

Research article

Costs and benefits of joint colony founding in Australian *Acacia* thrips

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Abstract. Facultative joint colony founding by social insects (pleometrosis) provides an outstanding opportunity to analyze the costs and benefits of sociality. Pleometrosis has been documented for a range of social insects, but most studies on the adaptive benefits of this behavior are restricted to the Hymenoptera. In this study, we provide the first analysis of costs and benefits associated with pleometrosis for Australian *Dunatothrips*, which form domiciles by glueing together phyllodes (leaves) of their *Acacia* host plant. In *Dunatothrips aneurae*, the distribution of foundress numbers per nest indicated that females formed associations non-randomly. Furthermore, average group size was independent of both the number of foundresses on the host plant and the number of mature colonies, suggesting that this behavior was not simply a response to limited availability of nesting sites. Although per capita reproduction declined with increasing group size, we also identified two benefits of pleometrosis: (1) individual foundresses in groups had higher survival than solitary foundresses during the brood development period, and (2) larger colony sizes resulting from pleometrosis provided a benefit later in colony development, because a higher proportion of *D. aneurae* adults survived invasions by the kleptoparasite *Xaniothrips mulga* when colony size was larger. These results demonstrate that the reproductive costs of pleometrosis are at least partially counterbalanced by survival benefits.

Keywords: Pleometrosis, *Dunatothrips*, evolution of cooperation, foundress survival, brood production.

Introduction

Studies of facultative joint colony founding by social insects have proven to be especially useful for identifying selective pressures that favor the evolution of sociality. Although the majority of social insect colonies are established by a single female (haplometrosis), facultative group-founding (pleometrosis) occurs in several social insect groups including ants (Herbers, 1993; Choe and Perman, 1997; Bernasconi and Strassmann, 1999; Johnson, 2004), wasps (Reeve, 1991; Ito, 1993), bees (Packer, 1993; Schwarz, 1997), termites (Shellman-Reeve, 1997; Hacker et al., 2005), mites (Saito, 1997), aphids (Miller, 1998a,b) and thrips (Crespi et al., 1997, 2004; Morris et al., 2002). Sharing a nest can be costly because individual females lose their reproductive monopoly within the nest, competition over resources is increased, and close grouping may facilitate the transmission of parasites and pathogens (Cahan and Julian, 1999). The evolution of pleometrosis in the face of such costs implies that they are counterbalanced by benefits, or that this behavior is a consequence of constraints on solitary nesting (e.g. a lack of suitable nesting sites) (Strassmann et al., 1987; Miller, 1998a), such that group-nesting females are simply 'making the best of a bad situation' (see Bull and Schwarz, 1996).

A number of benefits of pleometrosis have been identified including: (1) increased foundress survival (Waloff, 1957; Mintzer, 1987; Jerome et al., 1998; Tibbetts and Reeve, 2003; Johnson, 2004), (2) protection from parasites and predators during brood development (Abrams and Eickwort, 1981; Soucy et al., 2003) (3) higher per capita offspring production (Schwarz et al., 1998; Tierney et al., 2000), (4) larger eventual colony size, which may be advantageous in interactions with conspecifics or predators (Gamboa, 1978; Bartz and Holldobler, 1982; Thorne, 1982; Tschinkel and Howard, 1983; Rissing

and Pollock, 1987; Adams and Tschinkel, 1995; Jerome et al., 1998;), or allow for more efficient acquisition of resources (Cahan and Julian, 1999; Cahan, 2001) (5) reduction of costs associated with nest construction and maintenance (Abrams and Eickwort, 1981; McCorquodale, 1989; Pfennig, 1995; Cahan, 2001), or the ability to repair nest damage more rapidly (Strassmann, 1988), and (6) insurance-based advantages that result because the probability of total nest failure decreases with larger group size, or because an individual's investment can be preserved after her death by remaining group members (Gadagkar, 1990; Reeve, 1991; Queller, 1994; Tibbetts and Reeve, 2003). These considerations suggest that diverse ecological circumstances can select for pleometrosis. However, the relative importance of these selective factors is unclear, and because almost all previous studies on the costs and benefits of pleometrosis have been conducted with Hymenoptera, it is difficult to partition taxon-specific effects from general causal factors that would apply to all organisms that exhibit this behavior.

