Split sex ratios and virginity in a gall-inducing thrips

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Abstract

Split sex ratios have been predicted in haplodiploid populations with high proportions of reproductive virgins, but there has been little empirical support. We found such split sex ratios in the gall-inducing thrips, *Kladothrips rugosus*. Sex ratios of juveniles from 96 galls were determined using chaetotaxy over two consecutive summers. The population-wide sex ratio was unbiased, but bimodal. Twenty-four per cent of galls only contained male juveniles. These galls were induced by a female that was probably a virgin. The mean sex ratio of all other galls was 0.36 ± 0.02 , which is not significantly different from the theoretical evolutionarily stable sex ratio of 0.34, calculated from a previous model (Godfray, H.C.J. 1990. *J. Evol. Biol.* **3**: 3–17) for 24% constrained females in a pannictic population. These data provide the first empirical support for the constrained sex allocation model of Godfray.

Introduction

The study of sex ratio variation is important for understanding the causes and consequences of selective pressures that influence population structure, mating systems and sociality (Shaw & Mohler, 1953; Charnov, 1982; Bulmer, 1986; Crozier & Pamilo, 1996). Split sex ratios occur when some individuals produce male-biased sex ratios and colleagues produce female-biased sex ratios. Split sex ratios are expected when there is: (i) variation among females in the cost ratio of producing daughters and sons; (ii) a prevalence of virgin females in haplodiploid populations, as they can produce only sons (Grafen, 1986); (iii) worker-biased sex allocation in eusocial haplodiploid colonies with polygyny or polygamy (Boomsma & Grafen, 1990, 1991); and (iv) partial sib mating (Greeff, 1996). There have been numerous studies on Hymenoptera linking split sex ratios to relatedness asymmetries (e.g. Chan & Bourke, 1994; Pamilo & Seppä, 1994; Hastings et al., 1998; Aron et al., 1999; Chan et al., 1999) but few empirical studies have

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linked split sex ratios to virginity (Higgins & Myers, 1992; Guertin *et al.*, 1996; Ode *et al.*, 1997).

Godfray & Grafen (1988) and Godfray (1990) developed Grafen's (1986) argument that the existence of reproductive virgins in social haplodiploid species should lead to split sex ratios, and that this might facilitate worker-like behaviour in some colonies. Split sex ratios in haplodiploids may be important for the evolution of sociality, since female-biased sex ratios can lower selective thresholds for sib rearing. As an extension of Fisher's (1930) explanation for the near ubiquity of unbiased sex ratios in random mating populations, Godfray's (1990) model showed that the evolutionarily stable strategy for a population-wide sex ratio (proportion of males) produced by mated females in a panmictic population is 0.5(1-2p)/(1-p), where p is the proportion of constrained (e.g. virgin or sperm-depleted) reproductive females in the population. As *p* increases, mated females produce increasingly female-biased sex ratios until at p = 0.5 mated females are expected to produce only daughters. When p > 0.5 the sex ratio becomes male biased and equal to p, but there should be strong selection against such high proportions of virginity (Godfray, 1990). Indeed, virginity levels in haplodiploid populations have not been identified at higher than 30% (Godfray & Hardy, 1993), despite investigation in fig wasps (Godfray, 1988; West et al., 1997, 1998), parasitic

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wasps (Tagawa, 1987; Hardy & Godfray, 1990; Ode *et al.*, 1997; reviewed by Godfray & Hardy, 1993), other hymenoptera (reviewed by Godfray & Hardy, 1993) and thrips (Higgins & Myers, 1992; B. Kranz, unpublished data).

Fig wasps and other haplodiploid organisms with local mate competition (LMC) are probably not good organisms for investigating split sex ratios as a consequence of virginity, as competition among related males means that the offspring of virgin females will be at a disadvantage for gaining a mate (Godfray, 1990; Godfray & Hardy, 1993). In a comparison of 53 fig wasp species, there was no correlation between virginity and sex ratio (West et al., 1997). In fact, split sex ratios have been identified in only two haplodiploid species with constrained females; the parasitoid wasp, Bracon hebetor, due to sperm depletion (Guertin et al., 1996; Ode et al., 1997) and western flower thrips, due to virginity (Higgins & Myers, 1992). For both these species, the sex ratios of mated females were significantly more female biased than predicted by Godfray's (1990) model. Consequently, Godfray's model has yet to be quantitatively validated. Here, we present data indicating split sex ratios in a gallinducing thrips, where the mean sex ratio of mated females matches the predicted sex ratio of Godfray's (1990) model.

