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How many cooperators are too many? Foundress number, reproduction and sex ratio in a quasi-social parasitoid

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Abstract

1. In the parasitoid genus *Sclerodermus*, multiple foundresses produce and care for communal broods on large hosts, which can lead to greater reproductive success for group members than attempting to reproduce alone.
2. We explore the consequences of foundress group size on the benefits of cooperative brooding and on brood sex ratios by providing groups of 10–55 foundresses with a single host and no alternative reproductive options.
3. Within this range, increasing foundress group size leads to increasingly common failure in brood production and diminished *per capita* success. Group production of adult offspring declines once foundress number reaches around 25.
4. Brood failure is usually at the early developmental stages, and current evidence suggests that there may be competition among foundresses for oviposition sites, possibly involving reproductive dominance and ovicide, which also delays initial brood production. Once broods become established, their rate of development is enhanced by large foundress numbers.
5. The sex ratios of broods are very strongly female biased, irrespective of the foundress number. As this bias is not easily explained by standard models of local mate competition or by a recent model of local resource enhancement, we suggest an explanation based on control of sex allocation by a minority of dominant foundresses, which monopolise the production of adult males.

KEYWORDS
brood developmental failure, cooperation, dominance, offspring production, *Sclerodermus*, sex allocation

INTRODUCTION

The benefits of cooperation in insect societies are manifest in numerous ways, including the efficient exploitation of environmental resources (Sachs et al., 2004; West et al., 2015; Tang et al., 2014) and enhanced protection of acquired resources (Shen et al., 2017). Cooperative behaviour by an 'actor' individual is defined as providing direct or indirect fitness benefits to a 'recipient' individual (West et al., 2007). Its evolution requires that the actor also accrues fitness benefits, whether via kin selection (explaining altruistic cooperation that incurs a personal fitness cost to the actor, Hamilton, 1964), by-products benefit (a direct consequence of a self-interested act, Davies et al., 2012), reciprocity (preferentially helping individuals that have helped previously, Trivers, 1971; Dugatkin, 1997) or enforcement (rewarding cooperators and punishing non-cooperators, Franks, 2003; Davies et al., 2012). Cooperative reproduction in social insects is often

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associated with biased offspring sex ratios (Bono & Crespi, 2008; Crozier & Pamilo, 1996; Iritani et al., 2021; West, 2009), often due to the indirect fitness benefits of cooperation being greater when an actor helps to rear offspring of one sex rather than the other.

Cooperative systems are often liable to exploitation by the selfish actions of individual members, 'freeloaders' and 'cheats', which accrue benefits without bearing costs (Ghoul et al., 2014; Riehl & Frederickson, 2016; West et al., 2007; West et al., 2015), leading to reduced success or breakdown (Avilés, 2002; Kümmerli et al., 2015; Rankin et al., 2007). The spread of selfish behaviours may be countered by peer actions, such as worker policing of the production of male offspring by other workers in eusocial hymenopterans (Foster & Ratnieks, 2001; Ratnieks & Visscher, 1989) or by the actions of dominant individuals, such as a dominant female in a *Polistes* Latreille wasp nest eating or destroying eggs laid by subordinate females (Ratnieks & Wenseleers, 2008; Röseler et al., 1984). Maintaining dominance, however, may be difficult in larger groups (Clutton-Brock, 1998; Gilbert et al., 2018) and policing is not always completely successful (Oldroyd et al., 1994). Further, a scarcity of resources may lead to selfishness becoming selectively favoured over altruistic or mutually beneficial behaviours for most or all group members and thus the breakdown of an otherwise cooperative system (Boomsma & Gawne, 2018; Grinsted et al., 2014; Gunnels et al., 2008; Paul & Annagiri, 2018; Trunzer et al., 1998). Even without widespread cheating, there may be diminishing returns to individuals in larger groups (Bono & Crespi, 2008), and individuals might be expected to remain in, join or leave cooperative groups according to the conditions within that group and their opportunities for reproduction elsewhere (Grinsted & Field, 2017a, 2017b, 2018; Kennedy et al., 2021), but extra-group opportunities are not always available (Grinsted & Field, 2017b; Trunzer et al., 1998). Here, we examine the offspring production and sex ratio consequences of increasingly large groups of individuals of a cooperatively brooding parasitoid wasp being presented with fixed reproductive resources, such that *per capita* resource availability is greatly diminished, and there are no extra-group opportunities.

Members of the genus *Sclerodermus* Latreille may be the most socially complex of all parasitoid species. Multiple foundresses lay eggs onto the same host and then remain to tend the common brood together (quasi-social reproduction; Hu et al., 2012; Tang et al., 2014; Gao et al., 2016; Wang et al., 2016). Cooperative multi-foundress reproduction in *Sclerodermus* appears to have evolved due to large hosts being very challenging for individual females to attack, with mean *per capita* reproductive output being higher among multi-foundress groups (Tang et al., 2014). It has also been predicted that the mutual benefits of foundresses co-exploiting hosts select for female-biased sex ratios via local resource enhancement (LRE: Tang et al., 2014; Kapranas et al., 2016; Iritani et al., 2021) instead of, or in combination with, local mate competition (LMC: Hamilton, 1967), which is the more commonly applied explanation for female-biased parasitoid sex ratios (Godfray, 1994; West, 2009). Local mate competition and local resource enhancement are two aspects of the same theoretical framework for explaining sex ratio bias (Taylor, 1981; West, 2009); LMC emphasises how mothers bias their sex allocation away from members of the sex that competes among itself for a resource (e.g., males competing for mating opportunities), and LRE emphasises how mothers bias allocation towards members of the sex that enhance each other's ability to exploit a resource (e.g., suppression of a common host by females).

While multi-foundress host attack results in greater overall success, there is evidence that females within these groups selfishly adjust the risks they take (Abdi et al., 2020a,2020b; Liu et al., 2021; Mesterton-Gibbons & Hardy, 2021). Once hosts are suppressed, reproduction appears to be shared approximately equally between *Sclerodermus* foundresses (generally low reproductive skew), but there is nonetheless evidence that larger and earlier arriving females produce disproportionately more offspring and also that these females produce the majority of the male offspring within broods (Guo et al., 2022). Current evidence thus suggests that *Sclerodermus* reproduction is broadly cooperative but also subject to selfish exploitation by freeloaders during host attack and by dominants, via brood sex ratio control, during brood production.