In this study, we provide the first analysis of costs and benefits associated with pleometrosis for phyllode-glueing *Acacia* thrips. These thrips create domiciles on their host plants by using an anal secretion to join together phyllodes (leaf-like extensions of the petioles) to form an enclosed space for feeding and breeding. Several species in the genus *Dunatothrips* are known to exhibit facultative pleometrosis (Morris et al., 2002; Crespi et al., 2004), but the consequences of this behavior on individual fitness have not been assessed. In an earlier study, Morris et al., (2002) showed that females nesting in groups produced larger brood sizes than single foundresses, but they did not attempt to link larger colony size to any fitness advantage.

We used census data from *D. aneurae* colony collections to evaluate the causes and consequences of joint-nesting for this species. First, we evaluated whether average group size was correlated with the number of foundresses and/or the number of mature colonies on the host plant. A positive association between these variables could result if group formation is a consequence of limited nesting sites, (i.e. foundresses are 'making the best of a bad situation'), or if foundresses more easily find partners at higher densities. Second, we evaluated the costs and benefits of pleometrosis during two stages of colony development: before brood reached maturity (i.e. when foundresses were the only adults present in the domicile), and after brood reached maturity. For colonies with immature brood, we examined whether foundresses in groups had higher survival and/or higher per capita brood production than solitary foundresses. We expected that foundresses in associations would have higher survivorship in part because they would be better able to survive or repel invasions by the kleptoparasite *Xaniothrips mulga*, which frequently enters domiciles at this stage of development. Motivated by the earlier finding that pleometrotic colonies were generally larger once brood matured (Morris et al., 2002), we also examined whether

larger colony size was associated with higher adult survival when *X. mulga* was present in mature colonies.

Materials and methods

Life history and behavior of Dunatothrips and Xaniothrips

Species in the genus *Dunatothrips* create domiciles using a silk-like anal secretion, which is used to either enclose several phyllodes or create a tent-like structure on a phyllode surface. Several species of *Dunatothrips* exhibit facultative pleometrosis, whereby colonies are initiated by two or more females (Morris et al., 2002; Crespi et al., 2004). In at least two species, *D. aneurae* and *D. skene*, males are also sometimes present at colony initiation, particularly when there are large groups of females. At some point before domicile construction is completed, females become dealate (shed their wings). When construction is finished, females remain within the domicile, feeding on plant cell contents and producing a brood that develops to adulthood inside. Preliminary evidence suggests that at least some of the adult brood may remain within their natal domicile, apparently breeding and helping to expand it along the phyllode surface (*D. aulidis* and *D. skene*), or via incorporation of new phyllodes (*D. aneurae*, *D. armatus*, and *D. vestitor*). Female offspring that stay in the domicile become dealate, while males remain winged and presumably disperse. Mature colonies comprise up to 50 individuals in some species. The mating system and social system of *Dunatothrips* species have yet to be elucidated, but there is no evidence of morphological or behavioral division of labor as found in the soldiers castes of some gall-inducing *Kladothrips* species (Crespi et al., 2004). In this study, we focus on *D. aneurae*, which occurs on its host *Acacia aneura* in the eastern distribution of the plant's range (Queensland, New South Wales, Northern Territory, and South Australia).

The domiciles of *Dunatothrips* are invaded by parasitic species in five genera of *Acacia* thrips: *Akainothrips*, *Advenathrips*, *Schwarzithrips*, *Vicinothrips*, and *Xaniothrips* (Crespi et al., 2004). In this study, we focus on interactions with the kleptoparasite *X. mulga*, the most common parasite of *D. aneurae* domiciles. Although we know little about how *X. mulga* gains entry to host colonies, this species, like other members of the genus, has enlarged lateral abdominal spines that presumably facilitate invasion (Crespi et al., 2004).

We found *X. mulga* in *D. aneurae* domiciles under a variety of circumstances. A single parasite female was most commonly found with *D. aneurae* foundresses that had immature brood. Foundress mortality in these colonies was much higher than that in free-living colonies, with all foundresses being dead in the majority of cases. Given this, we infer that foundresses are commonly killed by a single invading parasite female (Bono, unpubl. manuscript). Less commonly, the parasite was found dead in these colonies; this could result from foundress aggression, but because this was relatively uncommon we cannot definitively rule out other causes. We also found the parasite cohabiting with the host, typically in older colonies where *D. aneurae* brood had reached maturity. These colonies often included more than one *X. mulga* adult, which are assumed to be the offspring of the original invader. Finally, in a smaller number of cases, we found the parasite alone in domiciles constructed by the host, but with no host adults present.

