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Pleometrosis in phyllode-glueing thrips (Thysanoptera: Phlaeothripidae) on Australian *Acacia*

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Pleometrosis, or colony founding by more than one female, is common in various social insects and it engenders opportunities for social cooperation as well as cheating. The life cycles of four species of thrips on Australian *Acacia* trees were examined to elucidate the extent and nature of colony founding by multiple individuals. Data from colonies of three species of thrips from the genus *Dunatothrips* Moulton and one species of *Lichanothrips* Mound were used to infer the prevalence of pleometrosis in each species. The results indicate that *Dunatothrips* species show high levels of cofounding, with up to 50% of colonies having more than one foundress. By contrast, colonies of *Lichanothrips* are predominantly established by a female and a male. As in some communal insects, pleometrosis is facultative in *Dunatothrips*, foundresses show more or less constant per capita reproduction with foundress number, and the selective pressures for pleometrosis may involve predation pressure during founding or survivorship insurance for the brood. In *Lichanothrips*, male founders are probably engaging in mate guarding, which also occurs in some species of gall-inducing thrips on *Acacia*. The differences in founding patterns between *Dunatothrips* and *Lichanothrips* may be due in part the nature of their domiciles: *Dunatothrips* engage in extensive construction of a domicile using anal secretions, whereas many *Lichanothrips* primarily improve a pre-existing partial enclosure. © 2002 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2002, **75**, 467–474.

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INTRODUCTION

The manner in which colonies are established can be an important factor in the evolution of social behaviour in insects. Most social insects begin new colonies by haplometrosis, i.e. by a single female or gyne. Pleometrosis is the mode of colony initiation in which two or more females or gynes cooperate to produce a new colony. Comparison of these two modes of founding has provided useful insights into selective pressures favouring sociality (Itô, 1993; Bourke & Franks, 1995; Schwarz *et al.*, 1998).

Pleometrosis has been reported in a variety of social insects including wasps, bees, ants and termites. Cofounding and its effects have been studied in a number of bees of the subfamilies Xylocopinae (Schwarz *et al.*, 1998) and Halictinae (Packer, 1993). In wasps, pleometrosis is common in some groups of Vespinae and Polistinae (Itô, 1993). Cofounding occurs in at least a dozen ant species from a number of genera (Rissing & Pollock, 1988; Bernasconi & Strassmann, 1999). Among termites, pleometrosis is known to occur in a number of species, primarily from genera such as *Nasutitermes* and *Macrotermes* (Shellman-Reeve, 1997; Thorne, 1997).

The benefits of pleometrotic colony founding appear to vary substantially among the different groups of insects that exhibit this behaviour. It has been proposed that the primary reasons for some paper wasp queens cooperating in establishment of new colonies are the benefits in terms of enhanced colony survival and growth resulting from mutualistic cofounding (Itô, 1993; Clouse, 2001). Among ants, queens may establish colonies as a group but usually, though not always, only one queen survives to dominate the colony

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(Rissing & Pollock, 1987; Tschinkel & Howard, 1983). Cofounding ant queens that do not survive will make little contribution to the production of future sexuals, and are therefore probably not cooperating for the same reasons as pleometrotic wasp queens (Herbers, 1993; Choe & Perlman, 1997). In ant species that exhibit pleometrotic colony founding, queens are typically sealed inside their nests until the first generation of workers eclose. By cofounding, queens reduce the time required for the first cohort of workers to be produced and this may confer selective advantages, resulting from more rapid growth of the colony during the claustral period (Herbers, 1993; Tschinkel & Howard, 1983). Another example of the benefits of pleometrosis is that of some weaver ant species, in which queens cooperate to facilitate the construction of a nest that would otherwise be difficult for a single queen to accomplish (Peeters & Andersen, 1989). Cofounding in bees is attributed to a number of potential advantages that may vary from species to species. In many allodapine species, evidence suggests that cofounded colonies are more successful in defending the brood from enemies at the nest (Bull & Schwarz, 1996).

