

# Life history of *Kladothrips ellobus* and *Oncothrips rodwayi*: insight into the origin and loss of soldiers in gall-inducing thrips

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**Abstract.** 1. The evolution of eusociality in Australian gall-inducing thrips cannot be understood without comparisons among closely related solitary species. The life history of two solitary, gall-inducing thrips, *Kladothrips ellobus* and *Oncothrips rodwayi*, was investigated, and data for solitary and eusocial species from previous studies were re-analysed. *Kladothrips ellobus* is in a clade that is closely related to the eusocial species. *Oncothrips rodwayi* is in the same clade as the eusocial species and appears to have undergone an evolutionary loss of eusociality. It is the only galling thrips on *Acacia* in temperate environments.

2. The brood size of *K. ellobus* is eight to 23 times larger than broods of foundresses in eusocial species whereas the brood size of *O. rodwayi* is not significantly different from those of foundresses in eusocial species.

3. In *K. ellobus*, the mean sex ratio was not significantly different from parity but in *O. rodwayi* the mean sex ratio was 0.13 male. In *O. rodwayi*, 77% of females were inseminated by their brothers before dispersal, which is consistent with high levels of inbreeding in eusocial species of the same clade. Sex ratios suggest random mating in *K. ellobus* whereas female-biased sex ratios in *O. rodwayi* are consistent with inbreeding and local mate competition.

4. Comparisons among solitary and eusocial species suggest that large brood size is an ancestral trait for eusociality in thrips, and this trait persists in solitary species as an *r*-selection strategy. Soldiers may have evolved in arid environments to minimise the risks of dispersal and the costs of latency to reproduction, and to maximise gall defence.

5. Temperate conditions could have facilitated the evolutionary loss of soldiers in *O. rodwayi*, as there should be a shorter, safer, more predictable window period between dispersal and gall induction, reducing the period of latency to reproduction following dispersal and lowering risks of dispersal.

6. The loss of soldiers in *O. rodwayi* is not associated with a reversion to the large brood sizes of solitary species in ancestral lineages.

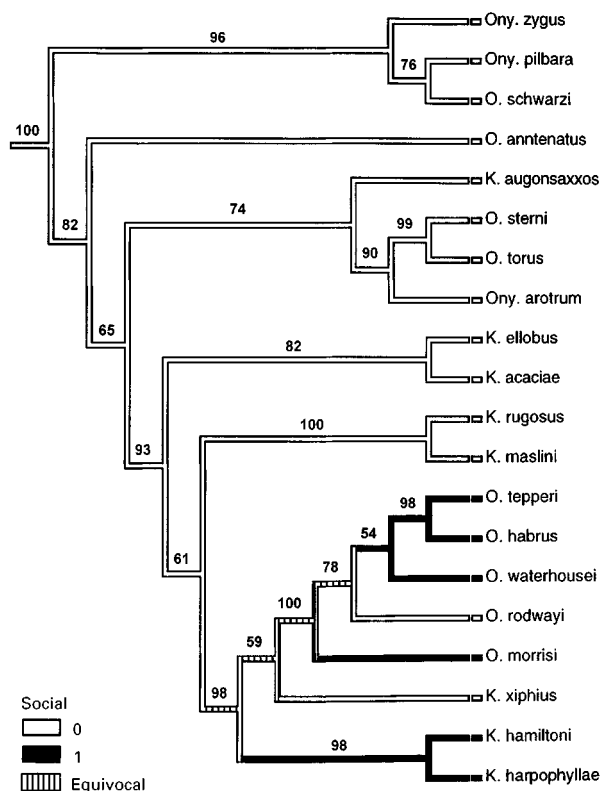
**Key words.** Brood size, eusociality, gall thrips, loss of soldiers, sex ratio, social evolution.

## Introduction

The implied directionality of such terms as quasisocial, semisocial, and primitively eusocial, with *highly eusocial* (Wilson, 1971) as the evolutionary end-point, has been a focus of concern in defining eusociality (Gadagkar, 1994; Crespi &

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Yanega, 1995; Sherman *et al.*, 1995; Wcislo, 1997). Losses of sociality have been identified in a variety of social taxa (reviews by Gadagkar, 1997; Wcislo & Danforth, 1997), including halictine bees (Eickwort, 1985; Packer, 1991, 1997; Richards, 1994; Danforth *et al.*, 1999), allodapine bees (Reyes & Schwarz, 1997; Schwarz *et al.*, 1998), termites (reviews by Myles, 1999; Thompson *et al.*, 2000), aphids (Stern, 1994, 1998), and thrips (Crespi *et al.*, 1998; Morris, 2000; Fig. 1), demonstrating that eusociality is not an evolutionary end-point but rather a strategy that has been selected for and against under varying conditions (Wcislo & Danforth, 1997). The selective factors underlying losses of sociality are often not clear, however, and the extent to which the losses are *reversions* to ancestral traits is not understood. Clearly, it is important to know the basic life history of both ancestral and secondarily derived solitary species to begin understanding how and why evolutionary losses of eusociality arise. The causes of the loss of eusociality in a gall-inducing thrips are explored here, by comparing its life history with the life history



**Fig. 1.** Phylogenetic tree for gall-inducing *Kladothrips*, *Oncothrips*, and *Onychothrips*. The tree is modified from Morris (2000) and is based on sequence data from four gene regions, COI, 16S, EF1- $\alpha$ , and Wingless. Bootstrap values are indicated above the nodes. Bold lines indicate clades with soldiers (or non-dispersing fighting morph), open lines indicate solitary clades, hatched lines indicate equivocal nodes. Equivocal nodes allow either one origin of soldiers with two losses or two origins with one loss in *Oncothrips rodwayi*.

of solitary thrips in a lineage closely related to the eusocial species.

