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FORAGING AND BUILDING IN SUBTERRANEAN TERMITES (ISOPTERA: TERMITIDAE): TASK SWITCHERS OR RESERVE LABORERS?

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Abstract Task-switching between foraging and building in workers of *Nasutitermes exitiosus* (Termitidae), a subterranean, mound-building termite, was investigated using mark-recapture. Foragers were collected from wood-filled drums and marked with Nile blue, whereas builders were collected from the mound by damaging it and collecting the termites that were undertaking repairs; these were marked with Neutral red. Two protocols were followed: the first marked foragers first and then damaged the mound; the second reversed this order, with up to eight drums sampled for foragers over 80 days. In the first protocol, the number of marked foragers that had switched tasks to building (blue-marked workers found in mound samples), was small compared with the number of blue-marked workers that remained foraging (0.7% cf. 1.8% of marked workers). The number of builders that had switched to foraging (red-marked workers found in the first drum sample) was also small in both the first and second protocols (0.3% of original number marked). The numbers of blue-marked foraging workers in drums decreased over time, whereas those for red-marked workers increased. The average decrease in blue-marked workers was ~1.5 workers (first protocol) and 0.5 workers (second protocol), the average increase in red-marked workers was ~2 workers (first protocol) and ~2.4 workers (second protocol). These results indicate that relatively few termite workers switch directly between foraging and building, but suggest that a pool of workers exists that could be directed readily to either task.
Key Words Termite, behaviour, *Nasutitermes exitiosus*

INTRODUCTION

The division of labor into different tasks and allocation of these tasks are central to the study of the organisation of social insect colonies. Workers in social insect colonies have many tasks to perform, such as caring for the reproductives and young, cleaning, foraging, including the search for new food and the collection of food from established sites, building and maintaining the nest, and defending the colony (Wilson, 1971; Michener, 1974; Oster and Wilson, 1978).

How tasks are allocated has been the focus of much study in the social Hymenoptera. Individuals choose their tasks according to internal factors, such as genetic response thresholds and hormone levels, and external factors, such as communication with other individuals and 'foraging for work' (Robinson et al., 1989, 1994; Gordon et al., 1992; Tofts, 1993; Franks and Tofts, 1994; Jeanne, 1996; Theraulaz et al., 1998; Gordon and Mehdiabadi, 1999; Beshers and Fewell, 2001). Furthermore, tasks may not be predictable. Allocation of sudden and urgent tasks have two hypotheses, the first suggests that workers switch from one task to another and the second suggests that colonies have a reserve of workers who are not active (Kolmes, 1985; Gordon, 1989, 1996; Johnson, 2002). Little task-allocation research has been performed on the Isoptera (Traniello and Rosengaus, 1997). There are similarities in social behaviours of isopterans and hymenopterans, but important differences also, such as development: termites are hemimetabolous, and therefore the younger immature instars can contribute to the tasks in the colony; whereas in contrast ants, bees and wasps are holometabolous and only the final 'adult' moult works. The lack of research in termites is due in part to the difficulty of studying insects that prefer closed spaces, total darkness, and still air with 100% humidity.

Mound-building termites present an opportunity to measure task-switching between two activities that can be observed and manipulated practicably in field experiments: foraging in artificial feeding stations and building damaged mounds. Mounds can be damaged unexpectedly, due to fire, tree fall or attack by large predators (e.g. aardvarks in Africa, echidnas in Australia or anteaters in South America). Individuals must be recruited to this building activity urgently, a situation which allows the testing of the task switching. Therefore, the aim of this study was to measure frequency of task switching behaviour between foraging and building in termite workers.

