Reproductive Caste Performs Intranidal Tasks Instead of Workers in the Ant *Mystrium oberthueri*

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Abstract

Division of labour improves the efficiency of animal societies. Efficiency is further improved in many social insects where morphologically specialized adults perform different tasks. In ants, the wingless worker caste performs non-reproductive activities and sometimes exhibits multiple phenotypes when requirements between brood care and expert foraging diverge. *Mystrium rogeri* from Madagascar is a specialist predator on large centipedes, and the worker caste is highly polymorphic in size. In contrast, *M. oberthueri* has only large workers. The replacement of the queen caste by wingless intermorphs much smaller than workers explains this evolutionary shift in *M. oberthueri*. Many intermorphs occur in each colony but only a few mate and reproduce. In order to determine their contribution to non-reproductive tasks, we performed multivariate analyses on behavioural data recorded by scan sampling from four *M. oberthueri* colonies in the laboratory. In unmanipulated colonies, workers and intermorphs exhibited two distinct behavioural profiles. Workers focused on guarding and foraging, while intermorphs performed brood care and nest cleaning, regardless of whether they reproduced or not. This pattern of polyethism where the reproductive caste completely takes charge of some non-reproductive tasks is novel, as confirmed by our observations of one colony of *M. rogeri* where non-reproductive tasks were restricted to workers, as in most ants. When isolated from one another, *M. oberthueri* workers and intermorphs developed less distinctive behavioural patterns. Some workers cared for the brood, but the intermorphs could not hunt because of their small mandibles. Such plasticity in polyethism at the colony level confers the ability to react to unexpected changes, including variable proportions of workers and intermorphs.

Introduction

Division of labour (polyethism) is a characteristic of many animal societies that enhances the fitness of the group. Indeed, repeating a specific task improves individual performance and reduces the time wasted at switching tasks (e.g. in honeybee workers: Seeley 1982). Moreover, helping relatives to rear their brood when direct reproduction is not an option benefits both helpers and reproductives (e.g. when nesting sites are scarce in birds: Koenig & Stacey 1990; when lone founding is rarely successful in *Ropalidia* and *Polistes* wasps: Reeve 1991; Premnath et al. 1994). Age polyethism, where only older individuals perform dangerous activities outside nests, limits the mortality of young individuals (e.g. in honeybee: Huang & Robinson 1996).

In most ants, the various non-reproductive tasks needed for group survival (brood care, nest construction and foraging) do not require conflicting morphological specializations. All members of the worker caste can perform all tasks, and in many species workers exhibit little morphological variability. Although polyethism is generally based on age, workers can readily switch between tasks, if needed (Tripet & Nonacs 2004). A minority of ant species have highly specialized foraging or predation, and this introduces an incompatibility between the morphological requirements of tasks carried out inside and outside the nest. This can lead to the evolution of either continuously polymorphic workers or discrete worker subcastes. For instance, in *Atta sexdens*, dwarf workers tend the fungus gardens while large workers harvest plant material (Wilson 1980a). Because adults are predetermined for a specific task and cannot switch, colonies gain in efficiency but lose in task plasticity, although this is buffered by large colony size (Gautrais et al. 2002).

Mystrium ants (subfamily Amblyoponinae) are a fine illustration of the severe constraints placed on worker morphology by very specific prey requirements. Predation on large centipedes requires long and strong mandibles that can hold these fast-moving arthropods before they are stung between the segments (as found in *Amblyopone*: Gotwald & Lévieux 1972; Masuko 1993). In *M. rogeri* from Madagascar, workers are very polymorphic with large individuals having mandibles and head muscles appropriate for such skilled hunting, while small individuals have slender mandibles appropriate for handling brood (Molet et al. in press). Surprisingly, *M. oberthueri* has only large workers. However, in contrast to *M. rogeri* colonies that have a single large dealate queen that monopolizes reproduction, *M. oberthueri* colonies produce many individuals belonging to a reproductive caste smaller than workers, called intermorphs (Molet et al. in press). Only a few mate and reproduce but the others do not disperse, suggesting that their presence is beneficial to the colony.

