

Kinship effects in quasi-social parasitoids II: co-foundress relatedness and host dangerousness interactively affect host exploitation

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Sclerodermus brevicornis is a parasitoid that exhibits cooperative multi-foundress brood production. Prior work showed that the time lag to paralysis of small-sized hosts is shorter when co-foundress relatedness is higher and predicted that the greater risks and greater benefits of attacking larger hosts would combine with co-foundress relatedness to determine the limits to the size of a host that a female is selected to attack as a public good. It was also predicted that the time to host attack would be affected by an interaction between host size and relatedness. Here, we show empirically that both host size and kinship affect *S. brevicornis* reproduction and that they interact to influence the timing of host attack. We also find effects of co-foundress relatedness after hosts have been suppressed successfully. A public goods model using parameters estimated for *S. brevicornis* again suggests that selection for individual foundresses to attack and, if successful, to share hosts will be dependent on both the size of the host and the relatedness of the foundresses to any co-foundresses present. Females will not be selected to bear the individual cost of a public good when hosts are large and dangerous or when their relatedness to the co-foundress is low. We conclude that although reproductive behaviours exhibited by *Sclerodermus* females can be cooperative, they are unlikely to be exhibited without reference to kinship or to the risks involved in attempting to suppress and share large and dangerous hosts.

ADDITIONAL KEYWORDS: host attack – host size – kinship – public goods – *Sclerodermus brevicornis* – sociality.

INTRODUCTION

The evolution and maintenance of social systems has been considered in many animal taxa (e.g. Costa, 2006, 2018; Schenider & Bilde, 2008; Davies *et al.*, 2012; Tanaka *et al.*, 2018; Ågren *et al.*, 2019; Downing *et al.*, 2020). Among parasitoid wasps, an extremely species-rich functional group (e.g. Dolphin & Quicke, 2001; Davis *et al.*, 2010; Dale-Skey *et al.*, 2016; Whitfield *et al.*, 2018; Chen *et al.*, 2019), sociality is unusual and relatively little explored. *Sclerodermus* (Hymenoptera: Bethyliidae) are among the most socially complex parasitoids known (Bridwell, 1920; Wheeler, 1928; Mamaev, 1979). Species in this genus are not members

of the monophyletic group that contains most hymenopterans that have parasitoid life histories (the Parasitica) but are aculeates ('stinging wasps'). Within the Aculeata, they are members of the Chrysidoidea, which forms the sister group of all other aculeate taxa, including the ants, bees and vespidae wasps in which eusociality has evolved (Peters *et al.*, 2017).

Female *Sclerodermus* not only exhibit maternal care of their own offspring, but also a group of 'foundress' females may cooperate to tend, in an apparently indiscriminate manner, a group of offspring produced collectively on a single host (Bridwell, 1920; Kühne & Becker, 1974; Casale, 1991; Hu *et al.*, 2012; Wu *et al.*, 2014). *Sclerodermus* are considered quasi-social because they exhibit cooperative brood care without generational overlap or apparent division of labour

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(Tang *et al.*, 2014; Costa, 2018). Tang *et al.* (2014) showed that co-exploitation of large hosts provides direct fitness benefits (in terms of average reproductive success) to individual females within *Sclerodermus harmandi* foundress groups and thus that quasi-sociality could be explained without reference to inclusive fitness benefits, an oft-invoked factor in social evolution studies (Hamilton, 1964; Costa, 2006, 2018; Davies *et al.*, 2012).

Although Tang *et al.* (2014) showed that kin selection need not be required to explain *Sclerodermus* sociality, a role for inclusive fitness effects in the reproductive cycle was not excluded. Abdi *et al.* (2020) subsequently showed that, in *Sclerodermus brevicornis*, kinship among foundress groups affects the timing of host attack, in that paralysis of standard sized hosts is more rapid when co-foundress relatedness is higher. Attacking hosts carries considerable mortality risks for *Sclerodermus* females, especially when hosts are large (Kühne & Becker, 1974; Liu *et al.*, 2011; Tang *et al.*, 2014; Wei *et al.*, 2014) and, although females must ultimately access a host in order to reproduce, they might be reluctant to take risks when reproductive benefits might be shared with non-kin. Using data from several *Sclerodermus* species, Abdi *et al.* (2020) used a simple public goods model based on Hamilton's rule (Hamilton, 1964; Cooper *et al.*, 2018) to explore how three parameters, the greater risks and greater benefits of attacking larger hosts and co-foundress relatedness, could combine to determine the size ranges of hosts that a female is selected to attack to provide reproductive resources to co-foundresses in addition to herself. This suggested that when foundresses are more closely related, larger hosts will be attacked by individuals as a public good. It also suggested that, in general, effects of kinship would be least marked when hosts are small and relatively safe to attack and might be greater when hosts are large and dangerous to attack, and thus that co-foundress relatedness and host dangerousness should interact to affect the timing of host attack.

Here, we test empirically the combined effects of host size and *S. brevicornis* co-foundress relatedness. We hold the number of foundresses constant, at two females, and vary relatedness such that co-foundresses are either brood-mates or non-siblings. We provide foundress pairs with a single host, drawn from a wide range of host sizes, with larger hosts being more dangerous to attack. We evaluate the timing and success of host attack behaviour and other aspects of reproductive success and find effects of kinship, including an interaction between co-foundress relatedness and host dangerousness. We also assay the success of single foundresses in attacking hosts of different sizes, the timing of the attack and the probability of dying during the attack, confirming that larger hosts are more dangerous for individual females to attack. We use our empirical estimates of the host

size-dependent risks of host attack and on offspring production on successfully suppressed hosts in a new model of host attack by *S. brevicornis*. As with models for other *Sclerodermus* species, this suggests that host size and foundress kinship will interact to influence host attack behaviour and, specifically, that individual *S. brevicornis* foundresses will be selected to attack and then share hosts as a public good only when their relatedness to co-foundresses is high and when the host is neither large nor very small.

MATERIAL AND METHODS

INSECT CULTURING

Sclerodermus brevicornis (Kieffer) (Hymenoptera: Bethyliidae) is a gregarious ectoparasitoid wasp, which is a parasitoid of European long-horned beetle larvae (Coleoptera: Cerambycidae) (Kieffer, 1914; Lupi *et al.*, 2017) that can be reared on several non-native, invasive cerambycids, including the larvae of the yellow long-horned beetle, *Psacothea hilaris hilaris* (Pascoe) (Lupi *et al.*, 2017), which was used as a host in the present study. Stocks of *P. h. hilaris* were maintained according to Lupi *et al.* (2017). Stocks of *S. brevicornis* were reared on late instar larvae of *P. h. hilaris*.

All cultures and experiments were maintained in a climatic chamber at 25 ± 1 °C, with a 16 h–8 h light–dark photoperiod and $60 \pm 5\%$ relative humidity. To synchronize parasitoid and host availability, newly emerged *S. brevicornis* adults were stored in a refrigerator at 5 ± 0.5 °C for a maximum of 7–10 days before use in experiments (following Abdi *et al.*, 2020).

TWO-FOUNDRESS EXPERIMENT

The experiment followed a 2×3 factorial design, varying foundress relatedness and host size and holding the number of foundresses constant. In each replicate, a larval host was placed individually into a plastic container (5 cm in diameter and 4 cm in depth), in which there was a thin layer (~1.5 mm) of cork oak granules to maintain the relative humidity and to allow the parasitoids to access the part of the host that would otherwise be in contact with the container. Hosts were classified as small (mean weight = 0.0476 g, range = 0.0213–0.0825 g, SD = 0.0197 g), medium (mean = 0.2851 g, range = 0.2142–0.3671 g, SD = 0.0415 g) or large (mean = 0.7020 g, range = 0.4921–1.0522 g, SD = 0.1367 g); the weight of the host in each replicate, not only its size class, was also recorded. Note that our 'small' size class corresponds closely to the standardized sizes of the factitious host used by Abdi *et al.* (2020) and also to the 'small' host size class of *P. hilaris* used by Lupi

et al. (2017). Two adult female *S. brevicornis* were added into each container. The relatedness between co-foundresses was varied such that foundresses were either brood-mates (often sisters) that had developed in the same brood or were non-siblings that had developed in different broods. To give adequate overall statistical power (Smith *et al.*, 2011), we set up 20 replicates of each foundress relatedness and host size combination (20 replicates \times 2 foundress relatedness levels \times 3 host size levels = 120 replicates overall).

Replicates were left undisturbed for 2 days because observing the wasps within this period has previously been found to disrupt their reproductive behaviours (D.L. & C.J., pers. obs.). We then observed each replicate once per day until the 23rd day. At each observation, we recorded whether the host had been paralysed, whether any oviposition occurred, whether any foundresses had died and the number and sex of adult offspring produced.

SINGLE-FOUNDRESS ASSAY

The assay consisted of presenting single female *S. brevicornis* with a host of known weight and varying host weight considerably across replicates (range = 0.0227–0.9408 g, mean = 0.3536 g, SD = \pm 0.2723 g, $N = 37$). In each replicate, a larval host was placed individually into a plastic container with cork granules, as described above. Then a single adult female *S. brevicornis* was added into each container. The container was covered with a white plastic cover and left undisturbed for 7 days. We then observed each replicate once per day for a further 14 days. At each observation, we recorded whether the host had been paralysed, whether any oviposition occurred, whether the foundresses had died and whether dead foundresses had been bitten into two parts by the host.

STATISTICAL ANALYSES

Unless otherwise stated, 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). All statistical tests were two sided. All analyses were carried out using the statistical software package *GenStat* (v.17; VSN International, Hemel Hempstead, UK).

