

Sex ratios, local fitness enhancement and eusociality in the allodapine bee *Exoneura richardsoni*

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Summary

Previous studies of a facultatively eusocial allodapine bee, *Exoneura richardsoni* Rayment, indicated that high levels of cooperative nesting among close relatives seem to be maintained by benefits that lead to increases in per capita brood production. These traits could lead to local fitness enhancement, which in turn could select for female-biased sex ratios. We show here that sex investment ratios in this species are female-biased in small colony sizes, becoming progressively male-biased in larger colonies, consistent with expectations for local fitness enhancement, but not explainable by alternative models. Our results support previous suggestions that local fitness enhancement can lead to sex ratio bias in primitively social Hymenoptera, but differ from previous studies by suggesting that patterns of bias could lower selective thresholds for sib-directed altruism in small colonies, but have an opposing effect in large colonies.

Keywords: eusociality; *Exoneura*; local fitness enhancement; sex allocation; social evolution

Introduction

Female-biased sex ratios have the potential to lower selective thresholds for eusociality in haplodiploids because of the high levels of relatedness between supersisters (Hamilton, 1964; Trivers and Hare, 1976). However, empirical evidence for such facilitation has proved elusive (Grafen, 1986). Three kinds of selective agents that can produce female-biased sex ratios have received empirical study in social haplodiploids: (1) worker-mediated sex ratio bias (Trivers and Hare, 1976), (2) partial bivoltinism (Seger, 1983) and (3) bias due to non-linear relationships between investment in one sex and subsequent fitness returns through that sex (general models described in Charnov, 1982).

The role of worker-mediated sex ratio bias in the evolution of eusociality has been controversial for two reasons. First, Crozier (1977) argued that it is unlikely to be important in the very early stages of eusocial evolution, since it requires that generational overlap and worker-like behaviour had already evolved; that is, the bias arises after sib-rearing is already in place. Secondly, there was initial doubt as to whether observed sex ratio biases (Trivers and Hare, 1976) were due to worker mediation or other factors, such as local mate competition (Alexander and Shermann, 1977). However, in a comprehensive review of studies on ants, Nonacs (1986) concluded that evidence for worker-mediated bias is strong, whereas evidence for local mate competition is weak. More recent empirical studies have also suggested that female bias in some social Hymenoptera may be better explained by worker bias in brood rearing (Mueller, 1991; Packer, 1994; Sundstrom, 1994).

Werren and Charnov (1978) and Seger (1983) suggest that female bias may arise in populations where males survive long enough to mate with females of both their own generation and the subsequent generation, which may be likely for partially bivoltine life-cycles. However, there is little empirical evidence to support partial bivoltinism in social insects (but see Brockmann and Grafen, 1992).

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Non-linear fitness return models have the potential to produce female-biased ratios before worker-like behaviour has evolved, and may therefore lower the selective thresholds for sib-rearing before eusociality has actually evolved. Two non-linear models have been considered as possible sources of female-biased ratios in social insects. Local mate competition has the potential to provide female-biased investment ratios, but there is no convincing empirical evidence to indicate that it may provide such bias in primitively social species. In contrast to local mate competition, which is a diminishing returns model, Frank (1987) has discussed sex allocation in scenarios where interactions between females may lead to increased colony efficiency. Frank based his models on social spiders and concluded that selection may operate to produce female-biased allocation patterns if this produces greater efficiency in subsequent generations, and that such relationships may lead to synergism between cooperation and relatedness. Similarly, Schwarz (1988a) argued that local resource enhancement explained the strongly female-biased sex ratios in a primitively social allodapine bee, *Exoneura bicolor*, and that this was due to the benefits of cooperative nesting among sisters. Schwarz (1994) developed this argument, introducing the term 'local fitness enhancement' as a broader umbrella for positive fitness interactions among same-sex siblings, and argued that local fitness enhancement could facilitate eusociality or eusocial-like altruism in some haplodiploids. He noted that, because of the potential importance of this model for social evolution, further empirical study of sex allocation in other primitively social Hymenoptera was needed.

