Behav Ecol Sociobiol (2011) 65:1499–1504
DOI 10.1007/s00265-011-1159-5

ORIGINAL PAPER

Active and effective nest defence by males in a social apoid wasp

Eric R. Lucas · Jeremy Field

Received: 11 November 2010 / Revised: 6 January 2011 / Accepted: 18 February 2011 / Published online: 3 March 2011

Abstract Altruism in the social Hymenoptera is generally considered to be a feature of females rather than males. A popular explanation for this is that in the solitary ancestors of today's social species, males provided little brood care. Males might therefore lack the preadaptations necessary to evolve altruism in social contexts. While anecdotal observations of male contributions to colony life have been reported, there are few reports of male participation in nest defence. In apoid wasps, there have been several reports of male nest-guarding behaviour in solitary species, potentially setting the evolutionary stage for similar behaviours in social lineages. Here, we present evidence of active and effective nest defence in males of the social apoid wasp *Microstigmus nigrophthalmus*. Males were observed chasing intruders away from the nest, and the presence of males had a significant effect on nest survival when females were removed. Males potentially obtained direct benefits through defence, so that defence may not represent male altruism. However, our results do show that males can perform acts that benefit their colony.

Keywords Male altruism · Sociality · *Microstigmus* · Crabronidae

Introduction

The order Hymenoptera is striking for its number and diversity of social taxa, as well as for the extreme adaptations associated with sociality in some of these taxa. With very few exceptions, however, social altruism in the Hymenoptera is found in females rather than males, contrasting strongly with some other social insects such as termites (Wilson 1971) and thrips (Crespi 1992).

This notable absence of altruism on the part of males has been attributed to several factors. The absence of male brood care and key behavioural suites such as hunting, even in solitary species, may have precluded males from being able to help on the nest in an efficient way (West-Eberhard 1975). Similarly, the absence of a sting in males makes it more difficult for them to help in nest defence (Starr 1985). Furthermore, the haplodiploid sex determination characteristic of the Hymenoptera may act to create relatedness asymmetries that favour sib rearing by females more than males (Hamilton 1972; Bartz 1982), or to promote the spread and fixation of sib-rearing alleles to a greater extent in females than males (Reeve 1993).

There are a few exceptions to this rule of exclusive female altruism. Males performing tasks on the nest, apparently for no personal gain, have been observed in a handful of species. In several polistine wasps, males sometimes perform tasks typically associated with females, such as provisioning of larvae and nest maintenance (Steiner 1932; Pardi 1977; Hunt and Noonan 1979; O'Donnell 1999; Sen and Gadagkar 2006). The instances of brood rearing never involve observations of the males returning to the nest with forage. Rather, it appears that they receive solid food from foraging females and pass it on to the larvae. In other taxa, male bumblebees may engage in energetic fanning to help control the temperature of the brood, though it is not clear that this is necessarily an altruistic behaviour (Cameron 1985), and male larvae provide silk used in nest construction in the weaver ant (Wilson and Hölldobler 1980).

Communicated by R. Moritz

E. R. Lucas (✉) · J. Field
School of Life Sciences, University of Sussex,
John Maynard Smith Building,
Brighton BN1 9QG, UK
e-mail: e.r.lucas@sussex.ac.uk

Although the idea that males do not engage in altruistic social behaviour because they lack the required pre-existing repertoire of behaviours remains an appealing one, their abilities are not so limited that they should be incapable of providing any helpful contributions (West-Eberhard 1975). Observations of male behaviour in some solitary species may give us some insight into what we can expect from males in related social taxa. In the solitary apoid wasp *Trypoxylon monteverdeae*, for example, males help in the construction of the nest, though they do not forage for nesting material (Brockmann 1992). Occasional anecdotal examples have also been presented of males playing a part in nest defence (Peckham 1977; Coville and Coville 1980; Brockmann 1980, 1992). Most of these studies include observations of males actively defending the nest, indicating that benefits are not simply a cost-free by-product of the male's presence.