Thrips are an important group for investigating social evolution. Sociality involving soldier morphs has been inferred for at least four species of haplodiploid, Australian gall-inducing thrips (Crespi, 1992a; Mound & Crespi, 1995; Crespi & Mound, 1997; Kranz *et al.*, 1999) and has been suggested for two other species (Mound *et al.*, 1996; Crespi & Mound, 1997). In this paper, we examine sex ratios in the gall-inducing species *Kladothrips rugosus* Froggatt, which is in a sister clade to social species (Mound & Crespi, 1995; Mound *et al.*, 1996; Crespi & Mound, 1997; Crespi *et al.*, 1998; Kranz *et al.*, 1999; D. Morris, unpublished data). We determined whether mated females had a sex ratio unequal to 1:1, and tested whether the sex ratio conformed to Godfray's prediction.

Materials and methods

Biology of Kladothrips rugosus

Kladothrips rugosus induces galls on at least 13 *Acacia* host species (Crespi *et al.*, 1998; B. Crespi & L. Mound, unpublished data). The life history and behaviour of *K. rugosus* have so far only been studied on the host *Acacia pendula* (Crespi, 1992b) and are summarized here. Females frequently fight for access to galling sites, which can result in one live foundress and one or more dead females enclosed in the gall. A male and female initiate about half the galls; solitary females induce other galls. The female commences egg laying once the foundress or founder-pair is enclosed. The offspring do not enclose as

adults in the gall while it is attached to the host tree, and second-instar larvae are the most mature stage of offspring observed in galls (Crespi, 1992b; Crespi & Mound, 1997).

Field collections

Kladothrips rugosus galls were collected from 10 *A. papyrocarpa* trees over two consecutive seasons at the Middleback pastoral station, 20 km north-west of Whyalla, South Australia. The habitat is semi-arid. Galls on this host are pouched and spherical to tubular in shape, 5– 35 mm deep and about 7 mm wide (Mound *et al.*, 1996; Crespi & Worobey, 1998).

Brood were censused from 96 galls collected over nine sampling dates: 13 December 1995 (five galls), 8 and 26 January (17 and 16 galls), 18 March (16 galls), 27 November (five galls) and 15 December 1996 (six galls), and 22 January (16 galls), 17 February (13 galls) and 16 March 1997 (two galls). For each date, approximately 25 galls were collected, placed in plastic bags, and transported on ice to Flinders University. Galls were stored at 8 °C and censused within one week of collection, or otherwise frozen at –70 °C. Galls invaded by kleptoparasites were not included in the study.

Demographic and sex ratio study

Individuals were removed from their gall and counted following the methods of Kranz *et al.* (1999). Firstinstar larvae were cleared in Hoyer's medium and sexed using chaetotaxy; females have three pairs of setae on the ninth abdominal segment and males have four (Heming, 1991; Kranz *et al.*, 1999). Second-instar juveniles could not be sexed. The gall founders were sexed by observing their body size and the shape of the ninth abdominal segment (Crespi, 1993). Where there was uncertainty about the sex, adults were mounted in Hoyer's and sexed by viewing the fustis of females and phallobase of males (Mound & Heming, 1991; Kranz *et al.*, 1999).

From 20 galls, the foundress was dissected to inspect the spermatheca for evidence of insemination. These galls consisted of four galls from each of the 8 and 26 January and 18 March 1996, and 22 January and 17 February 1997 collections. For each collection, half the selected galls had a single foundress and half had a male and female founder pair. In the galls with a male founder, males were dissected to inspect the development of testes.

Data analyses

Descriptive statistics, *t*-tests and ANOVAS were calculated using SPSS version 8.0.1 (SPSS Inc., 1997). Where necessary, data were transformed to produce homogeneity

of variances. Population-wide sex ratios were truncated at r = 1 (all males) and the distribution was binomial. Consequently, three approaches were used for sex ratio analysis. First, the sex ratio r and its corresponding standard error and confidence intervals were calculated both including and excluding the r = 1 data. Second, the effects of season, month and presence of male founder on sex ratio were examined by fitting negative binomial models to the data, using S-PLUS version 3.4 (Mathsoft Inc., 1996), as Poisson models showed large residual deviances (Lawless, 1987; Quinnell, 1992). Third, sex ratios excluding r = 1 data were approximately normal but, because the distribution was zero-bounded, were arcsine transformed prior to analysis with *t*-tests.

