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Assured fitness returns in a social wasp with no worker caste

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The theory of assured fitness returns proposes that individuals nesting in groups gain fitness benefits from effort expended in brood-rearing, even if they die before the young that they have raised reach independence. These benefits, however, require that surviving nest-mates take up the task of rearing these young. It has been suggested that assured fitness returns could have favoured group nesting even at the origin of sociality (that is, in species without a dedicated worker caste). We show that experimentally orphaned brood of the apoid wasp *Microstigmus nigrophthalmus* continue to be provisioned by surviving adults for at least two weeks after the orphaning. This was the case for brood of both sexes. There was no evidence that naturally orphaned offspring received less food than those that still had mothers in the nest. Assured fitness returns can therefore represent a real benefit to nesting in groups, even in species without a dedicated worker caste.

Keywords: assured fitness returns; insurance-based advantages; cooperative brood care; origin of sociality; *Microstigmus*

1. INTRODUCTION

To understand the evolution of animal societies requires understanding the selective pressures that determine the levels of cooperation and antagonism between conspecific individuals in a range of contexts. The decision to nest in reproductive groups is a critical first step towards the evolution of any society of organisms. Much attention has therefore focused on understanding what causes selection to favour nesting independently or in groups [1].

Hamilton's [2,3] concept of inclusive fitness provides a theoretical framework within which to pose explanations for the evolution and maintenance of social behaviours. What is still lacking, however, is a full understanding of the evolutionary history of selective pressures that have led to the origins of traits such as group living, cooperative brood care and reproductive division of labour. In other words, under which combinations of ecological conditions and life-history traits will Hamilton's rule be satisfied for these behaviours? One factor that may promote group living is the idea of assured fitness returns [4]. In order to obtain a return on its reproductive investments, an individual that nests solitarily must survive until its offspring are no longer dependent on it for their survival. If the individual dies before its offspring have become independent, the offspring will also die and the individual's fitness will be zero. In contrast, an individual that contributes only partially to raising young in a social group will not have wasted its investments when it dies, provided the surviving adults can complete rearing the offspring through to independence. This safeguard reduces the fitness cost of death, and therefore also allows individuals to engage in more risky, but potentially more rewarding, strategies [5]. The longer the brood are dependent on the continued presence of the adult for survival, the greater the potential advantages of this insurance. In progressive provisioning species, which have an extended period of brood dependence, assured fitness returns may therefore be especially important [6].

There are well-supported examples of assured fitness returns in social groups with dedicated workers, such as the hover wasp *Liostenogaster flavolineata* [7] and the paper wasp *Polistes dominulus* [8]. However, Queller [9] argued that assured fitness returns could also have been important in the origin of social behaviour, when dedicated workers are not present (Queller considered the origin of workers, and therefore a situation in which the focal individual has no offspring of its own, but the same arguments apply to an individual that does have offspring). So far, there is little empirical evidence to support this.

In communally nesting species, where reproductively active individuals share a nest without a dedicated worker caste, there is evidence of assured fitness returns in the form of defence: orphaned brood that no longer require active care, such as feeding, may still be defended against predators by surviving adults [10,11]. Evidence of assured fitness returns in the form of continued brood provisioning has been presented in some progressively provisioning bees, either among co-foundresses [12] or among offspring females who remain in their natal nest [13–17]. None of these studies, however, combined a thorough genetic analysis of maternity with direct observation of brood care in the form of foraging. Such an analysis has, to our knowledge, not yet been conducted in vertebrates or insects without dedicated workers.

The existence of offspring not belonging to any female present upon nest collection is not sufficient to conclude that care of orphaned brood is occurring. It is possible that the mother of the orphaned brood had only recently died, so that the brood are in fact destined to starve or be fed to other brood. Alternatively, the mother may simply

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have been absent when the nest was collected. To demonstrate the potential for assured fitness returns, it must be shown that individuals remaining in the nest after a female's death continue to provision her brood, or brood that she had been caring for. It must also be shown that such care is provided by individuals other than the female's own offspring. If care of orphaned brood is performed only by the daughters of the dead female, then an individual would still have to survive until her daughters reached adulthood before orphaned brood would be cared for. This would put her in the same position as a solitary foundress.

Microstigmus Ducke is a little-known genus of neotropical apoid wasps, characterized by their construction of nests from an amalgam of natural building materials and silk produced by the adult females [18,19]. In *Microstigmus nigrophthalmus*, nests contain up to six females and the brood is provisioned progressively with Cicadellidae nymphs, so that larvae require active parental care until they reach pupation [19,20]. As in all Hymenoptera, foraging is performed exclusively by females. Almost all adult females are mated and have developed ovaries [19]. Cooperative brood care occurs in this species, but there is no worker caste [21,22]. *Microstigmus nigrophthalmus* is therefore a good candidate for investigating the role of assured fitness returns before the origin of a worker caste. Here, we test the hypothesis that orphaned brood continue to be provisioned by surviving adults in *M. nigrophthalmus*.