Nest defence is therefore one area in which it might be expected that males could play a role in social species. Although the lack of a sting would make them less effective than females at fighting off large intruders (Starr 1985), mere physical presence and aggression can be enough to ward off at least small invaders. Particularly in small colonies, where the nest is frequently left with no females, either temporarily or because of the death of all resident females, active male defence could enhance brood survival.

Evidence of male defence in the social Hymenoptera is, however, scarce. In *Polistes dubia*, Steiner (1932) reports that males sometimes inspect individuals landing on the nest and will remove dead flies, placed on the nest, in a similar way to females. Houston (1970) describes what appears to be a male soldier caste, complete with morphological adaptations for nest defence, in an Australian halictine bee. Unfortunately, neither study presents evidence that males really do attack intruders or that they have a positive effect on nest survival. In the case of the apparent soldier caste for example, it seems more likely that this in fact represents a polymorphism of mating strategies, rather than a defensive caste (Wilson 1971; Kukuk and Schwarz 1988; Danforth 1991). To our knowledge there has as yet been no evidence of active and effective nest defence by males in any social species of Hymenoptera.

In several group-living species of apoid wasps, such as *Trypoxylon fabricator* and *Spilomena subterranea*, it has been documented that males are often nest residents (Melo 2000). *Microstigmus nigrophthalmus*, for example, nests in small groups of one to six females and is attacked mainly by parasitoids of small size that might potentially be chased away by a male. It is not rare for a nest to be temporarily left devoid of females. In these cases, males remaining on the nest could have a positive influence on nest survival. Furthermore, *Microstigmus* represents an origin of social behaviour independent of the commonly studied bees and vespid wasps (Matthews 1991), and may therefore display behavioural traits markedly different from what has been observed in other taxa. *M. nigrophthalmus* is therefore a good candidate for exploring the possibility of male nest defence. Here, we present an investigation into whether males of *M. nigrophthalmus* engage in active and effective defence of their nest.

Methods

Background to study species

Within the superfamily Apoidea, the most advanced forms of sociality are found in the Apidae (the bees). The rest of this superfamily, termed the apoid wasps, consists primarily of solitary species, though group-nesting species have been recorded in several lineages (Melo 2000). *Microstigmus* and its sister genera, which together form the Spilomenina (Menke 1988), represent the apoid wasp lineage in which the most advanced forms of sociality have been found (Matthews 1991). *Microstigmus* Ducke (Crabronidae) is a neotropical genus of apoid wasps characterised by a method of nest construction in which adult females fix organic material such as bark or leaf fibres in a matrix of silk which they produce. *M. nigropthalmus*, our study species, builds its nests under the leaves of trees in the forest. Though around half of the *M. nigrophthalmus* nests at our study site contained only one adult female, nests can contain up to six adult females and up to eight adult males, with up to 13 brood cells in use at any time (Lucas et al. 2011).

Field methods

Field work was conducted at the Mata do Paraiso, Viçosa, Minas Gerais, Brazil (20°48′ S, 42°51′ W), from 27 March 2008 to 11 September 2008. This field site is a reserve of inland Atlantic forest (Oliveira-Filho and Fontes 2000), covering around 200 ha at approximately 600–700 m elevation, belonging to the Universidade Federal de Viçosa.

M. nigrophthalmus builds spherical nests using a mixture of silk produced by the adult females and pieces of external material such as wood or bark. These nests are around 1–2 cm in diameter and hang by a silk petiole from the underside of leaves. There is a single entrance at the top of the nest, where it connects with the petiole.