Of the 21 species of gall-inducing thrips on *Acacia* (Mound *et al.*, 1996), five eusocial species, three in the genus *Oncothrips* and two in the genus *Kladothrips*, have a non-dispersing *soldier* caste that comprises the first generation offspring of a single gall-inducing foundress (Crespi, 1992a; Mound & Crespi, 1995; Crespi & Mound, 1997; Kranz *et al.*, 1999, in press; Chapman *et al.*, 2000). Soldiers have an enlarged prothorax and enlarged fore femora, reduced wings and antennae, and pale exoskeletons (Mound, 1971; Crespi, 1992a; Mound & Crespi, 1995; Mound *et al.*, 1996), and defend gall occupants from kleptoparasitic invaders, particularly thrips in the genus *Koptothrips* (Crespi, 1992a,b; Mound & Crespi, 1995; Crespi & Abbott, 1999). Phylogenetic studies have revealed that soldiers have either one or two evolutionary origins and one or two losses (Crespi & Mound, 1997; Crespi *et al.*, 1997, 1998; Morris, 2000; Fig. 1). The possibilities are (1) two origins, one in each of *Kladothrips* and *Oncothrips*, with a single loss of soldiers in *O. rodwayi* or (2) one origin in an ancestor of species in both genera, and two losses, one in *O. rodwayi* and one in *K. xiphius*.

In this paper, the life histories of the solitary thrips, *Kladothrips ellobus* Mound and *Oncothrips rodwayi* Hardy, which are in the same genera as the eusocial species (Fig. 1), are presented and data are synthesised from earlier studies to explore patterns underlying the evolutionary transitions from solitary to eusocial to solitary in this group of thrips. *Kladothrips ellobus* is in a clade that is closely related to the eusocial species (Crespi *et al.*, 1998; Morris, 2000; Fig. 1). It induces galls on *Acacia cambagei*, the same host plant as for the eusocial species, *K. hamiltoni* (Mound & Crespi, 1995; Kranz *et al.*, 1999), and the species are commonly found together on the same tree (Mound & Kranz, 1997). *Oncothrips rodwayi* is in the same clade as the eusocial *Oncothrips* species, and phylogenetic inference suggests that it has undergone a loss of soldiers (Crespi *et al.*, 1998; Morris, 2000; Fig. 1). *Oncothrips rodwayi* is of particular interest because it is the only galling thrips in the clade that occurs in the temperate regions of Australia. The only other species in the group that occurs outside the arid regions of Australia is *K. maslini* (Fig. 1), which is restricted to parts of subtropical eastern Australia (Mound *et al.*, 1996). A scenario for the evolution of soldiers in thrips is presented here and the possible reason for the loss of soldiers in *O. rodwayi* is discussed. Previous studies of eusocial thrips and their solitary congeners are drawn on to assess the extent to which the evolutionary loss of soldiers is a reversion to ancestral traits.

## Materials and methods

### Study organisms

Adult females of *K. ellobus* are  $\approx 3$  mm long and induce disc-shaped galls, with or without a male. Galls are  $\approx 20$  mm in diameter and 2 mm deep, and occur on *Acacia cambagei* along episodic waterways in the Lake Eyre Basin region of central

Australia (Mound, 1971; Crespi & Mound, 1997). Galls are dispersed but where found are common and can occur alongside galls of the congeneric eusocial thrips, *K. hamiltoni* (Mound & Kranz, 1997; Kranz *et al.*, 1999; Fig. 1).

*Oncothrips rodwayi* induces galls on *Acacia melanoxylon*, which occurs from Hobart, Tasmania, to Tamworth, New South Wales, and sporadically from south-eastern Victoria to the Mount Lofty ranges of South Australia. Galls are purse-shaped pouches,  $\approx 10\text{--}15$  mm long and  $7\text{--}10$  mm deep (Mound, 1971; Mound *et al.*, 1996). *Oncothrips rodwayi* does not have a non-dispersing micropteran morph, and female adults closely resemble gall foundresses of eusocial *Oncothrips* (Crespi *et al.*, 1998).

