

1 *Entomologia Experimentalis et Applicata*

2 **Special Issue: Mark Jervis Memorial**

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

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7 **Apostolos Kapranas^{1*}, Ian C.W. Hardy², Xiuyun Tang³, Andy Gardner⁴ & Baoping Li³**

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9 ¹ Institute of Biology, University of Neuchâtel, Emile-Argand 11, Neuchâtel 2000,
10 Switzerland, ²School of Biosciences, University of Nottingham, Sutton Bonington Campus,
11 Loughborough, LE12 5RD, UK, ³School of Plant Protection, Nanjing Agricultural
12 University, No. 1 Weigang, Nanjing, Jiangsu 210095, China, and ⁴School of Biology,
13 University of St Andrews, Sir Harold Mitchell Building, Greenside Place, St Andrews, KY16
14 9TH, UK

15

16 ***Correspondence:** Apostolos Kapranas, FARCE Lab, Institute of Biology, University of
17 Neuchâtel, Emile-Argand 11, Neuchâtel 2000, Switzerland

18 E-mail: akapranas@gmail.com, apostolos.kapranas@unine.ch

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20 **Running head:** *Sex ratios in a quasisocial parasitoid*

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22 **Key words:** *Sclerodermus harmandi*, Bethyilidae, LRE, LMC, developmental mortality, all-
23 female broods, Hymenoptera

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25 **Accepted: 31 August 2015**

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1 **Abstract**

2 *Sclerodermus harmandi* (Buysson) (Hymenoptera: Bethyridae) is an economically beneficial
3 species of parasitoid wasp that has an unusual level of sociality: groups of female foundresses
4 reproduce on a single host and exhibit cooperative post-ovipositional brood care. The
5 beneficial effects females have on each other's reproductive success provide, via the theory
6 of local resource enhancement (LRE), an explanation for their female-biased progeny sex
7 ratios, which is part of the same framework for understanding sex-ratio evolution as the more
8 often invoked theory of local mate competition (LMC). Here we show that *S. harmandi* sex
9 ratios are over-dispersed, with high variance largely attributable to the common occurrence
10 (60%) of developmental mortality. Developmental mortality is also positively associated with
11 the proportion of broods which contain only females at emergence (virgin broods). Virginity
12 is more common when broods are produced by fewer foundresses. Virginity is expected to be
13 disadvantageous under LRE, as it is under LMC, but theory for LRE is less extensively
14 developed. We suggest approaches for the development of LRE theory, in particular using
15 models of 'population elasticity' in which the intensity of kin competition is reduced because
16 extra resources are available to local populations that are more cooperative. For *S. harmandi*,
17 such extra resources may include large hosts that can only be successfully utilized if multiple
18 foundresses cooperate.
19

1 **Introduction**

2 Sex ratios in many species of gregarious and quasi-gregarious parasitoid wasps are female
3 biased. In the vast majority of cases this can be explained by the theory of local mate
4 competition (LMC) (Hamilton, 1967, 1979; Godfray, 1994; West, 2009). LMC theory
5 predicts that female-biased sex ratios are selected for when the offspring produced by one or
6 a few mothers, termed foundresses, mate among themselves before the female offspring
7 disperse away from the natal group, a common feature of many parasitoid species (Hamilton
8 1967, 1979; Godfray, 1994; Hardy, 1994; Godfray & Cook, 1997). LMC theory further
9 predicts that bias will be less extreme when more foundresses contribute offspring to the
10 mating group and such facultative adjustment of sex ratios is observed in empirical and
11 comparative studies of parasitoids (Charnov, 1982; Godfray, 1994; Hardy, 2002; Hardy et al.,
12 2005; West, 2009). In short, LMC theory has been a major key to the understanding of
13 parasitoid sex allocation (Charnov 1982; Godfray, 1994; West, 2009; a critique of this
14 success is provided by Orzack, 2002).