Nests were found by searching the underside of leaves in the forest. Behavioural observations were performed by videoing nests using Sony DCR SR32E digital camcorders placed approximately 30 cm away from the nest and positioned so that the entrance faced the lens as much as possible. Nineteen nests were observed, and total observation time for each nest ranged from 31 to 87 h, over a period of 4–11 weeks. Seventeen of these nests have been reported on in a previous study (Lucas et al. 2011). The remaining two had not been included in the previous study as they were subjected to an experimental pilot study, which involved removing one leg from each adult female for DNA analysis. Wasps were marked with enamel paint for use in other studies (Lucas et al. 2011). Nests and their entire contents were collected after nightfall to ensure all wasps were on the nest. Adults and brood were stored by killing them in 100% ethanol.

Experimental manipulation

We investigated whether the presence of males had a positive effect on nest survival in the absence of females. On 10 nests, adult females were removed, but not adult males. These 10 nests are referred to as “treatment” nests. As a control, all adults of both sexes were removed on a further 10 nests, which are referred to as “control” nests. Initial number of adult males and adult females in each nest, as well as the general area in which the nest was found, was recorded (Table 1). Removals were performed in pairs comprising one treatment and one control nest, for which removals were performed on the same days. Pairs were also matched as much as possible for initial number of adult females. We matched for number of females rather than males because this is a reflection of the number of foragers in the nest and therefore, potentially, of the nutritional state of the brood at the moment of removal. If the presence of males has a positive effect on nest survival, then nests in the treatment group should show higher survival than those in the control group.

Adults were removed by placing a small sealable plastic bag around the nest and tapping the leaf from which it was suspended, thus encouraging its inhabitants to leave and become caught in the bag, then using a pooter to remove any remaining individuals. This was repeated twice a day for two consecutive days on each nest to maximise the chances that all individuals were removed (with the exception of one pair where nests were checked for three consecutive days, with three checks per day for the last two days).

In order to keep track of the number of males on treatment nests, captured males were marked on their thorax with a single spot of enamel paint and then immediately released back next to or onto the nest. Markings were performed under a binocular microscope, using fine-meshed marking cages.

Nests were collected 14 days after the removal events and their contents recorded. The purpose of the experiment was to determine whether males were effective in nest defence, rather than maintenance, so nests were recorded as “intact” if they still contained brood, even if the brood had starved. Nests were recorded as “attacked” if all brood cells were empty, or if they contained parasitoid brood.

Statistical analysis

Statistical analyses were performed in R (R Development Core Team 2008). A generalised linear model with binomial errors and a logit link function was performed on the data from the removal experiment. Treatment type (treatment or control), pair number and nest location were included as categorical explanatory variables. The number of males and females in the nest before removal were included as continuous explanatory variables. We did not consider that a sample size of 20 (10 for each of treatment and control) was sufficient to test for interactions between five potential explanatory variables, therefore only main effects were included in the model.

The maximal model was compared to each of the five models obtained by removing one main effect. The main effect that caused the smallest non-significant deviance in the model likelihood was removed. This was repeated until no more main effects could be removed without causing a significant deviance in likelihood.

Results

Anecdotal video observations confirm that males can display defensive behaviour, but rarely do so. Whenever at least one female was present in the nest when a potential intruder appeared, it was always a female that chased away the intruder. As all the nests that were videoed were nests that contained females, the only opportunities to observe an intruder arriving on a nest containing only males arose when all the females had left the nest. On only four occasions did an intruder arrive on a nest when only males were present. None of these occasions involved an intruder which is known to be a threat to *M. nigrophthalmus*.

On one of these four occasions, no male emerged from the nest. On another, a male did emerge, and the intruder left, but it was unclear whether the male was simply walking around the nest (a common behaviour in both males and females of this species), unaware of the intruder's presence. On the other two occasions however, the male made clear darts towards the intruder, causing it to leave. One of these latter two occasions has already been reported in a previous paper (Lucas et al. 2011). The intruder on one of these occasions was a small fly. On the other, the quality of the video is less good and it is harder to identify the insect, but it also appears to have been a small fly.

