

Female ambrosia beetles adjust their offspring sex ratio according to outbreeding opportunities for their sons

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Abstract

Recent studies on the effect of local mate competition (LMC) on sex ratios have focused on the effect of post-dispersal mating success by males. A higher proportion of males is expected to be produced as the potential for outbreeding increases. Here we demonstrate that males of a haplodiploid ambrosia beetle with LMC disperse to seek additional matings, and brood sex ratios increase with outbreeding opportunities in the field. Manipulations in the laboratory confirm that females produce more sons when the post-dispersal mating prospects of their sons are experimentally increased. This is the first study showing that male dispersal options may influence individual female sex allocation decisions in species with strong LMC.

Introduction

Hamilton's concept of local mate competition (LMC; Hamilton, 1967, 1979) has inspired a great number of studies in the field of sex ratio theory. According to this theory, sex ratios should depart from equality if mating is not random within the population, but takes place within groups containing related individuals. In such situations, females maximize fitness by producing female-biased brood sex ratios. In the extreme case of strict local mating and a single founding female, the model predicts that the sex ratio should approach zero; broods should contain the minimum number of sons sufficient to fertilize all daughters. With increasing number of foundresses reproducing within one patch, female bias should be reduced and the sex ratio approach equality as predicted by Fisher (1930).

In fig wasps and parasitoid wasps a small number of females reproduce within a patch, mating takes place before female dispersal, and males are often unable to disperse as a result of reduced wings and body size. Numerous empirical tests have qualitatively confirmed Hamilton's theory of sex allocation (reviewed for fig

wasps: Herre *et al.*, 1997), but often more males than predicted are produced. One explanation could be constraints on females, preventing them from producing optimal sex ratios. For example, less-than perfect control of sex determination or developmental mortality (Hardy *et al.*, 1998) could increase the risk of producing all-female broods, which would result in unmated daughters (Oku & Nishida, 2001), and thus additional 'insurance males' could be produced. Similarly, limited insemination capacity of males should lead to an increase in sex ratio (but see Hardy *et al.*, 2000).

Alternatively, females may be behaving optimally, but the assumptions of LMC theory need not be correct. The original theory has been refined to include additional factors determining sex ratios in structured populations. In particular, the assumption of strict local mating has been relaxed in several models (e.g. Nunney & Luck, 1988; Ikawa *et al.*, 1993; Taylor, 1993). This situation has been termed partial LMC. It has been argued repeatedly that outbreeding or nonlocal mating should decrease the female bias of Hamiltonian sex ratios. In these models, a mother gains inclusive fitness through an extra son only if he is outbreeding.

Unfortunately, assumptions about mating and population structure are often indirect, and have only rarely been tested in studies of LMC (Molbo & Parker, 1996). Increasing evidence suggests that strict local mating may be the exception rather than the rule in typical

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inbreeders (see reviews by Nadel & Luck, 1992; Hardy, 1994; Hardy *et al.*, 1999). Comparative studies have shown a correlation between inferred male dispersal abilities and average sex ratios (Hardy & Mayhew, 1998; West & Herre, 1998a; Fellowes *et al.*, 1999). However, indirect inferences of population structure from morphological data should be treated with care (Drapeau, 1998). To our knowledge, no study has shown as yet that females individually adjust the sex ratio of their brood according to outbreeding opportunities.

The most popular taxon for testing LMC theory are the Hymenoptera, owing to the biology of fig wasps and parasitoids clearly exhibiting structured populations with limited male dispersal. However, nonlocal mating success in the field is difficult to study in Hymenoptera because of their small size and difficulties of tracking them individually after dispersal. The life history of certain ambrosia beetles (Scolytinae, Xyleborini) shows striking similarities with these hymenopteran groups; mated females disperse, and each female excavates a brood chamber with a single entrance/exit hole in freshly dead trees. Thus, offspring groups are produced by a single foundress. The female and her offspring feed on the fungi they cultivate on the gallery walls. Unfertilized eggs develop into haploid males, which are smaller than females and have reduced, nonfunctional flight wings. For the whole tribe Xyleborini, it is generally believed that mating occurs exclusively within the natal gallery, and males are assumed to die or be evicted by their sisters after mating, resulting in strict LMC (Kirkendall, 1993). Indeed, the whole group exhibits heavily biased sex ratios. However, there may be hundreds of galleries per tree, and males can be observed wandering on the bark surface and visiting other gallery entrances (Schneider-Orelli, 1913). This offers a unique opportunity to study male dispersal behaviour and outbreeding opportunities in a species with single foundress broods. If these males have some post-dispersal mating success, this should influence optimal sex allocation of the founding female.

