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Sex ratios, virginity, and local resource enhancement in a quasisocial parasitoid

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Abstract

Sclerodermus harmandi (Buysson) (Hymenoptera: Bethylidae) is an economically beneficial species of parasitoid wasp that has an unusual level of sociality: groups of female foundresses reproduce on a single host and exhibit cooperative post-ovipositional brood care. The beneficial effects females have on each other's reproductive success provide, via the theory of local resource enhancement (LRE), an explanation for their female-biased progeny sex ratios, which is part of the same framework for understanding sex-ratio evolution as the more often invoked theory of local mate competition (LMC). Here, we show that *S. harmandi* sex ratios are overdispersed, with high variance largely attributable to the common occurrence (60%) of developmental mortality. Developmental mortality is also positively associated with the proportion of broods which contain only females at emergence (virgin broods). Virginity is more common when broods are produced by fewer foundresses. Virginity is expected to be disadvantageous under LRE, as it is under LMC, but theory for LRE is less extensively developed. We suggest approaches for the development of LRE theory, in particular using models of 'population elasticity' in which the intensity of kin competition is reduced because extra resources are available to local populations that are more cooperative. For *S. harmandi*, such extra resources may include large hosts that can only be successfully utilised if multiple foundresses cooperate.

Introduction

Sex ratios in many species of gregarious and quasi-gregarious parasitoid wasps are female biased. In the vast majority of cases, this can be explained by the theory of local mate competition (LMC) (Hamilton, 1967, 1979; Godfray, 1994; West, 2009). LMC theory predicts that female-biased sex ratios are selected for when the offspring produced by one or a few mothers, termed foundresses, mate among themselves before the female offspring disperse away from the natal group, a common feature of many parasitoid species (Hamilton, 1967, 1979; Godfray, 1994; Hardy, 1994; Godfray & Cook, 1997). LMC theory

further predicts that bias will be less extreme when more foundresses contribute offspring to the mating group and such facultative adjustment of sex ratios is observed in empirical and comparative studies of parasitoids (Charnov, 1982; Godfray, 1994; Hardy, 2002; Hardy et al., 2005; West, 2009). In short, LMC theory has been a major key to the understanding of parasitoid sex allocation (Charnov, 1982; Godfray, 1994; West, 2009; a critique of this success is provided by Orzack, 2002).

There are, however, some species of parasitoid wasps in which observed sex ratios are more biased than predicted by current LMC theory and/or do not vary with foundress numbers according to LMC predictions (Shuker et al., 2004, 2005; Matthews et al., 2009; Innocent et al., 2010; Abe et al., 2014; Tang et al., 2014). For instance, Abe et al. (2014) recently highlighted that the extremely female biased (1–5% males), and relatively invariant sex ratios in the genus *Melittobia*

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(Hymenoptera: Eulophidae) are inexplicable using current sex-ratio theory. A concurrent publication by Tang et al. (2014) on parasitoids in the genus *Sclerodermus* (Hymenoptera: Bethylidae) similarly reported highly female-biased sex ratios, and although sex ratios increased significantly with foundress number, the effect was not strong. Like Abe et al. (2014), Tang et al. (2014) concluded that the observed sex ratios could not be explained by LMC but in contrast to Abe et al. (2014) it was concluded that current sex-ratio theory does provide an explanation: *Sclerodermus harmandi* (Buysson) is a quasisocial parasitoid (groups of females reproduce on a single host and exhibit cooperative brood care) and the beneficial effects females have on each other's reproductive success is expected to lead to female bias due to local resource enhancement (LRE), wherein an excess production of the sex that leads to a greater increase in fitness of the parents or their offspring is favoured (Taylor, 1981; West, 2009). This was the first report of LRE operating among parasitoid wasps and one of only a few reports on LRE within the Hymenoptera (Schwarz, 1988; Martins et al., 1999; Harradine et al., 2012). Although it is part of the same conceptual framework for understanding the evolution of sex allocation strategies, theory for LRE has not been as extensively developed as LMC theory (Taylor, 1981; West, 2009; Gardner & Ross, 2013). In consequence, expectations for sex-ratio means and variance and patterns of brood sexual composition in relation to other life-history variables such as foundress number, clutch size, or developmental mortality, are less well defined than under LMC (e.g., Green et al., 1982; Werren, 1983; Griffiths & Godfray, 1988; Heimpel, 1994; Hardy et al., 1998).