Allodapine bees are particularly suited to studies of factors influencing social behaviour because, with the probable exception of *Exoneura tridentata* (Houston, 1977), sociality is facultative and behavioural castes are not constrained by adult morphology (Schwarz *et al.*, 1997). Sociality in *Exoneura* encompasses a wide range of levels, including largely solitary behaviour in *E. lawsoni* (Michener, 1964), primitively eusocial behaviour in *E. variabilis* (Michener, 1965), semisociality and quasisociality in montane populations of *E. bicolor* (Schwarz, 1986), and eusocial behaviour in *E. tridentata* (P.S. Hurst, personal communication).

In *Exoneura*, multi-female colonies can arise in three ways: (1) by one or more adult daughters remaining in the nest with their mothers; (2) by groups of siblings re-using their natal nest for subsequent periods of brood rearing; and (3) by groups of females co-founding new nests. All three factors are well documented in *E. bicolor* (Schwarz, 1986; Bull, 1994). Recent work has shown that multi-female nesting is also common in *E. richardsoni*; most colonies comprise groups of females either re-using their natal nest or cooperatively founding new nests. In this species, high levels of kinship occur in both re-used ($r \pm \text{s.e.} = 0.759 \pm 0.087$) and newly founded (0.498 ± 0.152) nests (Schwarz *et al.*, 1996). Cooperative nesting appears to be selectively maintained by fitness benefits accruing to nest-mates, rather than by limited opportunities for independent nesting (Schwarz *et al.*, 1996). Schwarz (1994) argued that the same three characteristics in *E. bicolor* lead to local fitness enhancement and that they select for female-biased sex ratios. In particular, female bias should be largest in small brood sizes and less biased in larger colonies. Qualitative predictions were met in two populations of *E. bicolor* which differed in their overall levels of cooperative nesting. Schwarz *et al.* (1996) argued that similar patterns of sex allocation bias should occur in *E. richardsoni*. In this paper, we investigate sex allocation in *E. richardsoni* and examine whether it is consistent with local fitness enhancement.

Methods

Intact colonies of *E. richardsoni* were collected between 7 December 1992 and 3 February 1993 from the Dandenong Ranges National Park (latitude 37°54'10", longitude 145°22', altitude 300 m). This is the same site used by Schwarz (1986, 1987) for studies on *E. bicolor* and Schwarz (1988b)

and Schwarz *et al.* (1996) for *E. richardsoni*. In this area, *E. richardsoni* nests in the dead fronds of tree ferns, *Cyathea australis*, and less commonly in the dead pithy stems of *Senecio* spp. and *Rubus* spp. Intact nests were collected during rain or in early morning when all colony members could be assumed present. Nests were opened and adult and brood occupants recorded. When pupae were present in nests, they were sexed and freshly weighed to ± 0.5 mg. Colonies of *E. richardsoni* are occasionally infested with the inquiline bee, *Inquilina excavata* (Michener, 1983); infested nests were excluded from our analyses.

As with *E. bicolor* (Schwarz, 1986), nests of *E. richardsoni* can be categorized as either 'newly founded' or 're-used', the latter being occupied by females re-using their natal nest in subsequent years. In this study, newly founded or re-used status was determined by the condition of the lumen wall. The interior wall of re-used nests shows a characteristic darkening and blotchiness caused by decay of pollen and nectar traces from the previous year's brood-rearing activities. In contrast, the lumens of newly founded nests show a more pristine condition and pollen traces are bright yellow, rather than dark brown or black. However, in some nests, newly founded or re-used status was ambiguous.

Results

We obtained numerical sex ratio data for 19 newly founded nests, 40 re-used nests and 26 nests of unknown age, with wet pupal weights for 60 nests. Sample sizes, brood numbers, mean pupal weights and numerical sex ratios are summarized in Table 1.

Male and female pupal weights

Frequency histograms of male and female pupal weights for newly founded and re-used nests are summarized in Fig. 1. These data suggest differences in mean pupal weights between both males and females and between colonies in newly founded and re-used nests. We tested for gender and nest-age effects using a two-way ANOVA where nest age (newly founded or re-used) and pupal sex were crossed factors. Variances in pupal weight were not homoscedastic; we therefore log₁₀-transformed pupal weights and this produced homoscedasticity. The resulting ANOVA showed a significant effect of nest age ($F_{1,117} = 24.84$, $P < 0.001$) and pupal sex ($F_{1,117} = 44.76$, $P < 0.001$),