The aims of this study are:

- (i) to determine whether the xyleborine mating system is best described by strict or partial LMC;
- (ii) to determine the relationship between outbreeding prospects and sex allocation in a natural situation;
- (iii) to manipulate male post-dispersal mating opportunities in the laboratory, and to test whether or not females react according to the predictions of LMC theory.

Methods

Study population

Field work was carried out from the beginning of May until the end of September 2002 in the Bremgarten Forest surrounding the Hasli Ethological Station at Berne, Switzerland. *Xylosandrus germanus* (Blandf.) is

one of nine xyleborine species in Europe, which has been introduced from East Asia about 50 years ago (Groschke, 1953) and has a body length of about 2.2 mm. Dispersal flights last from May to June, when females colonize freshly fallen trees and start excavating a brood chamber or gallery. They carry spores of fungi in special structures (mycangia) and cultivate these fungi on the surface of the gallery walls. After the fungus has started to grow, females oviposit, and broods develop until the end of August. Around this time, many males leave their natal galleries and can be observed on the bark surface. Mated females overwinter in their gallery and disperse the next spring (Gauss, 1960; Heidenreich, 1960, 1964).

Male dispersal behaviour

We investigated male dispersal behaviour during late summer. The males of one subpopulation (tree log) were individually colour-marked, and their movements on the bark surface were recorded. Each observation session lasted for 1–2 h, and we observed a total of 23 males over a period of 4 days. We presumed any gallery within a radius of 2 cm of its movements to be within a potential 'perception range' of the male. As an index of gallery attractiveness for males, galleries were classified into three categories: 'ignored' (no contact with gallery entrance by any male coming within 2 cm of a gallery), 'visited' (at least one contact of a male with the entrance ≤ 1 min), or 'stayed' (at least one contact of a male with the entrance > 1 min). After completion of behavioural observations, we dissected galleries that had been within the range of wandering males and counted the number of females inside.

Female behaviour

The gallery entrance is often blocked by one of the females from inside the brood chamber. In order to judge the relevance of this blocking behaviour for extrafamilial male mating opportunities, we quantified this behaviour at the entrances of 24 galleries on three different trees. Blocking females were individually colour-marked, and each gallery entrance was observed on 7 days over a period of 3 weeks. On each observation day 6 consecutive scans were performed with an interscan-interval of 30 min. Frequency of blocking and the identity of the blocking females were recorded.

Sex ratio and outbreeding opportunities in the field

Post-dispersal mating opportunities are likely to be determined by the density of galleries on a tree, as males cannot fly. We selected 15 trees with varying levels of *X. germanus* colonization densities. After the end of the dispersal period, a grid with 470 cells of 2×2 cm was laid over the bark surface of each tree. The percentage of cells containing at least one gallery entrance of 50 randomly

selected cells was determined. This percentage was used as an index of colonization density. In addition, 45 gallery entrances were marked and emergence traps placed over them. The beetles that left their gallery were trapped in a plastic vial, which was checked once a week. At the end of the season, small chunks of wood containing the marked galleries were removed from the logs with hammer and chisel, and the numbers of males and females inside were counted under a dissection microscope in the laboratory. Thereby we obtained data on both dispersing and nondispersing individuals. Because of gallery failure, our final sample size was 36 galleries dispersed over 13 trees, with a mean of 2.2 ± 0.4 galleries per tree.

In the field, all-male broods are likely to result from an unfertilized female, whereas all-female broods are assumed to result from sampling error, because they occur in the laboratory only very rarely (3% in the laboratory vs. 19% in the field). Emergence traps were difficult to attach to the bark surface, so that sometimes small gaps occurred, through which males could escape. Therefore, all-female broods ($n = 7$) were excluded from the analysis of the relationship between colonization density and sex ratio in natural galleries.

Lab experiment

We tested the significance of nonlocal mating opportunities for brood sex ratios in an experiment with artificial breeding medium in tubes. Females were assigned randomly to treatments of one, two or three per tube. As galleries were never observed to merge in nature, any sex allocation change was assumed to be an adaptation to nonlocal mating opportunities for dispersing males (as opposed to outbreeding in multiple foundress broods). When there were several foundresses per tube, each female excavated her own gallery, although the galleries sometimes merged late during brood development. The resource volume per female was kept approximately constant between treatments by adjusting the tube diameter (11, 15 and 19 mm, respectively). To control for effects of tube size on sex ratio, single females were also put into tubes of these sizes. The medium was removed after the end of brood development and the numbers of male and female offspring in each tube were counted.