MATERIALS AND METHODS

Nasutitermes exitiosus (Hill) (Termitidae) was chosen for this study for four reasons. First, histological fat-stain markers are more reliable in *N. exitiosus* than in other species, due to lower mortality rates, longer marker persistence and no marker-transfer due to cannibalism (for a discussion see Thorne et al., 1996; Forschler and Townsend, 1996; Curtis and Waller, 1997; Evans, 1997, 2002; Evans et al., 1998, 1999). Second, the mound *N. exitiosus* builds is relatively soft but solid, so is easy to damage but the termites are protected from being crushed. Third, mound colonies of *N. exitiosus* were common near Canberra (35°17' S, 149°13' E, elevation ca. 800 m). Forth, echidna (*Tachyglossus aculeatus*, Mammalia, Monotrema) attacks on mounds are not uncommon in the area.

Testing Mound Damage Methodology

A damage-and-sampling procedure was devised and tested to measure the response of termites to experimental mound damage. Four mounds were chosen and damaged by sawing a wedge ca. 80 cm long and 30 wide (at the widest point) using a two-person, three metre long band saw. Cutting time was usually less then two minutes. The wedge (henceforth ‘undamaged wedge’) of mound material was solid and placed onto a tray easily, which was then put into a large plastic bag. The open section of the mound was covered with a plastic sheet and bricks, which was nailed to the mound to prevent entrance of ants or other predators and to maintain the elevated temperature and humidity inside the mound. The mound material wedge was returned to the lab, where the termites therein were separated (Gay et al., 1955). These termites were weighed and four reference samples of termites weighing 0.5 g were taken, which were used to determine the number of termites of each caste, with workers further separated into two size-classes, small (instars 1 and 2) and large (instars 3 to 5) (following Evans et al., 1998).

The broken-up mound-material from the wedge samples and the termites were returned to their mounds. The plastic covering the open section of the mounds was removed and the termites were released onto the open surface. After they had entered the mound, a stainless steel wire rack shaped appropriately was placed onto the open section of the mound, and the mound-material was placed on top. The plastic sheet was replaced over the mound-material and secured with nails into the mound. After three days, the plastic sheet was removed and the steel-rack was lifted from the mound, thus the repaired mound-material wedge (henceforth ‘damaged wedge’) and all the termites therein were collected in less than five seconds. The number and the proportions of termites in each size-class from the wedges were calculated as for the undamaged wedges, and then the number and proportion of each caste per kilogram of mound material, were compared using t-tests.

Task Switching Experiments

Task-switching between building and foraging was measured in two field experiments. Both experiments marked forager-termites (those were collected while foraging in bait-drums) with Nile Blue and builder-termites (those collected while building and repairing the mound wedge) with Neutral Red; in the first experiment the foragers were marked first and the builders were marked second, whereas in the second the reverse occurred (Figure 1; n.b. all drums were situated around and about 1.5 m from the mound-colony). The results from the two experiments were compared to determine whether the order of sampling had an effect on the results. Foragers were sampled from steel bait-drums (27 cm x 23 cm), filled with ca. 80 *Eucalyptus regnans* slats (0.7 cm x 5 cm x 24 cm) buried about 1.5 m from mound-colonies (as described in Evans et al., 1998) and builders were collected by cutting wedges from the mounds, as described above. All sampling of drums and mound-wedges occurred between 1200 and 1600 hours to minimise changes in termite numbers in drums due to daily foraging patterns. All drums were replaced immediately after their collection. 0.5 g reference samples were taken from every collection of termites from drums and mounds to assess whether castes responded differently.

In the first experiment (foragers first), the eight colonies chosen were sampled as above with the following changes (Figure1a). The experiment began for each colony when at least four of the eight bait drums dug around mounds were infested with foraging termites. The first bait-drum was collected (21-24 February), the termites therein separated and fast-marked with Nile Blue, and the blue-marked foragers returned to another infested drum around the mound. A second drum was collected between seven and 20 days later, the termites therein were separated and all blue-marked foragers were counted; this sample was used to calculate the average number of foragers that continued to forage under normal conditions. Mound-wedges were cut five minutes after the second drum was collected (2-16 March). The wedge was broken up immediately into chunks on large trays in the field, which were placed on a steel rack on the open cut in the mound, and a plastic sheet was secured over the top of the damage. It was hoped that this damage would affect task-decision making in foraging workers, drawing them from foraging into building and repairing the mound.