The current understanding of *Sclerodermus* reproduction has been attained by examining reproduction in relatively small groups of between 1 and 8 foundresses (Abdi et al., 2020a,b; Chen et al., 2019; Gao et al., 2016; Guo et al., 2022; Hu et al., 2019; Hu et al., 2019; Li et al., 2010; Li & Sun, 2011; Liu et al., 2011; Liu et al., 2017; Lupi et al., 2017; Tang et al., 2012; Tang et al., 2014; Wang et al., 2016; Wei et al., 2017; Yang et al., 2018). The natural range and distribution of foundress group size in *Sclerodermus* is largely undocumented but Liu et al. (2021) observed up to four *S. guani* wasps paralysing a single larva of *Saperda populnea* (L.) (Coleoptera: Cerambycidae) in nature. The laboratory study of Tang et al. (2014) found that on the largest class of hosts presented, *per capita* reproduction was greatest among groups of 8 foundresses, but larger group sizes are possible. For instance, in the most comparable parasitoid genus, *Melittobia* Westwood, Abe et al. (2021) found groups of up to 36 foundresses in the field. In this study, we extend the evidence for *Sclerodermus* to groups of between 10 and 55 foundress and explore whether cooperative reproductive system remains functional when there are large numbers of foundresses present and no alternative reproductive resources are available. We evaluate the probability and timing of brood production, identify where failures occur and examine the numbers of offspring produced in terms of the per foundress benefits of cooperative brooding. We use these data to infer patterns of cooperation and dominance, and we consider the sexual composition of successfully produced broods in terms of sex ratio theory (LMC and LRE) that predicts effects of foundress number and of foundress–foundress cooperation.

MATERIALS AND METHODS

Host and parasitoid

Psacothea hilaris hilaris (Pascoe) (Coleoptera, Cerambycidae, Lamiinae), a xylophagous beetle of plants belonging to Moraceae (Basset et al., 1997;

Kojima & Nakamura, 1986; Shintani et al., 2003) was detected in Italy in 2005 (Lupi et al., 2013). Like all Cerambycidae, *P. h. hilaris* adult females cut the epidermis of the host plant with their mandibles, leaving T-shaped incisions where they lay eggs. The larvae, after a first period of feeding under the bark, tunnel into the xylem of host trees and develop until pupation. Adults emerge by chewing a circular exit hole through the bark (Hanks, 1999; Lupi et al., 2013, 2015).

Sclerodermus brevicornis (Kieffer) was detected in Italy in 2011 in association with the larvae *P. h. hilaris* (Lupi et al., 2013). Members of the genus *Sclerodermus* (Hymenoptera: Bethylidae) are idiobiont ectoparasitoid wasps (Evans, 1978; Hu et al., 2012; Li & Sun, 2011) with, approximately 81 species distributed worldwide (Gordh & Móczár, 1990; Lanes & Azevedo, 2008). Their morphological characteristics [small size, flattened body, prognathous head (Lupi et al., 2017)] allow them to enter pre-existing tunnels in search of wood-boring beetle larvae (Evans, 1978; Jiang et al., 2015; Kühne & Becker, 1974). *Sclerodermus* has a wide range of hosts, from small to large species (Mendel, 1986; Yang et al., 2014). While a single female is most effective in attacking smaller hosts (Yang et al., 2014), multiple females, cooperating in host attack, can overcome the behavioural defences of large hosts (Abdi et al., 2020a, 2020b; Lupi et al., 2017; Tang et al., 2014). Larger hosts contain more resources than smaller ones, benefiting the offspring in fitness, number and size (Lupi et al., 2017; Tang et al., 2014).

Co-foundress females do not exhibit overt division of labour (Li & Sun, 2011; Liu et al., 2011; Wang et al., 2016) as all provide maternal care, such as ensuring eggs, and young larvae remain attached to the host and keeping them clean until their pupation and the emergence of new adults (Hu et al., 2012; Tang et al., 2014; Yang et al., 2012). Cooperation between females is influenced by the relatedness between females and also by host size. Sibling females paralyse the host in a shorter time than unrelated females, but, when hosts are larger, the relatedness does not correlate with the probability of successful parasitism (Abdi et al., 2020a). The first adult offspring to emerge from a new brood are the males, which are relatively short-lived and typically mate with the females before these exit their pupal cocoons (Hu et al., 2012; Kapranas et al., 2016).

Sclerodermus species are reported in association with xylophagous coleopterans (Gordh & Móczár, 1990; Lupi et al., 2017) and laboratory studies show that *Sclerodermus* females take less time to paralyse host of the species on which they have developed (Lupi et al., 2017; Wei et al., 2013). Nonetheless, factitious hosts, such as *Tenebrio molitor* L. and the lepidopteran *Corcyra cephalonica*, can be used to rear some species (Abdi et al., 2020a, 2021). The overall developmental time of *S. brevicornis* on both *C. cephalonica* and cerambycid beetle larvae (Lupi et al., 2017) is around one month, but may decrease as the number of foundresses increases (Abdi et al., 2021; Tang et al., 2014; Wei et al., 2017).

Rearing systems

The Yellow Longhorn Beetle, *Psacothea hilaris hilaris* (Pascoe) (Coleoptera: Cerambycidae), was used as the host species for *Sclerodermus brevicornis* Kieffer (Hymenoptera: Bethylidae). A colony of *P. h. hilaris* has been maintained since 2006 at the University of Milan, augmented annually with the addition of new adults from the field (Jucker et al., 2006; Lupi et al., 2013, 2015). Hosts were reared on the same diet used for *Bombyx mori* L. (Lupi et al., 2015) and maintained in a climate chamber at 26 ± 0.5°C, a 16 L:8 D diurnal cycle and a relative humidity of 70 ± 5%.

Sclerodermus brevicornis has been reared at the University of Milan for more than 30 generations on *P. h. hilaris*, deriving from individuals collected in Ponte Lambro (province of Como), in northern Italy in 2011, as described in Lupi et al. (2017). Five genetic lines of *S. brevicornis* have been maintained separately for more than 15 generations, and the current experiment used wasps randomly taken from each of these lines. After verifying the presence of at least one male, indicating that females would have mated, newly emerged *S. brevicornis* were collected (while females from broods without males were discarded). Females were then stored in a refrigerator (5 ± 0.5°C) to synchronise parasitoid and host availability on emergence and were around two weeks old when used in experiments. Previous studies have shown that such storage does not greatly affect their subsequent performance (Jucker et al., 2020). Cultures were maintained in a climate chamber at 25 ± 1°C, a 16 L:8D diurnal cycle and a relative humidity of 60 ± 5%.