During the course of the experiment, it turned out that the sex ratios produced by single foundresses in small tubes were unusually high compared with single-foundress broods in medium and large tubes, where no difference was expected (medians: 0.11 in small tubes, 0.06 and 0.06 in medium and large tubes; logistic regression, $\chi^2_1 = 18.59$, $P < 0.001$, $n = 30$, 17 and 21, respectively). One main assumption of the experiment was that resource quality is equal in all tube sizes, but in the smallest tubes the medium unexpectedly dried out more quickly than in the remaining tubes. If female

offspring suffer more from low resource quality, foundresses are expected to produce relatively more sons on low quality patches (Charnov *et al.*, 1981). Because of this confounding effect we had to exclude the broods in small tubes from further analyses.

We investigated the timing of male maturation relative to female maturation by dissecting tubes with single foundress broods in the laboratory at the age of 4 weeks, when about one-third of the offspring had reached adulthood. Sex and stage (pupal, adult) of the offspring was recorded.

Foundresses used for experiments were collected in the field during dispersal, with ethanol-baited live traps. The traps were checked every day, and the female were kept in plastic vials with filter paper for 2 days, already at densities according to experimental treatment. Before we transferred the beetles onto the medium on a sterile bench, they were rinsed for a few seconds in 70% ethanol and deionized water to prevent microbial contamination of the medium. Gallery structure, brood development and fungal growth were comparable with natural galleries in wood. All tubes were kept in constant darkness at 70% humidity and 22 °C ('night', 14 h) and 28 °C ('day'). The agar-based medium consisted of 0.35 g streptomycin, 1 g Wesson's salt mixture, 5 g yeast, 5 g casein, 5 g starch, 10 g sucrose, 20 g agar, 75 g pear tree sawdust, 2.5 mL wheat germ oil and 5 ml 95% ethanol (modified from Norris & Chu, 1985). All dry ingredients were mixed, and 500 ml of deionized water was added. The mixture was autoclaved for 20 min at 121 °C, and the hot medium was poured into sterile tubes, covered immediately, and left to dry for 4–5 days.

Statistical analyses

We used nonparametric statistics to examine the relationship between gallery attractiveness and gallery contents, because data were not normally distributed and variances were unequal between the groups. For all analyses, sex ratio was defined as the proportion of males in the total brood. Unless stated otherwise, the total sex ratio per tube was used in all calculations for tubes with multiple broods. Sex ratios were analysed using generalized linear models with binomial error distribution and a logit link function [weighted logistic regression (Crawley, 1993) using GLIM (Glim 4 © Royal Statistical Society, 1993) (Crawley, 1993; Krackow & Tkadlec, 2001)]. Brood sizes and number of males were analysed with Poisson regressions with a logarithmic link function using GLIM (Crawley, 1993). For both types of analyses, GLIM reports the significance of the effects based on the change in deviance from the model, which has a chi-square distribution. Whenever the final model was over- or underdispersed, variances were rescaled using Pearson's chi-square (Crawley, 1993). After rescaling, *F*-tests were used for testing significance of the change in deviance of logistic regressions (Crawley, 1993, p. 279;

Wilson & Hardy, 2002, p. 68), but not of Poisson regressions (Crawley, 1993, p. 263). To account for an effect of differential mortality (of females), brood size was always included in the analyses.

To compare sex ratios at different maturation stages, the data were arcsine transformed to attain normality. This was performed in order to allow for paired analyses. To determine the preciseness of sex determination, the ratio of observed sex ratio variance to expected variance under random sex determination with a binomial distribution was calculated [Green variance (GV); Green *et al.*, 1982; West & Herre, 1998b].

Results

Male and female behaviour

From the galleries equipped with emergence traps, data on male emergence rate could be collected. Of the 69 males found in 39 galleries, 47 (68%) had emerged before gallery dissection. From only eight (20%) of these galleries had not a single male emerged, and from three galleries (8%) males had already emerged although there were still female pupae present at the time of dissection. In galleries where the entire female brood had reached adulthood at the time of dissection, males had emerged on average 14 days before dissection, which makes it likely that at this time there were still female pupae and/or unmated females present.