2. METHODS

(a) *Field site and study species*

Fieldwork was conducted on a population of *M. nigrophthalmus* from the Mata do Paraiso, a reserve of Brazilian Atlantic forest belonging to the Universidade Federal de Viçosa (Viçosa, Minas Gerais, Brazil; 20°48′ S, 42°51′ W), from 27 March 2008 to 11 September 2008. Nests, which hang by a silk petiole from the underside of leaves, are roughly spherical and around 1.5–2 cm in diameter, with a single entrance in front of the petiole leading into the nest chamber. The bottom half of the sphere contains the brood-rearing cells, which open upwards into the nest chamber.

(b) *Unmanipulated nests*

Thirty-two nests containing at least one adult female were collected and their contents recorded. These were nests used in two other studies [21,22], and included nests on which adults had been paint-marked for individual recognition. Eggs and larvae were recorded as having been provisioned if prey was found in their cell. Collections were performed after nightfall to maximize the chances that all females had returned to the nest. No nests were collected when it had been raining before nightfall, as rain could have prevented individuals from returning to their nests. Adults and brood were preserved in 100 per cent ethanol.

(c) *Forager removal experiment*

Eleven additional nests containing at least two adult females were chosen for this experiment. Two of these nests had originally contained only one female, but were chosen for inclusion in the experiment after a second female emerged. The sample size was restricted because nests of this species are not found in large aggregations, and around half contain only one female [21]. As the purpose of the removal experiment was to demonstrate the existence of a behaviour (feeding of orphaned brood) rather than to quantify it, a small sample size is suitable.

On each nest, all adult females were marked using dots of enamel paint on the thorax [21]. The marking procedure cannot guarantee the capture of all females, and unmarked females were later observed on several nests. Each nest was video-recorded for 2 days, for around 6 h each day, using a Sony DCR SR32E camcorder mounted on a tripod. On one nest, filming time was cut short by rain (details of filming times are given in the electronic supplementary material). Foragers were identified as individuals seen returning to the nest with prey items. It should be noted that some foragers may not have been foraging during the observation periods, or may have returned to the nest from a direction that made it impossible to observe the contents of their mandibles.

On each nest, the female seen returning with prey most frequently was then permanently removed. Because foraging females are often the mothers of brood in the nest (around 75% of foragers are mothers, compared with 55% of all females [22]), this method maximized our chances of capturing a mother, which we could later confirm by genotyping (see §3*b*). Removals were performed in two ways. The first involved putting a small sealable bag around the nest and gently tapping the leaf from which it was suspended, causing most of the occupants to leave the nest into the bag. If the targeted forager was not caught in this way, a pooter [23] was used to remove any remaining nest inhabitants. The removed forager was placed in 100 per cent ethanol and all other individuals were replaced on the nest.

Eight out of the 11 nests were video-recorded again 4–5 days after the forager was removed. If foraging was observed and at least two items of prey were brought back, the nest was collected that night. If fewer than two foraging events were observed in the whole day, the nest was left for a further 4–5 days. This sequence was repeated for a maximum of two weeks, after which the nest was video-recorded and collected regardless of whether foraging was observed. The three remaining nests were simply left for two weeks and then collected on the final day. Further details are given in the electronic supplementary material.

(d) *Molecular work and genotyping*

Maternity and relatedness were analysed using microsatellite markers Mni001–003, Mni005, Mni007, Mni008, Mni011–014, Mni016, Mni019, Mni020, Mni023, Mni027–035, Mni038, Mni042–044, Mni047, Mni048 and Oni001 [24]. DNA was extracted and amplified using the methods described by Lucas *et al.* [21]. PCR products were analysed using an Applied Biosystems 3730 sequencer at the NERC Biomolecular Analysis Facility—Sheffield (NBAF-S; Sheffield, UK). Alleles were scored using the software GENEMAPPER v. 3.7 from Applied Biosystems.

(e) *Maternity analysis*

The software KINGROUP [25] was used to assign offspring to their mothers [21]. A few relationships were assigned indirectly; for example, if individual 1 was assigned as the daughter of individual 2 and as the full-sister of individual 3, then individual 3 would be assigned as the daughter of individual 2 as long as this relationship was not itself significantly rejected. In order to be as conservative as possible, this indirect method was not used in the forager removal experiment. In the case of one full-sib offspring group from the forager removal experiment, two larvae were assigned as the daughters of a particular female, but the third was incompatible with this hypothesis. In order to make the experiment more conservative, none of this sib-group was classed as offspring of the female.