15 There are, however, some species of parasitoid wasps in which observed sex ratios are
16 more biased than predicted by current LMC theory and/or do not vary with foundress
17 numbers according to LMC predictions (Shuker et al., 2004, 2005; Matthews et al., 2009;
18 Innocent et al., 2010; Abe et al., 2014; Tang et al., 2014). For instance, Abe et al. (2014)
19 recently highlighted that the extremely female biased (1-5% males), and relatively invariant
20 sex ratios in the genus *Melittobia* (Hymenoptera: Eulophidae) are inexplicable using current
21 sex-ratio theory. A concurrent publication by Tang et al. (2014) on parasitoids in the genus
22 *Sclerodermus* (Hymenoptera: Bethyridae) similarly reported highly female-biased sex ratios,
23 and although sex ratios increased significantly with foundress number, the effect was not
24 strong. Like Abe et al. (2014), Tang et al. (2014) concluded that the observed sex ratios could
25 not be explained by LMC but in contrast to Abe et al. (2014) it was concluded that current
26 sex-ratio theory does provide an explanation: *Sclerodermus harmandi* (Buysson) is a
27 quasisocial parasitoid (groups of females reproduce on a single host and exhibit cooperative
28 brood care) and the beneficial effects females have on each other's reproductive success is
29 expected to lead to female bias due to local resource enhancement (LRE), wherein an excess
30 production of the sex that leads to a greater increase in fitness of the parents or their offspring
31 is favoured (Taylor, 1981; West, 2009). This was the first report of LRE operating among
32 parasitoid wasps and one of only a few reports on LRE within the Hymenoptera (Schwarz,
33 1988; Martins et al., 1999; Harradine et al., 2012). Although it is part of the same conceptual
34 framework for understanding the evolution of sex allocation strategies, theory for LRE has

1 not been as extensively developed as LMC theory (Taylor, 1981; West, 2009; Gardner &
2 Ross, 2013). In consequence, expectations for sex ratio means and variance and patterns of
3 brood sexual composition in relation to other life-history variables such as foundress number,
4 clutch size, or developmental mortality, are less well defined than under LMC (e.g., Green et
5 al., 1982; Werren, 1983; Griffiths & Godfray, 1988; Heimpel, 1994; Hardy et al., 1998).

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

12

13 **Biology of *Sclerodermus harmandi***

14 *Sclerodermus harmandi* is a gregarious ectoparasitoid of wood-boring cerambycid beetle
15 larvae and is used extensively in biological control of coleopteran forest pests in China (Chen
16 & Cheng, 2000). These beetles damage trees directly by feeding on them and also vector the
17 extremely damaging pine wood nematode *Bursaphelenchus xylophilus* (Steiner & Buhrer)
18 Nickle which causes pine wilt disease (Yang et al., 2014).

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

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

33

34 **Materials and methods**

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

10 The number of adult female *S. harmandi* introduced into a glass vial (1.0 cm
11 diameter, 5.0 cm long) with one *M. alternatus* larva was varied (1, 2, 4, 6, or 8). The numbers
12 of eggs laid onto each host, and the numbers of adult male and female *S. harmandi* offspring
13 produced, were recorded. There were 220 replicates overall, with between 30 and 60
14 replicates for each number of foundress females. However, in about half of the replicates,
15 foundresses failed to produce any offspring; this was especially common when foundress
16 group sizes were small and/or hosts were large (Tang et al., 2014), and our current analysis is
17 restricted to those replicates in which some *S. harmandi* offspring matured. Of the 112
18 replicates producing surviving offspring, one brood produced by a single foundress, consisted
19 of eight males only, probably because the foundress had not mated. Another offspring group,
20 produced by two foundresses, had an unusually large number of males (19/44 offspring),
21 suggestive that one of the foundresses was unmated. Following procedures adopted by prior
22 studies of bethylid sex ratios (e.g., Hardy & Cook, 1995), these two replicates were excluded
23 from the reported analyses. The inclusion of the two-foundress replicate would not have led
24 to any different conclusion. There remained 110 offspring groups for analysis.

25 Data were mainly explored using logistic analysis (generalized linear modelling) in
26 the GENSTAT statistical package (v. 14.1; VSN International, Hemel Hempstead, UK). All
27 statistical testing was 2-tailed. Sex ratios were expressed as the proportion of adult offspring
28 that were males. When binary data were grouped, we assumed quasi-binomially distributed
29 errors to counter the effects of overdispersion (Wilson & Hardy, 2002). Sex ratio variance
30 and variance in mortality were each quantified using two descriptive statistics, the
31 Heterogeneity Factor (HF = residual deviance/residual degrees of freedom; West & Herre,
32 1998) and the variance ratio R (= variance in numbers observed/expected binomial variance;
33 Nagelkerke & Sabelis, 1998) and analysed using the Meelis test statistic U, which tests for
34 departures from binomial distribution (significant large negative values indicate

1 underdispersion and large positive values overdispersion; Nagelkerke & Sabelis, 1998;
2 Krackow et al., 2002). Values of R and U are calculated from sums of separate calculations
3 from each offspring group size and we note that our data consist of small numbers of clutches
4 or broods spread across a large range of group sizes. Although the approach we adopt is the
5 best currently available, it is known that when data consist of many small sub-samples
6 estimations can be distorted such that, for instance, larger values might not correspond to
7 stronger deviations from expected variances (Krackow et al., 2002).