The third drum and the repaired mound-wedge were collected simultaneously three days later. If the mound damage was great enough, it was predicted that there would be relatively fewer foragers in the third drum, and that there would be blue-marked 'ex-foragers' that switched tasks to building the mound-wedge. The number of unmarked and blue marked termites in the first, second and third drums were compared using paired t-tests. The mound-wedge and the drum were taken to the laboratory and the termites therein separated. After all blue marked termites were removed and counted, the number of builder-termites was determined, which were fast marked with Neutral Red. The mound material and red-marked builders were returned to the open cut in the mound, and the blue-marked and unmarked foragers to a drum.

The forth, fifth, sixth and seventh drums (if applicable) were collected at intervals of seven to 19 days (last collected 26 May 2000). The termites were separated and red and blue marked individuals removed and counted and the number of unmarked termites determined. The numbers of blue-marked foragers found repairing the damaged wedges (one sample for four mounds, and 2 samples for two mounds) were used to estimate rate of task switching from foraging to building. The numbers of red-marked builders found in drums 4-7 were used to estimate the rate of task switching from building to foraging, and the number of blue-marked foragers found in drums 2-7 was used to estimate the rate of not task switching, or task-maintaining. The proportion of originally blue-marked foragers and red-marked builders were regressed over the duration of the experiment to estimate task switching over time.

In the second experiment (builders first), the six colonies chosen were sampled as above with the following changes (Figure 1b). The experiment began for each colony when at least three of the four bait drums dug around mounds were infested with foraging termites. Builder termites were sampled and 'fast-marked' with Neutral Red as described above (13 - 31 March). The first bait-drum was collected 14 days later; the termites separated, sorted and any red-marked 'ex-builders' that were now foraging were removed and counted. The unmarked termites were then 'fast-marked' with Nile Blue. All termites were returned to the field and placed into an infested drum.

The second, third and forth drums (if applicable) were collected at intervals of seven to 21 days after the first drum (last drums collected 12 May 2000). The termites separated, and all red-marked 'ex-builders' and blue-marked foragers were counted. The unmarked termites were weighed and 0.5 g reference samples taken. All termites were returned to the field after being sorted and counted. As for the first experiment (foragers first), the numbers of red-marked builders found in drums 1 - 4 was used to estimate the rate of task switching from building to foraging. The number of blue-marked foragers found in drums 2 - 4 estimated the rate of or task-maintaining. The proportional of originally blue-marked foragers and red-marked builders, were regressed over the duration of the experiment to estimate task switching over time (Sokal and Rohlf, 1995). The results for the first experiment (foragers first) and the second experiment were compared to detect whether there was an effect of marker precedence.

RESULTS

Testing Mound-Damage Methodology

The undamaged wedges weighed an estimated average of 9.2 ± 0.6 kg and contained 3,429 ± 266 termites and all castes were found in approximately equal numbers and proportions (Fig 2). This was in stark contrast to the 'damaged' and repaired wedges, although these were the same size (9.2 ± 1.1 kg, $t_6 = 0.001$, $P = 0.999$) there was an estimated average of 39,912 ± 7161 termites, roughly ten times as many, but there were no larvae at all and fewer total and relatively fewer smaller workers. The differences in number of termites per kilogram of mound material in the wedges were all significant: fewer larvae ($t_6 = 6.35$, $P < 0.001$) and small workers ($t_6 = 3.39$, $P = 0.015$) and more large workers ($t_6 = 4.80$, $P = 0.003$) and soldiers ($t_6 = 5.92$, $P = 0.002$) (Figure 2a). The change in proportion of each size class in the sample was also significant: proportionately fewer larvae ($t_6 = 2.72$, $P < 0.035$) and small workers ($t_6 = 3.31$, $P = 0.016$) and more large workers ($t_6 = 3.28$, $P = 0.017$); but the difference was not significant for soldiers ($t_6 = 1.65$, $P = 0.150$) (Figure 2b).