In order to investigate whether the reproductive caste of *M. oberthueri* takes over some non-reproductive tasks that are usually restricted to workers in other species, we studied the pattern of polyethism between the two castes. We tested whether polyethism has changed relative to the strategy exhibited by *M. rogeri* (basal species as revealed by a molecular phylogeny of the genus; B. Noonan & B. Fisher, pers. comm.). Furthermore, we experimentally isolated the two castes to examine whether workers remain capable of performing the complete range of non-reproductive tasks. We analysed how behavioural differences are linked to the specialisation of the mandibles of *Mystrium* workers. Finally, we discuss the benefits brought by the intermorphs in *M. oberthueri*.

Methods

We collected four *M. oberthueri* colonies (11, 6, 16 and 20 workers, and 25, 18, 12 and 18 intermorphs, respectively) and one *M. rogeri* colony (30 workers and one dealate queen) in a primary rainforest in Madagascar (Parc National de Marojejy: 14°26′12″S, 49°56′30″E, altitude 450 m). In the laboratory, colonies were maintained in plaster nests with a glass roof that allows behavioural observations. The nests were kept humid at 25°C. Colonies were given live mealworms (*Tenebrio molitor*, Tenebrionidae) every 2 d as prey. These were well accepted although centipedes are the most commonly observed prey in the field (B. L. Fisher, pers. comm.). All the individuals in each colony were marked with paint dots. Two of the *M. oberthueri* colonies were not manipulated in order to study the natural behaviour of both workers and intermorphs. The two other *M. oberthueri* colonies were split into two artificial groups: one containing only workers and brood, the other having only intermorphs and the same number of brood. This setup allowed us to assess the behavioural plasticity of either caste in the absence of the other. Thus there were four different categories of individuals: 'unmanipulated workers', 'unmanipulated intermorphs', 'isolated workers' and 'isolated intermorphs'. Colonies that received similar treatments were pooled in this study because they exhibited similar responses, as confirmed by discriminant analyses and post hoc classifications of individuals that were 100% correct in unmanipulated colonies and 90% correct in isolated colonies. We did not perform the two treatments successively on each colony because this would have required keeping them in the laboratory for a much longer time, increasing the risks of mortality and colony decline. All intermorphs were dissected at the end of the experiment. Their ovaries were classified as undeveloped (infertile intermorphs) or developed with mature oocytes and yellow bodies that are evidence for oviposition (egg-laying intermorphs). The mating status of intermorphs was determined by checking whether the spermatheca was full.

In *M. oberthueri*, we recorded our behavioural data using the scan sampling method (Lehner 1996), during 5-min sessions (i.e. almost instantaneously) several times a day for 30 d. This allowed us to estimate the proportion of time spent on each type of

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behaviour by each individual. Preliminary observations led to a catalogue with 15 kinds of behaviours: rest in the periphery inside the nest (RP), walk in the periphery inside the nest (WP), activity outside the nest (AO) that includes foraging, rest near the brood (RM), walk near the brood (WM), self-directed behaviours like grooming and feeding (SB), egg care (EC), larva care (LC), pupa care (PC), grooming given to a worker (GW) or received (RW), grooming given to an intermorph (GI) or received (RI), nest cleaning (NM) and food handling inside the nest (HF).

As our data set was in a 15-dimensional space, we used multivariate analyses. First a correspondence analysis was performed, which makes no prior hypothesis about the category of each individual (e.g. Fresneau & Dupuy 1988). This method offers the most visually simplified yet accurate representation of our 15-dimensional data set in a two-dimensional projection. Thus we could examine whether unmanipulated and isolated individuals differ in behaviour. Then we performed a stepwise discriminant analysis, where our four categories are considered a priori (e.g. Cuvillier-Hot et al. 2004). This method maximizes the separation between the categories in a two-dimensional projection. It also statistically tests the classification of individuals in these categories and allowed for post hoc classification of *M. rogeri* workers and queen.