In the Hymenoptera, males are haploid and females are diploid. Brood were therefore sexed according to their homozygosity [21]. The software RELATEDNESS v. 5.0.8 [26] was used to calculate life-for-life relatedness [27] of adult females to orphaned brood, which is the genetic value of the brood to the females. Standard error values were generated by jack-knifing over nest and over loci. As it was not possible to know which female had provided prey to any given larva, the value of each larva to just the female that provisioned it could not be determined. Therefore, for each larva belonging to the removed forager, we calculated its genetic value (relatedness) to each remaining female, and considered only the largest of these values, which we call r_m. This value is the maximum estimate of the relatedness of the foraging female to the orphaned larva that she provisioned.

(f) *Foraging for orphaned brood*

For the 32 nests that were not used in the forager removal experiment, we calculated the proportion of eggs and larvae that had prey in their cells when the nest was collected, both for brood whose mothers were collected along with the nest and for brood that had apparently been orphaned. Brood that were ambiguously assigned as the offspring of a female on the nest were not included in the analysis. Multiple eggs are sometimes found in the same cell, but only one can survive to the larval stage [19,24]. If all the eggs in a shared cell could be placed in the same category (assigned to a mother or orphaned), then the cell contents were counted as one egg. Otherwise, all eggs in this cell were excluded from the analysis.

For the 11 nests used in the forager removal experiment, we examined whether any larvae that were found to belong to the removed forager had prey in their cells. As even small larvae of this species commonly consume prey in less than 5 days (E. R. Lucas 2008, personal observation), we could confidently assume that any provisioned larvae had received their prey since the removal event, and had therefore been provisioned by one of the females remaining in the nest.

3. RESULTS

(a) *Unmanipulated nests*

It was not uncommon to find eggs or larvae that could not be assigned as the offspring of any female in the nest but which, upon collection, were found to have prey in their cell. Out of 32 nests, 12 contained eggs or larvae that could not be assigned to any resident female. In five of these nests, some of the apparently orphaned brood were found with prey in their cells. Overall, 8 out of 29 (31%) apparently orphaned eggs and larvae were found with prey in their cell, compared with 33 out of 89 (36%) for larvae whose mothers were present in the nest when it was collected. This difference was not significant ($\chi^2 = 0.87$, d.f. $= 1$, $p = 0.35$).

The mean relatedness of orphaned brood to adult females was, for female brood and male brood, respectively, 0.43 (s.e. by nests = 0.06, s.e. by loci = 0.025, $n = 39$ female offspring from 19 nests) and 0.25 (s.e. by nests = 0.04, s.e. by loci = 0.023, $n = 24$ male offspring from 12 nests).

Table 1. Details of the larvae identified as daughters of the removed forager. *T*, number of days between initial forager removal and final nest collection; fem, number of females present on nest collection; LNA, number of larvae not assigned as offspring of removed female; r_m, maximum relatedness of adult females remaining on the nest to the orphaned larva (see §2*e*); *L*, 95% confidence interval for r_m generated by jack-knifing over loci; F, female; M, male.

nest characteristics				orphaned larvae characteristics		
nest	*T*	fem	LNA	sex	r_m	*L*
N2	15	2	1	F	0.42	±0.22
N3	14	5	1	F	0.21	±0.34
N5	5	1	2	M	0.12	±0.19
				F	0.49	±0.29
				M	0.20	±0.18
N8	9	2	2	F	0.33	±0.25

(b) *Forager removal experiment*

Brood that had been orphaned by the removal of their mother from the nest continued to be provisioned by females remaining on the nest. In 4 out of the 11 nests, we found such larvae with prey in their cells (table 1). Of these four nests, one (N2) belonged to the group that was left unobserved for two weeks before collection. The other three were monitored and collected when foraging was observed (N5 and N8) or after two weeks because no foraging was confirmed (N3).

Two of the remaining seven nests contained brood that were assigned as the offspring of the removed forager but did not have prey in their cells upon collection. Both nests contained other provisioned larvae that probably belonged to the removed forager, but had not been classed as such owing to the measures taken to make the test more conservative (see §2*e*). A further two nests contained no brood that were offspring of the removed forager, one contained no brood at all, one contained a provisioned larva for which genotype data are not available and one contained no adult females.

Provisioned orphaned larvae could be of either sex and their estimated relatedness to the females that fed them was low in several cases (table 1), though the confidence intervals are large. In three out of four nests, none of the remaining adults was the daughter of the removed forager; in the fourth nest, the removed forager and remaining female may have had a mother–offspring relationship, but other relationships could not be significantly rejected.

In one nest (N5), only one female remained after the removal event, so that it must have been she that was foraging for the orphaned brood. This female had her own offspring developing in the nest. She had therefore provisioned brood left behind by the removed female, despite having her own brood to care for at the same time.