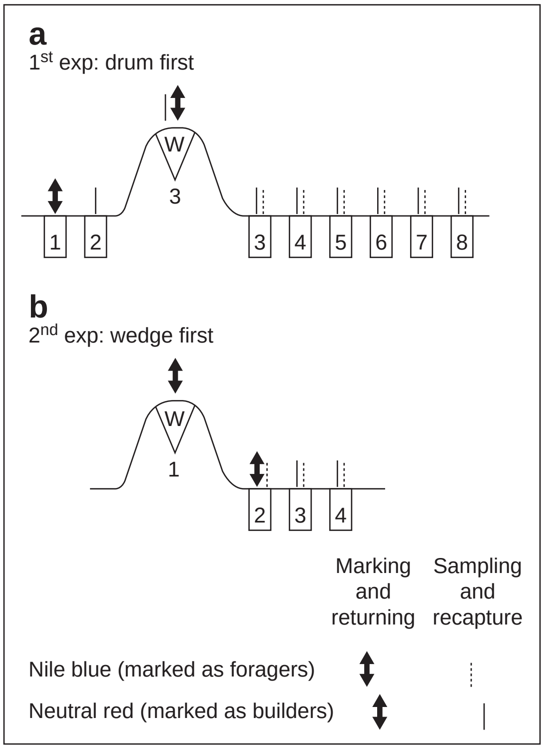

Figure 1. Schematic of the experimental set up. (a) the first experiment in which foragers were marked first. (b) the second experiment in which builders were marked first. n.b. The sample sequence is indicated by numbers, 'W' indicates the mound-wedge sample.

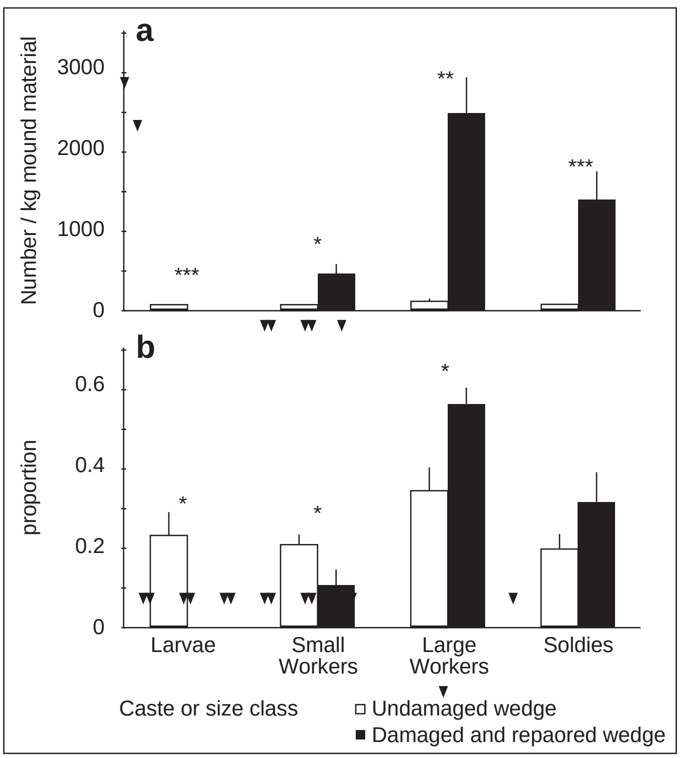

Figure 2. (a) Number and (b) proportion (average ± std error) of termites separated according to caste and size-class collected in wedge samples from the 'mound damage methodology' test. Open columns are wedge samples from undamaged mounds, filled columns are those from damaged and repaired wedge samples. Significant differences between paired columns indicated as * $P < 0.05$; ** $P < 0.01$, *** $P < 0.001$.