On each of the 4 days of behavioural observations, the tree was scanned for marked males. In total, 27 males were marked. Of those, four were seen the next day, three 2 days later, one 3 days later and one 4 days later. Males passed within 2 cm of 2.6 gallery entrances per hour, and they stayed at 50% of these for more than 1 min (median staying time not including visits up to 1 min was 9 min; $n = 23$). We never observed a male entering a gallery, but there were numerous interactions between males and females at the gallery entrances (i.e. touching with antennae, copulation attempts, it could not be determined whether those attempts were successful). Males were more attracted to galleries that contained a higher number of females [median number of females in different gallery categories: 0 (ignored), 1 (visited) and 11 (stayed), Kruskal–Wallis, $\chi^2_2 = 13.73$, $P < 0.001$, $n = 31$; Fig. 1].

Gallery entrances were occupied by a female on average for $60 \pm 6\%$ ($\bar{x} \pm \text{SEM}$) of the time, and there were on average two different females in succession (median = 2, interquartile range = 2–2.75, max = 6) attending the gallery entrance.

Brood sex ratio characteristics

Galleries with larger broods contained more males in natural and single foundress laboratory galleries (Poisson regression, field: $\chi^2_1 = 10.52$, $P < 0.001$, $n = 36$;

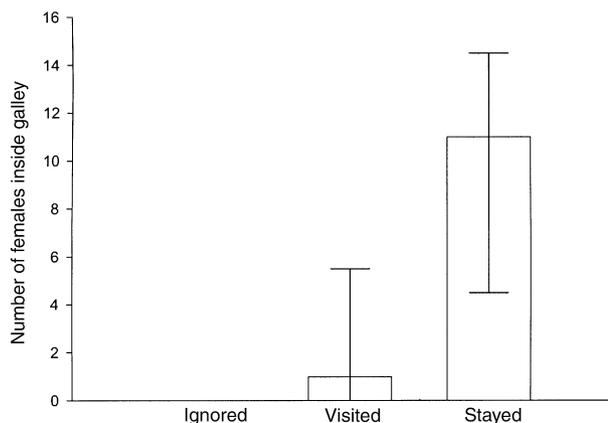


Fig. 1 Medians and interquartile ranges of the number of females in galleries that males ignored, visited, or where they stayed for several minutes.

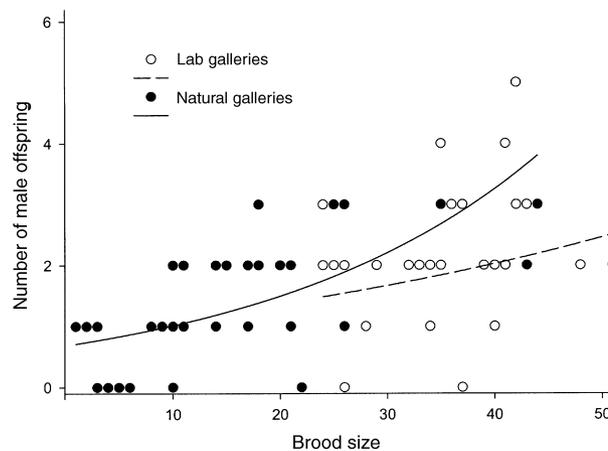


Fig. 2 The total number of males produced across different brood sizes in field and laboratory galleries, and Poisson regression line (field: $\ln y = -0.37 \pm 0.27 + 0.039 \pm 0.011 \times \text{brood size}$; laboratory: $\ln y = 0.067 \pm 0.32 = 0.019 \pm 0.007 \times \text{brood size}$).

laboratory: $\chi^2_1 = 6.223$, $P < 0.05$, $n = 38$; Fig. 2). Brood sizes were smaller in the field than in the laboratory ($\bar{x} = 14.6$ and 36.87 , respectively; Poisson regression, rescaled for overdispersion, $\chi^2_1 = 85.16$, $P < 0.001$), but mean sex ratios did not differ significantly ($\bar{x} = 0.1$ and 0.063 in the field and the laboratory, respectively; $\chi^2_1 = 1.07$, ns). GV was significantly lower than binomial variance for both field and laboratory data (field: $\text{GV} = 0.36$, $\chi^2_1 = 12.32$, $P < 0.001$, $n = 36$; laboratory: $\text{GV} = 0.2$, $\chi^2_1 = 6.93$, $P < 0.001$, $n = 38$).

The sex ratio of adult offspring of broods at the age of 4 weeks was higher than that of pupae (paired *t*-test on arcsine transformed sex ratios, $t = 7.592$, $P < 0.001$, $n = 32$). Thus, most males were between the first third of maturing offspring.