9 **Results**

10 Among the 110 broods in which some offspring matured, overall 61% offspring had died
11 during development (mean \pm SE egg-to-adult mortality = 0.614 ± 0.021), and mortality had
12 variance that was not significantly greater than binomial (HF = 28.3; Meelis test: R = 12.61,
13 U = 85.43, P = 1.0). It is already known that developmental mortality is unrelated to host
14 weight, the number of eggs laid on a host, or the number of foundress females present (Tang
15 et al., 2014). Unsurprisingly, the size of the offspring group at maturity was negatively
16 correlated with egg-to-adult mortality (Spearman's rank correlation: $r = -0.757$, $t = 12.12$, d.f.
17 = 109, $P < 0.001$). The sex ratios of groups of maturing adults were typically strongly female
18 biased (mean proportion of offspring that were male = 0.069 ± 0.004 – note that an incorrect
19 mean value of 0.032 was reported by Tang et al., 2014). Sex ratio variances were
20 overdispersed (HF = 1.48; Meelis test: R = 0.7208, U = 2.33, P = 0.020).

21 Sex ratios decreased weakly with adult offspring group size (Logistic ANCOVA
22 corrected for overdispersion: $F_{1,109} = 5.55$, $P = 0.02$, % deviance explained = 4.75; Figure 1)
23 and increased weakly with foundresses number ($F_{4,109} = 5.63$, $P < 0.001$, % dev = 4.81; Figure
24 1). There was no significant interaction between these two main effects ($F_{4,109} = 1.08$, $P =$
25 0.37). The number of males present in offspring group increased with group size ($F_{1,108} =$
26 80.97 , $P < 0.001$, % dev = 42.8). Sex ratio variance, quantified by HF, was not correlated with
27 the number of foundresses producing the brood (one: HF = 1.64, n = 9; two: HF = 0.816, n =
28 20; four: HF = 1.24, n = 31; six: HF = 0.595, n = 21; eight: HF = 2.25, n = 28; Spearman's
29 rank correlation: $r = 0.100$, $P = 0.20$). Sex ratios were significantly higher among broods that
30 had experienced higher proportions of developmental mortality ($F_{1,108} = 10.21$, $P = 0.002$, %
31 dev = 8.63; Figure 2). Sex ratio variance was significantly higher among broods that
32 experienced the highest percentages of developmental mortality ($\leq 24.9\%$ mortality: HF =
33 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,
34 n = 32; Spearman's rank correlation: $r = 0.800$, $P = 0.021$).

1 About 15.3% of adult offspring groups consisted of female offspring only. The
2 probability of an offspring group consisting only of females was lower among larger
3 offspring groups ($G_1 = 32.39$, $P < 0.001$, % dev = 34.0); no broods of more than around 50
4 maturing offspring contained females only (Figure 3). The probability of all-female offspring
5 groups was higher when developmental mortality was higher ($G_1 = 20.68$, $P < 0.001$, % dev =
6 21.7) and when foundresses number was lower ($G_4 = 5.26$, $P < 0.001$, % dev = 22.1; Figure 4).
7 The interaction between these two variables was not significant ($G_4 = 0.19$, $P = 0.95$).

