSION

Studies based on Hamilton's (1967) LMC theory predict that sex allocation bias may vary according to the relatedness among offspring (Frank, 1986, 1987), with related females producing a higher female-biased sex ratio than unrelated females in a similar patch. We used foundresses from the same or from different inbred populations to obtain the two levels of relatedness. In agreement with the prediction above, we found that the sex ratio among offspring of related females was significantly more female-biased than that of offspring of unrelated females. This result supports previous findings that *C. dactyliperda* beetles are able to discriminate between individuals originating from the same and from a different population (Gottlieb *et al.*, 2009) and we regard this as evidence for discrimination of relatedness.

Our results support the LMC hypothesis: the transition from one to several unrelated foundresses leads to an increase in the number of males and the sex ratio in the patch. However, the sex ratio did not increase further when the number of foundresses increased from three to seven. This may be explained by the LMC equation itself; as the number of foundresses increases, the sex ratio approaches an asymptote and the rate of change in the sex ratio gradually declines. Under certain assumptions that provide a reasonable approximation to our population structure, the offspring sex ratio for a haplodiploid species is predicted by the following equation, which takes account of the effect of inbreeding on the sex ratio (see Appendix):

$$S_n = \frac{1}{3} \frac{n-1}{n} \quad (1)$$

where S_n is the observed offspring sex ratio conditional on n , the number of foundresses. The results for $n = 3$ and $n = 7$ are 0.222 and 0.285. These slight changes in the sex ratio with increasing numbers of foundresses might be difficult to detect experimentally.

In the related foundress treatment, there was no difference in offspring sex ratio for one, three or seven foundresses in a patch. As the related foundresses were taken from populations with high inbreeding rate, the transition from one to several related foundresses did not decrease the relatedness among male offspring. Under such circumstances, only enough sons to ensure mating with all daughters should be produced to avoid competition among related males. A similar explanation was suggested for similar experimental results in a study of a highly inbred population of mites (Roeder *et al.*, 1996).

The present study clearly indicates that LMC theory is applicable to the female-biased sex ratios observed in offspring of *C. dactyliperda*. However, the observed sex ratios were extremely female-biased, more than expected from LMC theory [hereafter called *surplus* female-biased sex ratio, following Sato and Saito (2007)]. Three non-mutually exclusive mechanisms may explain the *surplus* female-biased sex ratio.

First, a *surplus* female-biased sex ratio may evolve in cooperative breeding species if females help in breeding (Hamilton, 1967; Taylor, 1981; Schwarz, 1988; Frank, 1998). *Coccotrypes dactyliperda* females often share a seed with other females, most commonly with their daughters (Herfs, 1950). Thus, if cooperation in brood care occurs (Crespi and Choe, 1997), this could explain the larger number of offspring in patches of related females. A positive effect of female helpers on the survival of the offspring has been shown by direct behavioural observations (Sitkov-Sharon, 2010). Cooperative breeding in *C. dactyliperda* females may improve the performance of certain tasks, such as excavating galleries and guarding offspring, thereby reducing offspring mortality and allowing foundresses to invest more energy in egg laying. In this case, a foundress is expected to produce more of the helpers' sex (females), thus contributing to the observed *surplus* of females among offspring.

Second, *Wolbachia* infection may further bias the sex ratio leading to a *surplus* of females. *Coccotrypes dactyliperda* is infected with *Wolbachia*, a cytoplasmic symbiotic bacterium (Zchori-Fein *et al.*, 2006). *Wolbachia*, which is maternally inherited and widely infects arthropods and nematodes, can distort the offspring sex ratio of its hosts towards females by various means, such as parthenogenesis (Stouthamer *et al.*, 1990; Stouthamer, 1997), feminization of genetic males (Rigaud, 1997; Kageyama *et al.*, 1998), and male killing (Hurst *et al.*, 1999). However, Zchori-Fein *et al.* (2006) found that uninfected (antibiotic-treated) females do not oviposit, thus making it difficult to estimate the effects of *Wolbachia* on offspring sex ratio.

Third, high levels of inbreeding may also favour a *surplus* female-biased sex ratio (Frank, 1985; Herre, 1985; but see Reece *et al.*, 2004; Shuker *et al.*, 2004). In haplodiploid taxa with frequent inbreeding, mothers may be more related to their daughters than to their sons (i.e. there is a strong asymmetry of inheritance between the sexes). Under haplodiploidy, daughters receive genes both from their fathers and mothers, whereas sons receive genes from their mothers only. Hence, diploid females in inbreeding haplodiploid taxa will gain more through inclusive fitness by producing a *surplus* female-biased sex ratio (Frank, 1985; Herre, 1985; Werren, 1987). The effect of inbreeding on sex ratio in LMC theory is incorporated in equation (1). Since the underlying assumption of the equation is that foundresses are unrelated, we compared the expected results to the observed results of unrelated females. When using $n = 3$ and 7 in the equation (as in our experiment), and *assuming* the highest level of inbreeding (resulting in a *surplus* female-biased sex ratio), the expected sex ratios are 0.222 and 0.286, respectively, and do not fall within the 95% confidence limits of offspring sex ratio of unrelated foundresses in our study. Thus, high inbreeding levels of *C. dactyliperda* (Gottlieb *et al.*, 2009) cannot fully explain the *surplus* female-biased sex ratio.