#### Study site and field collections

*Kladothrips ellobus* galls were collected from *Acacia cambagei* along Arckaringa Creek ( $28^{\circ}6'S$ ,  $135^{\circ}5'E$ ) in the southern Lake Eyre Basin,  $\approx 1100$  km north of Adelaide, South Australia. Arckaringa Creek is usually dry but floods on average every 2 or 3 years, mostly between late spring and mid summer (November to February). Temperatures in Oodnadatta, the closest weather station to the sites, range from  $-2$  to  $51^{\circ}C$ , the median monthly rainfall ranges from 2 to 10 mm, and the median annual rainfall is 65 mm (Commonwealth of Australia, 2001). Live broods, from galls without kleptoparasites, were censused from collections made on 7 and 28 December 1995 (11 and 20 galls respectively), 6 and 15 January and 14 May 1996 (seven, nine, and five galls), and 20 January and 31 May 1997 (six and five galls). Galls were also collected in February and March 1996 and 1997 but all galls were brown and dry and contained no living *K. ellobus* brood.

*Oncothrips rodwayi* galls were collected from two *A. melanoxylon* trees near Stirling ( $35^{\circ}0'S$ ,  $138^{\circ}7'E$ ), South Australia, and from about half a dozen roadside trees between Mount Gambier and Heywood ( $38^{\circ}1'S$ ,  $141^{\circ}6'E$ ), south-western Victoria. Both sites have a temperate climate. Stirling has temperatures ranging from  $-2$  to  $40^{\circ}C$  and a median annual rainfall of 1198 mm; Heywood has temperatures ranging from  $-5$  to  $43^{\circ}C$  and a median annual rainfall of 832 mm (Commonwealth of Australia, 2001). Live, unparasitised brood were censused from galls collected at Mount George on 26 December 1996 (nine galls), 3 and 15 January (six and six galls), 2 February 1997 (six galls), and 19 January 1998 (four galls). Galls were collected from Victoria on 8 January and 18 March 1999 (11 and 14 galls).

Galls were picked, placed in plastic bags, and kept on ice during transport to Flinders University. Galls were stored temporarily at  $8^{\circ}C$  and usually censused within a week of collection. Where this could not be done, galls were frozen at  $-70^{\circ}C$  for later examination. The total number of healthy, unparasitised galls censused was smaller than those dissected, as some galls were kleptoparasitised by thrips in the genus *Koptothrips*.

#### Demographic and sex ratio study

All individuals were removed from their galls and counted following the methods of Kranz *et al.* (1999). First-instar larvae were cleared in Hoyer's medium and sexed using chaetotaxy of the ninth abdominal segment; females have three pairs of setae on this segment and males have four (Heming, 1991; Kranz *et al.*, 1999). Adults were mounted in Hoyer's medium and sexed by viewing the fustis of females and phallobase of males (Mound & Heming, 1991; Kranz *et al.*, 1999). For *O. rodwayi*, five adult female brood from each of seven galls, collected on 18 March 1999, were dissected and the spermathecae were examined for evidence of insemination.

#### Data analysis

Data were analysed using SPSS<sup>®</sup> version 8.0.1 (SPSS Inc., Chicago, Illinois). Homogeneity of variances was assessed using Levene's test and data were transformed where necessary to produce homoscedasticity. Sex-ratio data were arcsin transformed prior to analysis.

## Results

#### Kladothrips ellobus

*Gall induction and development.* Galls were induced by either a female or a single male–female pair from late spring (November) to early autumn (March). Gall induction was asynchronous as indicated by the variation in brood size for January 1996 and the presence of both old and young galls in May 1996 and 1997 (Table 1). Brood development from early December to early January 1996 indicates that the foundress took  $\approx 6$  weeks to lay all of its brood, however galls became brown and dry and often cracked and open while brood were still in the second-instar stage. This is consistent with the life history of many gall-inducing thrips species, which apparently pupate after leaving the gall and presumably overwinter in the soil (Crespi, 1992b; Crespi & Mound, 1997; Kranz *et al.*, 1999, 2000, 2001, in press).

Thirty-four of 80 galls (45%) censused, including kleptoparasitised galls, were induced by a male–female pair, but in some of these galls there were other, dead *K. ellobus* adults. The presence of male founders in almost half of the galls is similar to that found in closely related *Kladothrips* spp. (Crespi, 1992b; Crespi & Mound, 1997; Kranz *et al.*, 2000). Six galls contained a living male–female pair and a dead female, two galls had a living male–female pair and a dead female and dead male, and one gall had a living female, a dead male, and two dead females. Thirty-nine of the 80 galls (49%) contained a single female, a further five galls contained a living and a dead female, and one gall contained one living female and three dead females.

**Table 1.** Summary life-cycle data for *Kladothrips ellobus*. *n* is the total number of galls censused. Brood size is the mean number of eggs and larvae ( $\pm$  SE). Per cent of galls with live foundress and per cent of galls with male founder are derived from the per cent of all galls sampled on the collection date. Other data are means  $\pm$  SE.