Foundress number variation

We evaluated the effects of the number of *S. brevicornis* foundresses that were presented with a single, size-standardised, host. Ten, 25, 35, 45 or 55 foundresses were placed with one *P. h. hilaris* larvae (0.47–0.52 g) into a transparent plastic container (5.5 cm diameter × 3.2 cm height) with an opaque plastic lid and a 2 mm layer of cork oak bark granules to maintain the relative humidity and make the larva more accessible to the parasitoid by increasing the contact surface area (Lupi et al., 2017). There were 21 replicates of each number of foundresses. All foundresses within each replicate came from the same brood (chosen randomly, after 14 days in the refrigerator): as these broods had been produced by several (in most cases sibling) mothers from the same genetic line, brood-mates were a mixture of siblings and closely related non-siblings. All replicates were maintained at 25 ± 1°C, 16D:8 L, 60 ± 10% HR, in a random design (changed at each examination) to avoid room and positional effects, and examined three times each week (Monday, Wednesday, Friday) by opening the lid, which also provided periodic ventilation. On each occasion, the presence or absence of parasitoid eggs, larvae and pupae was noted. Once the adults emerged, the numbers of males and females in the brood were recorded by counting and subtracting the number of foundresses originally present in the replicate from the total number of living and dead adult females found.

Statistical analyses

Data were analysed mostly using generalised linear models in the statistical software R (version 4.1.0). Factors potentially affecting binary response variables (e.g., success or failure) were analysed using logistic analyses assuming binomially distributed errors and a logit link function and analysis of grouped binary data (e.g., brood sex ratio) assumed quasi-binomial errors (Crawley, 1993; Wilson & Hardy, 2002). Factors potentially affecting integer data (e.g., brood size or numbers of males produced) were explored using log-linear analyses, a log-link function and the assumption of quasi-Poisson errors (Crawley, 1993). Data derived from integers (e.g., offspring production per foundress) were also analysed using log-linear models (Abdi et al. 2020a, 2020b; Faraway, 2006; Tang et al., 2014). The number of foundresses present was fitted as a continuous variable in all logistic and log-linear analyses. Following logistic and log-linear analyses, we give the percentage deviance explained (%Dev) as a descriptor analogous to r^2.

A life table approach (Kidd & Jervis, 2005; Varley & Gradwell, 1960) was used to identify how failures to progress between successive stages of brood production contributed to the overall probability of failure. How foundress number potentially affected the timing of brood production (overall and for each stage) was analysed via parametric cohort survival analyses (Weibull models with a time-dependent hazard function and foundress number fitted as a factor) with replicates that failed to progress treated as censors (Abdi et al., 2020a, 2020b; Aitkin et al., 1989; Crawley, 1993).

All statistical tests were two sided. Significance was assessed by sequentially deleting terms from initially complex models, and aggregating levels within factors, to achieve minimal adequate models (Crawley, 1993; Wilson & Hardy, 2002; R Core Team, 2021).

RESULTS

Probability of brood production

Fifty one percent of foundress groups presented with a host failed to produce any adult offspring (54/105, Table 1). The probability of success declined significantly as the number of foundresses in the group increased (logistic regression: $G_1 = 8.317$, $p = 0.004$, Figure 1). Brood production failed throughout the stages of brood development until the pupal stage; all broods that reached the pupal stage gave rise to adult offspring (Table 1). The stage of failure that contributed the most to the overall probability of failure differed across the different foundress numbers but was usually one of the earlier stages of brood production: a failure to oviposit was particularly common (Table 1). Logistic analyses of failures to transition to the subsequent stages of brood development showed that the probability of presented hosts not being oviposited on increased significantly as foundress number increased ($G_1 = 26.715$, $p < 0.001$), while the probabilities of broods of eggs not hatching into broods of larvae or of larval broods not pupating were unaffected by foundress number (hatching: $G_1 = 2.9866$, $p = 0.084$; pupating: $G_1 = 0.1733$, $p = 0.6772$). We conclude that brood production failure typically occurs during the early stages and when foundresses are more numerous.

TABLE 1 Life table of *S. brevicornis* brood development

Number of foundresses	Hosts presented	Hosts bearing eggs	% hosts not oviposited on	*k1* (oviposition failure)	Hosts bearing larvae	% of oviposited on hosts bearing no larvae	*k2* (hatching failure)	Hosts with pupae	% of larval broods failing to pupate	*k3* (pupation failure)	Hosts generating adults	% pupal broods failing to generate adults	*k4* (adult emergence failure)	% presented hosts from which no adult parasitoids were produced	*K* (overall reproductive failure)
10	21	19	9.52	0.043	14	26.32	0.133*	14	0	0	14	0	0	33.33	0.176
25	21	17	19.05	0.092*	15	11.76	0.054	13	13.33	0.062	13	0	0	38.10	0.208
35	21	18	14.29	0.067	16	11.11	0.051	10	37.50	0.204*	10	0	0	52.38	0.322
45	21	10	52.38	0.322*	8	20	0.097	8	0	0	8	0	0	61.90	0.419
55	21	6	71.43	0.544*	6	0	0	6	0	0	6	0	0	71.43	0.544
Overall	105	70	33.33	0.176*	59	15.71	0.074	51	13.56	0.063	51	0	0	51.43	0.314

Note: The number of broods of each stage of production that failed to develop further were used to obtain *k*-values (*k1*, *k2*, *k3*, *k4*), calculated as $k = $ (log10 number before failure − log10 number after failure), which indicate the probability of failure of broods during successive stages of development (for each number of foundress treatment and also overall). *K* is the sum of contributions of failures at each stage to the overall probability of failure ($K = k1 + k2 + k3 + k4$). * indicates the stage of mortality that contributed the most importantly to the overall mortality for each foundress number treatment and also overall.

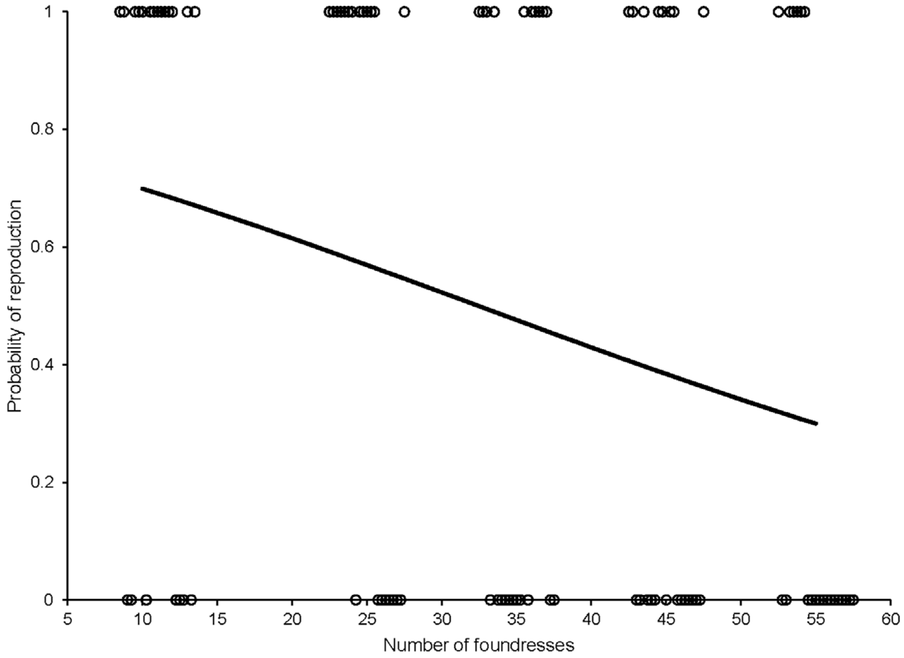

FIGURE 1 Probability of production of adult offspring according to the number of foundresses in the group provided with a host. Data are binary and are displaced horizanatally to illustrate sample sizes