Pleometrosis is not confined solely to the Hymenoptera and Isoptera. Crespi and Mound (1997) described 11 colonies of the thrips species *Dunatothrips aneurae* Mound, showing that, in this species, a colony could be established by either pleometrosis or haplometrosis. *Dunatothrips aneurae* is a species that builds a domicile by cementing together phyllodes (modified, leaf-like petioles) of *Acacia aneura* trees in Australia. Crespi and Mound also noted that colonies of a species of *Lichanothrips* were founded by multiple adults but they did not report the sexes of the adults. These indications of pleometrotic behaviour in Thysanoptera suggest that they would be fruitful subjects for further investigation of pleometrosis and the factors that give rise to this, and other, social behaviours. Thysanoptera have the potential to be a particularly useful group for studying the evolution of social behaviour because, being haplodiploid, they are one of the few groups that could be used in comparative studies with Hymenoptera, the primary focus of studies of insect social evolution to date.

In this study the mode of colony founding of four species of thrips (Insecta: Thysanoptera: Phlaeothripidae), *Dunatothrips aneurae*, *D. skene*, *D. vestitor* and *Lichanothrips* sp. nov., is discussed, and the extent to which pleometrosis occurs in these species is detailed. The life cycle of a species of *Lichanothrips* is also examined to determine the nature of cofounding in this species, and the prevalence of pleometrosis. With the data on colony structure for these species, some of the factors that might have facilitated the evolution of cofounding behaviour in thrips are evaluated.

MATERIAL AND METHODS

Thrips in three species of *Dunatothrips* were collected from *Acacia aneura* and *A. catenulata*. Samples of *D. aneurae* and *D. vestitor* Mound & Morris were collected from *Acacia aneura* at a site 11 km south-west of Broken Hill, New South Wales, Australia, in July and December 1997 and April 1998. The third species, *D. skene* Mound & Morris, was found on *Acacia catenulata* in April 1998 at a site approximately 80 km north of Adavale, Queensland. This species provides some comparison with the two species found on *A. aneura*. Samples of one species of *Lichanothrips* (as yet undescribed) were collected from *A. cana* at a site 26 km west of White Cliffs, New South Wales, in April, July and December 1997 and April 1998. Voucher specimens of all species discussed here have been deposited with the Australian National Insect Collection (ANIC).

The thrips were collected by removing the entire domiciles intact from the host plant and sealing them individually in plastic bags or tubes, which were then stored on ice until they were returned to the laboratory. Each domicile was opened and examined under a dissecting microscope, the contents were counted, and the internal dimensions of the domicile measured. The contents of each domicile were recorded as eggs (hatched and unhatched), first-instar larvae, second-instar larvae, prepupae, first-instar pupae, second-instar pupae, tenerals, and adults. The sex of each adult was recorded and, for the *Dunatothrips* species, whether the wings were present or torn off (dealate). In each of the *Dunatothrips* species studied, the dealate adults were assumed to be the original founders, as most of the colonies collected at an early stage of development contained only adults that had lost one or more wings. Alate or fully-winged adults were almost exclusively found in colonies where brood development was sufficiently advanced for adult brood to be present. In some colonies the number of foundresses could not be determined unambiguously (because adult brood were present and may have begun egg-laying or becoming dealate) and these colonies were excluded from the analyses. In *Lichanothrips* colonies, the exact number of founders was unknown except in domiciles obviously initiated recently, where none of the brood had developed beyond the larval stages. Domicile area was measured as length × width of the area delineated by the glue used to attach the phyllodes together, multiplied by the number of phyllodes used to create the domicile. The total brood size of each colony was estimated by adding the number of unhatched eggs to the number of larvae, pupae, and adult brood. The per capita brood production for each *Dunatothrips* colony was calculated by dividing total brood size by the number of foundresses present in the colony.

RESULTS

DUNATOTHRIPS

In total 141 domiciles of the three *Dunatothrips* species were collected over the three samples. Domicile sizes and contents are summarized in Table 1.