Table 1. Summary statistics for nests used in analysis of sex investment^a

Age of nest	% Nests where all brood could be sexed	Total number of sexed offspring	Mean male wet pupal weight (\pm S.E., N , n)	Mean female wet pupal weight (\pm S.E., N , n)
Newly founded	47.4	81	7.08 (0.29, 4, 31)	8.06 (0.34, 10, 21)
Re-used	15.0	200	8.12 (0.29, 9, 37)	9.52 (0.32, 11, 32)
Unknown	23.8	161	7.90 (0.22, 15, 78)	9.13 (0.20, 33, 137)
Total	28.2	442		

^a All nests were collected from the Dandenong Ranges National Park between 7 December 1992 and 3 February 1993. The mean pupal weights reported were calculated by averaging the mean pupal weight for each nest: N = number of nests where weight was recorded, n = number of individual pupae weighed. Not all sexed pupae were weighed, hence the discrepancy in sample sizes for numerical and pupal weight data.

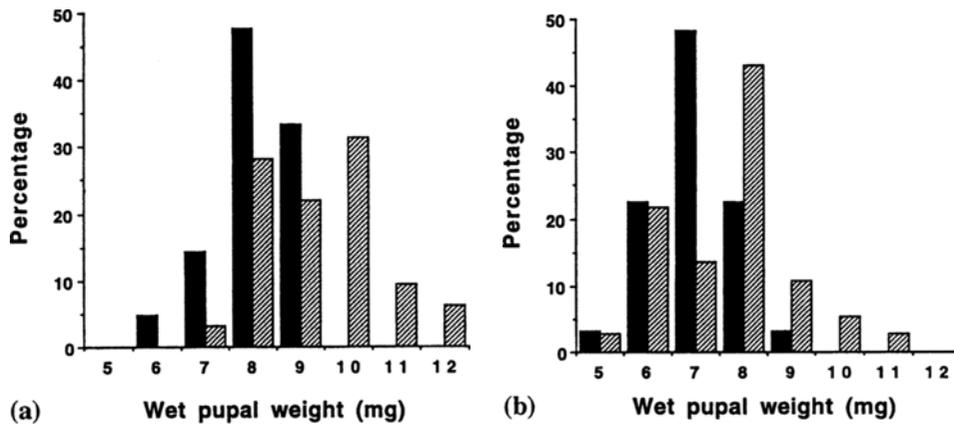


Figure 1. Percentage histograms of wet pupal weights for re-used nests (a) and newly founded nests (b). Female pupal weights are indicated by hatched bars and males pupal weights by solid bars.

but no interaction between these factors ($F_{1,117} = 3.06$, $P = 0.083$). Examination of mean pupal weights (summarized in Table 1) showed that mean pupal weights were greater for females than males, and that mean weights were greater in re-used than in newly founded nests.

Numerical and investment sex ratios

We then investigated the relationship between the total number of brood within a nest and the nest's sex ratio. In the following sections, we treat numerical sex ratios and investment ratios separately. Numerical ratios are calculated as (number of male pupae)/(total number of pupae); investment ratios are calculated as (summed wet weight of male pupae)/(summed wet weight of all pupae).

In our first set of analyses, we investigated relationships between total brood size and investment ratios. Because investment ratios are zero-truncated (many nests did not contain male pupae), we were unable to use ANCOVA with total brood size as a covariate. Consequently, we used non-parametric techniques. Because many of our sex ratio data came from nests whose age (newly founded or re-used) was not known, we began our analyses by comparing newly founded and re-used nests where age was known. We grouped our sex ratio data into five brood-size categories: 1–3, 4–6, 7–9, 10–14 and 15+ brood per nest (categories were based on all brood present within a nest, not the number of pupae). We then tested whether investment ratios differed between these two nest types using the Mann-Whitney U -test for each brood size category. Analyses suggested that for the smallest brood size category, investment ratios may be less female-biased in new than in re-used nests ($n_1 = 6$, $n_2 = 1$, $Z = -2.45$, $P = 0.014$), although the sample sizes were very small; all other comparisons were non-significant ($P > 0.2$). However, such repeated tests should be subjected to sequential Bonferroni adjustment of alpha levels (Rice, 1989), giving $\alpha = 0.01$. This adjusted α level suggests no significant differences for any brood size category.