Sex ratio adjustment in the field and lab

In the field, there was a significant increase of sex ratio with colonization density (sex ratio data were pooled over trees and variances rescaled for underdispersion, $F_{1,11} = 8.71$, $P < 0.01$, Fig. 3). The distribution of data points in Fig. 3 suggested that the result might be due to the two trees with the highest density estimates. We therefore repeated the analysis without these two data

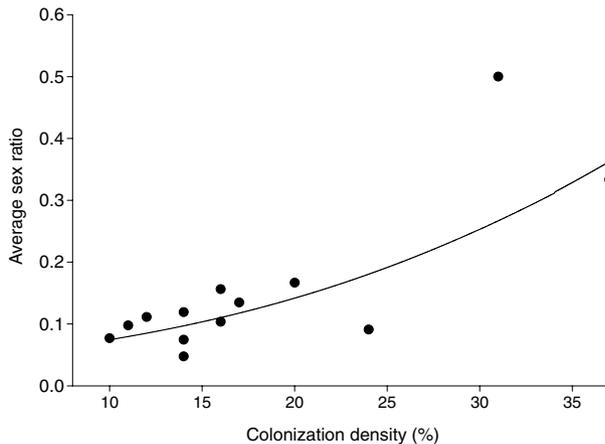


Fig. 3 Relationship between outbreeding opportunities and average sex ratios per tree in the field and logistic regression line; $\ln(p/q) = -3.24 \pm 0.37 + 0.072 \pm 0.02 \times \text{density}$, $P = 1/[1 + 1/(p/q)]$. Density is measured as the percentage of grid cells containing gallery entrances.

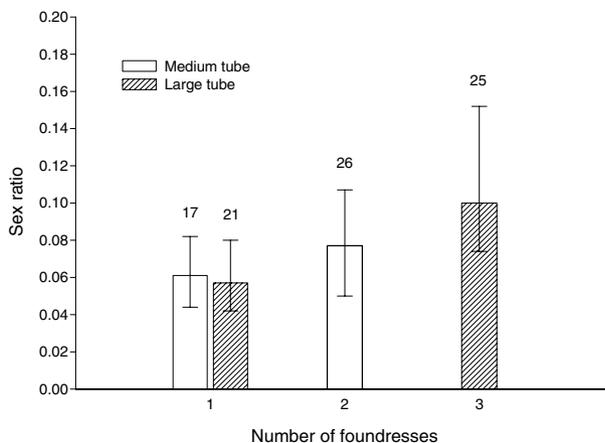


Fig. 4 Female adjustment of brood sex ratios according to outbreeding opportunities. Medians and interquartile ranges of brood sex ratios with different foundress numbers and tube sizes are shown. Sample sizes are given above bars. Available resource volume per foundress decreased from one to two and from one to three foundress treatments, but was constant between two and three foundress treatments.

points, after which the correlation was not significant ($F_{1,9} = 2.1$, ns). For the laboratory experiment, we investigated the effect of foundress number on brood sex ratio after 8 weeks, controlling for brood size and tube size. The effect of the number of foundresses was significant, whereas there was no effect of brood size or tube size (number of foundresses: $\chi^2_1 = 25.13$, $P < 0.001$; brood size: $\chi^2_1 = 2.37$, ns; tube size: $\chi^2_1 = 1.38$, ns, $n = 89$; Fig. 4).

To exclude an effect of differential resource availability, we also compared the tubes containing two vs. three foundresses with the same amount of resources per female. The sex ratio was significantly higher in tubes with three than in tubes with two founding females. The effect of brood size may be caused by mortality of late maturing individuals, which are females (number of foundresses: $\chi^2_1 = 12.9$, $P < 0.001$; brood size: $\chi^2_1 = 5.06$, $P < 0.05$, $n = 50$). Furthermore, we analysed the data from tubes, which were dissected after 4 weeks, when individual galleries could still easily be distinguished within tubes. Thus, sex ratios from individual broods could be analysed before mortality because of gallery fusion occurred. Including only individuals, which could already be sexed at this stage (pupae and adults), individual brood sex ratio was higher in tubes containing three broods than in those containing two broods. There was a strong effect of brood size, indicating that males matured first, and the sex ratio depended on the number of females having reached pupal or adult stage (rescaled for underdispersion; brood size: $F_{1,81} = 31.59$, $P < 0.01$, number of broods: $F_{1,81} = 4.49$, $P < 0.05$).