Each domicile of these *Dunatothrips* species consists of a number of *Acacia* phyllodes bound together to enclose a space within which the thrips live and breed. The phyllodes used are typically those at the apices of growing shoots. Presumably apical phyllodes are used because they are arranged closer together, but they might also be more nutritious than older phyllodes further down the stems. *Dunatothrips aneurae* and *D. vestitor* are both found on *A. aneura* and their domiciles are virtually indistinguishable from one another. Both species create their domiciles by forming a membrane of finely woven threads that join together the edges of closely opposing phyllodes. This process usually involves three phyllodes, or occasionally two phyllodes and part of the stem from which they arise. This results in an enclosure that incorporates the flat surfaces of two or more phyllodes, which become the feeding substrate for the thrips. The membrane is created by an anal secretion that is drawn out into long slender threads as it is stretched from one phyllode margin to the next. This process continues until the gaps between the phyllode edges are closed by a continuous sheet of interwoven threads.

The domiciles of *Dunatothrips skene* are created using anal secretion of the same type as in other *Dunatothrips*. However, in *D. skene* the secretion is stretched across a single phyllode to form a flat blister or tent-like structure. This unusual form of domicile is usually roughly circular and remarkably inconspicuous. In cases where the phyllode used is curved significantly from edge to edge, the thrips add columns of threadwork at the centre of the span, perhaps to anchor it or for support.

Colonies of *Dunatothrips* are established by adult females, most often singly, but with a moderate incidence of multiple females apparently cooperating to create a domicile. The degree of pleometrosis in each sample can be seen in Table 1, where all collections have some colonies with more than one foundress. It is not known at what point additional foundresses may join a colony, e.g. whether females join together prior to constructing the domicile or if, under certain circumstances, an established female will allow others to join. Collections of newly constructed domiciles showed several instances of multiple females within a domicile that was not yet complete or did not contain eggs, suggesting that females may join early in colony development. None of the colonies collected in the early stages of initiation contained males, suggesting that only females construct domiciles. There was no clear seasonality to colony establishment, with some new colonies found in each sample, although there may be a tendency to establish new colonies in spring and early summer when growth of the host plant is most vigorous.

Colonies typically begin with a small clutch of eggs, which are reared to adulthood as a discrete cohort. Observations suggest that a second clutch of eggs is

Table 1. Summary data for collections of *Dunatothrips* spp. The values given are arithmetic means with the range in brackets below

Species	Date	Dealate females	Winged males	Winged females	Unhatched eggs	Larvae	Pupae	Adult brood	Percent pleometrotic colonies	Mean domicile size (cm^2)
D. aneurae	July 1997	1.70	0.50	0.30	1.60	0.30	0.00	0.80	40%	–
	(*N* = 10)	(1–5)	(0–3)	(0–3)	(0–16)	(0–3)		(0–4)		
	Dec. 1997	1.33	0.93	1.80	4.07	0.67	0.60	2.73	26.7%	118.69
	(*N* = 15)	(1–3)	(0–4)	(0–7)	(0–19)	(0–3)	(0–5)	(0–10)		SE = 14.32
	April 1998	1.42	0.25	1.58	0.83	1.50	0.75	1.83	25%	77.75
	(*N* = 12)	(1–3)	(0–3)	(0–6)	(0–7)	(0–7)	(0–4)	(0–9)		SE = 18.60
D. vestitor	July 1997	2.25	0.25	0.25	0.00	0.00	0.00	0.50	75%	–
	(*N* = 4)	(1–4)	(0–1)	(0–1)				(0.2)		
	Dec. 1997	1.60	1.10	1.70	3.10	1.60	1.00	2.80	50%	132.00
	(*N* = 10)	(1–3)	(0–4)	(0–10)	(0–16)	(0–7)	(0–6)	(0–14)		SE = 31.99
	April 1998	0.83	0.33	0.50	3.67	1.17	0.33	0.83	33%	91.67
	(*N* = 6)	(1–2)	(0–2)	(0–2)	(0–12)	(0–4)	(0–2)	(0–2)		SE = 27.31
D. skene	April 1998	1.54	0.38	1.17	1.38	1.38	0.21	1.54	50%	67.90
	(*N* = 24)	(1–4)	(0–2)	(0–5)	(0–9)	(0–6)	(0–1)	(0–6)		SE = 8.39