We also performed scan sampling on the *M. rogeri* colony to determine which tasks are performed by workers in a queenright species. The behavioural catalogue was the same as in *M. oberthueri*. Twelve workers emerged during our study, and thus we could determine whether the behaviour of individuals in this single colony was linked to their age (young workers = less than 30 d; older workers = emerged before field collection). We took dorsal pictures of *M. rogeri* workers under a stereomicroscope and measured their maximum head width with ImageJ (http://rsb.info.nih.gov/ij) to check whether individual size was correlated with behaviour. This was not necessary in *M. oberthueri* as the size variability of workers is much lower (M. Molet, B. L. Fisher, F. Ito & C. Peeters, unpubl. data).

Our behavioural data consisted of 81 scans performed on the two unmanipulated *M. oberthueri* colonies (11 workers and 28 intermorphs; six workers and 18 intermorphs), 86 scans performed on the two groups with isolated workers (17 and 16 workers) and 85 on the two groups with isolated intermorphs (19 and 11 intermorphs). We also performed 45 scans on the *M. rogeri* colony (40 workers and one queen). In total, 6679 behavioural acts were recorded. These numbers do not always match earlier mentioned colony sizes because some individuals died and others emerged during the experiment. Individuals that did not have enough records because they died early or emerged subsequently were excluded from the analyses. All analyses were performed with Statistica 7.1 (http://www.statsoft.com).

Results

Behavioural Profiles of Intermorphs and Workers

A correspondence analysis (Fig. 1) was performed on the behavioural data from both unmanipulated and isolated *M. oberthueri* colonies. The two axes showed distinct groups of tasks and individuals. The first axis accounted for 36.51% of the inertia and mainly separated behaviours performed in the periphery (inside the nest) or outside the nest, from behaviours performed near the brood in the center of the nest (social interactions, brood care and nest cleaning). The second axis accounted for 13.23% of the inertia and separated non-social behaviours (rest, walk) and social behaviours (including brood care). Unmanipulated workers and intermorphs were clearly separated by the first axis (Fig. 1a). Indeed, workers performed most of their activities in the periphery of the nest (defence) or outside (foraging), while intermorphs stayed near the brood and performed grooming, nest cleaning and brood care. In contrast, experimental isolation led to workers and intermorphs performing a wider range of tasks (Fig. 1b). They could not be distinguished from unmanipulated intermorphs or from one another, although they were distinct from unmanipulated workers. Interestingly, all egg-laying intermorphs in unmanipulated colonies, mated or virgin (4 and 0 in one colony and 0 and 1 in the other), had similar behavioural profiles. They exhibited a higher proportion of rest than infertile intermorphs (RP+RM: $72.4 \pm 14.0\%$ of time, $n = 5$, against $50.7 \pm 16.8\%$, $n = 41$; Mann–Whitney test: $U = 42.5$, $p = 0.034$) because of a decrease in social interactions (GW+RW+GI+RI: $0.5 \pm 1.1\%$ against $4.6 \pm 5.2\%$; $U = 42.5$, $p = 0.034$) and brood care (EC+LC+PC: $4.9 \pm 3.0\%$ against $15.6 \pm 12.7\%$; $U = 49$, $p = 0.059$). Proportion of time spent walking or cleaning the nest did not differ significantly (WM+WP: $5.7 \pm 6.6\%$ against $10.2 \pm 7.5\%$; $U = 52$, $p = 0.075$; NM: $1.5 \pm 2.2\%$ against $3.8 \pm 3.8\%$; $U = 62.5$, $p = 0.16$). The overall proportion of work time (EC+LC+PC+GW+GI+AO+NM+HF) was higher in infertile intermorphs than in egg-laying intermorphs ($22.9 \pm 15.3\%$