In the two-foundress experiment, the explanatory variable ‘foundress relatedness’ was always fitted as a factor with two levels. In analyses of single-foundress and two-foundress data, host size was fitted as a factor with three levels in some analyses and as a continuous variable in others. The response variables were the parameters recorded during the daily observations and at the end of the experiment.

Binary data (on host paralysis, acceptance, foundress mortality and bisection) were explored using logistic analyses assuming binomially distributed errors and a logit link function; here, the test statistic is change in deviance, G , which is approximately χ^2 distributed (Crawley, 1993). Other logistic analyses of proportional data with denominators larger than unity (e.g. sex ratio) assumed quasi-binomial error distributions and adopted a logit link function; the test statistic was the F -ratio (Crawley, 1993; Wilson & Hardy, 2002). Logistic analyses comparing foundress mortality during the successive stages of host handling (two-foundress experiment) used mixed models [general linear mixed model (GLMM) and Wald χ^2 statistics], with replicate identity fitted as a random factor. Integer data (e.g. number of offspring produced) were explored using log-linear analyses assuming quasi-Poisson error distributions, adopting a log-link function and generating F -ratio test statistics (Crawley, 1993). Data derived from integers (e.g. offspring production per foundress) that were likely to exhibit an approximate Poisson distribution were also analysed using log-linear models (Faraway, 2006; Tang *et al.*, 2014). After logistic and log-linear analyses, we give the percentage of deviance explained (%Dev) as a descriptor analogous to r^2 .

Time-to-event data on host paralysis, oviposition and foundress mortality were analysed using parametric cohort survival analyses with censoring (Aitkin *et al.*, 1989; Crawley, 1993). We first compared exponential models (constant hazard function) against Weibull models (time-dependent hazard function); in all cases, the Weibull models provided a significantly better description of the data. The influences of the candidate explanatory factors (see above) were then explored by their inclusion into the Weibull models (Aitkin *et al.*, 1989; Crawley, 1993). In one case, we used a non-parametric log-rank test owing to poor fit to parametric assumptions.

Given that we performed many individual statistical tests, we controlled for possible type I errors using the false-discovery rate (FDR) procedure to control for multiple comparisons (Benjamini & Hochberg, 1995; McDonald, 2014). We treated the main results from the two-foundress experiment (Table 1) as a ‘family’ of tests (including evaluations of interactions; Cramer *et al.*, 2016) and set the family-wide α -value to 0.05, thus adopting a more stringent criterion than in the accompanying, more exploratory study (Abdi *et al.*, 2020). Likewise, we treated results from the single-foundress assay as a family of tests and used an FDR of 0.05. We report uncorrected interpretations in the main text and the results of FDR procedures in the results summary tables (Tables 1 and 2). The data analysed are available as supporting information (Supporting Information, Data set).

Table 1. Summarized main results from the two-foundress experiment*

Reproductive trait	Relatedness	Host size	Interaction
Foundress mortality (overall proportion)	Higher among brood-mate foundresses	NS	NS
Foundress mortality (timing)	Brood-mates die earlier than non-siblings	NS	NS
Paralysis of host (proportion)	NS	Lower probability with larger hosts	NS
Paralysis of host (timing)	Brood-mates often paralyse hosts earlier than non-siblings, but this depends on host size	Smaller hosts are paralysed earlier	Brood-mates paralyse smaller hosts earlier and larger hosts later than non-siblings
Oviposition on host (probability)	NS	NS	NS
Oviposition on host (timing)	Non-sibling foundresses oviposit earlier	NS	NS
Brood size (total)	Significance via interaction	Curvilinear response	Non-siblings produce larger broods than brood-mates except on small hosts
Brood size (per foundress)	Significant as main effect and via interaction	Curvilinear response	Non-siblings produce smaller broods than brood-mates on small hosts and relatively larger broods on large hosts
Sex ratio of offspring	NS	NS	NS

Abbreviation: NS, no statistically significant influence detected.

*All significant effects retained the same interpretation after multiple-comparisons correction using a false-discovery rate of 0.05.

Table 2. Summarized single-foundress assay results*

Trait	Effect of increasing host size
Host paralysis	Probability of paralysis decreased
Oviposition on paralysed host	NS
Foundress mortality	Probability of mortality increased
Bisection of dead foundress	Probability that a dead female was bisected increased
Timing of host paralysis	Smaller hosts were paralysed earlier than larger hosts
Timing of foundress mortality	NS

Abbreviation: NS, no statistically significant influence detected.

*All significant effects retained the same interpretation after multiple-comparisons correction using a false-discovery rate of 0.05.

PUBLIC GOODS MODEL OF HOST ATTACK

We consider the selective forces that might combine to influence the decision by an individual female *S. brevicornis* to attack a host by using a public goods model. Public goods models consider situations in which a focal individual produces, at personal cost, a benefit, which is then shared between the individual and its social partners. Hamilton's rule asserts that a trait will spread if its fitness benefits to the recipients

(b) multiplied by the relatedness (r) between social partners is greater than the fitness cost (c) to the actor ($rb - c > 0$; Hamilton, 1964; Cooper *et al.*, 2018). Given that approaches to calculating b and c are under ongoing debate (Gardner *et al.*, 2011; Abdi *et al.*, 2020), we proceed heuristically in making use of our empirical estimates of the host size-dependent probability of a foundress dying during host attack (cost, c) and of the fitness obtained from a successfully paralysed host of a given size (benefit, b) to explore, in a qualitative manner, how co-foundress relatedness (r) might affect selection for host attack as a public good. Given that the benefits and costs are affected by host size, our proxies of b and c are in the form of regression equations rather than being fixed values applied across all hosts. Cost is expressed as a proportional response to host size, and thus c takes values between zero and unity. Given that the relationship between the benefits provided by a host and the size of that host is domed (see below Fig. 6), we divided by the maximal value of the polynomial regression equation to scale benefits as a proportion; b thus takes values between zero and unity (following Abdi *et al.*, 2020). We use an open formulation of Hamilton's rule, in which the mechanism generating co-foundress relatedness is undefined (Cooper *et al.*, 2018), and explore values of r ranging between zero and unity.

RESULTS

TWO-FOUNDRESS EXPERIMENT

Results of analyses reported in this section are summarized in Table 1.

Foundress mortality

Approximately a quarter (23.75%, 57/240) of foundresses died by the 23rd day after presentation with a host. Foundresses that were brood-mates died earlier than non-sibling foundresses (cohort survival analysis with surviving females treated as censors: $G_1 = 5.7, P = 0.020, \%Dev = 1.98$; Fig. 1). In this analysis, the longevity of each one of the pair of foundresses was treated as if it were independent of the other; such pseudo-replication could have generated the significance. We therefore ran an additional analysis using a non-parametric log-rank test on the mean longevity of females in each replicate, thus analysing one observation per replicate; this also indicated

that brood-mates died earlier than did non-siblings ($z = 4.919, d.f. = 1, P = 0.027$). Time to death was not significantly affected by host size ($G_2 = 2.4, P = 0.301, \%Dev = 0.88$) or by its interaction with foundress relatedness ($G_2 = 2.9, P = 0.235, \%Dev = 1.10$).

Likewise, the proportion of foundresses in a replicate dying (number dying/2) was significantly higher when foundresses were brood-mates (logistic ANOVA: $G_1 = 5.23, P = 0.022, \%Dev = 3.15$; Fig. 2) but was not affected by host size ($G_2 = 1.14, P = 0.321, \%Dev = 1.37$) or its interaction with foundress relatedness ($G_2 = 1.52, P = 0.218, \%Dev = 1.84$). However, separate analyses within each host size class indicated that mortality of brood-mate foundresses was significantly higher when presented with medium-sized hosts (logistic ANOVA: $G_1 = 7.62, P = 0.006, \%Dev = 12.71$; Fig. 2) but did not differ when hosts were large ($G_1 = 0.62, P = 0.430, \%Dev = 1.09$) or small ($G_1 = 0.08, P = 0.774, \%Dev = 0.18$).

We also explored foundress mortality in relationship to the successive host-handling periods: pre-paralysis (host presentation to host paralysis), paralysis-to-oviposition

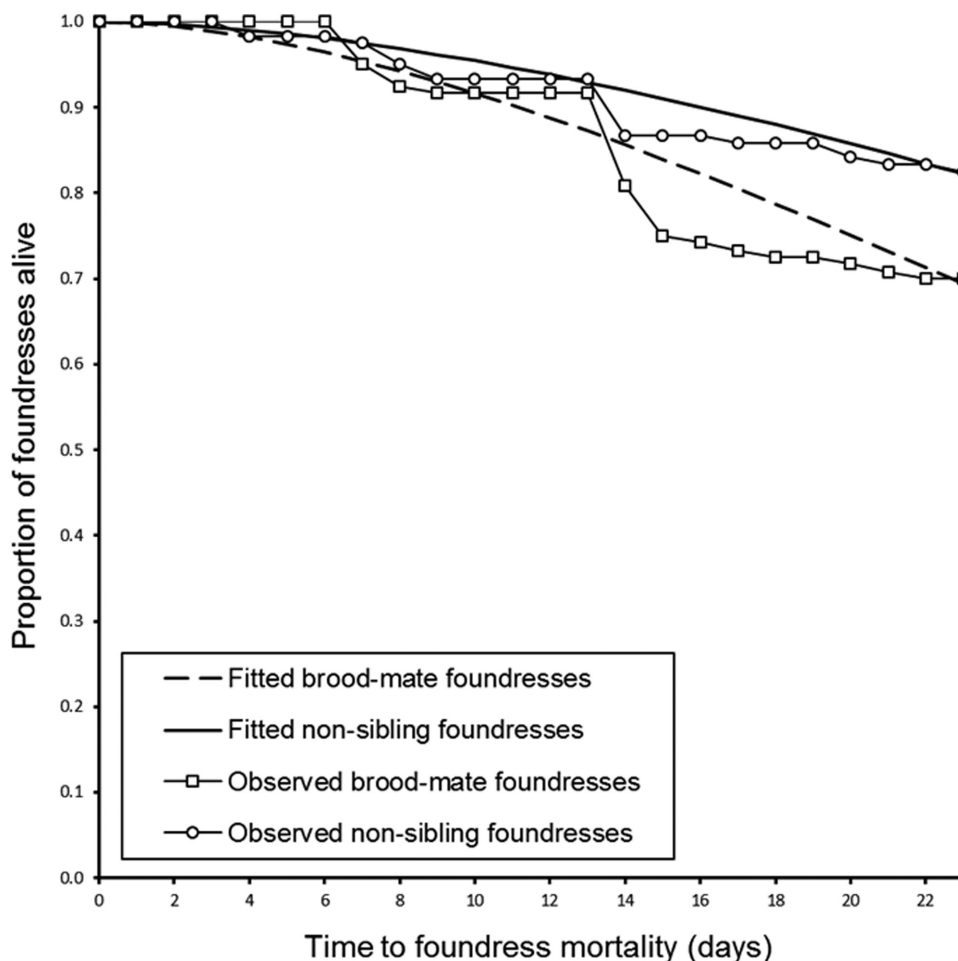


Figure 1. The effect of relatedness on foundress survival over time.