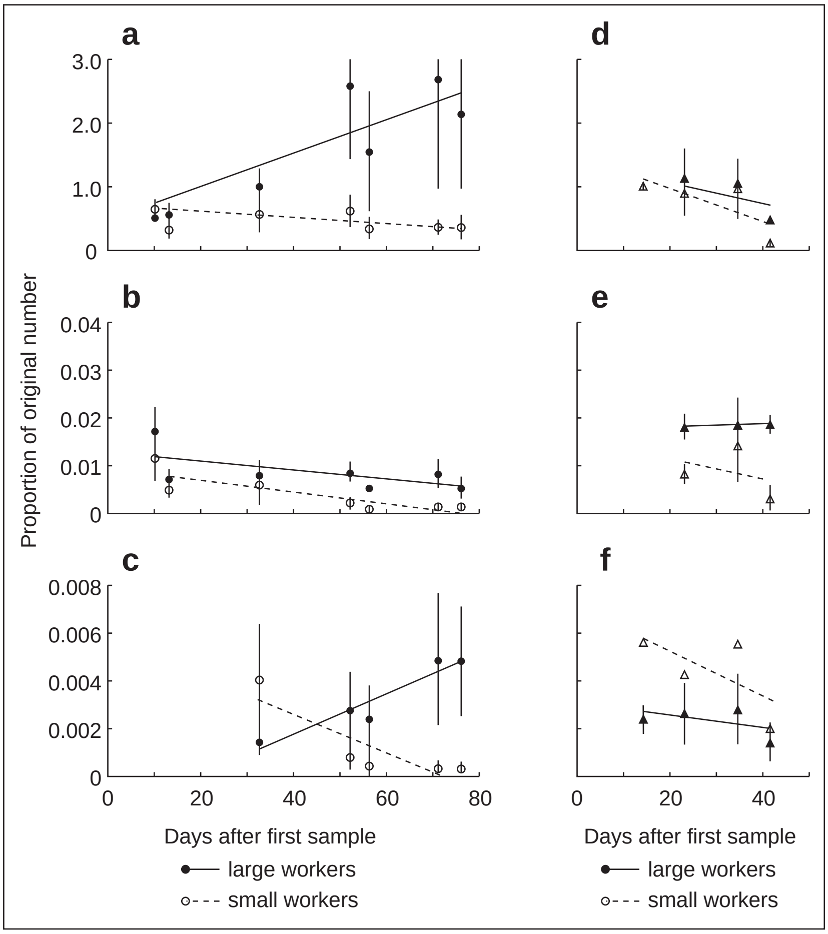

Figure 3. (a - c) Results from first task-switching experiment in which foragers were marked first (a) Average (± std error) proportion (compared with first drum sample) of termites collected from drums. (b) Average (± std error) proportion (of original marked sample) of recaptured blue termites. (c) Average (± std error) proportion (of original marked sample) of recaptured red termites. (d - f) Results from the second task-switching experiment in which builders were marked first. (d) Average (± std error) proportion (compared with first drum sample) of termites collected from drums. (e) Average (± std error) proportion (of original marked sample) of recaptured blue termites. (f) Average (± std error) proportion (of original marked sample) of recaptured red termites.

Task Switching Experiments

In the first task switching experiment, foragers first, data from only six of the eight colonies were used as two had insufficient contact to drums for adequate sampling. There was an average of ~13,000 foraging workers collected from the first bait-drums, which were then stained with Nile Blue. The second drums had significant fewer workers (an average of ~7,700) than the first drums (paired $t_5 = 6.188$, $P = 0.002$) (Table 1). This reduction coincided with a period of cool weather, an effect that would impact on all colonies simultaneously. The cutting of the wedge (9.8 ± 0.8 kg) was hoped to cause foraging workers to switch tasks to building and repairing the mound. The third drums contained fewer termites (an average of ~4,800 workers) however no consistent or significant pattern was observed (paired $t_5 = 1.477$, $P = 0.199$): two colonies had a ca. 90% decrease in the number of foragers in the third drum compared with the second, two colonies had about the same number of termites in the two drums, and two colonies had an ca. 100% increase. Temperatures were warmer when the third drums were collected, similar to those during collection of the first drums. There were significantly fewer termites in the third drums compared with the first in all six colonies (Table 1; paired $t_5 = 3.072$, $P = 0.028$). Perhaps a more telling comparison is with the number of recaptured, blue marked foragers. There were ~220 blue-marked, recaptured, foragers (1.76 ± 0.44 % of the original number marked) in the second drums and ~90 blue-marked, still foraging-foragers in the third drums (0.68 ± 0.19% of the original number marked) or a significant reduction of about 60% (Table 1, Figure 3; paired $t_5 = 3.551$, $P = 0.016$).