Date	<i>n</i>	Per cent of galls with live foundress	Per cent of galls with male founder	Eggs	First instars	Proportion male first instars	Brood size
7 December 1995	11	73	64	27 $\pm$ 7	0	–	27 $\pm$ 7
28 December 1995	20	80	45	60 $\pm$ 8	30 $\pm$ 3	0.50 $\pm$ 0.06	179 $\pm$ 13
6 January 1996	7	86	57	59 $\pm$ 10	37 $\pm$ 5	0.40 $\pm$ 0.07	403 $\pm$ 52
15 January 1996	9	56	55	16 $\pm$ 4	24 $\pm$ 5	0.21 $\pm$ 0.06	127 $\pm$ 25
14 May 1996	5	100	0	37 $\pm$ 9	17 $\pm$ 8	0.49 $\pm$ 0.18	82 $\pm$ 28
20 January 1997	6	100	50	22 $\pm$ 7	15 $\pm$ 7	0.20 $\pm$ 0.06	112 $\pm$ 60
31 May 1997	5	0	60	2 $\pm$ 2	11 $\pm$ 4	0.48 $\pm$ 0.14	286 $\pm$ 106

**Table 2.** Summary life-cycle data for *Oncothrips rodwayi*. *n* is the total number of galls censused. Adult brood is the mean number of adults, minus the foundress, in the gall. Brood size is the mean number of eggs, larvae, pupae, and adults. Per cent of galls with live foundress is the per cent of all galls sampled on the collection date. Other data are means  $\pm$  SE.

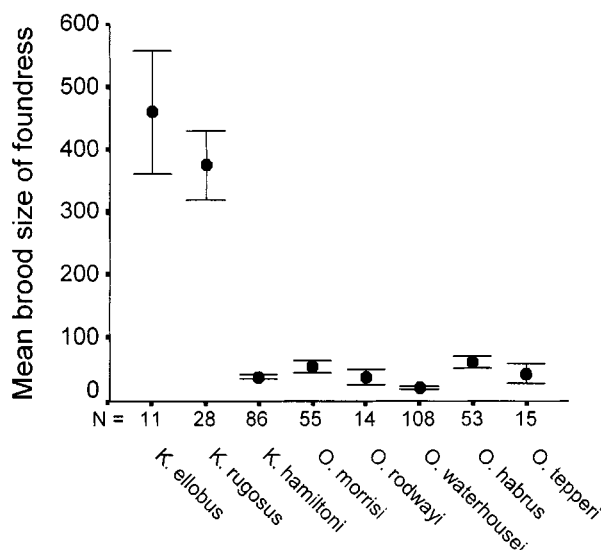
Date	<i>n</i>	Per cent of galls with live foundress	Eggs	First instars	Proportion male first instars	Adult brood	Proportion male adult brood	Brood size
<b>Mount George</b>								
26 December 1996	9	100	6 $\pm$ 2	3 $\pm$ 3	0.16 $\pm$ 0.00	9 $\pm$ 6	0.12 $\pm$ 0.01	7 $\pm$ 2
3 January 1997	6	100	19 $\pm$ 4	0	–	0	–	19 $\pm$ 4
15 January 1997	6	100	22 $\pm$ 6	0.2 $\pm$ 0.2	–	0	–	23 $\pm$ 5
2 February 1997	6	17	18 $\pm$ 5	6 $\pm$ 3	0.07 $\pm$ 0.04	14 $\pm$ 14	0.05 $\pm$ 0	40 $\pm$ 9
19 January 1998	4	0	8 $\pm$ 3	10 $\pm$ 5	0.13 $\pm$ 0.06	0	–	24 $\pm$ 6
<b>Heywood</b>								
8 January 1999	11	91	27 $\pm$ 3	23 $\pm$ 3	0.13 $\pm$ 0.03	0	–	52 $\pm$ 6
18 March 1999	14	0	0.2 $\pm$ 0.2	0.1 $\pm$ 0.1	–	27 $\pm$ 4	0.14 $\pm$ 0.06	35 $\pm$ 5

**Brood size.** The largest brood size (eggs and larvae) was 624 individuals. The mean brood size of galls censused from 6 January 1996, when brood sizes were largest (Table 1), was 403  $\pm$  52 SE ( $n=7$ ). The mean volume of corresponding galls was 270  $\pm$  49 mm<sup>3</sup>. A two-way ANOVA on square root-transformed data for all galls tested whether brood size differed between galls with a founder of both sexes and those with a single foundress, with collection date as a crossed factor. There was no significant interaction between the presence of a founding male and collection date ( $F_{4,36}=11.713$ ,  $P=NS$ ). 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 on brood size ( $F_{4,71}=13.78$ ,  $P<0.001$ ) but there was no effect on brood size due to the presence of a male founder ( $F_{2,47}=0.086$ ,  $P=NS$ ).

**Foundress and founder longevity.** The longevity of gall-inducers was determined from healthy, unparasitised galls. Forty-six of the 58 healthy galls (80%) had a living foundress. The foundress was alive in 77% of galls with a brood size up to 50, 84% of galls with a brood size of 51–100, 79% of galls with a brood size of 101–200, 85% of galls with a brood size of

201–400, and 67% of galls with a brood size greater than 400. There was no significant difference in longevity between females that induced a gall alone and females that induced galls with a male ( $\chi^2_2=0.683$ ,  $P=NS$ ). Of the 28 healthy galls with a male founder, 17 (61%) of the males were alive, and all were alive in early December 1996, before any eggs had hatched (Table 1).