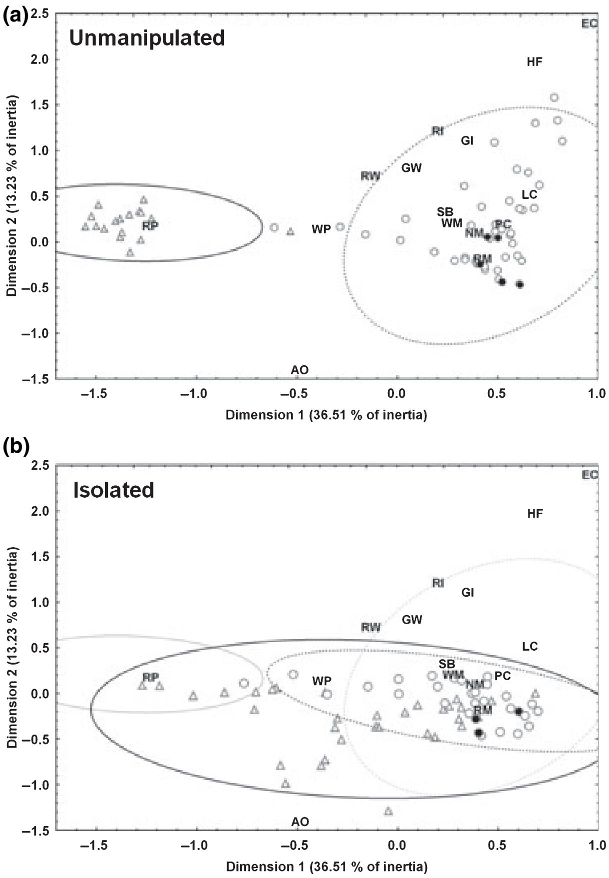

Fig. 1: Correspondence analysis of the behaviours of *M. oberthueri* individuals that were categorized a posteriori. Results are presented in two figures for more clarity, but they were obtained from a single analysis: (a) 16 unmanipulated workers (triangles), 46 unmanipulated intermorphs (circles); (b) 37 isolated workers (triangles) and 31 isolated intermorphs (circles). Ellipses are the 95% confidence limits. The ellipses of (a) are repeated in (b) in light grey. Spatial coordinates of the 15 behaviours are based on their frequency of occurrence in individuals. Reproductive intermorphs are solid circles. The 15 behaviours are: rest in the periphery inside the nest (RP), walk in the periphery inside the nest (WP), activity outside the nest (AO), rest near the brood (RM), walk near the brood (WM), self-directed behaviours like grooming and feeding (SB), egg care (EC), larva care (LC), pupa care (PC), grooming given to a worker (GW) or received (RW), grooming given to an intermorph (GI) or received (RI), nest cleaning (NM) and food handling inside the nest (HF)

against 6.4 ± 4.4%; U = 34, p = 0.016). As seen in Fig. 1a, b, egg-laying intermorphs did not change much in behaviour when comparing the unmanipulated and isolated situations.

Are Intermorphs and Workers Behaviourally Distinct?

We tested whether the four categories (unmanipulated workers and intermorphs, isolated workers and

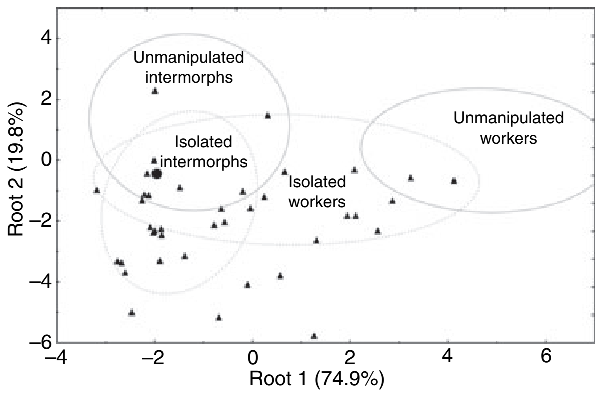

Fig. 2: Discriminant analysis of the behaviours of the same *M. oberthueri* individuals as in Fig. 1, but classified a priori into four categories: 16 unmanipulated workers, 46 unmanipulated intermorphs, 37 isolated workers and 31 isolated intermorphs. Only ellipses (95% confidence limits) are shown for more clarity: solid ellipses for unmanipulated setups and broken-lined ellipses for isolated setups. Two categories of *M. rogeri* individuals were then added to the projection: 40 workers (triangles) and one queen (circle)