Results

Gall induction and general life history

Forty of the 96 galls (42%) contained both a female and a male gall founder. All other galls contained a single foundress. Five of the 96 galls (5%) had both a living and a dead female in the gall. This was presumably a result of fighting between females for the gall site during or shortly after gall induction (see Crespi, 1992b).

Gall induction occurred mostly in late spring and early summer (November to December), but in 1996 galls were also induced in late summer, as indicated by the relatively small brood sizes in the March 1996 collections (Table 1). Brood development continued until late summer and early autumn (February to March), but galls dried and fell from the tree while brood were still in the second-instar stage. This is consistent with the life history of many of the gall-inducing thrips species on *Acacia* (Crespi, 1992b; Crespi & Mound, 1997; Kranz *et al.*, 1999).

Total brood size was estimated from galls collected on 26 January 1996, when mean brood size peaked for the 1995-96 season (Table 1). For this collection the maximum brood size was 692 individuals (maximum over both seasons) and the 50th and 75th percentiles were 238 and 535 individuals, respectively. A two-way ANOVA on log-transformed data tested whether brood size differed between galls with a founder of both sexes and those with a single foundress, with collection date (including both seasons) as a crossed factor. There was no significant interaction between the presence of a founding male with collection date ($F_{6,65} = 1.239$, P = 0.298). The interaction term was removed and a further two-way anova tested the effects of sampling date and presence of a male founder on brood size. Collection date had a significant effect ($F_{8,71} = 9.038$, P < 0.001), but there was no effect due to the presence of a male founder ($F_{2,71} = 0.620$; P = 0.541).

Sex ratio

The distribution of sex ratios for all first instars was bimodal and truncated at r = 1 (all male; Fig. 1). There was a slight decrease in the proportion of male first-instars in each season as broods developed (decrease of 0.24 ± 0.13 SEM males per collection in 1995–96 and 0.36 ± 0.18 males in 1996–97), which was marginally nonsignificant for both years (negative binomial 1995–96, $t_{46} = -1.83$, P = 0.074; 1996–97, $t_{33} = -1.99$, P = 0.055). The slight decrease in the number of males throughout each season suggests that the sex ratio was

Table 1 Summary data for gall inducers, brood development and sex ratio of *Kladothrips rugosus* for the 1995–96 and 1996–97 seasons. Data are means \pm SEM for eggs, first instars, *r* (proportion of males for first instars), and brood size. All other data are proportions: 'Propn live foundress' is the proportion of galls with a live foundress; 'Propn male founders' is the proportion of galls with a male founder; 'Propn *r* = 1' is the proportion of galls where all first instars are male.

		Proph live	Proph male		First		Propn	Brood
Date	n	foundress	founders	Eggs	instars	r	<i>r</i> = 1	size
1995–96								
13 Dec 1995	5	1.00	0	17 ± 11	0	-	0	17 ± 11
8 Jan 1996	17	0.77	0.47	30 ± 6	34 ± 5	0.55 ± 0.07	0.24	220 ± 48
26 Jan 1996	16	0.85	0.50	36 ± 8	39 ± 6	0.50 ± 0.09	0.31	316 ± 61
18 Mar 1996	16	0.75	0.38	19 ± 3	21 ± 2	0.57 ± 0.09	0.37	105 ± 13
Pooled	54	0.81	0.41	27 ± 3	28 ± 3	0.54 ± 0.05	0.28	193 ± 28
1996–97								
27 Nov 1996	5	1.00	0.40	49 ± 11	0	-	0	49 ± 11
15 Dec 1996	6	1.00	0.33	83 ± 7	36 ± 13	0.37 ± 0.07	0	127 ± 20
22 Jan 1997	16	0.54	0.25	35 ± 6	34 ± 5	0.63 ± 0.07	0.31	229 ± 33
17 Feb 1997	13	0.08	0.62	14 ± 5	17 ± 3	0.38 ± 0.04	0	202 ± 40
16 Mar 1997	2	0.50	0.50	19 ± 6	33 ± 23	0.30 ± 0.12	0	318 ± 239
Pooled	42	0.51	0.43	37 ± 5	25 ± 3	0.47 ± 0.04	0.12	186 ± 22
Seasons combined								
Pooled	96	0.67	0.42	32 ± 3	27 ± 2	0.51 ± 0.03	0.24	190 ± 18