Discussion

Under strict LMC with no dispersal before mating, single foundresses maximize their inclusive fitness by producing a single son only, regardless of brood size (Hamilton, 1967). In contrast to strict LMC theory, the number of males in *X. germanus* families increased with brood size. Together with our observations on male dispersal behaviour, this strongly suggests that mating is not restricted to the local patch (i.e. natal gallery).

There are several possible, not mutually exclusive explanations for the relationship between number of males and brood size. On the contrary, females may experience constraints in their optimal sex allocation. If male lifespan is not long enough to fertilize late born female offspring, foundresses may do best by producing a constant rate of males over the course of egg laying. However, as males always eclose first, our results cannot be interpreted as an insurance against a short lifespan of males. Neither is post-eclosion mortality of males a likely explanation, as males already dispersed when unmated females were still present in their natal gallery. Stochasticity in sex determination and male sperm limitation are also predicted to lead to an increase in number of males

with larger broods. (Nagelkerke & Hardy, 1994; Hardy *et al.*, 1998, 2000). Since sex ratio variance was significantly lower than binomial variance, stochasticity in sex determination is not likely to be a strong selective force. The observed variance in the field and in the laboratory was only 36% and 20% of the binomial variance, respectively. These values are substantially lower than those reported for species of parasitic wasps and fig wasps (Green *et al.*, 1982; West & Herre, 1998b). Similarly, sperm limitation is not likely to be expressed frequently in natural populations. In the only case of unfertilized females resulting from a laboratory brood, the brood contained only one male and 26 females. With the brood sizes observed in natural galleries, single males are unlikely to reach the limits of their insemination capacity.

On the contrary, females could make strategic decisions in their sex allocation according to outbreeding opportunities. Models of partial LMC predict that post-dispersal mating potential should decrease female bias in offspring sex ratios. Our observations on male dispersal behaviour show that males do not die after mating within their brood chambers. Instead, they apparently search for mating opportunities in neighbouring galleries for 1 to several days. The most likely mechanism by which males are able to locate occupied galleries and estimate the number of females inside is by chemical communication. A variety of bark beetle species use pheromones for both long- and short-distance communication (e.g. Klimetzek *et al.*, 1981; Wood, 1982; Teale *et al.*, 1994). Males spend more time at galleries with more adult females, which may raise their potential mating success. It is very likely that nonlocal mating success is the selective force shaping male dispersal behaviour. At present we cannot estimate the mating success of dispersing males. We have never observed a male entering a gallery, because females occupying the entrance were effectively blocking it. Although our data indicate that females were only blocking 60% of the time, average blocking frequency is likely to be higher. The entrance tunnel may be several millimetres long, and females may obstruct access to the gallery without being seen from outside. However, copulations at the entrance hole would allow dispersing males to reproduce. We have observed male copulation attempts with the guarding females. Since often two or more females (i.e. not only the founding female) participate in entrance blocking, males could propagate their genes without actually entering another gallery.

Even low levels of post-dispersal mating success may substantially influence the optimal sex ratio (Taylor & Bulmer, 1980; Taylor, 1993). According to theoretical models, sex ratios of 0.09–0.1 should result from a nonlocal mating probability of about 20%. In *X. germanus* this would correspond to successful copulations in another gallery for one male of five. A female bias in offspring sex ratio should

disappear almost completely if each male reproduces on average in two patches of reproductive females after dispersal (Nunney & Luck, 1988).

The biology of ambrosia beetles offers a unique chance to quantify post-dispersal mating opportunities. As males are unable to fly, they can reach other galleries only by walking. The density of galleries on a tree will thus determine their outbreeding opportunities. After dispersal flight, females spend considerable time walking around the surface of the tree (personal observation), apparently searching for a suitable place to start tunnelling. During this time, they repeatedly encounter other females or gallery entrances, and could potentially estimate the outbreeding opportunities for their prospective sons and adjust their offspring sex ratio accordingly. Indeed, brood sex ratios were correlated with gallery density in the field, although the significance of this result depends on two trees.

Our laboratory experiment confirmed that females adapt their offspring sex allocation to the potential outbreeding success of their sons. If alone, females always allocated less effort into male production than in the presence of additional females, and the proportion of males increased when the number of foundresses was experimentally raised from two to three with the same amount of resources available to each female. This is not probably due to higher mortality (of females) in tubes containing more broods. Although we do not have data on primary sex ratios, the result was the same for individual broods at the age of 4 weeks, when mortality because of competition has not become important yet. Recently it has been shown that in a pollinating fig wasp species with dispersing males the average sex ratio is higher than in regular species (Greeff, 2002), which matches results of comparative studies on other fig wasps (West & Herre, 1998a) and parasitoids (Hardy & Mayhew, 1998). However, individual adjustment of sex ratios to outbreeding opportunities had not been shown as yet.