not produced until the first cohort ecloses into adults. *Dunatothrips* can also continue to use a domicile for more than one generation. When this occurs, adult offspring of the first generation can remain in the original colony and produce their own offspring. If adult offspring remain in the domicile they usually lose their wings and at this stage it becomes very difficult to determine the number of original foundresses. Because of this, colonies that had progressed beyond maturation of the first brood were excluded from the analyses below. It is not known whether the original foundress or foundresses are still alive at this stage and continue to reproduce further. As the colony grows in size, the domicile is sometimes enlarged, and when this occurs in *D. aneurae* and *D. vestitor* nearby phyllodes are encompassed in a loose array of fine threads (Mound & Morris, 2001). Once the adult females from the first generation become reproductive, they usually also become dealate, presumably thereby foregoing any chance to disperse and establish their own colony. This process can be repeated several times, resulting in colonies of several dozen adults (one colony of *D. vestitor* found at a site in Queensland contained more than 75 adults (Morris, Mound & Schwarz, 2000)).

LICHANOTHRIPS

A total of 103 domiciles of one species of *Lichanothrips* were collected (over four samples). Domicile sizes and contents for those colonies where the number of foundresses could be readily indentified are summarized in Table 2.

Colonies of the *Lichanothrips* species are usually established in a domicile constructed from three or more phyllodes glued together at the edges to form an elongate tube-like structure. In the field collections it was noticed that new colonies were frequently established among phyllodes that had been tied together by lepidopteran larvae. These lepidopteran domiciles can be quite common and apparently provide the thrips with a starting point for domicile construction, usually requiring a little reinforcement and a patch to cover the hole left by the hatching lepidopteran. The anal secretion used by *Lichanothrips* differs from that used by *Dunatothrips* in that it resembles rubber cement and is spread onto the edges of the phyllodes and only rarely used to build partitions. Several different species of *Lichanothrips* tend to embed their eggs partially into this adhesive at the margins of a domicile (Crespi, 1992).

Lichanothrips colonies were founded by male–female pairs in about 60% of cases, with 30% being established by a single female. Most colonies appear to be established in spring and summer, with the brood developing to adulthood in autumn and early winter. This is indicated by the low number of recently established colonies in the late summer (April) and winter (July) collections, where the founders could be identified. The adult brood appear to remain in the natal domicile until favourable conditions allow them to disperse and establish new colonies the following spring. In many instances, a second clutch of eggs is produced while there are adult brood present and it is not then possible to distinguish between the original founders of the domicile and their adult brood. For this reason, only colonies in which the founders could be identified unequivocally (i.e. where there was no brood approaching maturity) have been included in the analyses. Four colonies contained more than one female, but there was only one case of unambiguous indication of pleometrosis, in the December sample where a single colony had two females. The remaining multi-female colonies contained two females with one male, three females with one male, and four females with two males, respectively, all of which were found in the July sample. Thus it is not

Table 2. Summary data for *Lichanothrips*. Values given are the arithmetic mean, with the range in brackets below

Date	Adult females	Adult males	Unhatched eggs	Larvae	Pupae	Percent colonies cofounded (1 male + 1 female)	Percent colonies with >1 adult female	Mean domicile size (cm^2)
April 1997	1.00	0.83	4.67	9.83	1.17	83	0	193.00
(*N* = 6)	(1)	(0–1)	(0–15)	(0–25)	(0–7)			SE = 33.49
July 1997	1.75	0.88	10.25	2.13	0.00	37.5	37.5	188.83
(*N* = 8)	(1–4)	(0–2)	(2–40)	(0–13)				SE = 19.86
Dec. 1997	1.07	0.60	8.40	1.47	0.00	60	6.7	140.80
(*N* = 15)	(1–2)	(0–1)	(0–20)	(0–10)				SE = 18.44
April 1998	1.00	0.60	3.40	1.40	0.00	60	0	209.86
(*N* = 5)	(1)	(0–1)	(0–10)	(0–7)				SE = 28.90

clear how the incidence of multiple females in these winter colonies should be interpreted, as most of the other colonies at this time contained only adults apparently waiting to disperse in spring (September).