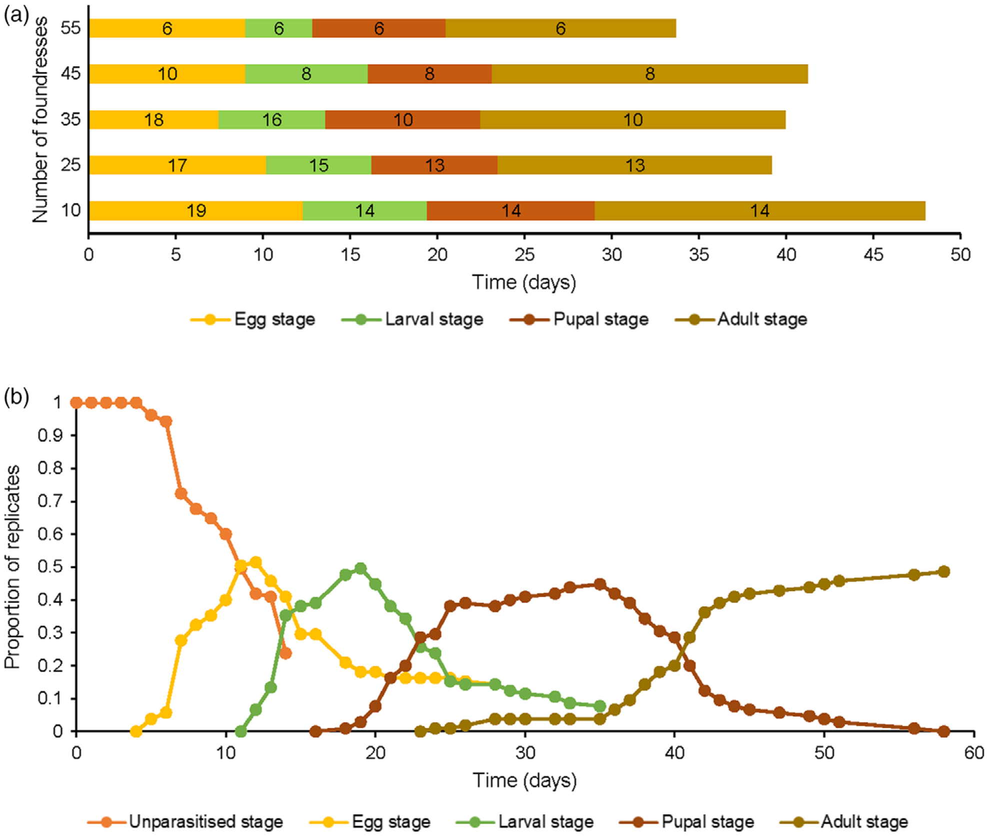

FIGURE 2 Overview of timing of *Sclerodermus* brood production. (a) The mean times taken for each stage of brood production and development, shown separately for each foundress number trialled (10, 25, 45 or 55 foundresses per host). The numbers within the stage-specific bars indicate the number of replicates from which each mean was estimated. The length of each bar shows the time taken for development. (b) Time-stage development of *Sclerodermus brevicornis*. The lines show the numbers of replicates at each developmental stage at any given time. Eggs were not laid on all hosts, and also some egg-stage and larval-stage broods failed to develop further, and the corresponding lines thus do not descend to zero (these broods were considered as censors in the cohort survival analyses, Figure 3). All broods reaching the pupal stage developed to the adult stage