In this companion paper to Tang et al. (2014), we summarise the pertinent biological details of *S. harmandi* and then, using the original data set of Tang et al. (2014), we further explore how its sex ratios are affected by foundress number and group size and also how developmental mortality and group size influence the incidence of virgin (all-female) broods. We go on to suggest how theory for LRE and quasisociality might be developed by consideration of the biology of *Sclerodermus* spp.

Biology of *Sclerodermus harmandi*

Sclerodermus harmandi is a gregarious ectoparasitoid of wood-boring cerambycid beetle larvae and is used extensively in biological control of coleopteran forest pests in China (Chen & Cheng, 2000). These beetles damage trees directly by feeding on them and also vector the extremely damaging pine wood nematode *Bursaphelenchus*

xylophilus (Steiner & Buhrer) Nickle which causes pine wilt disease (Yang et al., 2014).

In marked contrast to the aggressive behaviour observed when adult females in some other genera of the Bethylidae compete for exclusive access to a host (Hardy et al., 2013), *Sclerodermus* females appear to engage cooperatively in host suppression, oviposition, and offspring care (Bridwell, 1920; Wheeler, 1928; Kühne & Becker, 1974; Mamaev, 1979; Casale, 1991; Hu et al., 2012; Wu et al., 2013), often producing very large broods of offspring (>100). Using *S. harmandi*, Tang et al. (2014) demonstrated experimentally that individual females increase their reproductive success by jointly exploiting large hosts, thus identifying the selective advantage of their quasisocial behaviour.

Some *Sclerodermus* species exhibit extremely female-biased sex ratios (Griffiths & Godfray, 1988; Hardy & Mayhew, 1998; Li & Sun, 2011; Hu et al., 2012; Tang et al., 2014). Although most offspring groups consist mainly of females, some consist entirely of females ('virgin broods'). In *S. harmandi*, when males are present they are relatively short-lived and typically mate with maturing brood-mate females when these emerge or prior to their emergence by chewing entrances into their cocoons (Zhang & Tian, 1985; Hu et al., 2012).

Materials and methods

Sclerodermus harmandi was cultured at the Forestry Institute of Jiangsu Province, China, where it is mass-produced for release as an agent of biological control of *Monochamus alternatus* Hope (Coleoptera: Cerambycidae). *Monochamus alternatus* hosts were collected from forests in Liyang County (31.4°N, 119.4°E), China, during the winter of 2011, and maintained at 10 °C for 1–2 months before use in experiments. The foundresses used in the experiment were collected from laboratory colonies where females had been mated with siblings upon emergence. In the treatments with more than one foundress, each foundress was obtained from a different parasitised host. Laboratory experiments were conducted at 25 °C and 60–80% r.h.

The number of adult female *S. harmandi* introduced into a glass vial (1.0 cm diameter, 5.0 cm long) with one *M. alternatus* larva was varied (1, 2, 4, 6, or 8). The numbers of eggs laid onto each host, and the numbers of adult male and female *S. harmandi* offspring produced, were recorded. There were 220 replicates overall, with between 30 and 60 replicates for each number of foundress females. However, in about half of the replicates, foundresses failed to produce any offspring; this was especially common when foundress group sizes were small and/or hosts were large (Tang et al., 2014), and our current analysis is

restricted to those replicates in which some *S. harmandi* offspring matured. Of the 112 replicates producing surviving offspring, one brood produced by a single foundress, consisted of eight males only, probably because the foundress had not mated. Another offspring group, produced by two foundresses, had an unusually large number of males (19/44 offspring), suggestive that one of the foundresses was unmated. Following procedures adopted by prior studies of bethylid sex ratios (e.g., Hardy & Cook, 1995), these two replicates were excluded from the reported analyses. The inclusion of the two-foundress replicate would not have led to any different conclusion. There remained 110 offspring groups for analysis.