and post-oviposition (Fig. 3). The proportion of foundresses that died differed significantly according to relatedness (mortality was highest amongst brood-mates; GLMM: Wald $\chi^2 = 4.06$, d.f. = 1, $P = 0.046$) and between periods (post-oviposition mortality was lowest; $\chi^2 = 17.29$, d.f. = 2, $P < 0.001$) but without a significant interaction between relatedness and period ($\chi^2 = 2.12$, d.f. = 2, $P = 0.348$). Host size affected mortality through an interaction with period (size: $\chi^2 = 2.59$, d.f. = 2, $P = 0.279$; size \times period: $\chi^2 = 15.48$, d.f. = 4, $P = 0.005$), with pre-paralysis mortality being lowest when foundresses were presented with small hosts. There was no significant interaction between relatedness and size ($\chi^2 = 2.81$, d.f. = 2, $P = 0.250$) or between all three main effects ($\chi^2 = 0.04$, d.f. = 3, $P = 0.998$).

Paralysis

The percentage of hosts that were paralysed by *S. brevicornis* foundresses was 83.33% ($N = 120$). This

proportion decreased significantly with an increase in host size (logistic ANCOVA: $G_1 = 15.90$, $P < 0.001$, %Dev = 14.70; Fig. 4) but was unaffected by relatedness ($G_1 = 0.20$, $P = 0.653$, %Dev = 0.19) or its interaction with host size ($G_1 = 1.55$, $P = 0.213$, %Dev = 1.43).

Among the 100 replicates in which host paralysis occurred, the time taken to paralyse the host ranged up to 22 days. The 20 replicates in which there was no paralysis observed were treated as censors in the subsequent cohort survival analysis. Time to paralysis was significantly affected by host size ($G_2 = 96.5$, $P < 0.001$, %Dev = 37.36), with smaller hosts being paralysed faster than larger hosts. Foundress relatedness also affected time to paralysis ($G_1 = 9.5$, $P = 0.002$, %Dev = 5.97), and there was a significant interaction between relatedness and host size ($G_2 = 9.5$, $P = 0.009$, %Dev = 7.80): for small hosts, paralysis was significantly more rapid when foundresses were brood-mates ($G_1 = 20.4$, $P < 0.001$, %Dev = 46.99), for medium-sized hosts paralysis by

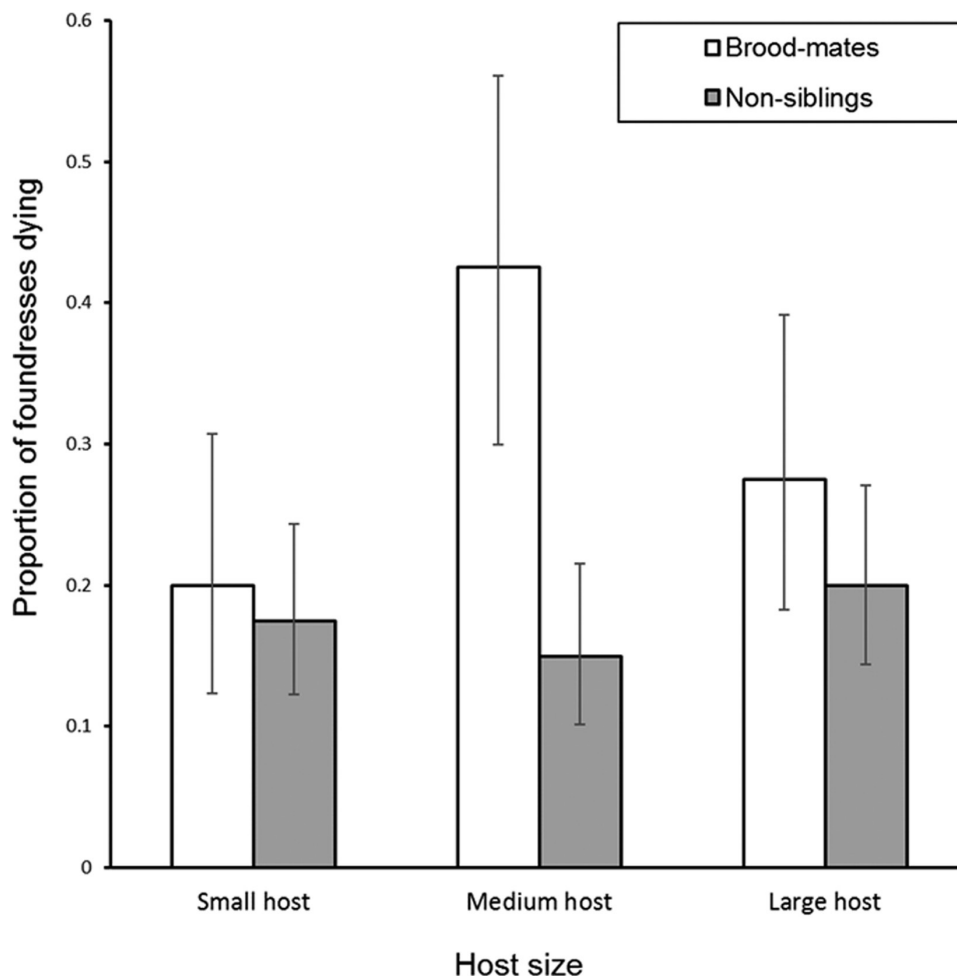


Figure 2. Foundress mortality according to host size and relatedness. Bars represent the SEM and are asymmetrical owing to back transformation from the logit scale. Differences between brood-mates and non-siblings on small or large hosts were not significant.

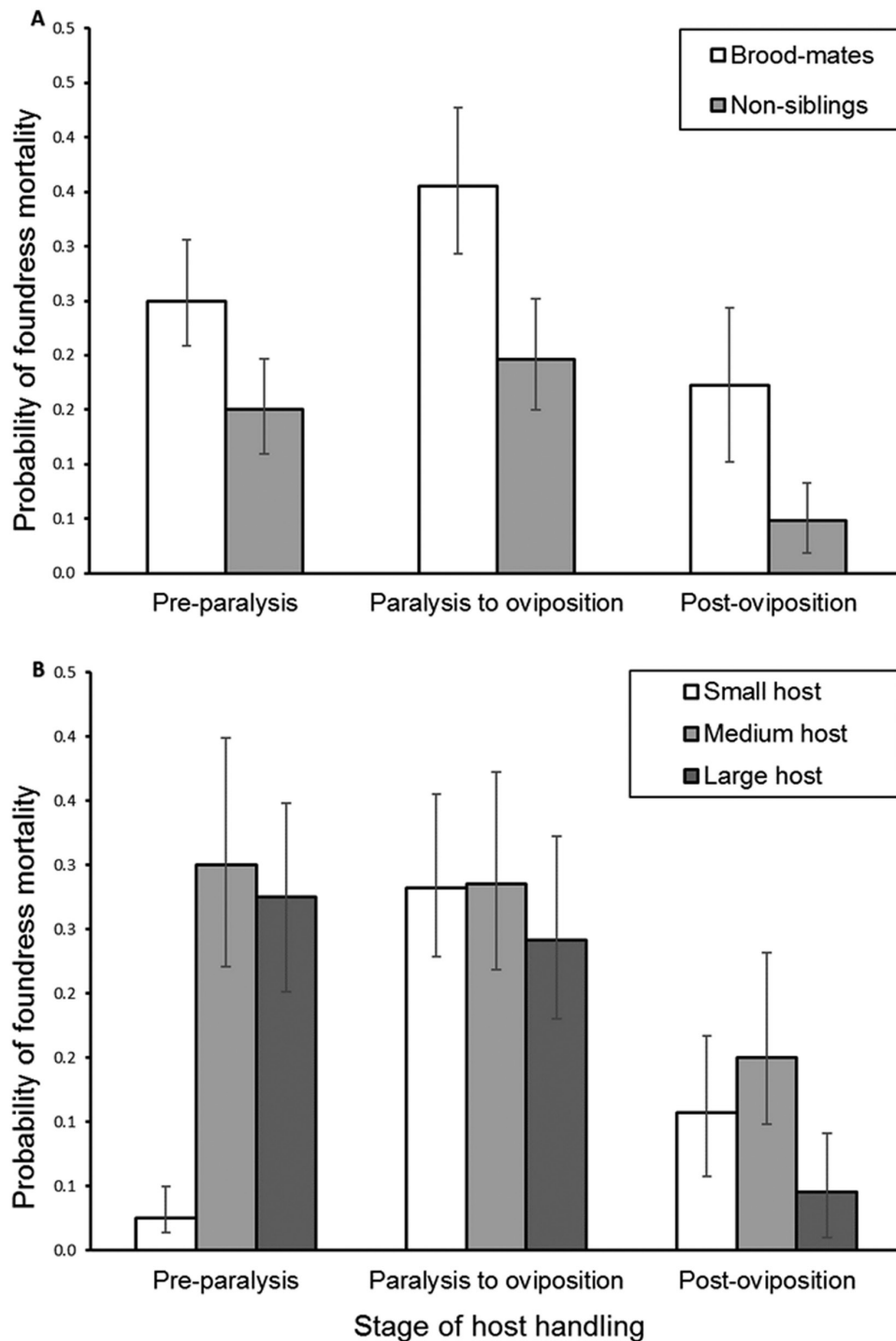


Figure 3. Foundress mortality according to relatedness (A) and host size (B) during the successive stages of host handling. Bars represent the SEM and are asymmetrical owing to back transformation from the logit scale.