We subsequently combined all nests in our study, regardless of age status. Brood sizes were categorized using the previous size groups, and the mean and standard error of the sex investment ratio was calculated for each brood size category. These are shown in Fig. 2 and suggest that sex investment ratios vary positively with brood size, with strongly female-biased ratios in smaller brood sizes and male-biased ratios in larger colonies. We examined this pattern statistically using Spearman's correlation coefficient between brood size and investment ratio, treating each nest as

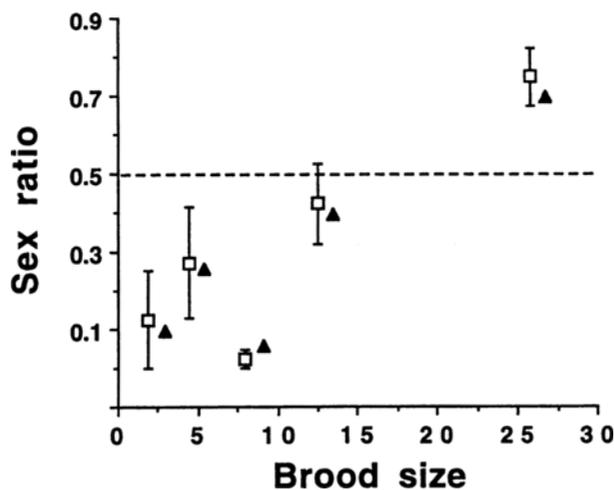


Figure 2. Mean sex investment ratios (\pm s.e.) (\square) and population-wide investment ratios (\blacktriangle) as a function of the number of brood per colony. Colonies were grouped into five brood size classes: 1–3, 4–6, 7–9, 10–14 and 15+ brood per nest. Mean investment ratios were calculated as mean over each colony in the sample; population-wide ratios were calculated as $(\sum \text{all male pupal weights})/(\sum \text{all pupal weights})$.

an independent data point. The results indicate a highly significant positive relationship between these variables ($r_s = 0.490$, $P = 0.002$). We also calculated numerical sex ratios for each brood size category as a mean of individual nest ratios. These were virtually identical to the investment ratios and are not shown here. At first this seems surprising, given the differences in pupal weights between males and females; however, many colonies, especially small ones, contained pupae of only one sex, and such colonies will have ratios of either one or zero for both numerical and investment ratios. When averaged over all colonies, numerical and investment ratios will therefore tend to be similar. As a final check that mean investment ratios as calculated above are indicative of population-wide trends, we calculated an 'overall' investment ratio for each brood size category as $(\sum \text{all male pupal weights})/(\sum \text{all pupal weights})$. These ratios are also shown in Fig. 2, but of course have no associated standard errors. These ratios agree closely with the mean investment ratios and further suggest a strong positive relationship between brood size and investment ratio.

Opisthandry and protandry

Because allodapine bees rear their brood progressively, it is not possible to remove larval instars from the nest and rear them through to pupation. *E. richardsoni* exhibits a range in developmental stages of immatures within most colonies, so we were not able to sex all brood within each nest (Table 1). It is therefore possible that some sex ratio bias apparent in the above results could be explained by unsexed brood. Indeed, there is a weak suggestion that the number of unsexed brood in a nest may be related to numerical sex ratio ($r_s = 0.300$, $P = 0.071$), although this relationship is not statistically significant. If such a relationship does actually occur, it could be for two reasons: (1) males eclose later than females (i.e. opisthandry) and are therefore under-represented among pupae when there are still substantial numbers of brood at larval stages; or (2) female bias is greatest in small broods, which by necessity must contain fewer unsexed brood.