8 9 **Discussion**

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

16 Current evidence suggests that *Sclerodermus* foundresses tend to each lay a small
17 number of male eggs in every clutch (Mamaev, 1979; Liu et al., 2011; Tang et al., 2014).
18 Mamaev (1979) reported that 1-2 males are laid among the first produced eggs in each clutch
19 (a pattern which may be associated with final clutch size uncertainty; Hardy, 1992).
20 Similarly, Tang et al. (2014) estimated that on average 0.8 adult males are produced per *S.*
21 *harmandi* foundress, suggesting that (given 61% developmental mortality) each foundress
22 lays an average of 1.31 male eggs in each clutch. Further, the brood sex ratios produced by
23 single foundresses are typically less female biased than the reciprocal of brood size (one male
24 per brood is expected under single-foundress LMC in the absence of developmental
25 mortality; Green et al., 1982; Griffiths & Godfray, 1988; Nagelkerke & Hardy, 1994), due to
26 mothers laying more males in larger broods than in smaller broods. Weak declines in sex
27 ratio with increasing brood size, as observed in *S. harmandi*, or a lack of relationship between
28 sex ratio and brood size, have been reported for the secondary sex ratios (at adult emergence)
29 of most examined sub-social bethylids in which broods are produced by a single foundress
30 and, as observed for *S. harmandi*, are typically associated with an increase in the number of
31 males per brood as brood size increases (Hardy et al., 1998). However, examination of the
32 primary sex ratio (at oviposition) in one sub-social species has shown that developmental
33 mortality may alter or obscure initially present relationships (Khidr et al., 2013). Given that
34 developmental mortality among *S. harmandi* offspring is more common than is observed in

1 many gregarious parasitoids (Hardy et al., 1998; Kapranas et al., 2011), empirical assessment
2 of the primary sex ratio is a desirable future step, especially as such evaluation could
3 potentially also reveal the relative contributions of individual foundresses to each offspring
4 group (Khidr et al., 2014) and thus provide insights into whether the apparently cooperative
5 reproduction observed is in fact tempered by reproductive dominance and skew (Tang et al.,
6 1994).

7 Sex ratio variances were overdispersed, most likely due to the scrambling effect
8 developmental mortality has on initially less variable group sexual compositions, as observed
9 within and across other species of gregarious parasitoids (Hardy et al., 1998; Kapranas et al.,
10 2011; Khidr et al., 2013). Theory for sex ratio variance under LRE is not well developed; but
11 under LMC, selection for low sex ratio variance can be less stringent in multiple-foundress
12 cases compared to single-foundress cases (Nagelkerke, 1996); our rather limited data do not
13 suggest a relationship between variance and foundress number. Further, selection for sex ratio
14 variance is expected to be related to the frequency at which different numbers of foundresses
15 naturally occur (West & Herre, 1998) but there is very little field data on the distribution of
16 foundress numbers in *S. harmandi* populations. The less female-biased sex ratios in broods
17 which experienced higher proportions of mortality is suggestive of higher mortality among
18 developing females than among males, which may be attributable to female larvae requiring
19 more resources than male larvae to grow large enough for successful pupation (Nagelkerke &
20 Hardy, 1994), and indeed *S. harmandi* females are larger than males (He, 2004), and could
21 also result from sexually differential care by brood-tending foundresses.

22 Whereas the current evidence suggests that developmental mortality increases brood
23 sex ratio variance in *S. harmandi*, there is much stronger evidence for an association between
24 mortality and a related aspect of brood sexual composition: all-female ('virgin') broods,
25 which can result from all males in a brood dying before maturity. Under single-foundress
26 LMC, hymenopteran parasitoids maturing in all-female broods are expected to have low
27 fitness due to being constrained to subsequently produce male-offspring only, and these will
28 have no reproductive opportunities unless some inter-group dispersal and non-local mating
29 occurs (Green et al., 1982; Godfray, 1990; Heimpel, 1994; Nagelkerke & Hardy, 1994; Hardy
30 et al., 1998, 2005). Virgin females co-founding broods with mated females can obtain fitness
31 via their sons mating locally with the offspring of the co-foundresses, but are not able to
32 produce offspring sex ratios close to the unconstrained optima and are thus also
33 disadvantaged (Godfray, 1990; West, 2009). Despite the disadvantage of virginity, virgin
34 broods are predicted to arise under LMC due to the trade-off between minimising the number

1 of male offspring produced and insuring against all the males dying before maturity (Green et
2 al., 1982; Heimpel, 1994; Nagelkerke & Hardy, 1994; West et al., 1997). In general accord
3 with these expectations from LMC theory, virgin *S. harmandi* broods were more common
4 when brood sizes were smaller, when mortality was more prevalent, and also when broods
5 were produced by fewer foundresses. Similar patterns have been observed in gregarious
6 parasitoids with LMC (Hardy et al., 1998; Kapranas et al., 2009, 2011) and across fig wasp
7 species with LMC (West et al., 1997). Further, the relationships between the prevalence of
8 virginity and the prevalence of mortality for *S. harmandi* broods produced by one or two
9 foundresses resemble explicit predictions for the one- and two-foundress cases under LMC
10 (Figure 1d in West et al., 1997). Whether these apparent matches to the predictions of
11 ‘extended’ LMC theory (West, 2009) counter the assertion (Tang et al., 2014) that ‘classical’
12 LMC does not explain sex ratios in *S. harmandi* is currently unclear and may require the
13 development of equivalent theory for virginity under LRE.