Data were mainly explored using logistic analysis (generalised linear modelling) in the GENSTAT statistical package (v.14.1; VSN International, Hemel Hempstead, UK). All statistical testing was two-tailed. Sex ratios were expressed as the proportion of adult offspring that were males. When binary data were grouped, we assumed quasi-binomially distributed errors to counter the effects of overdispersion (Wilson & Hardy, 2002). Sex-ratio variance and variance in mortality were each quantified using two descriptive statistics, the Heterogeneity Factor (HF = residual deviance/residual degrees of freedom; West & Herre, 1998) and the variance ratio R (= variance in numbers observed/expected binomial variance; Nagelkerke & Sabelis, 1998) and analysed using the Meelis test statistic U, which tests for departures from binomial distribution (significant large negative values indicate underdispersion and large positive values overdispersion; Nagelkerke & Sabelis, 1998; Krackow et al., 2002). Values of R and U are calculated from sums of separate calculations from each offspring group size and we note that our data consist of small numbers of clutches or broods spread across a large range of group sizes. Although the approach we adopt is the best currently available, it is known that when data consist of many small sub-samples estimations can be distorted such that, for instance, larger values might not correspond to stronger deviations from expected variances (Krackow et al., 2002).

Results

Among the 110 broods in which some offspring matured, overall 61% offspring had died during development (mean $\pm$ SE egg-to-adult mortality = 0.614 ± 0.021), and mortality had variance that was not significantly greater than binomial (HF = 28.3; Meelis test: R = 12.61, U = 85.43, P = 1.0). It is already known that developmental mortality is unrelated to host weight, the number of eggs laid on a host, or the number of foundress females present (Tang et al., 2014). Unsurprisingly, the size of the

offspring group at maturity was negatively correlated with egg-to-adult mortality (Spearman's rank correlation: r = -0.757, t = 12.12, d.f. = 109, P<0.001). The sex ratios of groups of maturing adults were typically strongly female biased (mean proportion of offspring that were male = 0.069 ± 0.004 – note that an incorrect mean value of 0.032 was reported by Tang et al., 2014). Sex-ratio variances were overdispersed (HF = 1.48; Meelis test: R = 0.7208, U = 2.33, P = 0.020).

Sex ratios decreased weakly with adult offspring group size (Logistic ANCOVA corrected for overdispersion: $F_{1,109}$ = 5.55, P = 0.02, % deviance explained = 4.75; Figure 1) and increased weakly with foundresses number ($F_{4,109}$ = 5.63, P<0.001, % dev = 4.81; Figure 1). There was no significant interaction between these two main effects ($F_{4,109}$ = 1.08, P = 0.37). The number of males present in offspring group increased with group size ($F_{1,108}$ = 80.97, P<0.001, % dev = 42.8). Sex-ratio variance, quantified by HF, was not correlated with the number of foundresses producing the brood (one: HF = 1.64, n = 9; two: HF = 0.816, n = 20; four: HF = 1.24, n = 31; six: HF = 0.595, n = 21; eight: HF = 2.25, n = 28; Spearman's rank correlation: r = 0.100, P = 0.20).

Sex ratios were significantly higher among broods that had experienced higher proportions of developmental mortality ($F_{1,108}$ = 10.21, P = 0.002, % dev = 8.63;
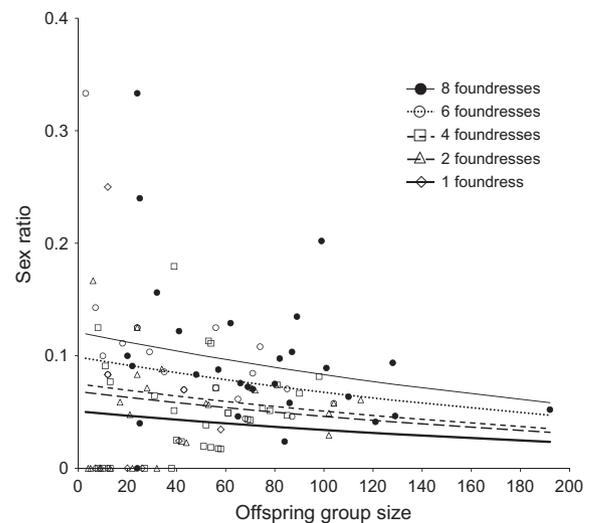