We examined the possibility of opisthandry using the following argument. If males tend to eclose later than females, then samples taken earlier in the year, when there are greater proportions of immatures which cannot be sexed, should show more female-biased ratios than samples taken later

in the season. We therefore compared the distribution of numerical sex ratios for our three main samples containing pupae or very recently eclosed callow adults. These samples were combined into the following sample groups: (1) 18–23 December 1992 ($n = 18$ colonies); (2) 3 January 1992 ($n = 17$); and (3) 16–22 January 1993 ($n = 37$). The samples sizes in this test were larger than in previous estimates of sex investment because they included some nests where pupae were not weighed, or where sexable brood were very newly eclosed adults where pupal weight could not be recorded. We then tested for a temporal (i.e. sample group) effect on the distribution of colony sex ratios using a Kruskal–Wallis non-parametric ANOVA. This indicated no sample effect (χ^2 corrected for ties = 2.041, d.f. = 2, $P = 0.360$). The mean numerical sex ratios for each of these three samples, weighting colonies equally, were $r = 0.56$, 0.46 and 0.40 respectively. Consequently, although numerical ratios do not change significantly over time, there may be a trend suggesting that males eclose earlier than females. Therefore, we conclude that the pattern of increased female investment in smaller brood sizes is unlikely to be due to opisthandry. Indeed, if the seasonal trend for decreasing proportions of males (suggesting protandry) is real, our numerical ratios could slightly underestimate the degree of female bias, particularly towards the end of the brood development period. This may have implications for selective thresholds for sib-rearing.

Mean pupal weight as a function of colony size

We also examined whether mean wet pupal weight is correlated with the number of adult females per nest. However, rather than use adult females per nest at the time of sampling, we used total number of brood; this may be a better indicator of initial colony size than the number of females per nest at the time of brood maturity (Schwarz *et al.*, 1996). This is because cumulative mortality of adult nest-mates is likely to be high by the time that brood begin pupation and hence confound initial adult/brood relationships. We used ANCOVA with nest age (newly founded or re-used) and sex as treatments, and total brood size as the covariate. Bartlett–Box and Cochran's C tests did not indicate heterogeneity of variances ($P > 0.6$). ANCOVA with simultaneous entry of treatments and the covariate indicated significant effects of nest age ($F_{1,29} = 14.69$, $P = 0.001$) and sex ($F_{1,29} = 15.53$, $P < 0.001$), no interaction between these factors ($F_{1,29} = 0.047$, $P = 0.822$) and no covariate effect ($F_{1,29} = 2.79$, $P = 0.106$). Mean pupal weights were greater for females than males, and greater in re-used nests than newly founded nests (Table 1, Fig. 1). Consequently, our data do not suggest that mean pupal weight within nests is a function of the total number of brood produced.

Brood sizes and the future numbers of cooperating sisters

Local fitness enhancement may lead to selection for female-biased investment when bias leads to increasing fitness returns through cooperation between the resulting adult daughters. Bias is only expected if optimal numbers of daughters cannot be produced when investment ratios are unbiased. Therefore, it is important to determine whether some colonies produce brood sizes that would not allow optimal returns through female investment without biased sex ratios. Data presented by Schwarz *et al.* (1996) suggest that, during periods of larval rearing, *per capita* brood production peaks at colony sizes of approximately three females per nest. These data were obtained in early spring to summer, approximately 10 months after adult eclosion occurs. It is likely that substantial adult female mortality occurs during the intervening period, so that provision of optimal numbers of females in early summer would require greater numbers of females to be produced when the brood are reaching maturity in the preceding summer.

We summarize brood sizes (calculated as the sum of all immature stages) in colonies collected from 3 to 22 January 1993 in Fig. 3. Brood size data from earlier samples were not included

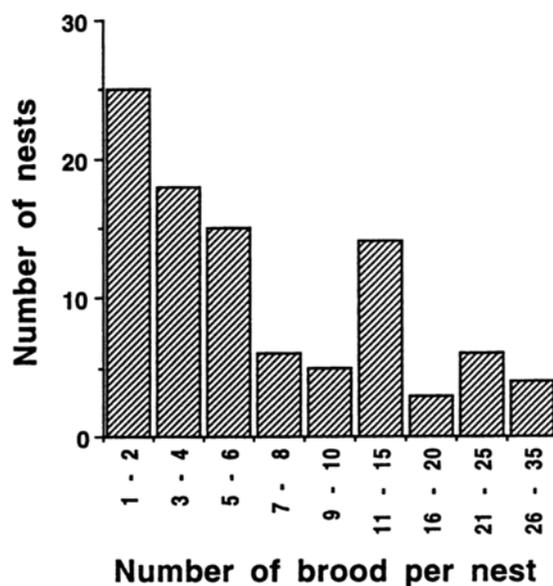


Figure 3. Total number of brood per nest in newly founded and re-used nests. Data are taken from nests collected from 3 to 22 January 1993 when brood were reaching maturity.

because these samples are less likely to reflect final numbers of brood reared to maturity; unpublished data indicate that in southern populations of *Exoneura* species, the number of brood per nest gradually decreases as brood rearing and concomitant larval mortality progress (M.P. Schwarz, unpublished, 1983–93). Our data indicate that there are many small colonies which would be unable to produce optimal numbers of daughters (≥ 3) for cooperation in the following summer without female-biased investment.