4. DISCUSSION

In *M. nigrophthalmus*, several individuals in a nest may reproduce simultaneously and it is often the breeders themselves that forage [22]. When a female dies, remaining adults may therefore have their own offspring to care for, and might not continue caring for the orphaned brood. We have shown that this is not the case. Orphaned larvae of both sexes continue to be cared for by surviving group members, even when the surviving females are not the daughters of the removed female and when the surviving females have their own brood. Furthermore, orphaned larvae are provisioned as often as the rest of the brood.

In species in which a dedicated worker caste provides brood care, evidence for assured fitness returns requires that a worker's efforts result in augmented brood size even in the event of her death [7,8]. If this were not the case, then the worker's efforts would be wasted. In *M. nigrophthalmus*, a foraging female's own offspring are cared for in the event of her death. It is therefore not necessary for her efforts to have had a lasting effect on overall brood size in order to have had a positive effect on her fitness. The remaining brood now include her own offspring and is therefore on average more genetically valuable to her than if she had not joined the nest (though mean relatedness of adult females to brood in their nest is about 0.5, that of male brood is only around 0.34 [21]). In effect, the female's legacy is to have replaced larvae less related to herself with her own offspring.

The frequent occurrence of brood with no assigned mother on the nest is convincing evidence that orphaning is frequent in this species, and that assured fitness returns are therefore likely to have important consequences for an individual's fitness. The high mean relatedness of motherless brood to nest-mate adult females suggests that most or all were orphans of a previous nest resident rather than offspring of conspecific intruders, for which we have no evidence. Nevertheless, direct evidence for assured fitness returns requires quantification of the consequences of death, in terms of inclusive fitness, for individuals in cooperative groups with alloparental care. Our finding that females care for orphaned brood strongly suggests that death will have less negative consequences for females in groups than for lone females. We therefore consider that our data provide powerful, though indirect, evidence for assured fitness returns in *M. nigrophthalmus*.

We found that females provide for larvae even when they are not closely related. A probable explanation is that *M. nigrophthalmus* females cannot assess their relatedness to individual larvae. Kin recognition systems in social insects tend to involve recognizing nest-mates [28], but there is little evidence that individuals can directly estimate their relatedness to individual nest-mates [29,30]. It seems more likely that females simply care for all brood in the nest because their mean relatedness to the brood is sufficiently high to make caring advantageous. *Microstigmus nigrophthalmus* females could remember the cells in which they lay their own eggs, but even this may not be straightforward, as cells can be shared by as many as four eggs, though only one egg ever survives [19,24]. A female may therefore not even be certain that the cells in which she laid contain her offspring. This may also explain why foragers of *M. nigrophthalmus* provision orphaned and non-orphaned brood equally.

To our knowledge, this study provides the first experimental evidence that assured fitness returns, in the form of active brood care by non-daughters, exist in species without a worker caste, and therefore that they may provide an important selective pressure in the evolutionary origin of group-nesting. However, it is unlikely that *M. nigrophthalmus* is rare or unique in this respect. Similar effects are likely to exist, for example, in allodapine bees. In natural nests of *Exoneura nigrescens*, there is evidence that two-female nests from which one female disappears produce more offspring than nests in which there has always been one female [12]. Genetic studies of kinship in social insects with no worker caste are currently rare, making it difficult to ascertain whether orphaned brood are indeed being cared for. Our genetic analysis not only allowed us to demonstrate that orphaned brood are fed by remaining adults, but also to provide evidence that there is no discrimination on the part of these carers between orphaned and non-orphaned brood.

Although *M. nigrophthalmus* is a progressive provisioner, the majority of *Microstigmus* species are mass provisioners: each cell is fully provisioned before the egg is laid (e.g. *Microstigmus comes* [31]); orphaned brood therefore do not need further provisioning by surviving females, though they may still need defending. In group-living taxa related to *Microstigmus*, mode of provisioning is also variable [32,33]. Assured fitness returns can occur in mass provisioners [11], but are likely to be more important in progressive provisioners, where offspring remain dependent on active care for a longer period of time [6]. In order to address whether assured fitness returns have been important in the origin of social nesting, a phylogeny will be required, including the related solitary taxa, on which group size and mode of provisioning can be mapped. The *Microstigmus* lineage may be ideal for this purpose. Assured fitness returns provide a significant fitness benefit only when there is a high probability that parents will die before they are able to completely rear their offspring. In vertebrate societies, the issue of assured fitness returns has so far been largely neglected, perhaps owing to the relatively low mortality rates found in vertebrate social groups [7,34]. In the Hymenoptera, however, assured fitness returns arguably represent the best-documented ecological benefit of helping in primitively eusocial taxa [7,8,11,13]. Our findings suggest that assured fitness returns can operate at the origin of sociality [9].

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