Figure 1 Relationships between sex ratio (proportion of adult offspring that were males) and brood size at emergence, for broods founded by 1–8 adult female *Sclerodermus harmandi*. Fitted logistic regression lines are provided for each foundresses group. Note that for visual clarity the fitted logistic regression line for 2-foundresses broods is slightly displaced below the 4-foundresses regression line.
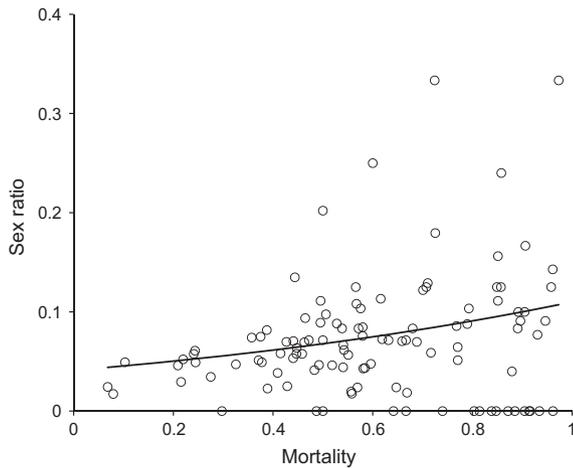
Figure 2 The relationship between sex ratio at adult emergence (proportion males) and the proportion of developmental mortality in offspring groups of *Sclerodermus harmandi*. The fitted line is from logistic regression.

Figure 2). Sex-ratio variance was significantly higher among broods that experienced the highest percentages of developmental mortality ($\leq$24.9% mortality: HF = 0.46, n = 9; 25–49.9%: HF = 0.953, n = 27; 50–74.9%: HF = 2.08, n = 42; $\geq$75%: HF = 1.13, n = 32; Spearman's rank correlation: r = 0.800, P = 0.021).

About 15.3% of adult offspring groups consisted of female offspring only. The probability of an offspring group consisting only of females was lower among larger offspring groups (G_1 = 32.39, P<0.001, % dev = 34.0); no broods of more than around 50 maturing offspring contained females only (Figure 3). The probability of all-female offspring groups was higher when developmental mortality was higher (G_1 = 20.68, P<0.001, % dev = 21.7) and when foundresses number was lower (G_4 = 5.26, P<0.001, % dev = 22.1; Figure 4). The interaction between these two variables was not significant (G_4 = 0.19, P = 0.95).

Discussion

The highly female-biased sex ratios observed in *S. harmandi* appear to be due to LRE (the mutually beneficial foundress–foundress interactions contribute to the value of female offspring; Taylor, 1981) rather than to the more usual explanation of LMC (Hamilton, 1967). We first consider the brood compositions observed in *S. harmandi* with regard to current literature and then suggest an approach for how models can be developed to better evaluate the assertion that *S. harmandi* sex ratios have principally evolved due to LRE.
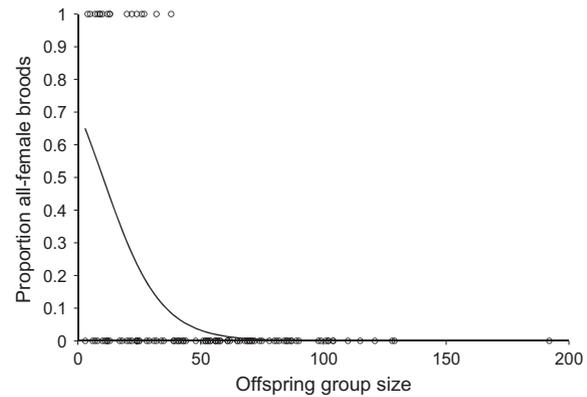