brood-mates was non-significantly earlier ($G_1 = 2.10$, $P = 0.147$, %Dev = 3.61) and for large hosts paralysis by brood-mates was non-significantly later ($G_1 = 0.1$, $P = 0.752$, %Dev = 0.16; Fig. 5). We checked these results by repeating the analysis with host size fitted

as a variate rather than as a categorical factor; the interpretation remained the same (host size: $G_1 = 60.1$, $P < 0.001$, %Dev = 29.09; relatedness: $G_1 = 4.3$, $P = 0.038$, %Dev = 2.64; interaction: $G_1 = 4.1$, $P = 0.043$, %Dev = 2.47).

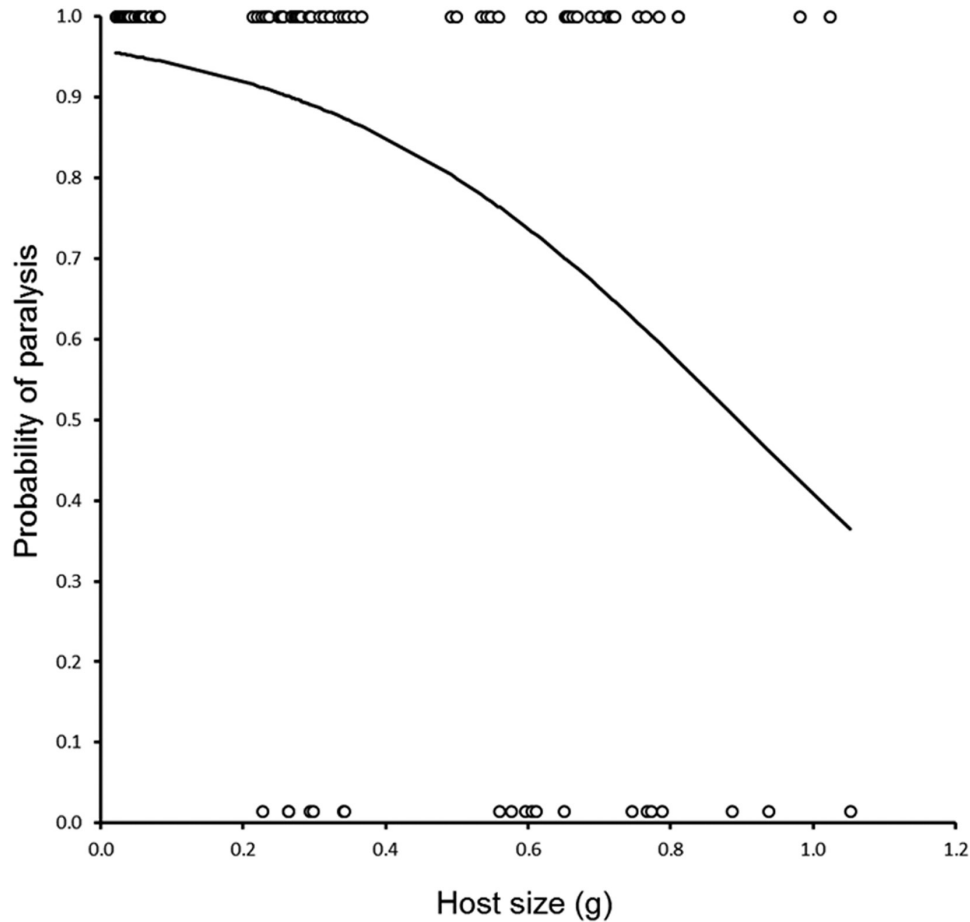


Figure 4. The effect of host size on probability of host paralysis.

Oviposition

The percentage of presented hosts on which oviposition occurred was 73.33% ($N = 120$); excluding the 20 hosts that were not paralysed, the percentage was 88%. The probability of oviposition on paralysed hosts was not significantly affected by host size (logistic ANCOVA: $G_1 = 0.07$, $P = 0.791$, %Dev = 0.10, $N = 100$), relatedness ($G_1 = 1.36$, $P = 0.243$, %Dev = 1.86) or by an interaction between host size and relatedness ($G_1 = 2.41$, $P = 0.121$, %Dev = 3.29). Once a host was paralysed, the time to oviposition was not affected by host size (cohort survival analysis with foundresses that did oviposit by day 20 treated as censors, $G_2 = 5.2$, $P = 0.074$, %Dev = 3.58) or by an interaction between host size and relatedness ($G_2 = 2.4$, $P = 0.301$, %Dev = 1.93), but non-siblings oviposited significantly earlier ($G_1 = 7.70$, $P = 0.006$, %Dev = 5.50). There was, however, no difference between non-siblings and brood-mates in the time taken to oviposition when data were analysed from the time of host presentation ($G_1 = 0.2$, $P = 0.655$, %Dev = 0.10).

Brood size

The total number of adult offspring produced from a host which had been oviposited on ($N = 59$) ranged between one and 163. Total brood size had a significantly curvilinear response to increasing host size (log-linear ANCOVA including a quadratic term: host size: $F_{1,55} = 14.50$, $P < 0.001$, %Dev = 13.95; host size²: $F_{1,55} = 32.41$, $P < 0.001$, %Dev = 31.18; Fig. 6A) and was also affected by foundress relatedness via a significant interaction with host size (relatedness: $F_{1,55} = 0.356$, $P = 0.064$, %Dev = 3.43; interaction: $F_{1,55} = 6.42$, $P = 0.014$, %Dev = 6.18; Fig. 6A); non-siblings typically produced larger broods. Examination of the same data in terms of mean per-foundress offspring production (brood size/number of foundresses surviving at the time of oviposition) also found a curvilinear response to increasing host size (host size: $F_{1,55} = 10.08$, $P = 0.002$, %Dev = 10.41; host size²: $F_{1,55} = 27.22$, $P < 0.001$, %Dev = 28.10) and an interaction between foundress relatedness and host size (relatedness: $F_{1,55} = 9.88$, $P = 0.003$, %Dev = 10.20;