Apart from a reduction in the degree of LMC for males, post-dispersal mating may have an additional effect on sex allocation. In haplodiploid species inbreeding leads to a relatedness asymmetry, in that mothers are more related to their daughters than to their sons. Females therefore have higher fitness gains through daughter reproduction and should bias their brood sex ratio towards females independently of LMC (Herre, 1985). If males mate after dispersal, this reduces inbreeding levels in the population, and the proportion of males should increase. Greeff (1996) suggested that this could lead to split sex ratios in populations with single foundress broods and partial LMC; if females are able to determine whether they have mated with a brother or an unrelated male, they should bias their progeny's sex ratio accordingly. Future studies the effects of male dispersal on fitness should allow predicting individual sex allocation decisions even quantitatively.

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References

- Charnov, E.L., Los-denHartogh, R.L., Jones, W.T. & van den Assem, J. 1981. Sex ratio evolution in a variable environment. *Nature* **289**: 27–33.
- Crawley, M. 1993. *GLIM for Ecologists*. Blackwell Scientific Publications, Oxford.
- Drapeau, M.D. 1999. Local mating and sex ratios. *Trends Ecol. Evol.* **14**: 235.
- Fellowes, M.D.E., Compton, S.G. & Cook, J.M. 1999. Sex allocation and local mate competition in Old World non-pollinating fig wasps. *Behav. Ecol. Sociobiol.* **46**: 95–102.
- Fisher, R.A. 1930. *The Genetical Theory of Natural Selection*. Oxford University Press, Oxford.
- Gauss, R. 1960. Ist *Xylosandrus germanus* Blandf. ein Primärschädling. *Anzeiger für Schadlingskunde Pflanzenschutz Umweltschutz* **23**: 168–172.
- Greff, J.M. 1996. Alternative mating strategies, partial sibmating and split sex ratios in haplodiploid species. *J. Evol. Biol.* **9**: 855–869.
- Greff, J.M. 2002. Mating system and sex ratios of a pollinating fig wasp with dispersing males. *Proc. R. Soc. Lond. B* **269**: 2317–2323.
- Green, F.G., Gordh, G. & Hawkins, B.A. 1982. Precise sex ratios in highly inbred parasitic wasps. *Am. Nat.* **120**: 653–665.
- Groschke, F. 1953. Der 'Schwarze Nutzholzborkenkäfer', eine neue Gefahr für Forstwirtschaft, Obst- und Weinbau. *Anzeiger für Schadlingskunde Pflanzenschutz Umweltschutz* **6**: 81–84.
- Hamilton, W.D. 1967. Extraordinary sex ratios. *Science* **156**: 477–488.
- Hamilton, W.D. 1979. Wingless and fighting males in fig wasps and other insects. In: *Reproductive competition, mate choice, and sexual selection in insects* (M. S. Blum & N. A. Blum, eds), pp. 167–220. Plenum, New York.
- Hardy, I.C.W. 1994. Sex ratio and mating structure in the parasitoid Hymenoptera. *Oikos* **69**: 3–20.
- Hardy, I.C.W. & Mayhew, P.J. 1998. Sex ratio, sexual dimorphism and mating structure in bethylid wasps. *Behav. Ecol. Sociobiol.* **42**: 383–395.
- Hardy, I.C.W., Dijkstra, L.J., Gillis, J.E.M. & Luft, P.A. 1998. Patterns of sex ratio, virginity and developmental mortality in gregarious parasitoids. *Biol. J. Linn. Soc.* **64**: 239–270.
- Hardy, I.C.W., Pedersen, J.B., Sejr, M.K. & Linderoth, U.H. 1999. Local mating, dispersal and sex ratio in a gregarious parasitoid wasp. *Ethology* **105**: 57–72.
- Hardy, I.C.W., Stokkebo, S., Bonlokke-Pedersen, J. & Sejr, M.K. 2000. Insemination capacity and dispersal in relation to sex allocation decisions in *Goniozus legneri* (Hymenoptera: Bethyridae): why are there more males in larger broods? *Ethology* **106**: 1021–1032.
- Heidenreich, E. 1960. Primärbefall durch *Xylosandrus germanus* an Jungeichen. *Anzeiger für Schadlingskunde Pflanzenschutz Umweltschutz* **23**: 5–10.