Collections

We collected *D. aneurae* domiciles from *A. aneura* host plants at sites in South Australia and New South Wales, Australia. *Dunatothrips aneurae* colonies are initiated throughout the year, but founding events appear to be synchronized around environmental cues such as rainfall. Thus, collections from a single population, or even a single tree, may include colonies at all stages of development, but they are generally organized into distinct cohorts.

We collected thrips by removing intact domiciles from plants and placing them into tubes with 20% dimethyl sulfoxide (DMSO)/saturated NaCl solution. We opened domiciles under a dissecting microscope and counted the number of adults of each sex that were alive and dead and the number of eggs, larvae and pupae. Because thrips were preserved prior to censusing colonies, we considered individuals to be dead when bodies were not fully intact or clearly desiccated. Although by using this method we may have failed to detect individuals who had died only recently, it nonetheless provides an unbiased, conservative estimate of mortality. For colonies that had been invaded by *X. mulga*, we counted the number of *Dunatothrips* adults of each sex (alive and dead), and the number of parasite adults of each sex (alive and dead).

To calculate the frequency of confounding we followed the methods of Morris et al. (2002) by excluding colonies with adult brood from the analysis (i.e. those with alate females). These colonies were excluded because it was not possible to distinguish the original dealate foundresses from any newly emerged adults that may have shed their wings and remained in the domicile.

Data analysis

To evaluate whether pleometrosis was a consequence of high foundress densities and/or a lack of suitable nest sites, we examined whether average group size (log-transformed) was positively correlated with the number of foundresses on the host plant (estimated by counting the number of foundresses belonging to immature colonies), or with the number of mature colonies on the host plant (which would also reduce available nesting sites). We used multiple linear regression with foundress number, number of mature colonies, and an interaction term as predictors. Non-significant terms ($\alpha=0.10$) were eliminated from the model starting with the interaction. We excluded trees from the analysis that had less than two immature colonies.

To assess whether females associated randomly, we used a chi-square test to compare the frequency distribution of foundress numbers with expectations from a zero-truncated Poisson distribution (Cohen, 1960), which assumes that associations are random. To avoid having cells with expected values of less than three, we pooled foundress classes with low expected values (Krebs, 1989). Because of sample size limitations, we were only able to perform this analysis on two trees from two different sites.

Brood production

We used linear regressions to determine whether foundress number influenced total brood production (transformed to $\log(\text{total brood}+1)$) and per capita brood production ($\log(\text{per capita brood}+1)$). We excluded from this analysis new colonies whose foundresses had not commenced laying eggs, colonies in which the foundress number could not be determined, and colonies that were parasitized.

Foundress survival

To test whether foundresses in groups had higher individual survival than solitary foundresses, we used a G-test of independence with Williams' correction to compare the proportion of foundresses that were alive in multiple vs. single foundress colonies with developing brood. Colonies with adult brood and colonies with no brood were excluded from this analysis. This test included both parasitized and unparasitized colonies and therefore represented the overall survival probability of joint vs. solitary foundresses without differentiating among possible causes of mortality. To determine whether the former result could be primarily attributed to survival benefits of confounding in interactions with parasites, we then did separate analyses for parasitized and unparasitized colonies.

Because vulnerability to successful invasion by *X. mulga* might be related to the number of foundresses in a colony, we used a G-test of

independence with Williams' correction to compare the proportion of pleometrotic colonies that were parasitized to that for single foundress colonies. We calculated these proportions using only data from trees that were infested with *X. mulga*. In addition, we used Fisher's exact test (sample sizes were low) to compare the proportion of colonies in which the *X. mulga* invader was dead in single vs. multiple foundress colonies.

Benefits of larger colony size

Because colonies initiated by more than one female were larger than single foundress colonies, we tested whether larger colony size provided an advantage in interactions with *X. mulga* when the parasite was present in older colonies with adult brood (i.e. colonies with alates). Specifically, we used linear regression to determine whether the proportion of *D. aneurae* adults that were alive in these colonies was positively correlated with colony size (number of *D. aneurae* adults alive and dead), and Spearman rank correlation to assess the relationship between the proportion of *X. mulga* individuals surviving and *D. aneurae* colony size. Young colonies with no adult brood were excluded from this analysis because benefits of increased brood production are assumed to result after offspring have reached maturity. In addition, we excluded several colonies that were invaded by more than one species of parasite (some colonies were invaded by *X. mulga* and up to two other parasite species).