BENEFITS OF PLEOMETROSIS

The finding of pleometrosis in the three *Dunatothrips* species raises the question of why adults cooperate in the construction and use of domiciles. Pleometrotic colony foundation could be associated with increased per capita brood production. This possibility was investigated here by looking at the relationships between the number of adult foundresses and total brood production, per capita brood production, and per capita domicile surface area. Domiciles containing adults from more than one generation (i.e. parent–offspring associations) were excluded from analysis. The census data from field collections are summarized in Table 1. Total brood production and per capita brood production are plotted against foundress number in Fig. 1. Total brood production increased with increasing foundress number for two of the three *Dunatothrips* species, with regression values as follows; *D. aneurae*, $F_{1,35} = 4.273$, $r = 0.330$, $P = 0.046$; *D. vestitor*, $F_{1,18} = 1.713$, $r = 0.295$, $P = 0.207$; *D. skene*, $F_{1,22} = 4.781$, $r = 0.423$, $P = 0.040$ (Fig. 1a). Thus, in all three species, each foundress contributed about 3–4 brood to the colony on average regardless of foundress number, and per capita brood production did not increase notably with the number of foundresses (Fig. 1b). This relationship was explored further by regressing per capita brood onto the number of founders separately for each species. This indicated no significant relationship (*D. aneurae*, $F_{1,35} = 0.093$, $r = 0.051$, $P = 0.762$; *D. vestitor*, $F_{1,18} = 0.017$, $r = 0.031$, $P = 0.897$; *D. skene*, $F_{1,22} = 0.221$, $r = 0.100$, $P = 0.643$). Similarly, regression of per capita domicile area onto foundress number was not significant for any species (*D. aneurae,* $F_{1,23} = 2.115$, $r = 0.290$, $P = 0.159$; *D. vestitor*, $F_{1,13} = 0.264$, $r = 0.141$, $P = 0.616$; *D. skene*, $F_{1,22} = 0.162$, $r = 0.085$, $P = 0.691$).

To assess the possible effect of cofounding involving both males and females in *Lichanothrips*, total brood size in singly founded colonies was compared with total brood size in colonies founded by a female/male pair. This test suggested that there was no significant difference between brood sizes in single female and cofounded (female/male) colonies (independent samples *t*-test, $F_{22} = 0.109$, $t = -0.518$, $P = 0.614$). It was not possible to investigate a relationship between cofounding and domicile size in *Lichanothrips* due to this species' habit of often using domiciles created by lepidopteran larvae. This behaviour meant that, for most of the colonies that were collected, the founding adults had little direct control over the size of the domicile.