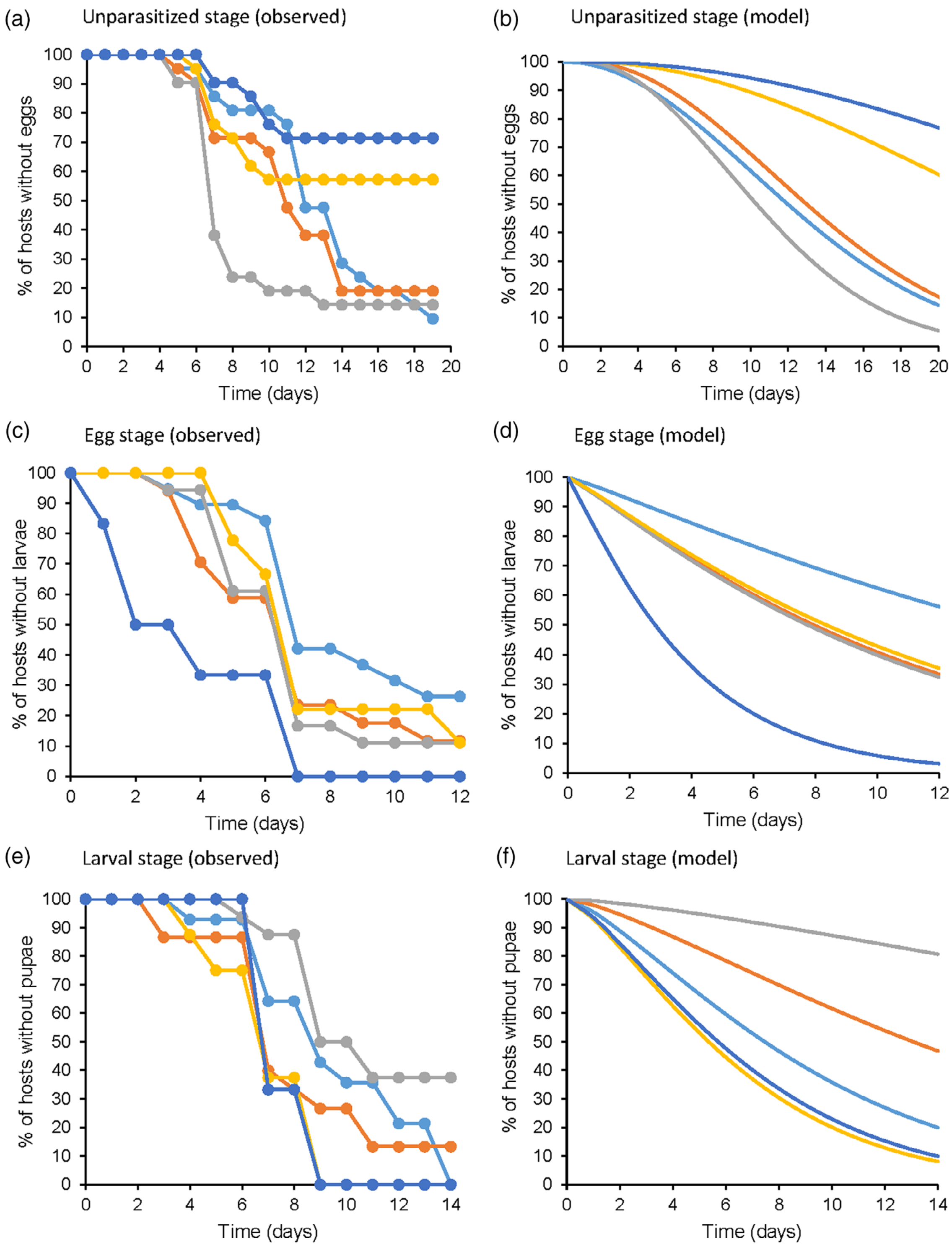

FIGURE 3 Cohort survival analysis of *Sclerodermus* brood production. (a) cohort plot of the timing of progression to the production of clutches of eggs on presented hosts for each number of foundresses. Lines that do not descend to zero indicate that eggs were not produced in some replicates. (b) Weibull model of time from presentation to oviposition taken to reach the egg stage, with replicates with no egg production treated as censors. (c) Cohort plot of the timing of development of egg clutches to the larval stage. (d) Weibull model, with censoring, for egg-to-larval development. (e) Cohort plot of larval-to-pupal brood development. (f) Weibull model, with censoring, of larval-to-pupal development. (g) Cohort plot of pupal-to-adult offspring development. (h) Weibull model of pupal-to-adult development. (i) Cohort plot of the overall timing of host presentation to adult offspring production. (j) Weibull model, with censoring, of offspring production following host presentation. Separate relationships are shown for each number of foundresses tested but the difference across these was marginally non-significant (see main text)

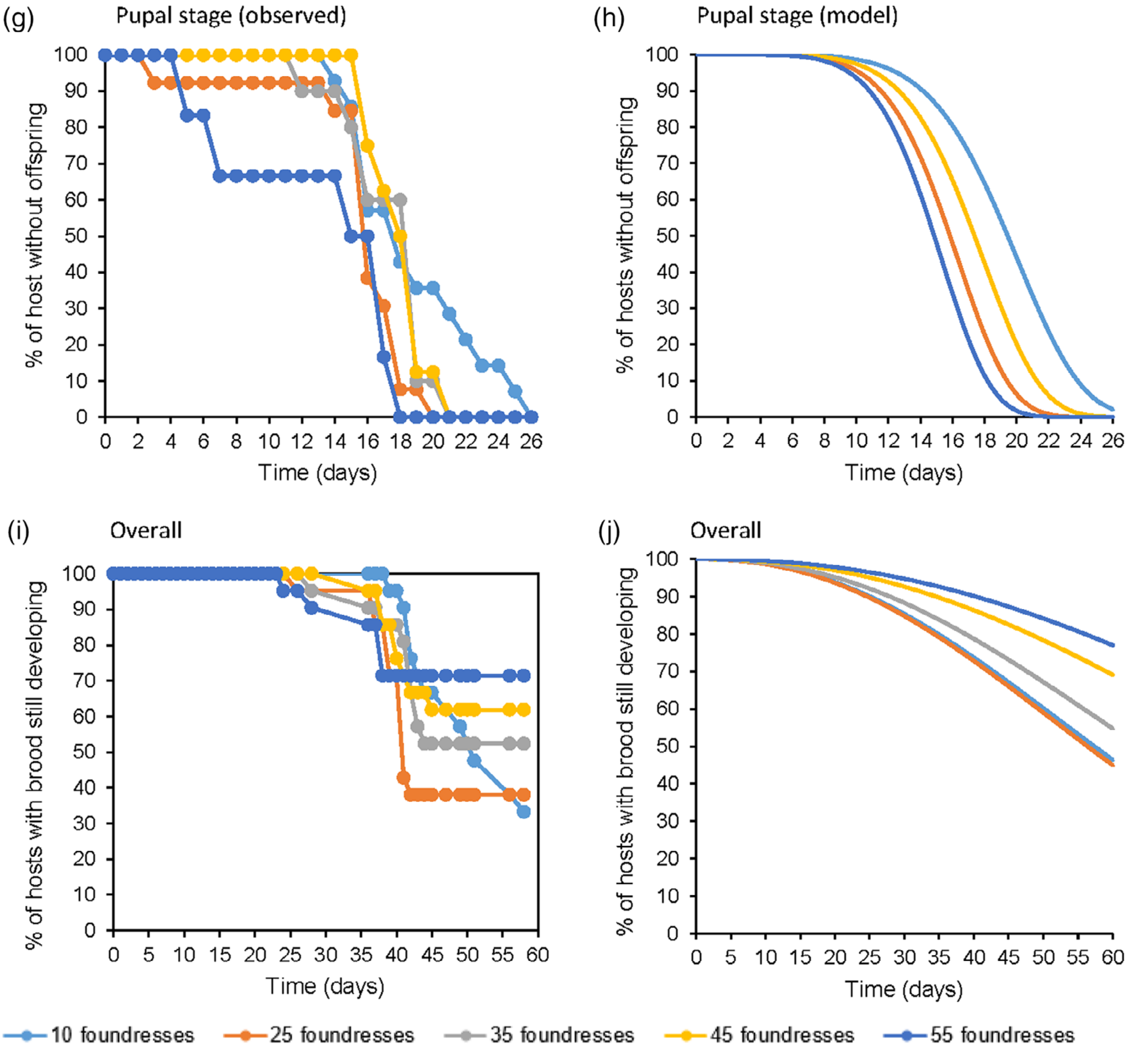

FIGURE 3 (Continued)

Timing of brood production

The overall time broods took to develop varied (host presentation to adult production range: 24 to 58 days) and development time also varied within each developmental stage (Figure 2). The overall time between the contact with the host and the emergence of adult offspring was not significantly influenced by foundress number (cohort survival analysis, with replicates in which no adult offspring were produced treated as censors: $G_4 = 8.76$, $p = 0.067$, $n = 105$, but note the marginal non-significance; Figure 3i,j).