14 In mixed sex broods, with female-biased sex ratios, current evidence suggests that
15 local (within brood) mating is the norm. Given a mean sex ratio of 0.069, individual males
16 will typically mate with around 14 females and evidence from other bethylids suggests that
17 they will have sufficient supplies of sperm with which to successfully inseminate all the
18 females (Hardy et al., 2005), although at high-mating frequencies males are expected (Abe &
19 Kamimura, 2015) and observed (e.g., in the bethylid *Goniozus legneri* Gordh; Gordh et al.,
20 1983) to transfer smaller ejaculates. The occurrence of virgin broods suggests that non-local
21 mating, via male dispersal, may also occur, due to the selection pressure on males to acquire
22 more mates (e.g., by immigrating into virgin broods) and that females may be receptive due
23 to the selective advantage for being able to produce female-biased offspring sex ratios. Male
24 *S. harmandi* typically possess wings which is suggestive of male dispersal but there is a lack
25 of direct evidence for the mating structure of *Sclerodermus* populations (as with other
26 bethylids; Hardy & Cook, 1995; Hardy & Mayhew, 1998; Hardy et al., 2000).

27 After maturing around the remains of a host, female *Sclerodermus* must disperse to
28 forage for a fresh host. Females typically do not possess wings and so forage by walking. It is
29 not currently known whether females disperse as individuals or as cohesive groups, although
30 reports that females overwinter in groups in host-made tunnels or cavities in trees (Zhang &
31 Tian, 1985; Xu et al., 2002) do suggest group cohesion. The direct selective advantage to
32 cohesive dispersal and foraging would be that it would promote successful reproduction on
33 large hosts (Tang et al., 2014). Cohesive dispersal would also enhance the relatedness
34 between foundresses, which may in turn select for more strongly biased sex ratios (and other

1 aspects of social behaviour) compared to situations when foundresses were not closely related
2 (Taylor & Crespi, 1994; Shuker et al., 2004; Gardner et al., 2009; Abe & Kamimura, 2012).

3 We, however, speculate that females maturing in virgin broods may not disperse as
4 cohesively as females from mixed-sex broods, due to the expected mating opportunities to a
5 virgin foundress's sons being greater when her co-foundresses are not also virgins.

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

16 We have suggested that mutually-beneficial cooperative interaction between
17 foundresses select for female-biased sex allocation through LRE to the extent that a female's
18 daughters tend to reproduce in close proximity of each other. However, whilst such a
19 'viscous' population structure can ensure high relatedness between social partners, it can also
20 lead to intense competition between kin for limiting reproductive resources (Hamilton, 1964),
21 and this kin competition effect can inhibit or even override the effects of increased
22 relatedness on sex allocation and other social evolutionary traits (Bulmer, 1986; Frank, 1986;
23 Taylor, 1988, 1992a; Gardner et al., 2009; Rodrigues & Gardner, 2015). Accordingly, a
24 theoretical analysis is required to establish under which circumstances (if any) limited
25 dispersal of females may lead to sex ratio bias via LRE. A promising avenue for exploration
26 will involve models of 'population elasticity', whereby the intensity of kin competition is
27 reduced because extra resources are made available to local populations that are more
28 cooperative (Taylor, 1992b; Gardner & West, 2006). In the context of *S. harmandi*, these
29 extra resources may include the larger hosts that can only be successfully parasitized by
30 multiple foundresses acting as a cooperative unit.