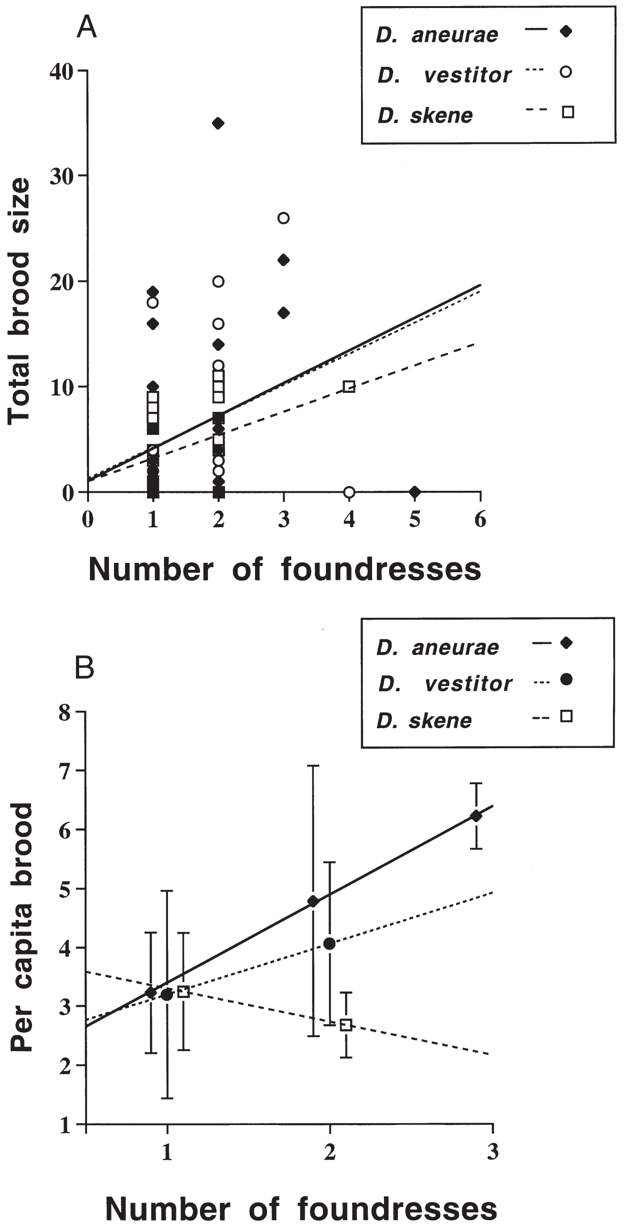

Figure 1. Plots of (a) total brood production and (b) per capita brood production vs. number of foundresses in *Dunatothrips* colonies. In (b), most colonies containing more than two foundresses are omitted as they are represented by single data points and so standard errors could not be calculated.

DISCUSSION

Despite the rapidly growing number of studies of social organization in thrips, very few species are known to show any incidence of cofounding behaviour. The only other thrips for which information on cofounding is known are some of the gall-inducing species found on *Acacia*. Among some species of the gall-inducing genus *Kladothrips,* up to 40% of galls are initiated by a male/female pair (Crespi & Mound, 1997; Kranz *et al*, 2000). Also, the corpses of dead conspecific males and females may be found in some of the galls, and there is an aggressive response towards any attempts at same-sex cofounding; females engage in lethal fighting with other females, and males engage in lethal fighting with other males, such that only one female or one male–female pair remain alive in the newly developing gall (Crespi, 1992).

These results indicate that at least some *Lichanothrips* species do not exhibit pleometrosis at appreciable levels, whereas in the *Dunatothrips* species studied pleometrosis occurs at rates between 25 and 50%. The fact that a significant proportion of *Dunatothrips* colonies are cofounded suggests that there are benefits to co-operating with conspecifics in order to establish a colony. These benefits could arise in a number of ways, and some potential benefits are related directly to the construction and maintenance of the domicile. A multi-female colony may be able to construct or repair a domicile more rapidly than a single female colony. This would be of great benefit as the environment in which these thrips are typically found is arid, and the domicile is critical for preventing desiccation and providing protection (e.g. from ants, which are common on these *Acacia*). Thus, pleometrosis may enhance survival during the founding period through better protection of the founders and defence of the incipient colony.

Pleometrosis might also confer benefits by allowing foundresses to build larger domiciles. Presumably the size of a domicile will place constraints on the number of offspring that can be produced, as there must be sufficient surface area to allow all of the brood to feed. Thus a larger domicile will permit a larger brood size. However, there was no evidence for increasing domicile size with increasing foundress number, and it may be that the size of the domicile is more limited by the choice of the site for the colony than the abilities of the founders.

Another potential benefit of cofounding is a greater ability to defend the domicile, whether from predators such as ants or from other thrips species that usurp the domicile, such as *Xaniothrips* (Mound & Morris, 1999). However, the incidence of successful invasion by kleptoparasites is low in *Dunatothrips* and therefore it is unlikely that kleptoparasitism is a selective factor underlying the evolution or maintenance of pleometrosis. However, invasion of the nest by parasites or conspecifics (i.e. brood raiding) is a significant factor in the incidence of pleometrosis in some ant species (Tschinkel, 1992; Tschinkel, 1998).