Results

We collected a total of 348 colonies from seven locations in South Australia and New South Wales, Australia (Table 1). Of these colonies, 27% were parasitized by *X. mulga*. We could identify the original foundresses in 185 colonies, of which 30% were initiated by more than one female (Range 1–8; Fig. 1A). Overall, more than half of all foundresses (57%) were involved in associations. Average group size was independent of the number of foundresses on a host plant and the number of mature colonies on a host plant (multiple linear regression, all terms eliminated; $\alpha=0.10$). For the two trees that we analyzed, foundresses did not appear to associate ran-

Table 1. Summary collection data showing the percentage of *D. aneurae* colonies that were pleometrotic and the percentage that were parasitized by *X. mulga*. Sample sizes for column one represent all colonies collected at a particular site, while sample sizes given in column two are for colonies where foundress number could be determined. NSW = New South Wales; SA = South Australia

Site location (N)	% pleometrotic colonies (N)	% parasitized
1. 60 km S of White Cliffs, NSW (3)	50 (2)	0
2. 45 km S of White Cliffs, NSW (13)	67 (9)	0
3. 92 km SW of White Cliffs, NSW (130)	38 (60)	29
4. 10 km W Mutawintji NP, NSW (67)	15 (40)	43
5. 132 km N of Port Augusta, SA (53)	41 (29)	2
6. 5 km N of Glendambo, SA (52)	21 (28)	29
7. 1 km S of Glendambo, SA (30)	12 (17)	37

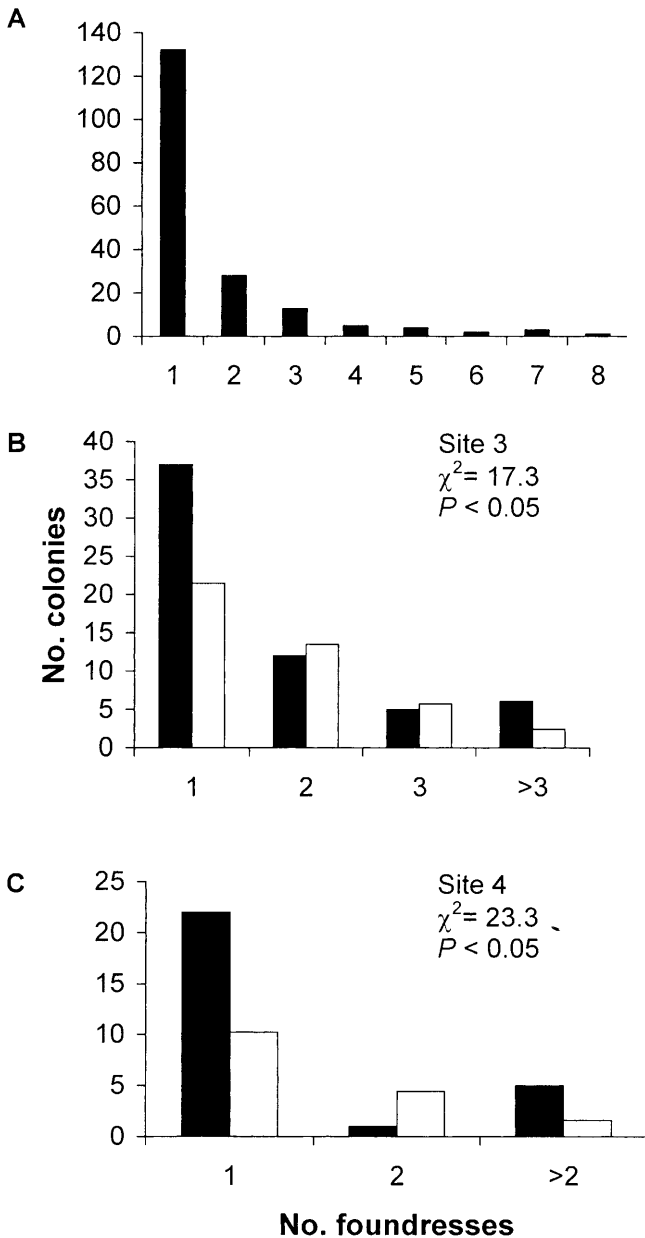


Figure 1. The distribution of foundress numbers per nest (dark bars) for (A) all colonies, and individual trees from site three (B) and site 4 (C). Open bars in (B) and (C) represent expectations derived from a zero-truncated Poisson distribution.