The following analyses of the timings of successive stages of brood production are based on progressively declining sample sizes, due to brood production failures at previous stages, with failures during a focal stage being treated as censors: the statistical power of these analyses thus declines. The time between contact with the host and the commencement of oviposition differed significantly according to foundress number (cohort survival analysis with censors: $G_4 = 34.5$, $p < 0.001$, $n = 105$). Groups of 35 foundresses were the earliest to produce clutches of eggs but were not significantly earlier than groups of 25 and 10 foundresses ($G_2 = 3.12$, $p = 0.21$, mean for these treatment levels combined $= 10.02 \pm 3.54$ days). Groups of 45 or 55 foundresses were slower to oviposit than the smaller group sizes but did not differ significantly from each other in terms of timing ($G_1 = 1.87$, $p = 0.17$; combined mean ± SD $= 8.21 \pm 1.58$ days; Figure 3a,b).

The time taken for clutches of eggs to reach the larval stage differed significantly according to foundress number (cohort survival analysis with censors: $G_4 = 11.09$, $p = 0.026$, $n = 69$; Figure 3c,d). Clutches produced by groups of 10, 25, 35 and 45 foundresses took similar times ($G_3 = 4.42$, $p = 0.22$; combined mean ± SD $= 6.49 \pm 1.96$ days), while groups of 55 foundresses took less time (mean ± SD $= 3.83 \pm 2.64$ days). The number of foundresses also affected the time taken for broods to develop from the larval to the pupal stage (cohort survival analysis with censors: $G_4 = 31.91$, $p < 0.001$, $n = 60$). Broods produced by 55 and 45 foundresses took similar times ($G_1 = 0.00$, $p = 0.95$) and were the most rapid (combined mean ± SD: 7.36 ± 1.55 days), broods produced by 10 and

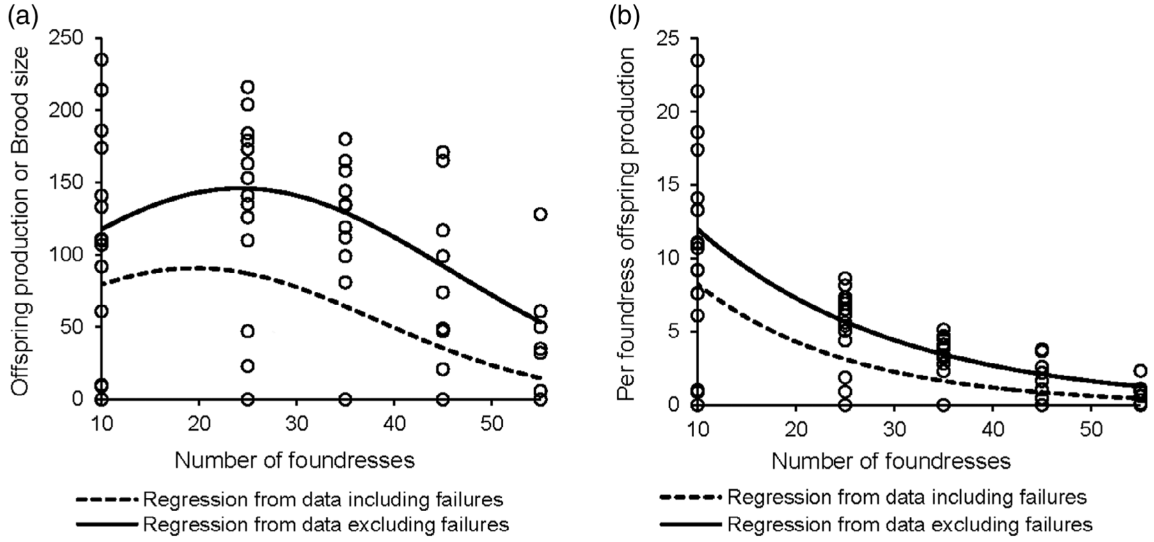

FIGURE 4 Offspring production and brood size. (a) Total number of adult offspring produced (including replicates in which no offspring were produced) and brood size (excluding production failures) in relation to the number of foundresses present. (b) Mean per foundress production of offspring (including failures) and mean per foundress brood size (excluding failures)

25 foundresses took significantly longer but were similar to each other ($G_1 = 3.14$, $p = 0.077$; combined mean ± SD = 8.48 ± 3.01 days) and broods produced by 35 foundresses took the longest (mean ± SD = 8.9 ± 1.52 days) and were statistically distinct from broods produced by 10 and 25 foundresses ($G_2 = 28.26$, $p < 0.0001$; Figure 3e,f).

The time taken for pupae to develop to adulthood also differed according to foundress number (cohort survival analysis with censors: $G_4 = 12.02$, $p = 0.017$, $n = 51$; Figure 3g,h). Development was fastest among broods produced by 25 and 55 foundresses (with no significant difference between these treatment levels: $G_1 = 0.47$, $p = 0.49$; combined mean ± SD = 14.89 ± 4.64 days), followed by the 35 and 45 foundresses ($G_1 = 0.02$, $p = 0.89$; combined mean ± SD = 17.77 ± 2.26 days) with broods produced by groups of 10 foundresses taking significantly longer than other broods ($G_2 = 11.42$, $p = 0.0033$; mean ± SD = 18.93 ± 3.85 days).

Offspring production and brood size

Results for 'offspring production' within replicates include cases were no adult offspring matured while results for 'brood size' refer to the numbers of adults when at least some adults matured. Offspring production had a significantly curvilinear response to increasing numbers of foundresses (log-linear regression including a quadratic term: Foundresses: $F_{1,103} = 14.42$, $p < 0.001$, %Dev = 11.25; Foundresses^2: $F_{1,102} = 6.19$, $p = 0.014$, %Dev = 4.83), showing little change when foundress numbers were relatively small (10 and 25 foundresses typically produced almost 100 offspring) then declining to around 15 as foundress numbers further increased (Figure 4a). Per foundress production (offspring/foundress group size) declined significantly, from 8 offspring to 0.5 offspring, as the number of foundresses increased ($F_{1,103} = 81.24$, $p < 0.001$, %Dev = 2.60, Figure 4b). Among the 51 groups of foundresses that produced adults, indicated in Figure 2a for each treatment, brood sizes ranged between six and 235 (mean ± SD = 115.59 ± 59.82). As with offspring production, there was a curvilinear relationship between brood size and foundress number (Foundresses: $F_{1,49} = 5.63$, $p = 0.02$, %Dev = 1.45; Foundresses^2: $F_{1,48} = 9.89$, $p = 0.003$, %Dev = 2.56, Figure 3a) and a significant decline in mean per foundress contribution to broods as foundress number increased ($F_{1,49} = 94.02$, $p < 0.001$, %Dev = 1.38, Figure 4b).