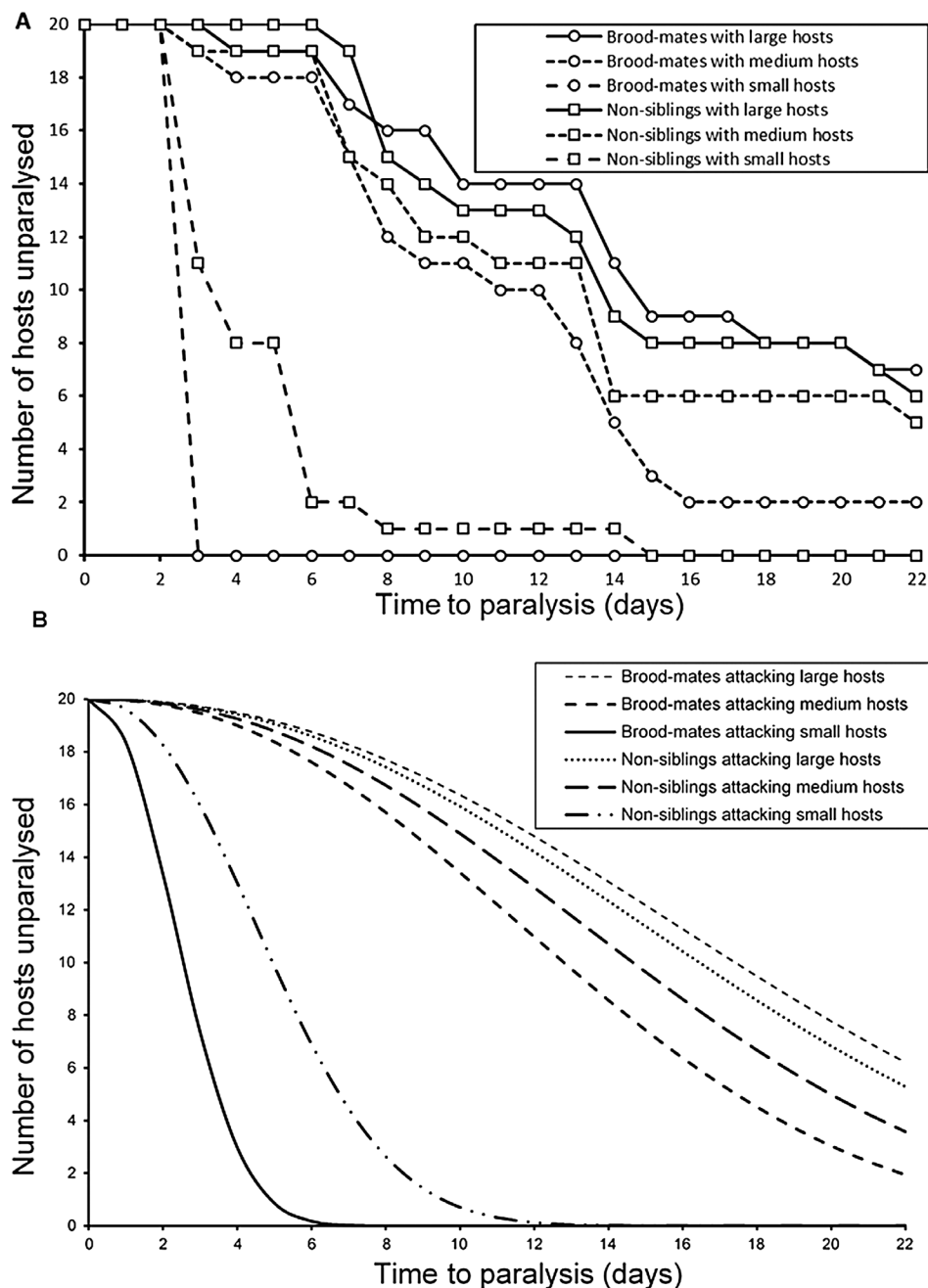


Figure 5. The effects of co-foundress relatedness and host size on time to paralyse the host. A, cohort data from the six treatment combinations. B, fitted survival model, estimated from Weibull analysis with unparalysed hosts treated as censors. To avoid disruption of the behaviour of the females, no observations were made during the first 2 days, and the statistical model was fitted assuming that no hosts were paralysed during this period. Foundress relatedness and host size interacted to influence time to paralysis; effects of kinship were significant only when hosts were small.

interaction: $F_{1,55} = 11.40$, $P = 0.001$, %Dev = 11.77; Fig. 6B); non-siblings typically produced smaller broods than brood-mate foundresses when hosts were small but relatively larger broods when hosts were large.

Sex ratio

Offspring brood sex ratios were strongly female biased; the mean proportion of offspring that were male was 0.0339 (+SE = 0.0039, -SE = 0.0035, $N = 59$). Owing to the mortality of some foundresses

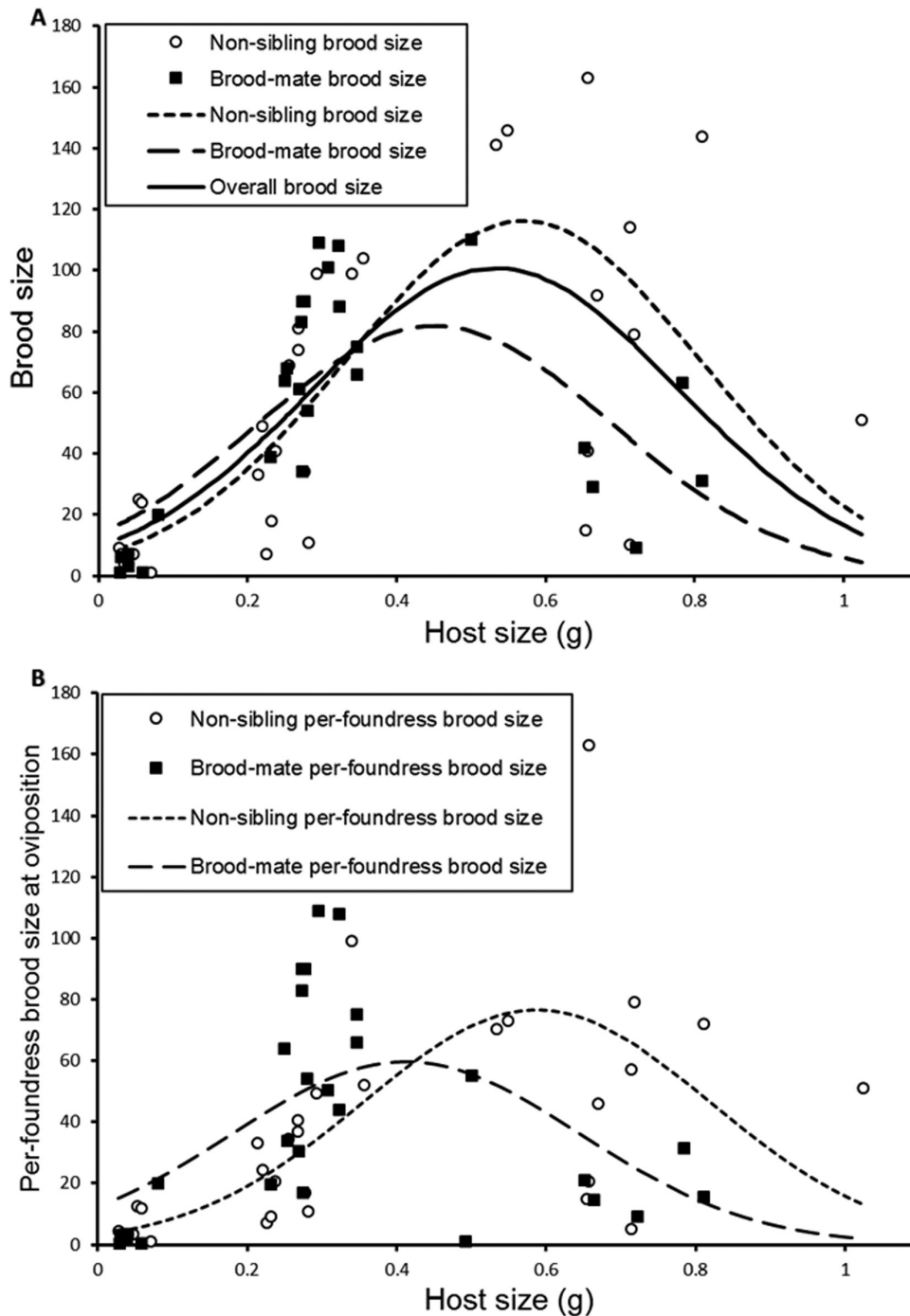


Figure 6. Adult offspring produced according to relatedness and host size. A, total brood size. B, per-foundress offspring production. Regression lines were obtained by log-linear ANCOVAs including a quadratic term. Offspring production differed according to relatedness, hence separate lines are shown for brood-mate and non-sibling foundresses. The regression line for overall brood size in panel A is used as the host size-dependent benefit, b , in the public goods model: fitness benefits obtained from parasitised host = $\exp(8.82 \times \text{host size} - 8.27 \times \text{host size}^2 + 2.261)$.

before oviposition, broods were produced by a single surviving foundress from a sibling group or by a single surviving foundress from a non-sibling group or by two surviving sibling foundresses or two surviving

non-sibling foundresses. The effect of varying the number of foundresses at oviposition was explored by fitting the number of foundresses as a two-level factor along with relatedness and host size in a

three-way logistic ANOVA. Sex ratios were less female biased when pairs of foundresses oviposited together ($F_{1,58} = 4.08$, $P = 0.049$, %Dev = 7.19; Fig. 7) but were not significantly affected by relatedness ($F_{1,55} = 0.00$, $P = 0.948$, %Dev = 0.01), host size ($F_{2,57} = 0.40$, $P = 0.670$, %Dev = 1.42) or by any interactions between these main effects (relatedness \times host size interaction: $F_{2,54} = 1.22$, $P = 0.304$, %Dev = 4.29).

Sex ratios were not significantly affected by brood size (logistic regression: $F_{1,57} = 3.08$, $P = 0.085$, %Dev = 5.12). The number of male offspring produced increased significantly with an increase of brood size (log-linear regression: $F_{1,58} = 25.39$, $P < 0.001$, %Dev = 30.82; Fig. 8). No other measured variables or their interactions affected the number of males per brood significantly.

SINGLE-FOUNDRESS ASSAY

Results

of analyses reported in this section are summarized in Table 2.

Probability of paralysis and oviposition

Almost 60% (22/37) of hosts presented to a single *S. brevicornis* foundress became paralysed. The probability of paralysis decreased significantly with an increase in host size (logistic regression: $G_1 = 11.68$, $P < 0.001$, %Dev = 23.39; Fig. 9A). Once a host was paralysed, the probability that the foundress oviposited on it was also almost 60% (13/22) and was not affected by the size of the host (logistic regression: $G_1 = 0.00$, $P = 0.957$, %Dev = 0.01).