**Sex ratio.** The mean sex ratio (proportion of males) of *Kladothrips ellobus* was 0.41  $\pm$  0.04 ( $n=46$  galls). There was no evidence of either protandry or protogyny, and the population-wide distribution of sex ratios was approximately normal. In order to detect any bias in the sex ratio resulting from young galls with small numbers of brood (i.e. less than five), the overall sex ratio was also determined by summing the total count of first-instar males and females and determining the proportion of males. The summed sex ratio was also 0.41, indicating that sex ratios from small numbers of individuals did not bias the overall sex ratio. The mean sex ratio was not significantly different from 0.5 (one sample *t*-test, arcsin-transformed data against 0.5,  $t_{45}=-1.097$ ,  $P=NS$ ). The mean sex ratio of first-instar larvae in galls induced by a single female did not differ significantly from that in galls induced by



**Fig. 2.** The mean brood size and 95% CI bars of the foundress for *Kladothrips ellobus*, *K. rugosus* (solitary species in the ancestral lineage to the eusocial species), *K. hamiltoni*, *Oncothrips waterhousei*, *O. habrus*, and *O. tepperi* (eusocial species), *O. morrisi* (which has a non-dispersing, fully reproductive fighting morph), and *O. rodwayi* (secondarily solitary). See text for details of sources and calculation of data.  $n$ =number of galls for each species in the analyses.

a male–female pair (independent  $t$ -test, arcsin-transformed data,  $t_{42}=0.108$ ,  $P=NS$ ).

#### *Oncothrips rodwayi*

**Gall initiation and development.** Solitary females (i.e. no male founder) induced all of the 72 *O. rodwayi* galls that were censused, including those that were kleptoparasitised. The absence of male founding is consistent with all other *Oncothrips* spp. (Crespi, 1992b, 1993; Mound *et al.*, 1996; Crespi & Mound, 1997; Kranz *et al.*, 2001, in press; B. Crespi, unpublished). Gall induction appeared to be asynchronous from mid spring (October) to late summer (February), as indicated by the overlap of very young galls and galls with adult brood in December 1996 (Table 2). Unlike *Kladothrips ellobus* and many other gall-inducing thrips, including all social species except *O. tepperi* (Crespi & Mound, 1997; Kranz *et al.*, 1999, 2000, 2001, in press; Fig. 1), larvae of *O. rodwayi* pupate and eclose as adults in their natal gall. The development time from egg to adult eclosion took  $\approx 6$  weeks (Table 2). The total brood size (eggs, larvae, and adults) in galls where offspring had eclosed as adults was  $37 \pm 5$  ( $n=14$ ) and the corresponding mean gall volume was  $172 \pm 18 \text{ mm}^3$ . The foundress was dead in all galls with adult brood.

**Mating structure and sex ratio.** Dissections of adult female brood and inspection of their spermathecae revealed that  $77 \pm 7\%$  of females were inseminated prior to dispersal from

the natal gall. These females must have mated with their brothers. Whether the brothers were full or part siblings depends on whether their mother mated prior to and/or after dispersal from the natal gall.

The sex ratio (proportion of males) of *Oncothrips rodwayi* was highly female biased (first instar  $r=0.12 \pm 0.03$ ,  $n=18$  galls; adults  $r=0.14 \pm 0.05$ ,  $n=17$ ). There was no evidence of either protandry or protogyny and the population-wide distribution of sex ratios was approximately normal. As for *Kladothrips ellobus*, the population-wide sex ratio was also determined by summing all females and all males, in order to account for any bias resulting from the sex ratio in galls with a small number of individuals. The summed sex ratio for first instars was 0.12 and for adults 0.14, indicating that the sex ratios from small numbers of individuals did not bias the overall sex ratio. There was no significant difference between sites in the sex ratio of first instars (independent  $t$ -test, arcsin-transformed data,  $t_{16}=-0.509$ ,  $P=NS$ ) or adults ( $t_{15}=-0.420$ ,  $P=NS$ ). There was also no significant difference between the mean sex ratio of larvae and adults (independent  $t$ -test, arcsin-transformed data,  $t_{33}=-0.393$ ,  $P=NS$ ), suggesting that sex-specific mortality in the juvenile stages did not contribute to the female bias. The mean sex ratio resulting from pooling larvae and adults was  $0.13 \pm 0.03$  ( $n=35$ ).