- Heidenreich, E. 1964. Ökologische Bedingungen für Primärbefall durch *Xylosandrus germanus*. *J. Appl. Entom.* **54**: 131–140.
- Herre, E.A. 1985. Sex ratio adjustment in fig wasps. *Science* **228**: 896–898.
- Herre, E.A., West, S.A., Cook, J.M., Compton, S.G. & Kjellberg, F. 1997. Fig-associated wasps: pollinators and parasites, sex-ratio adjustment and male polymorphism, population structure and its consequences. In: *The Evolution of Mating Systems in Insects and Arachnids* (J. C. Choe & B. J. Crespi, eds), pp. 226–239. Cambridge University Press, Cambridge.
- Ikawa, T., Shimada, M., Matsuda, H. & Okabe, H. 1993. Sex allocation of parasitic wasps: local mate competition, dispersal before mating and host quality variation. *J. Evol. Biol.* **6**: 79–84.
- Kirkendall, L.R. 1993. Ecology and evolution of biased sex ratios in bark and ambrosia beetles. In: *Evolution and Diversity of Sex Ratio in Insects and Mites* (D. L. Wrensch & M. A. Ebbert, eds), pp. 235–345. Chapman & Hall, New York.
- Klimetzek, D.K., Kiesel, K., Möhring, C. & Bakke, A. 1981. *Trypodendron lineatum*: reduction of pheromone response by male beetles. *Naturwissenschaften* **68**: 149–150.
- Krackow, S. & Tkadlec, E. 2001. Analysis of brood sex ratios: implications of offspring clustering. *Behav. Ecol. Sociobiol.* **50**: 293–301.
- Molbo, D. & Parker, E.D. 1996. Mating structure and sex ratio variation in a natural population of *Nasonia vitripennis*. *Proc. R. Soc. Lond. B* **263**: 1703–1709.
- Nadel, H. & Luck, R.F. 1992. Dispersal and mating structure of a parasitoid with a female biased sex ratio: implications for the theory. *Evol. Ecol.* **6**: 270–278.
- Nagelkerke, C.J. & Hardy, I.C.W. 1994. The influence of developmental mortality on optimal sex allocation under local mate competition. *Behav. Ecol.* **5**: 401–411.
- Norris, D.M. & Chu, H.-M. 1985. *Xyleborus ferrugineus*. In: *Handbook of Insect Rearing*, Vol. I (P. Singh & R. F. Moore, eds), pp. 303–315. Elsevier, Amsterdam.
- Nunney, L. & Luck, R.F. 1988. Factors influencing the optimum sex ratio in a structured population. *Theor. Popul. Biol.* **33**: 1–30.
- Oku, S. & Nishida, T. 2001. Presence of single-sex broods under local mate competition in *Trypoxylon malaisei* (Hymenoptera: Sphecidae): adaptation or maladaptation? *Ann. Entomol. Soc. Am.* **94**: 550–554.
- Schneider-Orelli, O. 1913. Untersuchungen über den pilzzüchtenden Obstbaumborkenkäfer *Xyleborus (Anisandrus) dispar* und seinen Nährpilz. *Zentr. Bakteriolo., Parasitenk.* **Abt. II** **38**: 25–110.
- Taylor, P.D. 1993. Female-biased sex ratios under local mate competition: an experimental confirmation. *Evol. Ecol.* **7**: 306–308.
- Taylor, P.D. & Bulmer, M.G. 1980. Local mate competition and the sex ratio. *J. Theor. Biol.* **86**: 409–419.
- Teale, S.A., Hager, B.J. & Webster, F.X. 1994. Pheromone-based assortative mating in a bark beetle. *Anim. Behav.* **48**: 569–578.
- West, S.A. & Herre, E.A. 1998a. Partial local mate competition and the sex ratio: a study on non-pollinating fig wasps. *J. Evol. Biol.* **11**: 531–548.

West, S.A. & Herre, E.A. 1998b. Stabilizing selection and variance in fig wasp sex ratios. *Evolution* **52**: 475–485.

Wilson, K. & Hardy, I.C.W. 2002. Statistical analysis of sex ratios: an introduction. In: *Sex Ratios – Concepts and Research Methods* (I. C. W. Hardy, ed.), pp. 48–92. Cambridge University Press, UK.

Wood, D.L. 1982. The role of pheromones, kairomones, and allomones in the host selection and colonization behavior of bark beetles. *Ann. Rev. Entomol.* **27**: 411–446.

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