The fact that, as in many other insects with pleometrosis, not all colonies are founded through pleometrosis suggests there are costs as well as benefits to colony founding by multiple females (Crespi & Choe, 1997), although this may simply be a result of the difficulty of finding a cofounder. One cost might be that some females produce fewer offspring as a result of dominance hierarchies within the colony. Also, the difficulties inherent in finding another individual to cofound with (in terms of increased risk of mortality through predation or exposure) may often be sufficient to outweigh the advantages of pleometrosis.

Cofounding may also enhance brood production by allowing greater reproductivity per foundress. This could result if foundresses can accrue energetic savings by sharing the costs of constructing a domicile, but there is little evidence to suggest that this occurs in *Dunatothrips*. The data do not indicate that increases in per capita brood production result from additional foundresses. However, at least in *D. aneurae*, there may be a trend towards an increase in per capita brood production with increasing foundress number, and such a relationship could be revealed by more exhaustive sampling. In some communal bees there is a similar, roughly linear increase in total brood production with increasing number of adult females, with no per capita increase (Kukuk & Sage, 1994). In eusocial species, the relationship between per capita brood production and the number of adult females varies, from increases in per capita brood production with additional females, as in allodapine bees (Schwarz *et al.*, 1998; Tierney *et al.*, 2000), to decreases in per capita brood in some halictine bees (Michener, 1964), polistine and polybiine wasps (Clouse, 2001 and references therein) and fire ants (Tschinkel & Howard, 1983; Tschinkel, 1998). One hypothesis used to explain cofounding behaviour, independently of per capita brood production, is the *survivorship insurance* model (Reeve, 1991). This model suggests that cofounding behaviour can provide significant benefits in cases where survivorship of solitary foundresses is low, since surviving foundresses will aid in the rearing of the offspring of females who die before brood maturity. This model may be applicable where pleometrotic behaviour has arisen in species that do not display increased per capita brood production. In this scenario, there may be a trade-off between reproductivity and survivorship for foundresses; solitary founding can produce a larger number of brood but, should a solitary foundress die, all of the brood may also die.

The presence of males in newly established colonies is unusual in the *Acacia* thrips studied thus far, occurring in only a few species of gall-inducing thrips. In thrips species where male founders occur with foundresses, there is no evidence that males provide any benefits in terms of enhancing gall size or brood numbers (Kranz *et al*., 2000; Kranz, 2000). The presence of male founders in these species therefore appears to be a strategy to guard mates during domicile establishment (Crespi, 1992); thus, mate-guarding in newly founded domiciles has apparently evolved convergently in *Lichanothrips* and in *Kladothrips*.

The data on *Lichanothrips* do not suggest that there are any significant differences between brood sizes of single female colonies and brood sizes of female–male colonies. Furthermore, the tendency of this species to establish colonies in empty lepidopteran domiciles meant that it was not possible to compare the effect of cofounding on domicile size. It is possible that male cofounders in *Lichanothrips* provide benefits in terms of repairing domiciles, enabling colonization of sites that would be unavailable to a single female, or in deterring enemies. If such benefits do arise (and there is no evidence for such benefits), they would be different in one important respect from cofounding by females; namely, males do not compete with female cofoundress for egg-laying opportunities.

Pleometrosis in phyllode-glueing *Dunatothrips* is similar to that in some communal taxa, such as bees (Kukuk & Sage, 1994) and embiids (Edgerly, 1997) in that it is facultative with some females founding alone, and it appears to engender more or less constant per capita reproduction among females in haplometrotic and pleometrotic colonies. In the species of *Lichanothrips* studied here, the lack of female pleometrosis may be due in part to the observation that in this genus the females primarily improve a pre-existing domicile (started via a lepidopteran tie), rather than creating a domicile more or less de novo, as in *Dunatothrips*, which may be more energetically expensive and risky in terms of predation. Future studies of phyllode-glueing thrips should focus on the speed of formation and survival rates of haplometrotic and pleometrotic *Dunatothrips* colonies, the behaviours involved in domicile creation and use, and the genetic relatedness of cofoundresses. Such studies will provide further extremely useful comparative information, from a taxon highly divergent to Hymenoptera, on the selective pressures involved in pleometrosis.

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