#### Comparison between solitary and eusocial thrips taxa

Previous studies on Australian gall-inducing thrips have suggested that the relatively large brood size of solitary species is an ancestral character for the eusocial clade of thrips and a distinguishing characteristic of an  $r$ -selection strategy (Crespi *et al.*, 1997; Kranz *et al.*, 2000, 2001; Chapman *et al.*, in press). To investigate brood size further, data were combined from the current study with foundress brood size data (i.e. only brood produced by the foundress, not brood produced by soldiers in the eusocial species), synthesised and re-analysed from previous studies for the solitary species *K. rugosus* (Kranz *et al.*, 2000), the eusocial species *K. hamiltoni* (Kranz *et al.*, 1999), *O. waterhousei* and *O. habrus* (Kranz *et al.*, in press), *O. tepperi* (B. Kranz, unpublished), and *O. morrisi* (Kranz *et al.*, 2001), which has a fully reproductive non-dispersing morph (see Fig. 1 for phylogenetic positions). As the life history and available data varied among groups of species, brood size was determined separately for the groups *K. ellobus* and *K. rugosus*, the eusocial species, and *O. rodwayi*. For *K. ellobus* and *K. rugosus*, the mean brood size was determined from all galls with a brood size greater than the lower 95% CI of the mean for the month where brood sizes were largest (see above, Table 1; Kranz *et al.*, 2000). For the eusocial species, *K. hamiltoni*, *O. waterhousei*, *O. habrus*, and *O. tepperi*, and also for *O. morrisi*, the following method was used to differentiate brood produced by the foundress and the soldiers or fighting morph. Using the rationale of Kranz *et al.* (2001, in press), galls with a brood size greater than the maximum number of soldiers were selected, to be confident that dispersing brood were being produced and that the brood were approaching

maturity. For these galls, the number of brood produced by the foundress ( $b_f$ ) was calculated as:

$$b_f = s + [(1 - p_s) \times d_{fs}]$$

where  $s$  is the number of soldiers in the gall,  $p_s$  is the proportion of dispersing brood produced by all soldiers, calculated for each species by Kranz *et al.* (2001) and Chapman *et al.* (in press), and  $d_{fs}$  is the total number of dispersing brood, produced by both the foundress and the soldiers. For *O. rodwayi*, the brood size was determined from all galls with more than one adult brood.

The mean number of brood produced by foundresses in each species is shown in Fig. 2. As data were heteroscedastic and could not be transformed to produce homoscedasticity, 95% CI bars for general comparisons among species are shown in Fig. 2. The mean brood sizes for *K. ellobus* and *K. rugosus* were 460 ( $\pm 44$  SE;  $n = 11$  galls) and 375 ( $\pm 27$ ;  $n = 28$ ) respectively, and 95% CI bars overlapped; however the mean brood size of the foundress in the eusocial species and *O. morrisi* ranged from 20 to 61, and for *O. rodwayi* was 37 ( $\pm 5$ ;  $n = 14$ ), and the 95% CI bars did not overlap with *K. ellobus* and *K. rugosus* for any of these species. The 95% CI bars did not overlap for all eusocial species but the means for each species are in the same general range. *Oncothrips rodwayi* has a mean brood size that is not significantly different from the mean brood size of the eusocial species and *O. morrisi* combined (independent  $t$ -test,  $t_{329} = 0.296$ ,  $P = \text{NS}$ ).

## Discussion

The life histories of *Kladothrips ellobus* and *Oncothrips rodwayi* enable traits to be identified on why non-dispersing soldier castes have evolved and been lost in the *Oncothrips* + *Kladothrips* clade. *Kladothrips ellobus* and *O. rodwayi* are solitary species belonging, respectively, to a clade that never evolved soldiers and to a lineage where soldiers were evolutionarily lost (Fig. 1). As *K. ellobus* occupies a relatively basal position to the eusocial *Kladothrips* clade (Fig. 1), it could be important for identifying traits that are ancestral to the social species, especially when considered in conjunction with closely related solitary species.

The population-wide sex ratio of *K. ellobus* was not significantly different from parity and there was no evidence of population structure such as split sex ratios (cf. *Kladothrips rugosus*; Kranz *et al.*, 2000), whereas in *O. rodwayi* the sex ratio was highly female biased. These sex ratios suggest random mating in *K. ellobus*, and for *O. rodwayi* are consistent with data showing within-gall sibmating and, therefore, probable local mate competition. High levels of inbreeding have been found in all but one (*Oncothrips waterhousei*) of the *Oncothrips* and *Kladothrips* species with soldiers (Chapman & Crespi, 1998; Chapman *et al.*, 2000, in press). Indeed, phylogenetic inference arguments indicate that inbreeding is a plesiomorphic trait for the soldier clade (Chapman *et al.*, 2000). At the same time, sex ratios vary widely in the soldier-producing species (Table 3), indicating evolutionary lability in

this trait and suggesting the existence of underlying causal factors that lead to very different sex-ratio strategies, despite broad similarities in ecology and sociality. While *K. ellobus* exhibits a sex ratio that is not significantly different from parity, *K. hamiltoni*, which often forms galls on the same host trees as *K. ellobus* (Mound & Kranz, 1997), shows a strongly female-biased sex ratio in the dispersing generation. Further data are required before the difference in sex ratio between *K. ellobus* and *K. hamiltoni* can be explained, and estimates of inbreeding in *K. ellobus* and other solitary species are particularly important here.