intermorphs) could be mistaken for one another from their behavioural profile by performing a stepwise discriminant analysis (ellipses in Fig. 2). This generated three roots explaining all the variance (global model: Wilks' $\lambda = 0.063$, $F_{33,330} = 15.52$, $p < 10^{-4}$; root1: canonical $R = 0.90$, $\lambda = 0.063$, $\chi^2_{33} = 324.0$, $p < 10^{-6}$, 74.9% of variance; root2: $R = 0.74$, $\lambda = 0.348$, $\chi^2_{20} = 124.0$, $p < 10^{-6}$, 19.8%; root3: $R = 0.49$, $\lambda = 0.761$, $\chi^2_{9} = 32.2$, $p < 10^{-3}$, 5.3%). The model led to 81.0% correct classification of the individuals within the four groups. Unmanipulated workers and intermorphs formed two distinct and homogeneous groups, with 94.1% and 82.6% correct classifications, respectively. They were segregated by the first root of the discriminant analysis. Moreover, they were never mistaken for one another (a stepwise discriminant analysis including only these two groups yielded a 100% and 97.8% correct classification, respectively), although they often resembled isolated intermorphs or workers. A few isolated intermorphs (16.7%, including the three egg-laying intermorphs) continued behaving like unmanipulated intermorphs, although most of them (83.3%) behaved distinctly from unmanipulated workers and intermorphs. They were segregated from unmanipulated workers by the first root and from unmanipulated intermorphs by the second root. A few isolated workers (6.1%) continued behaving like unmanipulated workers, but some (9.1%) started behaving like unmanipulated intermorphs. Most of them (84.8%) behaved distinctly from

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unmanipulated workers and intermorphs. Isolated workers were segregated from unmanipulated workers by the first root and from unmanipulated intermorphs by the second root.

Time Budgets of Intermorphs and Workers

Finally we pooled intranidal behaviours in five categories that we considered as being meaningful relative to division of labour: rest (RP+RM), walk (WP+WM), social interactions (GW+RW+GI+RI), nest cleaning (NM), brood care (EC+LC+PC) and activity outside the nest (AO). We did not include food handling (HF) because it was rare (0% of time in workers, <1% of time in intermorphs), as well as self-directed behaviours (SB) because they are not related to polyethism. In unmanipulated colonies, workers spent more time resting than intermorphs (Fig. 3), while intermorphs spent more time cleaning the nest and caring for the brood. Workers' resting time decreased when isolated, because of an increase in brood care, nest cleaning and activity outside, while walking and social interactions did not change. Intermorphs' resting time did not change when isolated, because they increased time spent walking and decreased time spent in social interactions, while nest cleaning, brood care and activity outside did not change. The global consequence of isolating both castes was that workers compensated for the lack of intermorphs by performing both brood care and nest cleaning, while intermorphs compensated for the lack of workers by exploring the nest. Workers changed their behavioural pattern more than did intermorphs,