Sex ratio

Sex ratio analysis is constrained to include only those replicates in which some adult offspring were produced ($n = 51$). Adult offspring brood sex ratios were strongly female biased overall and had greater than binomial variance (proportion of offspring that were male = 0.08397 + SE = 0.00739, −SE = 0.00684, heterogeneity factor = 3.87). Brood sex ratio was unrelated to foundress number (logistic regression: $F_{1,49} = 3.4408$, $p = 0.99$, %Dev = 0.001; Figure 5a) but decreased significantly with increasing brood size (logistic regression: $F_{1,49} = 5.88$, $p = 0.01$, %Dev = 0.03; Figure 5b). The number of males per brood increased with brood size in a curvilinear relationship (log-linear regression: brood size: $F_{1,49} = 13.53$, $p < 0.001$, %Dev = 1.70; Brood size^2: $F_{1,48} = 7.25$, $p < 0.001$, %Dev = 1.44; Figure 5c). The mean numbers of males and females produced per foundress decreased significantly with the increasing numbers of foundresses (log-linear ANCOVAs: Male: $F_{1,49} = 34.04$, $p < 0.001$, %Dev = 0.14; female: $F_{1,49} = 85.77$, $p < 0.0001$, %Dev = 0.86). The mean per

FIGURE 5 Sexual composition of broods. (a) Relationship between brood sex ratio and number of foundresses, line fitted by logistic regression. (b) Relationship between brood sex ratio and the size of the brood, line fitted by logistic regression. (c) relationship between number of males per brood and brood size, line fitted by log-linear regression including a quadratic term

foundress production of male adult offspring was 0.49 (+SE $= 0.074$, −SE $= 0.0064$, heterogeneity factor $= 0.499$), showing that many foundresses did not produce any adult sons. One brood of 92 offspring produced by ten foundresses contained 40 males (Figure 5c): this unusual sexual composition may have been due to one or more of the foundresses being unmated. Only three of the 51 broods produced contained female offspring only ('virgin broods', Kapranas et al., 2016), and the probability of a brood being all-female was unaffected by the number of foundresses (logistic regression: $G_1 = 21.26$, $p = 0.12$).

DISCUSSION

Cooperation between *Sclerodermus* females in the suppression of the host and subsequent brood care can, in overview, be seen as a 'collective action benefit' (Shen et al., 2017) that enhances group reproduction. Multi-foundress brooding is beneficial both in terms of the probability of group reproduction and the mean reproductive output of foundresses within groups, provided hosts are sufficiently large: large hosts are difficult for individual foundresses to suppress but once suppressed can support the development of many offspring (Abdi et al., 2020a, 2020b; Liu et al., 2011; Mesterton-Gibbons & Hardy, 2021; Tang et al., 2014). However, even large hosts represent finite nutritional resources for offspring development and thus members of increasingly large groups of foundresses are ultimately likely to experience decreasing benefits of cooperation and the overall reproductive performance of the foundress group may also be affected (Bono & Crespi, 2008; Grinsted & Field, 2018; Kennedy et al., 2021; Reeve, 2000). Lupi et al. (2017), for instance, reported that in *Sclerodermus brevicornis*, broods failed to pupate when the host resource was insufficient to enable feeding larvae to attain critical size. In some cooperative breeding systems, group members with low *per capita* fitness returns may have the option of leaving and attempting to initiate or join a group elsewhere (Grinsted & Field, 2017a, 2017b, 2018; Kennedy et al., 2021). Such options may naturally be available to adult *Sclerodermus*, although relevant ecological and behavioural aspects are largely undescribed. Here, we have focussed on the consequences of foundress group size in the absence of facultative dispersal.

We found that as foundress numbers increased from 10 to 55, measures of group performance generally declined: the probability of successfully producing some adult offspring and the mean per foundress reproduction both declined monotonically, while the total numbers of adults produced remained relatively stable (with a slight dome) between 10 and 25 foundresses and then declined. Similar declines in *per capita* reproduction as foundress number increases have been reported in some other social insects (Bono & Crespi, 2008). This result is analogous to the classical pattern from studies of clutch size in gregarious parasitoids: a monotonic decline in individual offspring fitness as the clutch size laid on a fixed resource increases and a domed response in the sum of the individual fitness of clutch members (Godfray, 1987a, 1994; Hardy et al., 1992; Zaviezo & Mills, 2000). Many foundress groups (51% overall) failed to produce any offspring at all, and even among the smallest group size studied here (10 foundresses), the mean failure rate was 33%. Broods tended to fail at the earlier stages of production. In the high foundress density replicates, the quality of hosts for subsequent brood production may have been severely diminished by large numbers of foundresses feeding on host haemolymph prior to oviposition (Wei et al., 2014). We also observed that when foundress densities were high, so many eggs were laid that they were often on top of each other or were not on the host but next to it, possibly, because they had been actively removed from the clutch. While we did not observe ovicide taking place, it is also possible that some eggs were eaten by foundresses (Lupi et al., 2017; Pérez-Lachaud et al., 2002, 2004) possibly in association with reproductive dominance (Ratnieks & Wenseleers, 2008; Röseler et al., 1984). However, such dominance would seem more likely if foundresses were to differ in body size or in temporal priority to the host (Guo et al., 2022). In further analogy to theory for the evolution of clutch size, that predicts shifts between solitary development and gregarious development (Godfray, 1987b), the discrepancy between productivity at the level of the foundress group and the reproductive interests of individual females may select for a switch from scramble competition to contest competition between group members (Reeve, 2000). However, Lupi et al. (2017) reported that *Sclerodermus brevicornis* foundresses may switch from brood care to infanticide when the brood begins to fail due to host decay. During the regular inspections, we observed fungus growing on hosts, and consequently on broods produced, in some of the high-density foundress treatments.

The overall time required for offspring production following presentation of the host was similar across the foundress number treatments used (differences were marginally non-significant), but there were differences in timing within the individual stages of brood production. Larger foundress groups (45 and 55) took longer than smaller groups to oviposit onto hosts. If individual females varied independently in terms of the propensity to initiate host attack or egg maturation physiology, we would mechanistically expect the time to the first observed presence of eggs on a host to be shorter among larger groups (Liu et al., 2011). We might also expect this pattern if foundresses enhanced each other's speed of reproduction (Gao et al., 2016) via, for instance, cooperative host attack. That the opposite pattern was observed is indicative of a net disruptive effect of co-foundresses on each other's speed of host suppression and/or oviposition at high densities, or that early-oviposited eggs are more frequently eaten (prior to experimental observation).

Once clutches were observed, the time taken for eggs to hatch, and thus for the brood to reach the larval stage, was similar among most foundress densities studied but was more rapid for the highest density foundress groups, and larval broods also developed more rapidly to the pupal stage in the two highest density treatments (45 and 55 foundresses). Density-dependent disruption thus appears to be largely absent once eggs have hatched, although whether the observed patterns are due mechanistically to individual variation or to active enhancement is unknown. Patterns in the timing of pupal development to adulthood were not clearly associated with increasing foundress density but the slowest developing pupal broods were those tended by the smallest number of foundresses, as also observed by Liu et al. (2011). Overall, our results suggest that at high densities, foundresses disrupt each other's initiation of reproduction, but once a brood is established, developmental speed is generally enhanced by a larger number of foundresses tending the brood.