The average gall and brood sizes for *K. ellobus* and other solitary species in the basal lineages, including *K. maslini* (the only species besides *O. rodwayi* to occur in a mesic environment), are larger than those of all eusocial species (Mound *et al.*, 1996; Crespi & Mound, 1997; Crespi & Worobey, 1998; Kranz *et al.*, 2000; Morris *et al.*, 2001; Table 3, Fig. 2). Foundresses of *K. ellobus* and *K. rugosus* produce between about six and 23 times that of foundresses of eusocial species (Fig. 2), and some solitary species, such as *O. torus* and *K. augonsaxos*, have brood sizes  $> 800$  (Mound *et al.*, 1996; Fig. 1), which is up to 40 times that of eusocial foundresses. [The total brood size of *O. morrisi*, which has a fully reproductive non-dispersing fighting morph, is larger than that of most solitary species but foundresses of this species produce similar brood sizes to the eusocial species (Kranz *et al.*, 2001; Table 3, Fig. 2)]. Conversely, the total number of eggs produced by *O. rodwayi* foundresses is similar to the number of eggs produced by foundresses in the eusocial species, although less than the total number of dispersing brood, which are produced by both the foundress and soldiers (Table 3, Fig. 2). [This is also true for the number of eggs produced by *O. morrisi* foundresses (Fig. 2).] This is a very important point because it indicates that the evolutionary loss of soldiers in *O. rodwayi* is not a simple reversion to the ancestral characteristic of foundresses inducing large galls and producing large numbers of eggs. Rather, *O. rodwayi* seems to have lost the soldier generation without any changes to foundress fecundity. As relatively large gall volumes and brood sizes are typical of all solitary species except *O. rodwayi* (Mound *et al.*, 1996; Crespi & Worobey, 1998; Table 3), it appears that large brood sizes are plesiomorphic for gall-forming thrips on *Acacia*, that the evolution of small brood sizes probably occurred once a micropteran generation had evolved, and that the loss of micropterans in *O. rodwayi* is not associated with a reversion to the large brood sizes of the solitary species.

*Oncothrips rodwayi* is the only galling thrips in the clade that occurs in temperate areas (Mound, 1971; Mound *et al.*, 1996). Consequently, growth of the *A. melanoxylon* host is probably more regular, making the gall-inducing window period longer, safer, and more reliable in *O. rodwayi* than in other species. It is very likely that the risks of desiccation during dispersal and gall induction are much higher in arid zone galling thrips than for *O. rodwayi*. Indeed, galls are present on *A. melanoxylon* for about 9 months of the year compared with about 3–5 months in arid regions (B. Kranz, unpublished) because there is often an overlap of gall generations on the host tree (Table 1). The longer and more

**Table 3.** Comparison of solitary and social species. Social species have an asterisk. †*Oncothrips morrissi* has a soldier-like morph but lacks reproductive skew between females, so is not typical of the social species (Kranz *et al.*, 2001). Gall volume is for galls with complete broods. Per cent male founders is the per cent of galls censused with a male founder. For the social species, mean number of foundress-produced brood includes soldiers and dispersers (see text for details), and mean number of dispersing brood includes dispersing brood produced by the foundress and soldiers. Data are from this paper, and modified from Kranz *et al.* (1999, 2000, 2001, in press) and B. Kranz (unpublished). SE in parentheses.

	Mean gall volume	Per cent male founders	Adult dispersers in natal gall	Mean number of foundress-produced brood	Mean number of dispersing brood	Sex ratio of dispersers
<i>K. rugosus</i>	338 (27)	42	No	375 (27)	375 (27)	Unbiased
<i>K. ellobus</i>	270 (49)	45	No	460 (44)	460 (44)	Unbiased
<i>K. hamiltoni</i> *	246 (12)	6	No	39 (2)	115 (7)	Female biased
<i>O. morrissi</i> †	1020 (37)	0	No	55 (5)	619 (63)	Female biased
<i>O. rodwayi</i>	172 (18)	0	Yes	37 (5)	37 (5)	Female biased
<i>O. waterhousei</i> *	50 (3)	0	No	21 (1)	79 (4)	Unbiased
<i>O. habrus</i> *	135 (43)	0	No	61 (5)	105 (8)	Unbiased
<i>O. tepperi</i> *	136 (56)	0	Yes	43 (7)	60 (10)	Female biased

reliable window period for inducing galls could explain partly why dispersers leave the gall as adults, ready to induce new galls, rather than overwintering as juveniles, as do most social and many solitary galling thrips (Crespi, 1992b; Mound & Crespi, 1995; Crespi & Abbott, 1999; Kranz *et al.*, 1999, 2000, 2001, in press).

Brood size could be an indicator of the strategy for minimising the fitness costs associated with *Koptothrips* invasion. Crespi *et al.* (1997) suggested that large brood sizes are analogous to an *r*-selection strategy, whereas eusocial species, with a soldier morph and small brood sizes, are analogous to having a *k*-selection strategy. On average, the rates of *Koptothrips* invasions appear to be lower for the *r*-selected solitary species than for the *k*-selected social species, suggesting that high rates of kleptoparasitism may have been important in both the selection and maintenance of soldier morphology and behaviour (Crespi & Abbott, 1999). In *O. rodwayi*, however, *Koptothrips* appear to have lower successful invasion rates than most other gall-inducing species (Crespi & Abbott, 1999; B. Kranz, unpublished). It is possible that temperate conditions mean that variable and asynchronous gall induction in *O. rodwayi* makes it more difficult for the *Koptothrips* to track gall induction than in those of arid zone thrips, a scenario that has been suggested to explain low rates of parasitism in some bees (Weislo, 1987).