Figure 3 The influence of offspring group size at adult emergence on virginity (proportion of broods that were all-female) in *Sclerodermus harmandi*. The fitted line is from logistic regression.
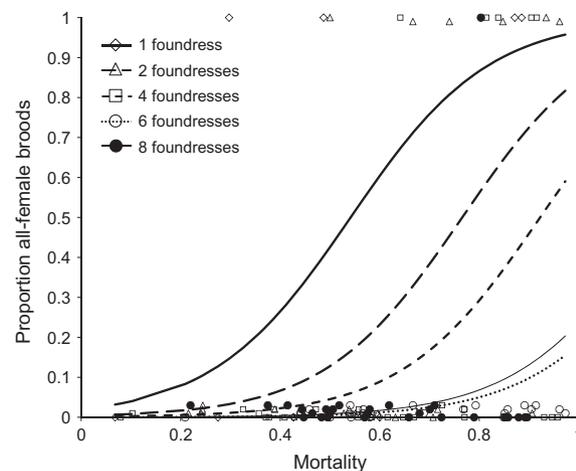

Figure 4 The influence of foundress number and mortality on virginity (proportion of broods that were all-female) in *Sclerodermus harmandi*. The fitted lines are based on logistic analysis of covariance, treating foundress group size as a discrete factor.

Current evidence suggests that *Sclerodermus* foundresses tend to each lay a small number of male eggs in every clutch (Mamaev, 1979; Liu et al., 2011; Tang et al., 2014). Mamaev (1979) reported that 1–2 males are laid among the first produced eggs in each clutch (a pattern which may be associated with final clutch size uncertainty; Hardy, 1992). Similarly, Tang et al. (2014) estimated that on average 0.8 adult males are produced per *S. harmandi* foundress, suggesting that (given 61% developmental mortality) each foundress lays an average of 1.31 male eggs in each clutch. Furthermore, the brood sex ratios produced by single foundresses are typically less female biased than the reciprocal of brood size (one male per brood is

expected under single-foundress LMC in the absence of developmental mortality; Green et al., 1982; Griffiths & Godfray, 1988; Nagelkerke & Hardy, 1994), due to mothers laying more males in larger broods than in smaller broods. Weak declines in sex ratio with increasing brood size, as observed in *S. harmandi*, or a lack of relationship between sex ratio and brood size, have been reported for the secondary sex ratios (at adult emergence) of most examined sub-social bethylids in which broods are produced by a single foundress and, as observed for *S. harmandi*, are typically associated with an increase in the number of males per brood as brood size increases (Hardy et al., 1998). However, examination of the primary sex ratio (at oviposition) in one sub-social species has shown that developmental mortality may alter or obscure initially present relationships (Khidr et al., 2013). Given that developmental mortality among *S. harmandi* offspring is more common than is observed in many gregarious parasitoids (Hardy et al., 1998; Kapranas et al., 2011), empirical assessment of the primary sex ratio is a desirable future step, especially as such evaluation could potentially also reveal the relative contributions of individual foundresses to each offspring group (Khidr et al., 2014) and thus provide insights into whether the apparently cooperative reproduction observed is in fact tempered by reproductive dominance and skew (Tang et al., 2014).

Sex-ratio variances were overdispersed, most likely due to the scrambling effect developmental mortality has on initially less variable group sexual compositions, as observed within and across other species of gregarious parasitoids (Hardy et al., 1998; Kapranas et al., 2011; Khidr et al., 2013). Theory for sex-ratio variance under LRE is not well developed; but under LMC, selection for low sex-ratio variance can be less stringent in multiple-foundress cases compared to single-foundress cases (Nagelkerke, 1996); our rather limited data do not suggest a relationship between variance and foundress number. Furthermore, selection for sex-ratio variance is expected to be related to the frequency at which different numbers of foundresses naturally occur (West & Herre, 1998) but there are very few field data on the distribution of foundress numbers in *S. harmandi* populations. The less female-biased sex ratios in broods which experienced higher proportions of mortality is suggestive of higher mortality among developing females than among males, which may be attributable to female larvae requiring more resources than male larvae to grow large enough for successful pupation (Nagelkerke & Hardy, 1994), and indeed *S. harmandi* females are larger than males (He, 2004), and could also result from sexually differential care by brood-tending foundresses.