This is the first study to consider large numbers of *Sclerodermus* foundresses. We found that the sex ratios of broods produced were similar to those reported by studies examining reproduction by smaller numbers of foundresses (e.g., Kapranas et al., 2016; Tang et al., 2014): brood sex ratios are consistently strongly female biased. This constitutes further evidence that *Sclerodermus* does not respond to foundress number in the manner predicted by prior models of local mate competition (LMC). With large numbers of foundresses, classical LMC theory would predict sex ratios of approximately 0.5 (Hamilton, 1967, 1979) and extended theory, that considers modifications to the assumptions of the original models, would predict sex ratios of around 0.3 (Tang et al., 2014; West, 2009), but *Sclerodermus* sex ratios are typically around 0.1. The extremely biased sex ratios within broods produced by multiple *Sclerodermus* foundresses have been suggested to be due to the local resource enhancement (LRE: Taylor, 1981) that foundresses provide to each other when co-exploiting hosts: females encountering large hosts have greater *per capita* reproductive success when in groups than when acting alone and mothers are thus selected to bias their reproduction towards daughters, which tend to cooperate, rather than sons, which tend to compete (Kapranas et al., 2016; Tang et al., 2014). While formal modelling has recently supported this suggestion qualitatively (Iritani et al., 2021), the predicted reduction in brood sex ratios (an increase in female bias) is insufficient to provide a close match to observations, although it remains possible that refinement of the modelling assumptions employed may provide a better match. Other studies have tested for possible relationships between the kinship of *Sclerodermus* foundresses (either directly experimentally controlled or inferred from wing dimorphism) and sex ratio, since reproducing with close relative co-foundresses is predicted to select for female bias (Abe et al., 2021; Gardner & Hardy, 2020; see also Abdi et al., 2020c) but have found no effect (Abdi et al., 2020a, 2020b).

A further possibility is that some foundresses monopolise the production of male offspring, either via suppression of oviposition of male eggs by other foundresses or via post-ovipositional infanticide (Lupi et al., 2017; Pérez-Lachaud et al., 2002, 2004). Current evidence, from a study of smaller groups of *Sclerodermus* foundresses, suggests that some may become dominant, by being larger or by commencing reproduction earlier, and produce the majority, or even all, of the male offspring within broods (Guo et al., 2022), and our result that the mean number of sons per foundress is *ca*. 0.5 also indicates that many foundresses could not have produced any sons (either because they did not lay male eggs or because their male offspring did not survive to adulthood). Such selfish control of group reproduction by a minority of foundresses would be expected to lead to very female-biased group sex ratios under a range of foundress numbers. For instance, under strict LMC, a single foundress would be expected to produce the lowest number of sons that can inseminate her numerous daughters (Godfray, 1994; Green et al., 1982; Hardy et al., 1998; West, 2009). Two foundresses, each with control of their own sex allocation, are expected to each produce more sons than this minimum as a game-theoretic response to the sex ratio that will be produced by the other co-foundress: standard LMC theory predicts the evolutionarily stable strategy (ESS) sex ratio to increase from effectively zero (for one foundress) to 0.25 (for two foundresses: Hamilton, 1967; Godfray, 1994; West, 2009).

However, if one foundress could control the sex allocation of the other, we would expect that the ESS for the dominant foundress would be to produce only as many sons as could inseminate all female offspring maturing within the group and to allow the subordinate foundress to produce female offspring only. If sex allocation dominance were substantial, we would expect sex ratios to be very strongly female biased, irrespective of foundress number (as observed in this study and previously by Hong et al., 2008; Li et al., 2010; Li & Sun, 2011; Tang et al., 2014; Lupi et al., 2017; Wang et al., 2016; Wei et al., 2017; Yang et al., 2018; Abdi et al., 2020a; Jucker et al., 2020; Zhao et al., 2020). We would also expect that, due to limited mating capacity of adult males, the numbers of males in broods would increase gradually as brood sizes increase (as observed in this study and previously by Kapranas et al., 2016; Abdi et al., 2021). Until these possibilities are further evaluated, the extremely biased sex ratios exhibited by *Sclerodermus* constitute one of the remaining sex allocation puzzles among parasitoid hymenopterans (Abe et al., 2021).

CONCLUSION

Sclerodermus foundresses cooperate in brood production such that individuals within multi-foundress groups can be more reproductively successful than individuals reproducing alone. This situation occurs when hosts are large and foundress numbers are moderate. However, further increasing foundress group sizes, for a given host size, leads to diminished *per capita* success and the common occurrence of complete developmental failure of the brood. From the perspective of an individual foundress, reproduction is likely to be maximised in groups of up to around 10 foundresses and group productivity is likely to peak at numbers lower than around 25 foundresses. Although the overall timing of brood production was similar across the range of foundress group sizes examined, early-stage reproduction was slower when groups were larger, suggesting density-dependent disruption when eggs are laid and enhancement once broods are more established. Our study employed regular, rather than continuous, observations and did not record any interactions that were overtly indicative of contest competition between foundresses (such as aggressive exclusion of individuals from the vicinity of the host); it remains possible that foundresses differ in terms of dominance and/or may commit ovicide via the removal or ingestion of eggs. The occurrence of eggs positioned on top of other eggs within clutches produced by large groups of foundresses suggests scramble competition for oviposition sites and, possibly, for host resources once eggs eclose. In natural situations, foundresses may opt to disperse from high-density groups and forage for alternative reproductive opportunities: future studies will investigate foundress behaviour when provided with such options. The sex ratios of *Sclerodermus* broods remained highly biased even when foundress numbers were extreme. Sex ratio theories assuming that each foundress within a group controls her own sex allocation cannot currently provide a quantitative explanation for these observations. We suggest that covert dominance within foundress groups, that leads to the production of males being by a minority of females, could explain the sex ratio bias observed.

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CONFLICT OF INTEREST

All authors declare that they have no competing interests.

AUTHOR CONTRIBUTIONS

All authors designed the experiment. Serena Malabusini, Daniela Lupi, Sara Savoldelli and Costanza Jucker collected the data. Serena Malabusini and Ian C.W. Hardy analysed the data and wrote the manuscript. Serena Malabusini, Ian C.W. Hardy, Daniela Lupi and Costanza Jucker revised the manuscript. All authors discussed the work at all stages and approved the manuscript.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available on request from the first, last and corresponding authors.

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