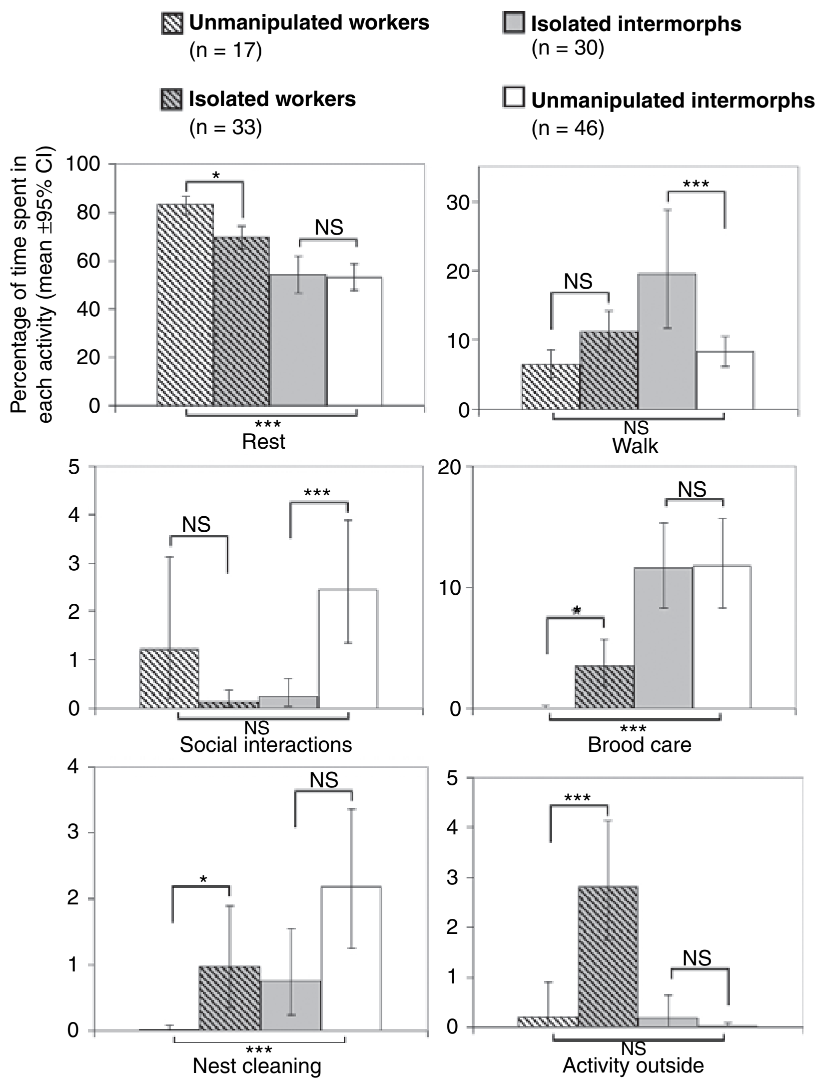

Fig. 3: Behavioural patterns of isolated *M. oberthueri* workers and intermorphs relative to unmanipulated individuals. Data were transformed using the function ArcSin$\sqrt{x}$ to ensure a normal distribution. Significance of the pair-wise *t* tests with Bonferroni correction is indicated with ***p ≤ 0.001; *p ≤ 0.05 and NS: p > 0.05

demonstrating a higher degree of behavioural plasticity. Intermorphs had a tendency to spend more time outside the nest when isolated although much less than workers, but they could not grab live mealworms so they had to be fed fresh pieces placed directly inside the nest.

Behavioural Profiles of *M. rogeri* Queen and Workers

We performed a post hoc classification of the *M. rogeri* workers and queen, using a stepwise discriminant analysis restricted to the unmanipulated *M. oberthueri* workers and intermorphs. According to their behaviour, 12 *M. rogeri* workers were classified as intermorphs, and 28 as workers (plotted in Fig. 2). The *M. rogeri* queen was classified as an intermorph with 100% probability. We examined whether the size of workers was correlated with their tasks, as in *A. sexdens* (Wilson 1980b). The head width of *M. rogeri* workers was not correlated with their coordinate on the first root (Pearson's correlation: $r = -0.036$, $n = 36$, $p = 0.84$). Knowing that this first root separates unmanipulated workers and intermorphs of *M. oberthueri*, this means that the head width of *M. rogeri* workers was not correlated with an intermorph-like or worker-like behaviour. Thus, bigger workers did not forage more than smaller workers, and the latter did not care for brood more than the former.