Although the current evidence suggests that developmental mortality increases brood sex-ratio variance in *S. harmandi*, there is much stronger evidence for an association between mortality and a related aspect of brood sexual composition: all-female ('virgin') broods, which can result from all males in a brood dying before maturity. Under single-foundress LMC, hymenopteran parasitoids maturing in all-female broods are expected to have low fitness due to being constrained to subsequently produce male-offspring only, and these will have no reproductive opportunities unless some inter-group dispersal and non-local mating occurs (Green et al., 1982; Godfray, 1990; Heimpel, 1994; Nagelkerke & Hardy, 1994; Hardy et al., 1998, 2005). Virgin females co-founding broods with mated females can obtain fitness via their sons mating locally with the offspring of the co-foundresses, but are not able to produce offspring sex ratios close to the unconstrained optima and are thus also disadvantaged (Godfray, 1990; West, 2009). Despite the disadvantage of virginity, virgin broods are predicted to arise under LMC due to the trade-off between minimising the number of male offspring produced and insuring against all the males dying before maturity (Green et al., 1982; Heimpel, 1994; Nagelkerke & Hardy, 1994; West et al., 1997). In general accord with these expectations from LMC theory, virgin *S. harmandi* broods were more common when brood sizes were smaller, when mortality was more prevalent, and also when broods were produced by fewer foundresses. Similar patterns have been observed in gregarious parasitoids with LMC (Hardy et al., 1998; Kapranas et al., 2009, 2011) and across fig wasp species with LMC (West et al., 1997). Furthermore, the relationships between the prevalence of virginity and the prevalence of mortality for *S. harmandi* broods produced by one or two foundresses resemble explicit predictions for the one- and two-foundress cases under LMC (Figure 1d in West et al., 1997). Whether these apparent matches to the predictions of 'extended' LMC theory (West, 2009) counter the assertion (Tang et al., 2014) that 'classical' LMC does not explain sex ratios in *S. harmandi* is currently unclear and may require the development of equivalent theory for virginity under LRE.

In mixed-sex broods, with female-biased sex ratios, current evidence suggests that local (within brood) mating is the norm. Given a mean sex ratio of 0.069, individual males will typically mate with around 14 females and evidence from other bethylids suggests that they will have sufficient supplies of sperm with which to successfully inseminate all the females (Hardy et al., 2005), although at high-mating frequencies males are expected (Abe & Kamimura, 2015) and observed (e.g., in the bethylid *Goniozus legneri* Gordh; Gordh et al., 1983) to transfer smaller ejaculates. The occurrence of virgin broods suggests that non-local mating, via male dispersal, may also occur, due to the selection pressure on males to acquire more mates (e.g., by

immigrating into virgin broods) and that females may be receptive due to the selective advantage of being able to produce female-biased offspring sex ratios. Male *S. harmandi* typically possess wings, which is suggestive of male dispersal but there is a lack of direct evidence for the mating structure of *Sclerodermus* populations (as with other bethylids; Hardy & Cook, 1995; Hardy & Mayhew, 1998; Hardy et al., 2000).

After maturing around the remains of a host, female *Sclerodermus* must disperse to forage for a fresh host. Females typically do not possess wings and so forage by walking. It is not currently known whether females disperse as individuals or as cohesive groups, although reports that females overwinter in groups in host-made tunnels or cavities in trees (Zhang & Tian, 1985; Xu et al., 2002) do suggest group cohesion. The direct selective advantage to cohesive dispersal and foraging would be that it would promote successful reproduction on large hosts (Tang et al., 2014). Cohesive dispersal would also enhance the relatedness between foundresses, which may in turn select for more strongly biased sex ratios (and other aspects of social behaviour) compared to situations when foundresses were not closely related (Taylor & Crespi, 1994; Shuker et al., 2004; Gardner et al., 2009; Abe & Kamimura, 2012). We, however, speculate that females maturing in virgin broods may not disperse as cohesively as females from mixed-sex broods, due to the expected mating opportunities to a virgin foundress's sons being greater when her co-foundresses are not also virgins.