Pedigrees for adult nestmates and brood in the nests subjected to behavioural observations were available

Table 1 Summary of the removal experiment showing, for each nest, the value of each of the five explanatory variables included in the model (columns 2–5) and the result after 2 weeks (column 6)

Nest	Treatment type	Pair i.d.	Fem	Mal	Location i.d.	Status after 2 weeks
N438	Control	1	1	1	1	Intact
N354	Treatment	1	1	1	2	Intact
N373	Control	2	1	1	2	Intact
N456	Treatment	2	1	1	1	Intact
N329	Control	3	2	4	3	Intact
N349	Treatment	3	1	2	3	Intact
N451	Control	4	1	1	1	Intact
N309	Treatment	4	2	1	2	Attacked
N493	Control	5	4	1	4	Intact
N498	Treatment	5	4	4	4	Intact
N324	Control	6	1	1	4	Intact
N515	Treatment	6	2	2	4	Intact
N284	Control	7	4	3	3	Attacked
N288	Treatment	7	4	1	3	Attacked
N399	Control	8	2	2	2	Attacked
N289	Treatment	8	1	2	3	Intact
N487	Control	9	3	1	4	Intact
N491	Treatment	9	4	2	4	Intact
N285	Control	10	4	1	3	Attacked
N464	Treatment	10	4	1	1	Intact

Fem number of females in the nest before removal, *Mal* number of males in the nest before removal

from a previous study (Lucas et al. 2011). On both the occasions where a male was seen actively defending the nest, he was found to be related to the brood in the nest: he was either the father or the son of the mother of the brood, but it was not possible to distinguish between these hypotheses, as both predict the same pattern of genetic similarity. The males could therefore have been the grandfathers or brothers of the brood which benefited from their defence.

Removal experiment

Treatment type was found to have an effect on nest survival. Of the 10 treatment nests, 9 were found to still contain brood on collection. Of the 10 control nests, only 6 were found to still contain brood. The results for each nest are given in Table 1. Of the five nests that were found to have been attacked, three contained an adult parasitoid, along with parasitoid pupae or parasitoid larvae feeding on the *M. nigrophthalmus* brood, one contained an adult parasitoid but was otherwise empty and one was empty, with no brood of any kind inside.

After model simplification, the final model retained only treatment and pair as explanatory variables. Removing either of these caused a significant deviance in the likelihood of the model (deviance=8.32, $df=1$, $p=0.004$ and deviance=19.96, $df=9$, $p=0.02$ respectively). This model was also significantly better than the null model, in which no explanatory variables were included (deviance=22.49, $df=10$, $p=0.01$). We note, however, that neither treatment nor pair on its own significantly improved the null model (deviance=2.53, $df=1$, $p=0.11$ and deviance=14.18, $df=9$, $p=0.12$ respectively). Only when both are combined does their inclusion become significant.

Discussion

Video observations revealed that males can chase away intruders while the nests' resident females are away. Furthermore, experimental removal of adults shows that the presence of males does affect the probability of a nest's survival: in the absence of females, nests on which adult males remained survived better than those on which they were removed. Males of *M. nigrophthalmus* are therefore capable of active nest defence, and have a positive effect on nest survival when females are absent. This could be of importance in two situations. First, even in multi-female nests of this species, all resident females can sometimes be away at the same time, so that none of them would be able to defend the nest should an intruder arrive. Particularly in single-female nests, in which the nest must be regularly left unattended by the female in order for her to forage, the presence of males on the nest could affect brood survival. Second, if all the females present on a nest disappear, they leave their brood at the mercy of parasitoids. Although males would almost certainly not be able to raise immature larvae to adulthood, any post-provisioning brood such as prepupae and pupae that require only time to develop could see their chances of survival to adulthood significantly increased by the presence of adult males.

To our knowledge, this study provides the first evidence of a positive effect of male defence on nest survival in the Hymenoptera. Social altruism in male Hymenoptera is generally considered to be extremely rare, and several potential explanations have been put forward to explain this (Hamilton 1972; West-Eberhard 1975; Bartz 1982; Starr 1985; Reeve 1993). Though *Microstigmus* represents an origin of social behaviour independent of other Hymenoptera, most of these arguments apply to it.