We assessed the link between age and behaviour in *M. rogeri* workers. The coordinates of the 12 young workers (<30 d) and 24 older workers on the first root were not different (t-test: $t_{34} = 1.02$, $p = 0.31$), and thus there was no evidence of age polyethism. Age polyethism is the general rule in ants (Hölldobler & Wilson 1990, Table 8-3; in Ponerinae: Peeters 1997). Our study of *M. rogeri* does not show this phenomenon although the results are insufficiently robust because of the observation of only one colony. We had selected a small colony (i.e. founded fairly recently: Molet et al. in press) to facilitate our behavioural study; division of labour may be more marked as colonies get larger. Moreover, some of the 'older workers' studied may have emerged a few days before field collection and thus this age category is heterogeneous. The experiment lasted 30 d, and young workers that emerged after field collection were accordingly older at the end, maybe even older than some of the 'older workers' at the beginning. Studies about age polyethism are not always consistent, e.g. Traniello (1978) did not detect age polyethism in the closely related *Amblyopone pallipes*, but Lachaud et al. (1988) did.

Discussion

Novel Polyethism in *M. oberthueri*: Intranidal Tasks Restricted to the Reproductive Caste

Mystrium rogeri exhibits a classical division of tasks between the fertile queen that only reproduces and stays near the brood, and the sterile workers that perform all other tasks, ranging from hunting to brood care. Although we did not find any behavioural difference between large and small workers in the laboratory, it is obvious that the latter cannot hunt as their mandibles are smaller than the centipedes. In *M. oberthueri*, winged queens have been replaced by intermorphs, of which a small proportion mate and reproduce while the others are infertile, similar to *M. 'red'* (Molet et al. in press). Intermorphs perform the intranidal tasks (such as brood care, grooming of nestmates and nest cleaning) done by workers in *M. rogeri*. Thus, intermorphs largely remain close to the brood. Even egg-laying intermorphs work, albeit at a lower rate than infertile ones. Workers stay in the periphery of the nest, with their mandibles generally pointing outwards (Fig. 4a). The nests of *M. oberthueri* are typically superficial, under stones, and lacking constructed walls, so workers could defend the nest using mandible snaps, a strong blow that pushes intruders

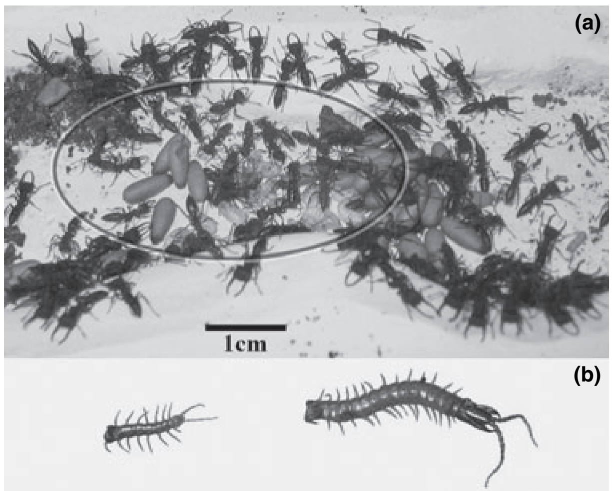

Fig. 4: (a) Laboratory nest viewed from above in the closely related *M. 'red'*. Intermorphs (smaller, mostly inside the ellipse) are always found in the center of the chamber, close to the brood, while workers stay in the periphery of the nest with their mandibles pointing outwards. (b) Fragments of centipedes found in a nest of *M. rogeri*, same scale as ants in (a). Intermorphs cannot capture such prey because of their reduced mandibles, unlike workers which have large toothed mandibles

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away and stuns them (Gronenberg et al. 1998), or biting. In the field, workers clearly performed such defence behaviours when we disturbed their colonies. Workers also forage outside the nest. The size and shape of their mandibles is adapted to hunt centipedes (Fig. 4b). The method used to kill mealworms in the laboratory was the same as that observed in the field with centipedes, and similar to that described in *Amblyopone silvestrii* (Masuko 1993). Workers grabbed this elongated prey with their enlarged mandibles, compressed it using their large mandible muscles (Paul & Gronenberg 1999) and stung it through the intersegmental membranes. Intermorphs, with their short slender mandibles and small heads that limit space for muscles, were not able to hunt. *Mystrium* intermorphs are the first case of a reproductive caste that takes charge of some tasks that are normally performed by workers. Casual observations suggest that all our results can be generalized to the two other *Mystrium* species (*M. mysticum* and *M. 'red'*) with intermorphs from Madagascar.