Foundress mortality

Typically, when a female *S. brevicornis* attacks a host, either the host is paralysed or the wasp is killed (Table 3). In three of the 37 replicates the female apparently did not attack the host within the 21 day observation period because neither was the host paralysed nor did the foundress die (Table 3); these replicates were excluded from estimation of the probability of mortality as a consequence of attack (cost parameter, c , in the public goods

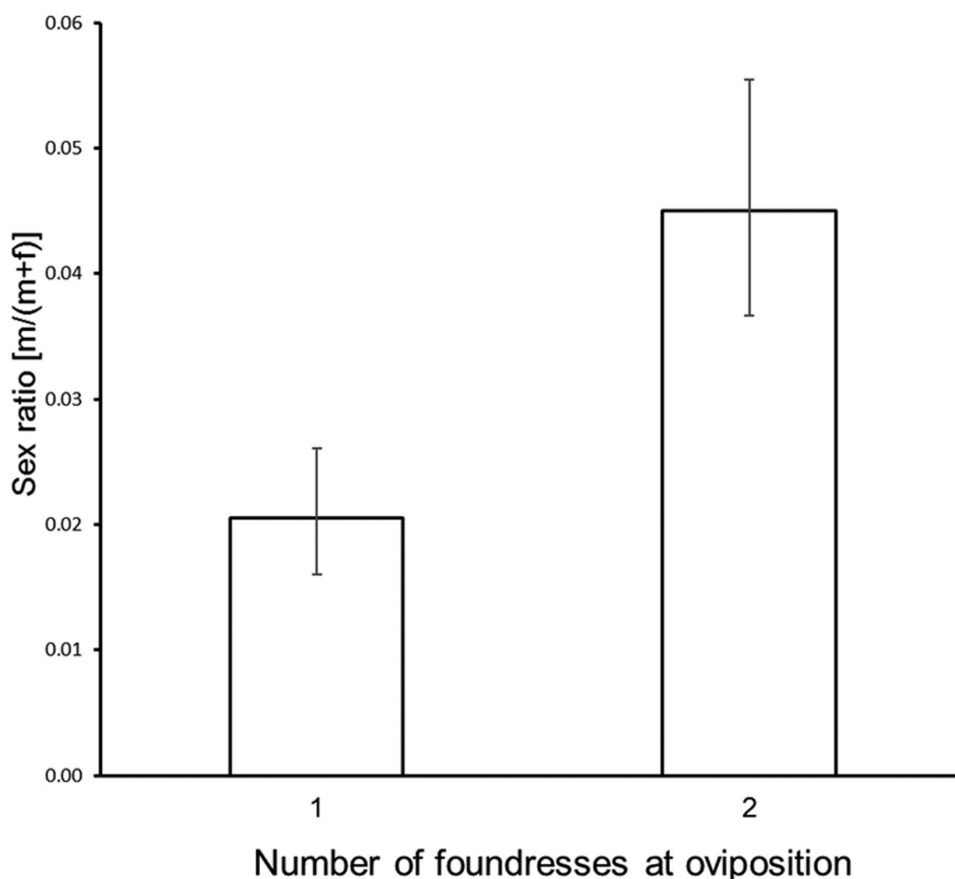


Figure 7. Sex ratios of broods according to the number of foundresses surviving to the time of oviposition. Bars represent the SEM and are asymmetrical owing to back transformation from the logit scale.

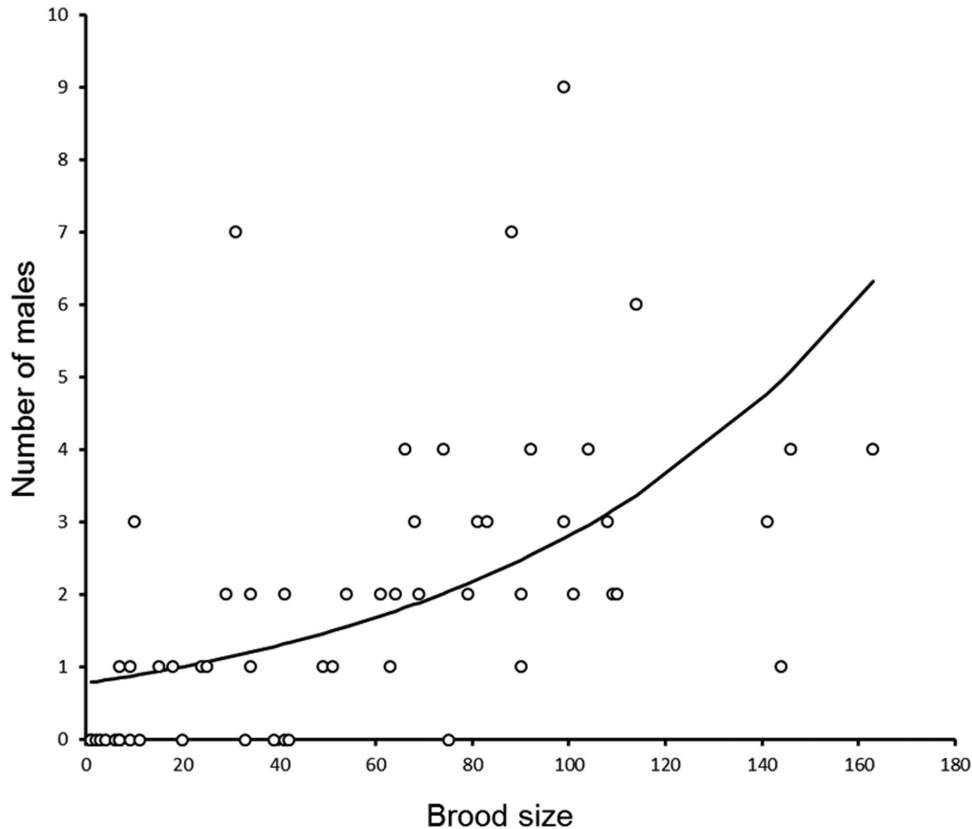


Figure 8. The relationship between the number of males in a brood and brood size.

model; see below). Among the remaining replicates, ~40% (14/34) of the foundresses died. In two cases, the foundress died and the host was paralysed (Table 3): in one of these the foundress was cut in half, suggesting that the host killed it during wasp attack, and in the other case the foundress died intact, suggesting that the cause of death might have been unconnected to host attack. Whether or not these replicates were excluded from analysis, the probability of mortality increased significantly with an increase in host size (all data: $G_1 = 5.18$, $P = 0.023$, %Dev = 11.25; excluding only the foundress that died intact: $G_1 = 7.03$, $P = 0.008$, %Dev = 15.54; excluding both females that died along with host paralysis: $G_1 = 8.22$, $P = 0.004$, %Dev = 18.62; Fig. 9B shows the regression for the second case). We observed that some dead females had been severed into two parts, such as the head being separated from the rest of the body or the head and thorax separated from the abdomen. The probability that a dead female was bisected increased significantly with an increase of host size (logistic regression: $G_1 = 7.97$, $P = 0.005$, %Dev = 43.67, $N = 14$; Fig. 9C).

Timing of paralysis and mortality

Among the 22 replicates in which host paralysis occurred, the time taken to paralyse the host ranged up to 19 days. Time to paralysis was significantly affected by host size, with smaller hosts being paralysed earlier than larger hosts ($G_1 = 18.4$, $P < 0.001$, %Dev = 37.15); in this analysis, replicates in which the foundress died before host paralysis or in which both the foundress and the host were alive at the end of the experiment were treated as censors. The time to foundress mortality also ranged up to 19 days but was unaffected by host size ($G_1 = 2.8$, $P = 0.095$, %Dev = 5.34; females that did not die were treated as censors). There was no relationship between time to foundress mortality and whether a female was bisected by the host (logistic analysis: $G_1 = 0.00$, $P = 0.947$).

PUBLIC GOODS MODEL OF HOST ATTACK

An estimate of the host size-dependent probability of a foundress dying during host attack (a proxy for cost, c) was obtained from the single-foundress assay (Fig. 9), and an estimate of how fitness benefits

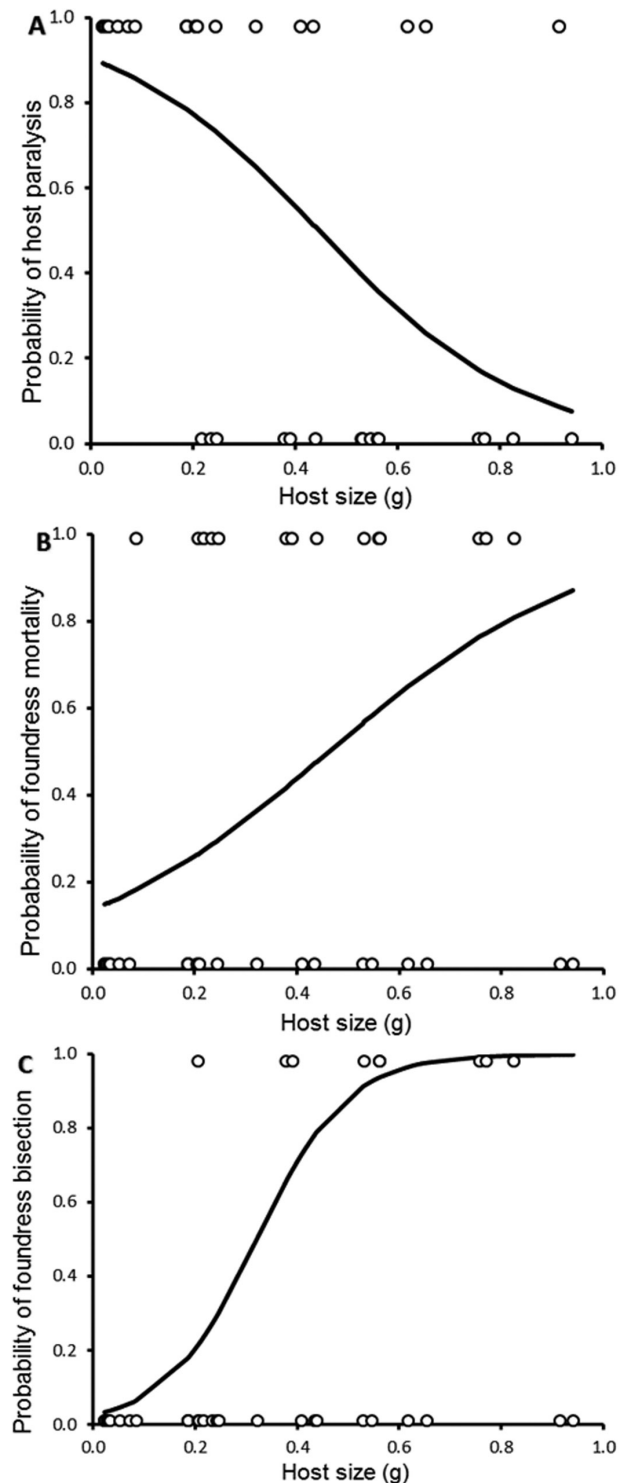


Figure 9. Probabilities of host paralysis [$N = 37$] (A), foundress mortality [$N = 34$] (B) and the foundress being bitten in half by the host [$N = 14$] (C). The logistic regression line in panel B is used as the host size-dependent cost, c , in the public goods model: probability of death when attacking host = $1/[1+(1/\{\exp[3.99 \times \text{host weight}] - 1.847\})]$, excluding the replicate where the female might have died after successful host attack.

obtained from a successfully paralysed host (a proxy for benefit, b) are influenced by host size was obtained from the two-foundress experiment (Fig. 6). Following Abdi *et al.* (2020), these relationships were then used in Hamilton's rule ($rb - c > 0$; Hamilton, 1964) to explore how variation in *S. brevicornis* co-foundress relatedness (r) might affect selection for host attack as a public good (Cooper *et al.*, 2018).