In summary, many patterns in the sexual composition of *S. harmandi* broods are similar to those observed in other gregarious, but sub-social, bethylids and also in some socially solitary species. Sex ratios in these other species are typically interpreted in the context of LMC theory whereas, on current evidence, *S. harmandi* sex ratios are better explained by LRE. This does not preclude that LMC effects are also operating and indeed they are expected given that within-brood mating occurs. While LMC and LRE are part of the same theoretical framework (Taylor, 1981), models for sex allocation under LRE are less extensively developed than are LMC models (West, 2009). We now turn considering how best to develop LRE theory to probe the current explanation for sex-ratio bias in *Sclerodermus*.

We have suggested that mutually beneficial cooperative interaction between foundresses select for female-biased sex allocation through LRE to the extent that a female's daughters tend to reproduce in close proximity of each other. However, while such a 'viscous' population structure can ensure high relatedness between social partners, it can also lead to intense competition between kin for limiting reproductive resources (Hamilton, 1964), and this kin

competition effect can inhibit or even override the effects of increased relatedness on sex allocation and other social evolutionary traits (Bulmer, 1986; Frank, 1986; Taylor, 1988, 1992a; Gardner et al., 2009; Rodrigues & Gardner, 2015). Accordingly, a theoretical analysis is required to establish under which circumstances (if any), limited dispersal of females may lead to sex ratio bias via LRE. A promising avenue for exploration will involve models of 'population elasticity', whereby the intensity of kin competition is reduced, because extra resources are made available to local populations that are more cooperative (Taylor, 1992b; Gardner & West, 2006). In the context of *S. harmandi*, these extra resources may include the larger hosts that can only be successfully parasitised by multiple foundresses acting as a cooperative unit.

Although the extent of female bias under LMC is expected to strongly depend upon the number of foundresses in the breeding group (Hamilton, 1967), the extent of female bias observed in *S. harmandi* does not appear to be strongly dependent upon foundress number (Tang et al., 2014). Formal theoretical exploration is needed to determine whether this is a general feature of LRE, or whether this relative invariance owes to a particular feature of *S. harmandi*'s biology. Moreover, whereas a 'fertility insurance' effect, that curbs the evolution of extreme female-biased sex ratios to ensure the presence of at least some mating opportunities for daughters in the context of stochastic death or sterility of males, has been explored in the context of LMC (particularly in relation to protozoan parasites; West et al., 2002; Gardner et al., 2003), the impact of the threat of daughter virginity on a foundress's sex allocation decision remains to be explored in the context of LRE. The ability of unmated females to produce male offspring adds further complexity for sex-ratio evolution (Godfray, 1990; West, 2009; Gardner, 2014).

In addition to improving our understanding of the sex allocation of these bethylid wasps, the proposed model development could also be used to understand the evolution of their quasisociality, both in terms of the evolution of reduced female dispersal and also in terms of the evolution of reduced aggressiveness and the emergence of coordinated cooperation between co-foundresses. In line with Gardner & Ross's (2013) suggestion that a positive feedback between female-biased sex ratios and female-biased cooperation can promote eusociality, it would also be useful to assess the potential for such feedbacks to occur in this quasisocial context. In particular, whereas Gardner & Ross's (2013) model required that some (unexplained) level of female cooperation be present at the outset, the biology of *S. harmandi* provides a ready explanation for cooperative breeding, i.e., a direct fitness benefit (Tang et al., 2014).

We conclude that considerations of the sex ratios of *S. harmandi* and its quasisocial congeners are currently constrained to be somewhat heuristic. This is essentially the same conclusion as reached by recent studies of sex ratios in *Melittobia*, another parasitoid genus in which similar degrees of sociality are observed (Innocent et al., 2010; Abe et al., 2014). This further understanding will likely develop best via a combination of field-based observations, experiments, and theoretical modelling.

Acknowledgements

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