Discussion

Our finding that mean pupal weights are smaller in newly founded nests than in re-used nests is similar to findings for the sympatric population of *Exoneura bicolor* (Schwarz, 1994). Greater pupal weights in re-used nests could be due to the longer period of time available for brood provisioning (allodapines rear their brood progressively), since larvae eclose 2–3 months earlier than in newly founded nests, allowing more extended opportunities for feeding. This could suggest some benefit for females to remain within their natal nests rather than disperse as foundresses. We also found that, in both newly founded and re-used nests, female pupal weights tend to be greater than male weights. Schwarz (1994) found that in montane populations of *E. bicolor*, where males reach adult eclosion later than females, mean male pupal weights are larger than for females. In contrast, in a heathland population of *E. bicolor*, where males and females reach adult eclosion at the same time, mean male and female pupal weights do not differ (Schwarz, 1994). Covariance between eclosion times and pupal weights could be related to the allodapine trait of progressive rearing, in that pupal weight could reflect the duration of time spent feeding, which in turn could influence the timing of pupation (Schwarz and Woods, 1994). That is, individuals that feed for longer will be heavier and eclose later.

Our most interesting results are that sex ratios in *E. richardsoni* are frequently female-biased and that bias varies with brood size. Investment and numerical ratios in *E. richardsoni* are most

strongly female-biased in small brood sizes and become less biased or male-biased as brood sizes increase. This relationship also occurs in montane and heathland populations of *E. bicolor*, and Schwarz (1994) argued that such patterns are consistent with local fitness enhancement but not with other potential sources of investment bias. These arguments also apply to *E. richardsoni* and we will briefly outline them here:

1. Local fitness enhancement can arise if the mean fitness of daughters increases with the number of daughters able to cooperate in subsequent brood rearing, and if brood sizes are sometimes so small that optimal numbers of daughters can only be produced by skewing investment away from sons. The need for such skew is more likely to occur in small than large brood sizes, and this should lead to a negative relationship between female bias and total number of brood. Schwarz *et al.* (1996) have shown that in *E. richardsoni*: (a) relatedness among cooperating females is moderately high to very high, indicating that cooperating females are mostly or entirely comprised of sisters; (b) colony *per capita* output increases with the number of cooperating females. Our results show that smaller colonies would be unable to produce an optimal number of daughters without biasing investment towards females, but larger colonies could produce an optimal number of daughters. Consequently, *E. richardsoni* meets the requirements for local fitness enhancement to operate and we would expect bias to occur in small colonies, but not large colonies.

2. Local mate competition (Hamilton, 1967, 1979) could arise if males mate close to their natal nest, or brothers compete for limited resources. However, local mate competition will select for increasing female bias as brood size increases; this trend is opposite to that seen here for *E. richardsoni*.

3. Local resource competition (Clark, 1978) could select for male-biased ratios in larger brood sizes if sisters compete with each other for limited resources, such as nesting sites. This could potentially produce female bias in small broods because the excess of males in larger broods will increase the value of those daughters that are not limited by resource availability. However, Schwarz *et al.* (1996) have shown that *per capita* brood production in *E. richardsoni* tends to increase, rather than decrease, as colonies become larger.

4. Frank and Crespi (1989) suggested that if offspring size increases with the number of cooperating parental-generation females, and if larger body size is more advantageous for females than males, then larger colonies should bias investment towards females. The same argument could also apply to males, if male body size enhances reproductive success. However, our results do not indicate that pupal weight varies with colony size independently of colony age. Schwarz *et al.* (1996) found that colonies in re-used nests are larger than in newly founded nests, and we have shown here that mean pupal weights are greater in re-used nests. However, we found that investment ratios for different brood size categories did not differ between colonies in newly founded and re-used nests. Rather, it seems that differences in overall investment ratios between new and old colonies are due to differences in the total number of brood produced by these colony types.