31 Whereas the extent of female bias under LMC is expected to strongly depend upon
32 the number of foundresses in the breeding group (Hamilton, 1967), the extent of female bias
33 observed in *S. harmandi* does not appear to be strongly dependent upon foundress number
34 (Tang et al., 2014). Formal theoretical exploration is needed to determine whether this is a

1 general feature of LRE, or whether this relative invariance owes to a particular feature of *S.*
2 *harmandi*'s biology. Moreover, whereas a 'fertility insurance' effect, that curbs the evolution
3 of extreme female-biased sex ratios in order to ensure the presence of at least some mating
4 opportunities for daughters in the context of stochastic death or sterility of males, has been
5 explored in the context of LMC (particularly in relation to protozoan parasites; West et al.,
6 2002; Gardner et al., 2003), the impact of the threat of daughter virginity on a foundress's sex
7 allocation decision remains to be explored in the context of LRE. The ability of unmated
8 females to produce male offspring adds further complexity for sex ratio evolution (Godfray,
9 1990; West, 2009; Gardner, 2014).

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

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

27

28 **Acknowledgements**

29 We thank the late Dr Mark Jervis, who always showed an interest in our work on parasitoids
30 and was always able to suggest connections to other research areas or study systems. He also
31 engaged in several blues jam sessions with AK and ICWH, both in Cardiff and in Sutton
32 Bonington, playing both guitar and bass guitar very adeptly. We greatly miss these academic
33 and non-academic interactions with him. We further thank Ling Meng, Fuyan Xu, Xie
34 Chunxia, Zheng Huayin, Xu Ming, Liu Conghui, Wu Shaolong, and Richard Wilkinson for

1 their help. This study was supported by Natural Science Foundation of China (31570389).
2 AK was supported by a Marie Curie Fellowship (FP7-PEOPLE-2010-IEF 273431). AG was
3 funded by a Natural Environment Research Council (UK) Independent Research Fellowship
4 (NE/K009524/1).

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8

9 **Figure captions**

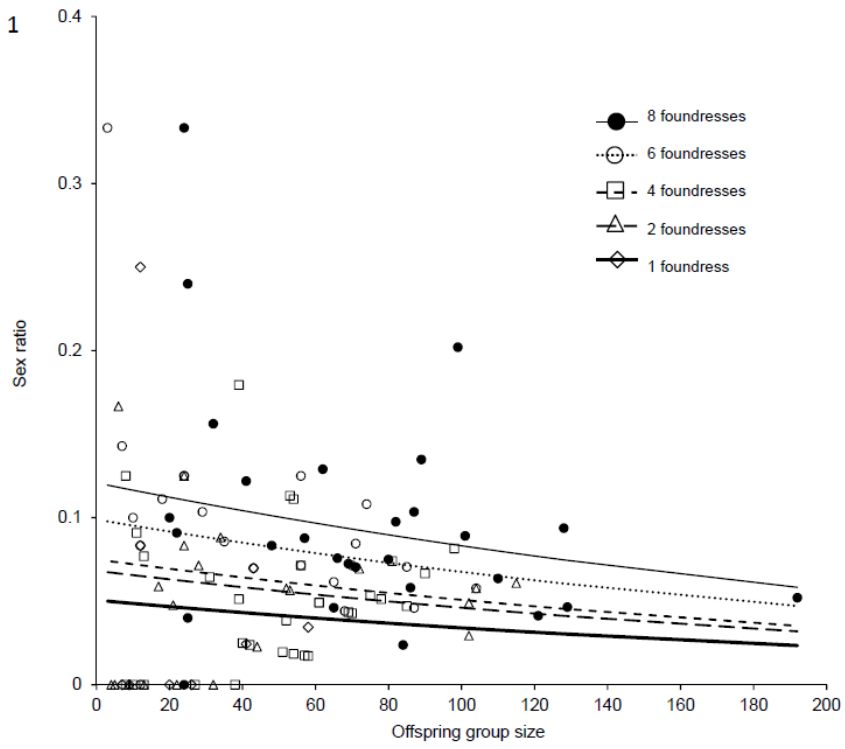
10 **Figure 1** Relationships between sex ratio (proportion of adult offspring that were males) and
11 brood size at emergence, for broods founded by 1 to 8 adult female *Sclerodermus harmandi*.
12 Fitted logistic regression lines are provided for each foundresses group. Note that for visual
13 clarity the fitted logistic regression line for 2-foundresses broods is slightly displaced below
14 the 4-foundresses regression line.
15

16 **Figure 2** The relationship between sex ratio at adult emergence (proportion males) and the
17 proportion of developmental mortality in offspring groups of *Sclerodermus harmandi*. The
18 fitted line is from logistic regression.
19