Thus, the three mechanisms suggested above – namely, cooperative breeding, *Wolbachia*

infection, and high inbreeding levels – might contribute to the observed extremely high female-biased sex ratios. Other mechanisms suggested in previous studies to explain a surplus biased sex ratio do not apply in this system, for reasons outlined below. These mechanisms include competition between offspring, male–male combat, and offspring manipulation of the sex ratio. Competition between offspring – the prediction of LMC theory – will differ if local competition for resources occurs during development of offspring and if there is an asymmetry between the competitive abilities of male versus female offspring (Godfray and Werren, 1996; but see Sykes *et al.*, 2007). An increase in competition for food or space may occur as the number of foundresses increases. We do not have information about possible asymmetric competition among males versus females in all developmental stages of the beetle. Our results, however, do not support such an effect, since even after controlling for number of offspring per patch, a significant difference between sex ratio of related and unrelated foundresses was still apparent.

Lethal combat among males, leading to male mortality, may also distort the sex ratio towards a more female-biased sex ratio. That is, a foundress ovipositing on a previously attacked host may refrain from producing male offspring, as these later-emerging males would be killed by older males (Abe *et al.*, 2003b). Combat among unrelated males is expected to be more severe than among related males, because unrelated males lack the benefit of inclusive fitness (Abe *et al.*, 2003a, 2003b, 2005). However, in *C. dactyliperda* the sex ratio is more female biased among related foundresses than among unrelated foundresses. Thus, it is unlikely that high mortality rate of males due to direct competition can explain the *surplus* female-biased sex ratio in *C. dactyliperda*.

In summary, offspring manipulation of the sex ratio seems an unlikely explanation, as neither resource competition nor male combat appear to play a role in determining the sex ratio (see above). Nevertheless, whether offspring can manipulate the sex ratio within the patch should be further examined.

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APPENDIX BY PETER TAYLOR

We approximate the *C. dactyliperda* population structure with an infinite island model in which each island is composed of a large number N of breeding patches. The patches are the seeds of the model and the islands are local configurations of seeds. We assume that the number n of breeders on each patch is variable, and that breeders can observe and respond to the n -value of their breeding patch. We assume that male and female offspring mate at random on each patch and mated female offspring leave their natal patch but with high probability settle to breed on a random patch on their natal island. Otherwise, with small probability, the female disperses to a random island in the population. Finally, we assume that a female knows whether or not she is breeding in her natal island. For this simple model, this is equivalent to the assumption that breeders can assess their level of relatedness to their breeding patch-mates.

Let:

- r_i be the relatedness of a female to her sex i offspring;
- R_i be the relatedness of a female to a random sex i offspring on her natal patch;
- \tilde{R}_i be the relatedness of a female to a random sex i offspring on her natal island;
- v be the reproductive value of a female offspring relative to that of a male offspring;
- s be the sex ratio (proportion of males) in a focal breeding patch.

Let w_i be the inclusive fitness effect on a breeding female of having an extra sex- i offspring. Then:

$$w_m = (r_m - R_m) \frac{1-s}{s}$$

$$w_f = (vr_f + R_m) - (v\tilde{R}_f + \tilde{R}_m)$$

In the equation for w_m , the female must subtract her relatedness to the male offspring that will be displaced by her extra son. And then this is multiplied by the female-male ratio on her patch. In the equation for w_f , the female must add her relatedness to the male who will get an extra mating with her extra daughter, but then she must also subtract her relatedness to the mated female offspring that will be displaced by the resulting mated female. Here we make the assumption that dispersal outside the island is rare, so that competition for next generation breeding sites is essentially within an island.

Now we consider the simple case of a mated female who happens to disperse to a distant island. In this case, the \tilde{R}_i are both zero, and $R_i = r_i/n$. We get:

$$w_m = \left(1 - \frac{1}{n}\right) r_m \frac{1-s}{s}$$

$$w_f = vr_f + \frac{1}{n} r_m$$

At equilibrium, $w_m = w_f$ and, solving for s :

$$s_n = s = \frac{n-1}{n} \frac{r_m}{vr_f + r_m}$$

This is the ESS sex ratio conditional on n . Our assumptions of rare dispersal from the island give us an expected inbreeding coefficient of 1, and this gives $r_m = r_f = 1$. With $v = 2$ (haplodiploidy), we get:

$$s_n = \frac{1}{3} \frac{n-1}{n}$$