domly, as higher than expected values were observed for single foundress colonies and for colonies with large numbers of foundresses (tree from site 3, $\chi^2 = 17.3$, $P < 0.05$, Fig. 1B; tree from Site 4, $\chi^2 = 23.3$, $P < 0.05$, Fig. 1C).

Brood production

Total brood production increased with foundress number for *D. aneurae* (linear regression, $P = 0.02$, $R^2 = 9\%$, $N = 61$; Fig. 2A), but per capita brood production de-

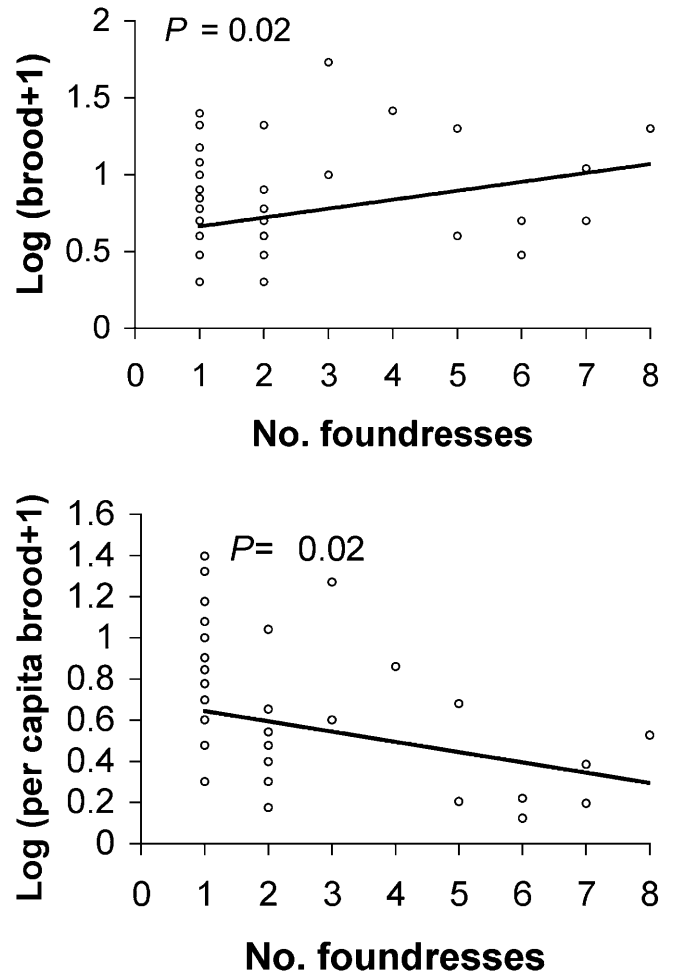


Figure 2. The relationship between the number of foundresses and (a) total brood production, (b) per capita brood production for *D. aneurae* colonies.

creased (linear regression, $P = 0.02$, $R^2 = 8\%$, $N = 61$; Fig. 2B). Thus, while colony founding by multiple females generally resulted in larger colonies overall, average foundress productivity was reduced.

Foundress survival

Individual foundresses in associations had higher survivorship than single foundresses (G-test of independence; $G = 5.66$, $P = 0.02$; Table 2). This did not reflect higher survival of joint foundresses in interactions with *X. mulga* (G-test of independence; $G = 0.291$, $P = 0.59$; Table 2), but rather was explained by higher survivorship in non-parasitized colonies (G-test of independence; $G = 4.21$, $P = 0.04$; Table 2).

There was no difference in the proportion of single vs. pleometrotic colonies that were invaded by *X. mulga* (G-test of independence; $G = 0.258$, $P = 0.61$). Moreover, there was no difference in the proportion of single vs.

Table 2. Survivorship of *D. aneurae* foundresses for haplometrotic and pleometrotic colonies. *P*-values are from G-tests of independence with Williams' correction.