20 **Figure 3** The influence of offspring group size at adult emergence on virginity (proportion of
21 broods that were all-female) in *Sclerodermus harmandi*. The fitted line is from logistic
22 regression.
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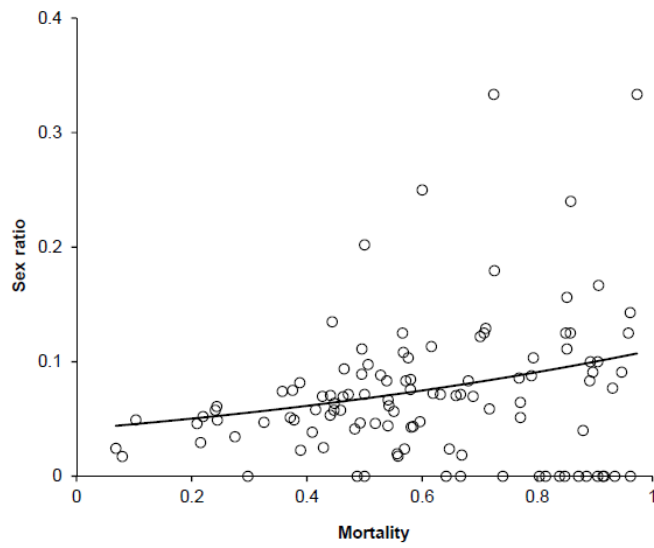
24 **Figure 4** The influence of foundress number and mortality on virginity (proportion of broods
25 that were all-female) in *Sclerodermus harmandi*. The fitted lines are based on logistic
26 analysis of covariance, treating foundress group size as a discrete factor.
27

Figure 1



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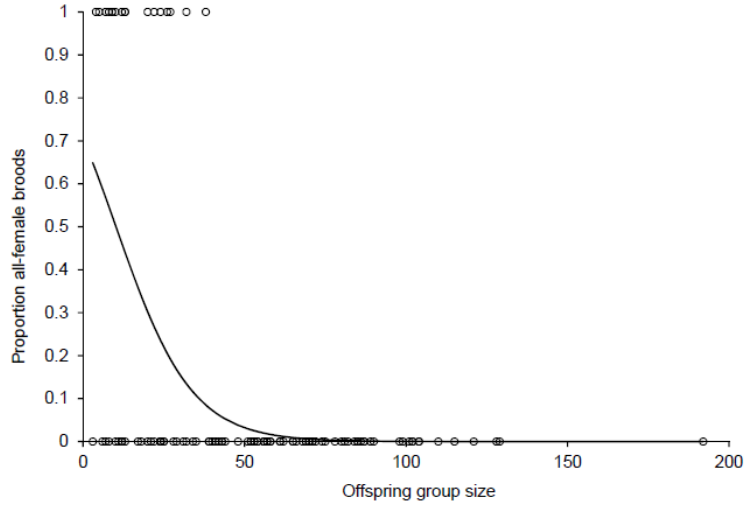
Figure 2



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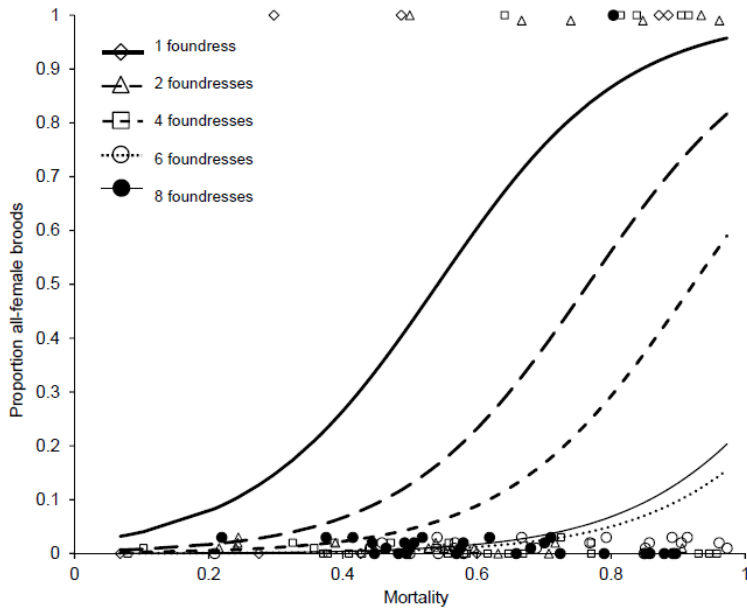
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Figure 3



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Figure 4



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