Did foragers switch tasks? There were ~12,500 ± 4,300 workers collected in the mound-wedges. Very few of these builders were blue-marked ex-foragers: around 80 (0.66 ± 0.20 % of the original number marked) blue-marked, ex-foragers-turned-builders were collected from the mound wedges (Figure 3). There was no consistent or significant pattern observed for blue-marked builders (i.e. collected from the mound-wedges) compared with blue-marked foragers (collected in the third drums) (paired $t_5 = 0.838$, $P = 0.440$): three colonies had more blue-marked foragers than blue-marked builders, one had a similar number, and two colonies had fewer. The similar number (and proportion) of blue-marked foragers continued to forage during the disturbance to the mound suggested that a strong shift from foraging to building had not occurred.

The number of foragers increased from forth to eighth drums (Table 1, Figure 3). This was probably due to the change in temperature, as during the later samples summer had passed and autumn was progressing. *Nasutitermes exitiosus* gather at feeding sites close to their mound during the colder months (Evans and Gleeson, 2001). The number of blue -marked termites recaptured in these latter drums decreased from ~100 workers (or 0.74 ± 0.24% of the original number marked) in the forth drums to about 50 workers in the eighth drums (0.39 ± 0.13%) (Table 1, Figure 3). This suggested that foragers were switching to other tasks slowly; about 1.6 blue-marked workers per day on average over the duration of the experiment. At the same time, the number of red-marked builders recaptured in drums as foragers increased from under 20 workers (0.27 ± 0.16% of the original number marked) to around 100 (0.43 ± 0.21%) in the same drums (Table 1, Figure 3). This was equivalent to an increase of 2.2 red-marked workers in drums on average per day.

In the second task switching experiment, builders first, data from only four of the six colonies were used as two had insufficient contact to drums for adequate sampling. The wedges cut from the mounds weighed an average of 9.1 ± 0.6 kg and contained nearly 28,000 termites; double the number from the first task-switching experiment, foragers first, but a few less than the number from the methodology test (Table 2). Two weeks later when the first drum was collected, there were a little more than 10,000 foragers, of which ~80 were red-marked ex-builders, or 0.27 ± 0.16% of the original number marked; the same proportion as observed in the first experiment. The numbers of termites collected from the second and third drums did not differ greatly, but they were much lower in the forth drum (Table 2, Figure 3). The number of recaptured, red-marked ex-builders now foragers increased to a little over 100 in the third drum (0.33 ± 0.20% of the original number marked), a rate of task-switching of 2.4 workers per day, but then halved in the forth sample (0.15 ± 0.09%). The number of recaptured blue-marked foragers fluctuated between 160 - 180 workers (1.39 - 1.76% of the original number marked); which was similar to the proportion found in the second drums of the first experiment, i.e. before mound-wedges were cut (Tables 1 and 2, Fig 3). It is evident from these data that there was a higher recapture rate of blue-marked foragers compared with red-marked builders in the drums. There were roughly double the numbers of blue-marked foragers compared with those of red-marked builders that had switched tasks to foraging (Table 2, Figure 3) This difference is even greater when proportional data are considered: there were roughly five times the proportional recapture rate of blue-marked foragers compared with red-marked builders (Figure 3).

Table 1. The sequence of sampling drums and mound-wedges, numbers (mean ± standard error) of forager and builder termite workers sampled, marked and recaptured for the first task switching experiment, 'foragers' first.