Fig. 1 Frequency distribution of first-instar males in galls of *Kladothrips rugosus* for the 1995–96 and 1996–97 seasons.

approximately constant throughout the season and there was a lack of protandry or protogyny. As sex ratio was obtained only from first instars, data between collections was pooled to analyse the sex ratio of the entire brood of the season. There was no significant difference in mean sex ratio between the 1995–96 and 1996–97 seasons (negative binomial $t_{81} = -0.668$, P = 0.498) so data were pooled over seasons for all analyses unless otherwise stated.

The population-wide mean sex ratio of first-instar larvae was 0.51 ± 0.03 , with an associated 95% CI of 0.45-0.58 (n = 83 galls), indicating that the population sex ratio was not significantly different from 0.5. Twenty of the 83 galls (24%) where juveniles were present had only male first-instars (r = 1), and these data were outside the 95% CI limits (0.48–0.58) for the population mean.

It is likely that females who produced only males were virgins. All foundresses dissected from 10 galls with a male founder were inseminated and each had female offspring (mean $r = 0.36 \pm 0.05$). All the male founders in these galls had well-developed testes. However, three of the 10 foundresses dissected from galls without a male founder were uninseminated, and all first instars were male. The other seven galls with a single, inseminated foundress contained first instars of both sexes.

A two-way ANOVA tested whether log-transformed brood size differed between foundresses who produced only males and foundresses who produced offspring of both sexes, with collection date as the crossed factor. Only collection dates containing galls with r = 1 were included in the analysis. There was no significant interaction between galls with $r = /\neq 1$ and collection date ($F_{3,43} = 1.482$, P = 0.233), so the interaction term was removed. A further two-way ANOVA revealed that sampling date had a significant effect ($F_{3,46} = 2.941$,

P = 0.043), but there was no significant difference in brood size between galls with r = 1 and those with r < 1 ($F_{1,46} = 0.023$; P = 0.880).

All galls with r = 1 were induced by a lone foundress (n = 20 galls). The mean sex ratio of galls induced by a single female was 0.64 ± 0.05 , 95% CI = 0.54-0.74(n = 47 galls) and in galls induced by a female and a male was 0.35 ± 0.03 , 95% CI = 0.30–0.40 (n = 36). The number of male offspring in galls induced by a single female was significantly higher than the number of males in galls induced by an adult of both sexes (negative binomial $t_{81} = -4.020$, P < 0.001). Because the proportion of galls with r = 1 did not differ significantly between seasons ($\chi_1^2 = 3.61$, P = 0.057), and neither did the sex ratio of galls when r = 1 was excluded (*t*-test on arcsine transformed data, $t_{61} = -1.422$, P = 0.160), these data were pooled between seasons. When galls with r = 1were excluded, the sex ratio in galls with a single female was not significantly different from the sex ratio in galls induced by a male and female (t-test on arcsine transformed data, $t_{61} = 0.675$, P = 0.502).

The mean sex ratio of first instars when galls with r = 1 were excluded was 0.36 ± 0.02 , 95% CI = 0.32-0.40 (n = 63 galls), which is significantly female biased (one sample *t*-test using arcsine transformed data against 0.5, $t_{62} = -5.991$, P < 0.001). This sex ratio is not significantly different to the predicted sex ratio of 0.34 (Godfray, 1990) for the offspring of mated females in a panmictic population with 24% virgin females (one sample *t*-test using arcsine transformed data against 0.34, $t_{62} = 1.508$, P = 0.137).

Discussion

The sex ratios of *Kladothrips rugosus* provide the first quantitative support for Godfray's (1990) sex ratio model for panmictic haplodiploid populations with a proportion of females constrained to produce male-only brood. Other studies suggesting split sex ratios due to constrained females have not supported the predictions of this model (Higgins & Myers, 1992; Guertin *et al.*, 1996; Ode *et al.*, 1997).