An important question, therefore, is whether observed nest defence can be considered altruistic. On both occasions where we saw males defending, they were related to the brood in their nest, so males can obtain inclusive fitness benefits from their actions. However, is it possible that direct benefits alone could suffice to explain the defensive behaviour?

We have noticed that males often remain in nests that have been totally abandoned by females, to the extent that the nests are empty and damaged to the point of near destruction (Lucas et al. 2011). These nests contain no brood, so nest defence is clearly not the reason why males stay put for such a long time. The most likely explanation seems to be that these males continue to look for matings throughout their lives and that these bedraggled nest remnants provide the safest base available to them. In this case, the males have an interest in keeping the nest safe regardless of the survival of its contents. If the benefit to the male in terms of long-term direct reproductive success is greater than the cost of nest defence, then the behaviour cannot be considered altruistic.

The cost of nest defence is probably relatively small. Among the 19 nests mentioned here, we observed adults (male and female) defending their nest a total of seven times. We have also seen this behaviour 11 times on nests observed for other purposes. In all cases, the defending individual did not appear to be injured. The only cost to nest defence therefore appears to be energetic. It seems very possible that this cost is not sufficient to outweigh the risk of losing a safe haven and having to spend nights exposed to predators.

A final question we can address is that of why male defence has not been observed before in other species. Of importance here is the fact that *Microstigmus* is an apoid wasp, and that sociality in this group has been very little studied. Male persistence in nests has been found in many apoid wasps, both social and solitary, although sometimes apparently for the purpose of mate guarding (Peckham 1977; Coville and Coville 1980; Brockmann 1992; see Melo 2000 for notes on the social species). It is therefore tempting to conclude that the pre-existing potential for male nest residence and defence in apoid wasps facilitated the evolution of defensive behaviour in a social species.

Another contributing factor could be the different threats faced by many of the large colony social bees and wasps compared to *Microstigmus*. Starr (1985) points out that large colonies suffer greatly from predation by large vertebrates, which may be deterred by the painful sting which females can deliver, but that small groups like those of *Microstigmus* rather tend to be threatened by insects, which can be deterred without a sting (but see Kukuk et al. 1989). In the study of social insects, a disproportionate amount of attention has focused on species with relatively large colonies, in which males may be ineffective at defence.

Alternatively, the fact that males seemed to defend only when females were absent may be important. Most of the well-studied groups of social bees and vespids are large by the time that males emerge, and nests are therefore rarely abandoned by all females simultaneously. If male defensive behaviour occurs only in the absence of females, it would not be observed in these species.

Conclusion

We have shown that males of *M. nigrophthalmus* engage in active and effective nest defence. This result must nevertheless be considered with caution. As males appear to benefit from having a nest within which they can stay, ensuring that they do not lose the one they have may provide sufficient direct benefits to explain the defensive behaviour without having to invoke altruism.

Further research into male defensive behaviour in the Hymenoptera should concentrate on small groups in which females may at times all simultaneously be away from the nest, and should focus on threats from small attackers which can be deterred without the use of a sting. The majority of social groups in apoid wasps are small, and as there is evidence that males of apoid wasps can be active in nest-related activities, we suggest that this group be the focus of such investigations.

Acknowledgments Specimens were collected under the CNPq Scientific expedition Processo EXC 014/07-C. Rogerio Parentoni was of great help in obtaining permits. Goumercindo Lima kindly allowed us access to the Mata do Paraiso field site. Lucio Campos first introduced us to the field site and gave helpful advice. Jonathan Macedo was invaluable in the field. Og De Souza provided great support in Brazil. Genotyping was performed at the NERC Biomolecular Analysis Facility—Sheffield with the help of Terry Burke, Gavin Horsburgh, Deborah Dawson and Andy Krupa. We thank two anonymous referees for the useful comments on the manuscript. This work was supported by the Natural Environment Research Council (UK) PhD studentship.

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