Drum (sequence)	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**
Sample day[1]	1 ± 0	10 ± 2	13 ± 2	33 ± 2	52 ± 8	56 ± 7	71 ± 7	76 ± 5
Number of colonies	6	6	6	6	5	3	3	3
Unmarked foragers in drum	13,109[2] ± 2,653	7,669 ± 2,156	4,778 ± 1,413	12,546 ± 4,529	23,582 ± 8,874	13,597 ± 5,178	23,685 ± 9,955	19,548 ± 7,792
Blue foragers in drum		222 ± 64	88 ± 27	107 ± 50	81 ± 22	54 ± 8	75 ± 17	51 ± 9

Unmarked builders in wedge[3]	12,354 ± 4,288					5,758 ± 2,047
Blue marked builders in wedge[4]	81 ± 28					24 ± 23
Red marked builders in 2nd wedge						170 ± 7
Red marked foragers in drums[5]		17 ± 6	59 ± 44	54 ± 37	110 ± 75	105 ± 63

[1]Sample day 1 = day that first drum was collected to sample and mark foragers blue. [2]Foragers from the first drum were marked blue. [3]First wedges were cut after the second drum and were collected simultaneously with the third drum. Builders were marked red. Second wedges were cut for 2 mounds only, simultaneously with the seventh drum and collected with the eighth drum. [4]Blue-marked builders were marked as foragers, therefore task-switchers. [5]Red-marked foragers were marked as builders, therefore task-switchers.

Table 2. The sequence of sampling mound-wedges and drums, numbers (mean ± standard error) of builder and forager termite workers sampled, marked and recaptured for the second task switching experiment, 'builders' first.

Drum sequence	**Wedge**	**1**	**2**	**3**	**4**
Sample day[1]	1 ± 0	14 ± 0	23 ± 2	35 ± 3	42 ± 4
Number of colonies	4	4	4	4	2
Unmarked builders in wedge[2]	27,865 ± 4,221				
Unmarked foragers in drum		10,339[3] ± 2,302	11,713 ± 5245	11,010 ± 5,133	4,451 ± 1,306
Red marked foragers in drums[4]		82 ± 33	86 ± 55	103 ± 70	49 ± 33
Blue marked foragers in drum			167 ± 42	184 ± 83	162 ± 13

[1]Sample day 1 = day that damaged wedge was collected to sample and mark builders red. [2]Builders were marked red. [3]Foragers from the first drum were marked blue. [4]Red-marked foragers were marked as builders, therefore task-switchers.

Table 3. The regression equations of worker termites sampled from drums over the duration of both experiments, where 'y' is the number of termites and 'x' is the day number. N.b.: for unmarked termites, 'y' is the proportion of workers relative to number sampled from the first drum; for blue marked termites, 'y' is the number of recaptured blue termites expressed as a proportion of the number marked blue and released (the foragers in the first drum); and for red marked termites, 'y' is the number of recaptured red termites expressed as a proportion of the number marked red and released (the builders from the mound-wedge)

Experiment Worker type	Worker size	Regression equation	r^2	*F*	d.f.	*P*
1: Foragers first						
Unmarked	Large	y = 0.026x + 0.498	0.74	16.95	1, 6	0.006
	Small	y = -0.005x + 0.733	0.41	4.12	1, 6	0.089
Blue	Large	y = (-9x + 1260) x 10-5	0.38	3.03	1, 5	0.142
	Small	y = (-10x + 940) x 10-5	0.71	12.18	1, 5	0.017
Red	Large	y = (8x - 170) x 10-5	0.90	26.19	1, 3	0.014
	Small	y = (-8x + 580) x 10-5	0.74	8.45	1, 3	0.062
2: Builders first						
Unmarked	Large	y = -0.016x + 1.379	0.44	1.61	1, 2	0.333
	Small	y = -0.026x + 1.482	0.56	2.52	1, 2	0.254
Blue	Large	y = (3x + 1740) x 10-5	0.80	3.96	1, 1	0.297
	Small	y = (-20x + 1480) x 10-5	0.10	0.11	1, 1	0.794
Red	Large	y = (-3x + 300) x 10-5	0.25	0.54	1, 2	0.540
	Small	y = (-10x + 700) x 10-5	0.46	1.68	1, 2	0.325