5. Worker-mediated sex allocation bias arises when worker-like individuals are able to choose between investment in sexes that are less or more closely related to them. Such asymmetry arises when the relationship between workers and brood is one of sibship. However, in *E. richardsoni*, potentially worker-like adult females belong to the same generation as reproductive females, and therefore there is no indirect fitness benefit to be gained by biasing the sex ratio.

6. With respect to the partial bivoltinism model (Seeger, 1983), in both *E. bicolor* and *E. richardsoni* some large and old colonies may show patterns of egg production that are so protracted, that older brood reach adult eclosion at a time when some younger brood are still at a early developmental (feeding) stage (Schwarz, 1994; Schwarz *et al.*, 1996). Although this gives the appearance of bivoltinism, the more developmentally advanced female brood do not reproduce until the following season, so that the populations are effectively univoltine.

Consequently, we conclude that, as with *E. bicolor*, sex ratio patterns in *E. richardsoni* are consistent with local fitness enhancement and not explainable by other potential sources of sex ratio bias. It is not surprising that local fitness enhancement might operate in *E. richardsoni*, since it resembles *E. bicolor* in terms of nesting substrates, colony foundation patterns, re-use of natal nests, augmentation of *per capita* brood production, and intra-colony relatedness. However, sex ratio patterns for *E. richardsoni* differ from the sympatric population of *E. bicolor*, in that sex ratios become male-biased for the largest brood sizes in the former but not the latter species (Schwarz, 1994). It is likely that this is linked to the number of females cooperating in nest use. Mean and maximum colony sizes in *E. richardsoni* are smaller than in *E. bicolor*, and *per capita* brood production peaks at smaller colony sizes in the former species than the latter. This suggests that the benefits of cooperation might saturate with a fewer number of daughters in *E. richardsoni* and that selection might operate on large colonies to produce male-biased ratios to exploit the underproduction of males by small colonies. Such compensatory ratios are also expected under other models predicting female bias for some colony types in hymenopteran species (Stubblefield and Charnov, 1986; Godfray and Grafen, 1988), and can potentially lead to what Grafen (1986) termed 'split sex ratios'. We discuss the implications of such sex ratio variance in *E. richardsoni* below.

Our results provide further evidence that local fitness enhancement may be able to produce female-biased investment ratios in facultatively social haplodiploids. However, if such a source of female bias is to facilitate eusociality, life-cycles must permit the possibility for older, adult siblings to invest in younger, immature siblings at the expense of investment in their own offspring. This kind of investment is precluded in montane populations of *E. bicolor* because synchrony of brood development largely precludes the adult eclosion of older daughters when younger brood are still present and require rearing (Schwarz, 1986). However, Schwarz *et al.* (1996) have shown that a small proportion of *E. richardsoni* colonies contain both newly eclosed daughters and younger immature stages that still require feeding, and that such overlap can occur in both large and small colonies. Consequently, it is possible that in some montane nests of *E. richardsoni*, older adult daughters may be able to rear younger siblings, and sex ratio biases in smaller colonies could facilitate such sib-rearing.

Grafen (1986) argued that split sex ratios may lead to a situation where sib-rearing is facilitated in some colonies (where sex allocation is female-biased), but a reverse situation occurs in others (where allocation is male-biased). Montane populations of *E. richardsoni* could potentially fall into this situation, in that sex allocation is female-biased in small colonies and is unbiased or male-biased in large colonies. Our data suggest a (statistically non-significant) trend for protandry. If such a trend were to be real, it would have the effect of increasing female bias among larvae in the latter part of the brood-rearing period. Opportunities for sib-rearing are greatest at this time because of the increased likelihood of co-existence of recently emerged adults and larvae that still require feeding.

In conclusion, our results provide further evidence that local fitness enhancement can lead to female-biased sex allocation in primitively social haplodiploids. Whether or not such a bias can facilitate eusociality depends on the pattern of bias as well as the existence of opportunities for sib-rearing. In *E. richardsoni*, opportunities for sib-rearing do occasionally arise and protandry could serve to augment female-biased ratios at times when sib-rearing opportunities are more likely.

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