The result (Fig. 10) suggests that selection for public goods attack should depend on a combination of host size and relatedness. Specifically, the model suggests that individual foundresses will be selected to attack and then share hosts as a public good only when the host is neither large nor very small (i.e. within the range ~ 0.1 – 0.7 g) and, furthermore, only when their relatedness to co-foundresses is high ($r > 0.5$). The model also suggests that a wider range of host sizes will be attacked as a public good when inter-foundress relatedness is higher.

Given that the relationships between host size and benefits differ according to the relatedness of co-foundresses (Fig. 6), we constructed a version of the model using the fitted quadratic log-linear regression for brood-mate foundresses when relatedness, r , is equal to 0.75 or one, and the regression for non-sibling foundresses when $r = 0.0$ or 0.25. The form of the prediction was very similar to results shown in Figure 10, but brood-mate females would be expected to carry out public good host attack on very small hosts and to have a slightly lower maximal host size that they should attack as a public good.

DISCUSSION

For *Sclerodermus* females, attacking a host is a challenging step in the reproductive cycle and yet, to be able to reproduce, a female parasitoid must gain access to a suppressed host. Our estimates indicate that, when presented with a healthy host, between 25 and 40% of *S. brevicornis* foundresses die before host suppression (estimates from two-foundress and single-foundress cases, respectively). Furthermore, foundress mortality is related to host size, with larger hosts being considerably more dangerous to attack, as is also the case for other *Sclerodermus* species (Liu *et al.*, 2011; Wei *et al.*, 2014). The observation that many of the dead wasps in the single-foundresses assay were severed into two pieces indicates that hosts engage in active, and often successful, behavioural defence against parasitism, as also observed by Li & Sun (2011) and Liu *et al.* (2011).

A female can avoid the risks of host attack by using a host that has been attacked successfully by another female ('free-rider' behaviour; Rankin *et al.*, 2007). *Sclerodermus* females have not been observed to

Table 3. Outcomes of single-foundress interactions with hosts

Foundress status	Host not paralysed	Host paralysed but not oviposited on	Host paralysed and oviposited on
Foundress died (bisected)	8	1	0
Foundress died (intact)	4	1	0
Foundress lived	3	7*	13

*Six of these hosts might have been too small (0.0005–0.0592 mg, mean = 0.0287 mg, SD = 0.0215 mg) to support offspring development.

defend paralysed hosts against usage by conspecifics (in contrast to some sub-social bethylids; [Hardy et al., 2013](#)), and post-ovipositional brood care is cooperative, without apparent inter-foundress conflict ([Hu et al., 2012](#); [Wu et al., 2014](#)); as such, the reproductive resource represented by a paralysed host is shared between co-foundress females. In *S. brevicornis* (present study) and *Sclerodermus pupariae* ([Wei et al., 2014](#)), there is a domed relationship between offspring production and host size, whereas for *S. harmandi* larger hosts, once suppressed, provide a larger collective reproductive benefit for co-foundresses ([Liu et al., 2011](#); [Tang et al., 2014](#)). Although there are several estimated forms of the relationship between host size and *Sclerodermus* brood size, in all cases the total reproductive benefits of host exploitation are host size dependent ([Abdi et al., 2020](#); present study).

Although a female can avoid the risks of attacking a host by joining one or more conspecifics in the exploitation of a previously suppressed host, the converse question concerns whether a female should be prepared to attack a host to obtain a resource that will then be shared with others. A guide to whether individuals should attack, and then share, a host of a given size (with the associated risk of death and benefits of successful suppression) is provided by the public goods modelling approach using Hamilton's rule. A discussion of the caveats associated with using empirically obtained parameter estimates as proxies for parameters in Hamilton's rule is provided by [Abdi et al. \(2020\)](#), and we also note that defining fitness benefits, b , simply in terms of numerical offspring production does not take into account the fact that host size might affect further components of fitness. One example is the size of female offspring ([Wei et al., 2014](#)) which, in turn, might influence performance, including the ability to attack hosts of a given size (affecting c). Using Hamilton's rule nonetheless suggests that both host size and co-foundress relatedness will be important influences on the decision by an *S. brevicornis* female to attack. When hosts are very small, the risks associated with host attack are low but the benefits of host suppression are also small; even when the relatedness of a female to any co-foundresses present is high, a female is unlikely to attack a host

as a public good because the personal fitness costs to the female outweigh the fitness benefits. When hosts are medium sized, the risks during host attack are intermediate and the benefits of success large. In these circumstances, a female is expected to pay the private cost of providing a public good but only if her relatedness to co-foundresses is high. Use of empirically estimated cost and benefit parameters suggests that inter-foundress relatedness of 0.75 (the relatedness of full sisters under haplo-diploid genetics; [Hamilton 1964](#)) is sufficient for selection to favour public goods attack on medium-sized hosts. When hosts are large and very dangerous, such that most attacking females are killed, and the benefits of successful host suppression are small, females are not expected to engage in public goods attack. We note that we have implicitly considered host attack to be an individual activity, carried out by one foundress while others present stand to benefit from her actions, but it remains possible that multi-female *Sclerodermus* attack, whether simultaneous or sequential, influences the probability of success.

The public goods approach functions to indicate whether an *S. brevicornis* female should attack and then share a host, rather than whether a female should attack a host to support only her own offspring. Females that do not obtain access to a suppressed host (whether shared or not) cannot reproduce and thus might be expected to attack all sizes of hosts when there are no other options. Following [Abdi et al. \(2020\)](#), we interpret the public goods model to suggest patterns in the latency of host attack, i.e. how long a female encountering a dangerous host should wait for other females to attack the host before eventually attacking it herself. We might expect the reluctance of a female to attack to be reduced by potential inclusive fitness benefits when other females present are kin and, indeed, we found from the two-foundress experiment that females tended to die both earlier and with a higher probability when they were with brood-mates rather than non-siblings (in contrast to the lack of effect found by [Abdi et al., 2020](#), when assessing attack on small hosts only).

The models constructed by [Abdi et al. \(2020\)](#) for other *Sclerodermus* species and the model constructed