Twenty-four per cent of *Kladothrips rugosus* galls had male-only brood. The sex ratio in other galls compensated for the male-biased subpopulation by having a mean sex ratio that was female biased and not significantly different from the predicted value of 0.34 from Godfray's (1990) model. None of these latter galls displayed sex ratios that approached r = 1 (Fig. 1), indicating that sex ratios were split, rather than just skewed. The population-wide sex ratio was unbiased. Brood size and sex ratios did not differ significantly between galls induced by a single female and those by both sexes, suggesting that the presence of male founders did not influence the fitness of a foundress or the sex ratio of her offspring, except by preventing virginity. As all dissected foundresses with male-only brood were uninseminated, and all females with male-only brood did not have a male founder in the gall, it is most likely that females with male-only brood were virgins. In the wasp *Bracon hebetor*, overproduction of males has been linked to sperm depletion (Ode *et al.*, 1997), but our data are inconsistent with this explanation because the production of first-instar males did not increase as the season progressed; if anything, male production decreased slightly. The relatively large size of spermathecae in female galling thrips, compared with free-living thrips (Heming, 1970, 1995; B. Kranz, unpublished observations), could be a strategy to avoid sperm depletion.

Our data support the sex ratio for mated females that Godfray (1990) predicted for a panmictic population with virgin females, assuming equal costs to the production of both sexes. Godfray (1990) presents a similar model for constrained females in populations with local mate competition (LMC). This model predicts sex ratios for offspring of unconstrained females in diploids with patches of two founding females. The sex ratio in this model is relatively insensitive to changes in the proportion of constrained females. For our data, the LMC-based model predicts a sex ratio of 0.24 for unconstrained females of K. rugosus, which is considerably more female biased than the sex ratio of mated females. While this suggests that LMC might not be important in the K. rugosus population, the assumptions of Godfray's (1990) LMC-based model do not apply to our data, and we do not know the population structure of this species.

We have yet to determine why virgin foundresses and all-male sex ratios are relatively common in this population of K. rugosus, when such proportions have not been found in closely related species, either solitary or social (Crespi, 1993; Kranz et al., 1999; B. Kranz, unpublished data). The proportion of virgin females ranges from zero to 2% in the related gall-inducing species K. ellobus, K. hamiltoni, Oncothrips waterhousei, O. habrus and O. rodwayi (B. Kranz, unpublished data), and virgins have been identified in low numbers in O. antennatus (Mound, 1971). However, in a greenhouse study of western flower thrips (Frankliniella occidentalis), which is not a gall-inhabiting species, virgin females comprised up to 24% of ovipositing females and, although there were difficulties in determining individual sex allocation patterns, there was evidence of split sex ratios (Higgins & Myers, 1992).

Thrips are unable to fully control their flight patterns and are effectively aerial plankton, except at very local scales (Lewis, 1964, 1973; Johnson, 1969; Taylor, 1974; Cheer & Koehl, 1987) and within about 0.20 m from the ground (Taylor, 1974). Consequently, high levels of virginity in thrips are not unexpected because it may be difficult to locate a mate after dispersal. In galling thrips, the period for finding a mate is short, as gall induction occurs following new foliage growth of the host plant, and rain is infrequent and unpredictable in the arid habitats where most galling thrips occur (Mound *et al.*, 1996; Kranz *et al.*, 1999). While we have no evidence of fitness costs associated with virginity in *K. rugosus*, it seems likely that when population density is low, production of all-male broods may be disadvantageous because of the risk that males might not find a mate. Indeed, even when females produce both sons and daughters, the risk of not finding a mate might select for mating prior to dispersal, and this in turn might partly explain the high levels of inbreeding observed in the social gall-inducing thrips (Chapman & Crespi, 1998; Chapman *et al.*, 2000).

It is interesting to note that eusociality in both galling thrips and aphids is associated with extraordinarily high levels of intragroup relatedness. In eusocial aphids this is due to parthenogenesis (Stern & Foster, 1996, 1997), and in thrips it is largely due to inbreeding (Chapman & Crespi, 1998; Chapman *et al.*, 2000). Both taxa are minute in body size, such that their flight control is limited, and so it is possible that parthenogenesis and inbreeding are evolutionary responses to the risks of not being able to find a mate after dispersal. If such is the case, it might be that minute body size has had an influence in setting the stage for the evolution of eusociality in these taxa.

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