In most social insects, there appears to be a positive association between brood size and social complexity (Bourke, 1999, and references therein), and large brood sizes have also been identified as promoting anti-predator social interactions in mammals and birds (Elgar, 1989; Quenette, 1990; Blumstein *et al.*, 1999). The Kalotermitidae and Termopsidae termite families demonstrate this well, as small brood sizes appear to be a trait of primitively eusocial species in lineages that never evolved more complex social behaviour, as well as secondarily derived primitively eusocial species (Thompson *et al.*, 2000). This example contrasts directly with eusocial thrips, as for

termites small brood size is ancestral, and the secondarily derived solitary state involves re-acquiring small brood sizes. In this sense, the life history of *O. rodwayi* cannot be considered a complete reversion to solitary behaviour.

To the authors' knowledge, *O. rodwayi* is the first example of a loss of eusociality where the species does not have a complete reversion to ancestral traits, however this is not necessarily an indication of a novel situation but more likely a lack of basic life-history information that compares ancestral and derived solitary species with eusocial species. In horned aphids, for example, the loss of a first-instar soldier morph in two species of *Ceratovacuna*, *C. nekoashi* and *C. sp.* (undescribed), is associated with host shifts from perennial bamboo to an annual and perennial grass respectively (Stern, 1998; Kurosu & Aoki, 1999; U. Kurosu, pers. comm.). Monomorphic juveniles of *C. nekoashi* are effective at defensive behaviour (Kurosu & Aoki, 1999) but it has not been contrasted with the behaviour of species in ancestral lineages to soldier-producing species. The significance of the host shift in the loss of soldiers in *Ceratovacuna* could be related indirectly to increasing vigilance of the ant species that interacts mutualistically with aphids by reducing their predatory pressure (U. Kurosu, pers. comm.). If so, this is similar to the low kleptoparasitism rates in *O. rodwayi* that appear to be associated with temperate conditions.

Packer (1997) found that losses of eusociality in halictine bees were associated with high altitudes or latitudes, and suggested that these cold environments are unfavourable for multivoltine life histories. While *O. rodwayi* occurs in a cooler environment than the eusocial thrips, temperate conditions appear to enable a longer window period for gall induction and are likely to be linked intrinsically to the low kleptoparasitism rates in *O. rodwayi* (Crespi & Abbott, 1999). Paradoxically, the conditions promoting secondarily solitariness in *O. rodwayi* could be more analogous to secondarily solitary halictine bees that occur in warmer (more temperate)

environments than some of their eusocial congeners, although intrinsic factors to the *Halictus* genus may also be important for the losses of eusociality in these halictine bees (Danforth *et al.*, 1999).

The contrast of trends between brood sizes and social complexity in thrips with Hymenoptera and Isoptera (Bourke, 1999, and references therein) is a reasonable indicator that the selective pressures underlying the evolutionary timing of morphological dimorphism and reproductive skew differ between these taxa. Kranz *et al.* (2001) suggested that morphological dimorphism preceded the evolution of reproductive skew in thrips and that a scenario for soldier evolution could have been: (1) selection for non-dispersal due to the value of galls for food and shelter, and reduction of latency period to reproduction, (2) selection for fighting morphology and behaviour to protect offspring and collateral relatives, and (3) a possible trade-off between fighting and reproductive effort, and selection for smaller gall sizes to elude predators and increase gall longevity. Chapman *et al.*'s (in press) microsatellite and census data for eusocial thrips showed a trend of low to high reproductive skew from the basal to derived lineages and is consistent with the scenario that fighting morphology evolved before reproductive skew. This scenario has also been suggested for aphids (Stern & Foster, 1997). In all Hymenoptera, however, morphological dimorphism appears to have evolved between already subfertile workers and the dominant reproductive (Wilson, 1971; Oster & Wilson, 1978; Brian, 1979; Bourke & Franks, 1995). In termites, the evolutionary timing of subfertility and morphological dimorphism remains controversial (Noirot & Pasteels, 1987, 1988; Roisin, 1994, 1999; Thompson *et al.*, 2000).

The loss of a non-dispersing soldier in *O. rodwayi* may be associated with the invasion of a temperate, more predictable environment, lowering the risks of dispersal and latency to reproduction, and which may also have lowered rates of kleptoparasitism. Phylogenetic analyses based on DNA sequence data indicate the possibility of an additional loss of soldiers in the lineage leading to *K. xiphys* (Morris, 2000; Fig. 1), and life-history data are being collected for this species (D. Morris and T. Chapman, unpublished). Long-term rearing experiments that manipulate temperature, length of necessary overwintering period, availability of galling sites, and parasitism rates might elucidate further the key factors involved in the loss of soldiers in *O. rodwayi*. Similarly, mapping the overwintering period throughout their distribution and relating this to ambient conditions and predation pressure would elucidate further the key extrinsic factors involved in the origin, maintenance, and loss of soldiers in gall-inducing thrips on *Acacia*.

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