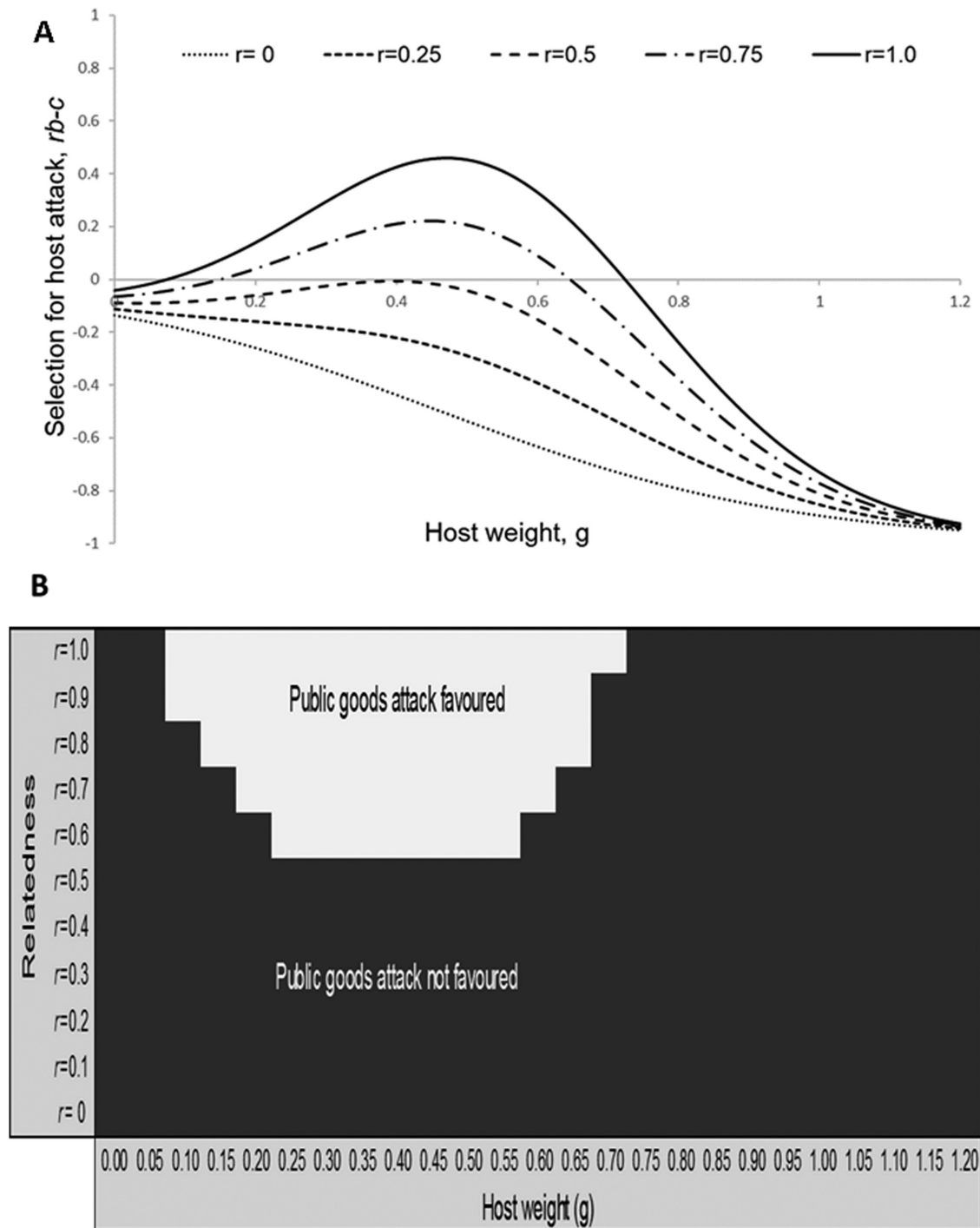


Figure 10. Public goods model of relatedness-mediated host attack for *Sclerodermus brevicornis*. The model combines the estimate of the host size-dependent probability of a foundress dying during host attack (cost, c), presented in Figure 9B, with the estimate of fitness benefits of successful attack (b), shown in Figure 6, into Hamilton's rule ($rb - c > 0$) to illustrate how co-foundress relatedness (r) might affect selection for host attack as a public good. The model suggests that selection for public goods attack depends on a combination of host size and co-foundress relatedness and will be strongest when hosts are medium sized and relatedness is > 0.5 . In panel A, values from Hamilton's rule are plotted against host weight, and the benefit curve was scaled to a maximum of one, following Abdi *et al.* (2020). Panel B highlights the combinations of relatedness and host weight when public goods attack is favoured.

here for *S. brevicornis* all suggest that co-foundress relatedness and host size will interact to influence the time that females wait before host attack. We have found empirically that time to paralysis is affected by host size (in accord with Lui *et al.*, 2011, studying *S. harmandi*), by relatedness (in accord with Abdi *et al.*, 2020) and also by their interaction, as predicted. The observed time to paralysis for *S. brevicornis* (Fig. 5A & 5B) suggests the greatest effect of relatedness when hosts are small, with hosts being paralysed more rapidly when co-foundress relatedness is higher, whereas the public goods model (Fig. 10) suggests greater effects for medium-sized hosts. When hosts are large, the time-to-paralysis data, the cohort survival model and the public goods model all suggest that relatedness has little effect on host attack rates. We conclude that using empirically estimated benefit and cost parameters in Hamilton's rule provides a broadly useful heuristic method with which to understand host attack in *Sclerodermus*.

After the successful suppression of a host, mortality among pairs of foundresses was common, especially during the period between paralysis and oviposition. We suggest that this mortality might result from inter-foundress conflict over resource exploitation, although such conflict is not obvious visually. Further work is required to probe the apparently cooperative nature of post-paralysis behaviour and brood production in *Sclerodermus* [e.g. to test for disproportionate reproduction by some foundresses (reproductive skew)] and any mediating effects of co-foundress kinship. Although we detected no effect of relatedness on foundress mortality after host suppression, we did find that brood-mate females produced slightly greater numbers of offspring on small hosts (as also found by Abdi *et al.*, 2020) and that on larger hosts the brood sizes were considerably larger when co-foundresses were not siblings. We suggest that *Sclerodermus* oviposition decisions might comprise a dynamic game between co-foundresses, involving a trade-off between brood size and offspring fitness and a tragedy of the commons scenario, whereby individual foundresses tend selfishly to add their own offspring, leading to broods being larger than the size that would optimize group fitness; we also expect that such behaviour would be mediated by kinship (Rankin *et al.*, 2007; van Dijk *et al.*, 2014; Ferrari *et al.*, 2015; Smith & Schuster, 2019). Furthermore, given that communal brood production in *Sclerodermus* usually leads to some reproductive output, we suggest that a tragedy of the commons would be a 'component tragedy', in which selfishness reduces average fitness in part, but not completely (Rankin *et al.*, 2007).

Maturing offspring had extremely female-biased sex ratios, as previously observed in *S. brevicornis* (Lupi *et al.*, 2017; Abdi *et al.*, 2020) and congeners (Kühne &

Becker, 1974; Li & Sun, 2011; Liu *et al.*, 2011; Hu *et al.*, 2012; Tang *et al.*, 2014; Wei *et al.*, 2014; Gao *et al.*, 2016; Kapranas *et al.*, 2016). We detected no effects of co-foundress relatedness on sex ratios but, in common with Tang *et al.* (2014), we found a slight decrease in bias as the number of foundresses increased. Sex ratio bias in *Sclerodermus* is likely to be selected for by the advantages accrued by co-foundresses from communal exploitation of hosts that are too large for single females to reproduce on alone (i.e. mutually beneficial female–female interactions increase the reproductive value of daughters; Tang *et al.*, 2014; Kapranas *et al.*, 2016); however, there are currently no models of optimal sex allocation in *Sclerodermus* and therefore no formal predictions concerning the likely influences of co-foundress relatedness.

CONCLUSIONS

This study set out to evaluate the importance of host size on the host attack and further reproductive behaviour of *S. brevicornis*. This followed a prior study (Abdi *et al.*, 2020), which identified that co-foundress relatedness affects the timing of host attack and suggested (using data on reproductive patterns in congeners and a public goods approach) that host size should interact with relatedness and thus mediate the observed effect of kinship. We have shown that effects of both host size and kinship operate during several of the stages of *S. brevicornis* host attack and reproduction and that they interact to influence the timing of host attack, as predicted.

A public goods model of host attack using parameters estimated for *S. brevicornis* gives broadly similar results to the previous models, again suggesting that selection for an individual foundress to attack and then, if successful, share their hosts will depend on both the size of the host and the relatedness of the foundress to any co-foundresses present. We also found that co-foundress relatedness influences some reproductive behaviours after host suppression, and we suggest that future studies are likely to reveal further effects.

Our overall conclusions are that females attune their behaviour to the risks involved in attempting to suppress large and dangerous hosts and that although reproductive behaviours exhibited by *Sclerodermus* females can be cooperative, they will not always be exhibited without reference to kinship.

CODA: COOPERATIVE REPRODUCTION IN THE GENUS *SCLERODERMUS*

Tang *et al.* (2014) showed that it is to the direct fitness advantage of individual female *Sclerodermus*

to exploit hosts as part of a multi-foundress group, provided that the host is not small. This is because individual females have very low probabilities of successfully suppressing and reproducing on medium- and large-sized hosts, whereas larger groups of foundresses have greater collective success and the mean per foundress production of offspring is higher than when females attempt to reproduce alone. However, [Tang *et al.* \(2014\)](#) did not assess variation in behaviour or success within foundress groups, nor did they control inter-foundress relatedness. Our new evidence from the present study and from the accompanying study ([Abdi *et al.*, 2020](#)) suggests that individuals within apparently cooperative foundress groups might attune their contributions to their own direct and inclusive fitness interests and thus that there is conflict within cooperation, as noted in numerous other biological systems and societies ([Schenider & Bilde, 2008](#); [Ågren *et al.*, 2019](#); [West & Ghoul, 2019](#); [Levin *et al.*, 2020](#)).

We suggest that the present understanding of *Sclerodermus* cooperative reproduction can be summarized broadly by considering inter-foundress relatedness simply as 'high' or 'low' and hosts as 'small' or 'large' and by classifying cooperation very simply in terms of inner conflict ([Table 4](#)); we note that when hosts are either very small or very large, any selection for cooperation may break down (owing to very low benefits or very high costs of attack, respectively). Depending on the combination of inter-foundress relatedness and host size, a female might be selected to attack a host or to leave host attack to others and also to share or not to share a successfully attacked host. When hosts are small and attack incurs low cost, *Sclerodermus* may share them with related females owing to inclusive fitness benefits but attempt to exclude non-related females to maximize direct fitness gains from host exploitation (as in sub-social bethylids; [Hardy *et al.*, 2013](#)), although aggressive inter-female behaviour has not currently been reported in *Sclerodermus*. When hosts are large and attack incurs high cost, females might gain both

direct and inclusive fitness from sharing with relatives but will gain only direct fitness when co-foundresses are not kin. In the latter case, cooperation might not be conflict free and is likely to be characterized by forms of exploitation, manipulation and enforcement ([Ågren *et al.*, 2019, 2020](#); [Engelhardt & Taborsky, 2020](#)).

Sclerodermus are aculeate parasitoids that have evolved quasi-sociality (communal brood care), but no parasitoid hymenopteran has evolved the eusociality (also involving reproductive division of labour and overlapping generations) that is observed in some non-parasitoid aculeate sister taxa ([Peters *et al.*, 2017](#)). It seems unlikely that lineages of *Sclerodermus* could transition readily to eusocial reproduction, because generational overlap would necessitate multi-generational cooperative groups colonizing fresh hosts in concert. Furthermore, if foundress groups are commonly formed from mixtures of kin and non-kin, selection for greater social complexity, such as reproductive specialization, might be limited ([Downing *et al.*, 2020](#)).

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Table 4. *Sclerodermus* reproductive strategy: a synthesis

	Small host	Large host
High relatedness	Attack and share host: conflict-free cooperation	Attack and share host: conflict-free cooperation
Low relatedness	Attack host but do not share host: no cooperation	Avoid host attack but share host attacked by others: conflict within cooperation

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SUPPORTING INFORMATION

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Data set. [Abdi et al., 2020](#) Part II.