Colony Class	% dead haplo (N)	% dead pleo (N)	<i>P</i> -value
All colonies	40.0 (65)	22.4 (98)	0.02
Parasitized	70.0 (20)	61.9 (21)	0.59
Unparasitized	26.7 (45)	11.7 (77)	0.04

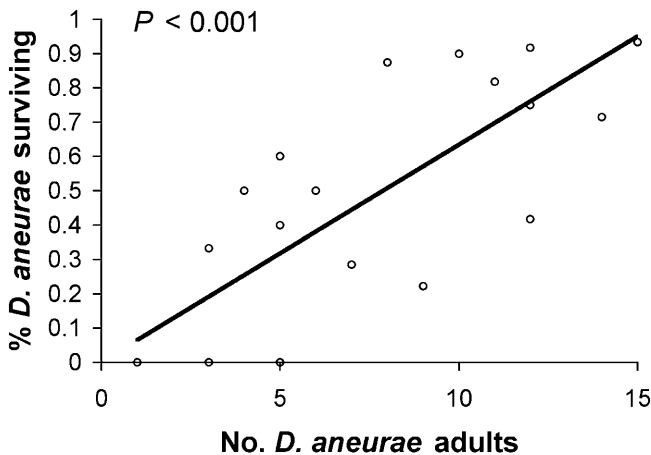


Figure 3. The relationship between the size of *D. aneurae* colonies and the percentage of adults that were alive in colonies where *X. mulga* was cohabitating with the host.

pleometrotic colonies in which the *X. mulga* invader was found dead (Fisher's exact test; $P=0.55$).

Benefits of larger colony size

There was a strong positive correlation between colony size and the percentage of *D. aneurae* adults surviving in mature colonies with the parasite present (linear regression; $P < 0.001$, $R^2 = 53\%$, $N = 20$; Fig. 3). There was not, however, a significant correlation between parasite mortality and *D. aneurae* colony size (Spearman rank correlation, $P = 0.77$, $N = 20$).

Discussion

In this study, we provide the first analysis of the costs and benefits associated with pleometrosis for Australian *Acacia* thrips. Our data suggest that foundresses did not join associations simply in response to ecological constraints such as a limited availability of nesting sites. While our inference is limited to some degree by a lack of information on the actual number of nesting sites available on each tree, several lines of evidence seem to support this conclusion. First, we did not find a significant positive relationship between average group size and the number of foundresses or the number of mature colonies on the host plant, both of which would be expected under

a nest-site limitation scenario. Second, for those host plants that we analyzed, the frequency distribution of foundress numbers did not conform to a random distribution, further suggesting an alternative explanation for this behavior. Finally, on some trees pleometrosis occurred when foundress numbers were low enough that nest-site limitation was almost certainly unlikely. For example, on one tree we found 13 foundresses total, yet only two of these initiated a domicile independently. Given the size of the host plant and number of phyllodes (trees can exceed three meters in height), it seems unlikely that these foundresses were constrained by a lack of suitable nesting sites.

We identified two contexts in which pleometrosis provided an advantage for foundresses. First, during the early stages of colony development foundresses that formed associations showed increased survivorship compared to solitary foundresses. Interestingly, this effect was evident only in unparasitized colonies; in parasitized colonies individuals in groups and solitary females suffered similarly high mortality rates. Although we have yet to identify the mechanisms leading to the survival advantage for individuals in groups, one possible explanation is that cofoundresses share the energetic burden of constructing a domicile, ultimately resulting in increased longevity. Females use a considerable amount of a silk-like anal secretion to build an enclosure, which probably represents a significant energetic cost. Moreover, during the initial stages of construction foundresses face a high risk of desiccation and predation because they are exposed to an extremely arid desert environment, and ants are common on the host plant. Working in groups may reduce these costs if multiple females construct a domicile more rapidly and/or individual energetic investment declines with group size. Similar benefits of group nesting have been proposed for bees and wasps that dig burrows in arid environments (McCorquodale, 1989; Wcislo, 1997), and for mites that also build a silken enclosure (Saito, 1997). This hypothesis is, of course, predicated on the fact that all foundresses contribute to the construction of a domicile. Although we know that groups form before domicile construction is complete, we have no data on the relative contributions of individual foundresses to the creation of the enclosure.