Plasticity in Division of Non-Reproductive Tasks

We found that when workers and intermorphs were isolated from one another, workers decreased their resting time in the periphery of the nest and spent time caring for brood and cleaning the nest. Some workers exhibited intermorph-like behavioural patterns, others remained worker-like, and some performed new combinations of tasks. Intermorphs started to explore the periphery of the nest and to exit the nest, but they never behaved like workers. They did not attack prey and had to be fed fresh pieces of mealworms. As workers cannot reproduce (Molet et al. in press) and intermorphs cannot hunt, the two castes are mutually dependent. The decrease in social interactions following isolation suggests that the presence of the two castes is important for the social dynamics in the colony. Although polyethism at the colony level is strict for reproduction and hunting, it is plastic for intranidal tasks. The proportion of intermorphs in field-collected *M. oberthueri* colonies can vary widely (from 36 to 75% of total adults, i.e. intermorphs and workers), but this may not affect colony efficiency dramatically because a shortage of either intermorphs or workers can be compensated by a switch in the behavioural pattern of the other caste. In ants, nurses have been observed to become foragers, and foragers can switch back to being nurses depending on colonial needs (Tripet & Nonacs 2004). Major workers can take over brood care in the absence of minors (e.g. *Pheidole pubiventris*, Wilson 1985; *Oligomyrmex*, Wilson 1986). Such plasticity is very important in small colonies where random events can lead to disequilibrium in caste ratios. For instance, in *Atta cephalotes*, small incipient colonies produce workers of intermediate size that can perform all tasks with an average efficiency (Wilson 1983). In the termite *Reticulitermes fukienensis*, workers of early instars can perform a wide range of tasks, including those that workers of late instars are specialized in, so incipient colonies with only young individuals are plastic (Crosland & Traniello 1997). Generally, large colony sizes favour a high specialization of individuals and a low plasticity in the tasks that they perform (Gautrais et al. 2002).

Influence of External Morphology on the Division of Non-Reproductive Tasks between Intermorphs and Workers

Intermorphs primarily evolved for reproduction and generally lack other morphological specializations. Many Myrmicinae intermorphs have the same external morphology as workers, and two behavioural studies showed that they perform the same tasks as workers, including foraging (in *Ocymyrmex foreli*: Forder & Marsh 1989; in *Eutetramorium mocquerysi*: Heinze et al. 1999). In contrast, *Mystrium oberthueri* intermorphs have small mandibles that make them unable to hunt centipedes and restrict them to a simplified behavioural repertoire that includes brood care. They are cheaper to produce than workers (relative to intermorphs in Myrmicinae) and yet efficient labourers. As intermorphs perform brood care, workers can focus on hunting, and larger individuals have well-adapted mandibles for this. These morphological specializations probably increase the efficiency of non-reproductive tasks.

Multi-purpose Reproductives Improve Colonial Economy

One characteristic common to all species with intermorphs is that they are produced in large numbers, even though most of them remain infertile. This apparent excess would be a waste in queenright species, where virgin queens that fail to found new colonies do not work. Young virgin winged queens and dealate queens do sometimes contribute to non-reproductive tasks in some species (Buschinger 1983; Fresneau & Dupuy 1988; Bourke 1991; Ito et al. 1996). However, they occur in small numbers relative to workers. Moreover, young virgin winged queens are only present in the colonies for a short period of the year to store metabolic reserves before the nuptial flight. In contrast, intermorphs in *M. oberthueri* do not disperse and benefit the colony for their entire lives by caring for the brood, grooming their nestmates and cleaning the nest, and even foraging in some myrmicine species. Intermorphs can also become reproductives whenever colony fission occurs. The replacement of winged queens by reproductively competent wingless adults that can double as labourers provides organizational plasticity, which can help compensate for small colony size or unpredictable environments (Forder & Marsh 1989). The gamergate strategy exhibited in ant species where all workers can mate (Peeters 1997) is an extreme case where all individuals are potential labourers and reproductives, thus providing the colony with maximal plasticity.

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