Higher foundress survivorship has also been identified as a benefit favoring pleometrosis for some ants (Waloff, 1957; Mintzer, 1987; Jerome et al., 1998; Johnson, 2004) and wasps (Tibbetts and Reeve, 2003). In these cases there is a clear link between foundress survival and fitness; ant queens reproduce continually over the course of their lifetime so longevity and fitness are positively correlated, and, for wasps, foundress survival is critical because offspring must be provisioned throughout development. Here, we show that joint-nesting *D. aneurae* females survived longer through the period when brood was developing, but we cannot, at this point, definitively link this to a fitness advantage. Because *D. aneurae* offspring are not provisioned during development, found-

dress survival after egg-laying might not be essential to offspring survival. Nevertheless, without adults present the brood may suffer higher predation or parasitism, as has been demonstrated for mass provisioning bees (Eickwort et al., 1996; Smith et al., 2003; Soucy et al., 2003). Moreover, brood would be particularly susceptible to ant predation or desiccation if the domicile was damaged, and without adults present there would be no way for damage to be repaired.

Although our results show that in parasitized colonies individual survivorship was not enhanced for foundresses in groups, pleometrosis may provide other advantages in this context. For example, though the effect was not statistically significant, *X. mulga* was found dead in a higher percentage of pleometrotic colonies than in colonies with a single foundress (28.5%, N=7 vs. 10.5%, N=19). Clearly, small sample sizes limited power in this analysis, and the potential link between *X. mulga* mortality and foundress number deserves further investigation.

While we did not identify clear benefits of pleometrosis in interactions with *X. mulga* early in colony development, this behavior did provide an advantage for colonies in which the parasite was found cohabiting with adult *D. aneurae* brood. Like Morris et al. (2002), we found a positive correlation between brood production and foundress number. Here, we show that this increase in colony size for pleometrotic colonies is important because survival of *D. aneurae* adults was positively correlated with colony size when *X. mulga* was present in mature colonies.

Larger colony size resulting from pleometrosis is apparently one of the primary adaptive benefits for many ant species that exhibit this behavior (Rissing and Pollock, 1987; Tschinkel, 1992; Adams and Tschinkel, 1995; Choe and Perman, 1997; Bernasconi and Strassmann, 1999; but see Pfennig, 1995; Brown, 2000). Colonies started by multiple females in these species become large more rapidly, which results in superior competitive ability in aggressive interactions with conspecifics. For thrips, the reason why larger colony size leads to increased survival in parasitized colonies remains unclear. We found no evidence to suggest that this effect was attributable to better defense in larger colonies, as survival of the parasite did not correlate negatively with colony size. Other possible explanations are that there is a dilution effect in larger colonies, or that *X. mulga* adopts a less aggressive invasion strategy in larger colonies.

The fact that pleometrosis is facultative in *D. aneurae* suggests that the advantages of this behavior are balanced by costs or constraints. Indeed, our results show that group formation is reproductively costly for some foundresses, as it results in lower average brood production. Although Morris et al. (2002) found no relationship between the number of foundresses and per capita brood production for *D. aneurae*, sample sizes in their study were much smaller, and thus statistical power was limited. Per capita brood production is probably lower in groups

because of limits imposed by the finite size of domiciles. While larger groups could theoretically construct larger domiciles, foundresses are likely constrained by the location and position of surrounding phyllodes (Morris et al., 2002).

Lower per capita brood production in groups is not uncommon for other social insects, being documented in bees, ants, and wasps (Michener, 1964; Tschinkel and Howard, 1983; Clouse, 2001), though Clouse (2001) points out potential problems with calculating this accurately. Without knowing the relatedness of *D. aneurae* cofoundresses and the degree of reproductive skew in these colonies, it is difficult to interpret our findings other than to say that at least some individuals suffer reproductive costs. For example, if there is high skew in these colonies than fecundity of a dominant female might actually be enhanced, while other members of the association have reduced reproductive output. Current work aimed at elucidating the social structure and degree of reproductive skew in *D. aneurae* colonies will help clarify the nature of reproductive costs associated with joint-nesting for these insects.

Our results have shown that pleometrosis provides direct benefits to *D. aneurae* foundresses both early and later in colony development. These benefits are counterbalanced by costs or constraints such as lower productivity for some foundresses, which may help to explain why this behavior is facultative. Future studies that elucidate the mating and social systems of *Dunatothrips* should clarify the links between behavior, demography, and fitness in this genus, and provide a novel comparative database for understanding the evolution of pleometrosis.

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