A comparison of small (instars 1 and 2) and large (instars 3, 4 and 5) worker termites revealed that there were different patterns between these groups. In general, the number of large worker foragers in drums increased, whereas the number of small foragers decreased, during the course of the experiment. These patterns become clearer when expressed as proportions of the original number of foragers (numbers sampled in the first drums), or as the proportion of those marked originally (numbers of foragers in first drum marked blue and released or numbers of builders in the mound-wedge marked red and released). In the foragers first experiment, the increase in the proportion of large worker foragers in drums over the course of the experiment is significant, but the decrease proportion of small foragers is not quite significant (Table 3, Figure 3a). The decrease in the proportion of blue-marked recaptured foragers in drums over the course of the first experiment is not significant for large workers, but is for small workers (Table 3, Figure 3b). The increase in the proportion of red-marked large worker in drums over the course of the experiment remains clear and is significant, and the decrease the proportion of small foragers is not quite significant in the foragers first experiment (Table 3, Figure 3c). There were no significant patterns in the builders first experiment, probably due to the fewer drum samples and large variability, yet the slope of the regression was similar for small unmarked foragers, both large and small blue marked foragers, and small red-marked foragers (Table 3, Figure 4d, e, f).

DISCUSSION

The results of this study show that *N. exitiosus* workers did switch tasks; damaging the mound lowered the forager population, although this was confounded with temperature changes, and blue-marked foragers became builders and red-marked builders became foragers. However they did not switch between tasks in any great numbers, nor did they do so quickly. Only very few (0.6%) of the blue-marked foragers switched tasks from foraging to building in the first experiment, which was fewer than the blue-marked foragers that continued to forage at the same time (~1.7%). This result seems notable given the damage done to the mound. The red-marked builders switched tasks, but as was seen for their blue-marked siblings, they did so slowly, at a rate of about two workers per day for both experiments. There was evidence that larger and smaller workers responded differently: fewer small workers became builders than large workers, a result similar to that seen by McMahan (1977). Smaller workers were recaptured less frequently and were decreasingly represented in drums as foragers over time.

How to interpret these results? Was the methodology flawed? The similar rate of task switching in both experiments indicates that neither the order of the marking nor the damaging of the mound affected the outcome greatly. Nile Blue and Neutral Red are not perfect markers; they do fade over time. Evans et al. (1998) reported that ca. 60% of marked workers, both small and large, were recovered after seven days, and 20% of large workers only after over 200 days, in a laboratory experiment that mimicked mound conditions. This suggests that the recaptures in this study were low due to marker fading, yet doubling or tripling the recaptures increases task switching to a mere 5 - 7 workers per day. The lack of marked small workers after 217 days in the laboratory experiment of Evans et al. (1998) suggests that some of the decrease in marked small worker over the duration of the experiment is a consequence of growth. It must be noted that the mortality rate of worker termites in the field is unknown.

Even with marker fading, *N. exitiosus* workers did not switch from foraging to building when sudden and urgently needed. This is supported by two simple calculations of the worker population. First, about 0.6% of blue-marked foragers become builders when the mound wedges were cut. If this percentage is representative for all foragers, and if all builders had switched tasks from foraging, then the 12,000 builders in damaged wedges equates to 2,000,000 foragers in total. Second, ca. 13,000 foraging workers were collected from drums around undamaged mound-colonies, and *N. exitiosus* colonies have around 40 feeding sites (calculated from Gay and Greaves 1940), suggesting that about 520,000 workers would be out foraging on a summer's day. Clearly, the estimated number of foragers based on task-switching blue-marked foragers turned builders is inaccurate, and builders must come from other tasks.

Of course, there were other tasks that were not monitored, including feeding and tending the queen, collecting eggs, nursing the young, cleaning the mound, and so forth. The termites that became builders after the mound was damaged could well have switched from these tasks. This suggestion has merit, given that these activities are confined to the mound-nest, whereas foraging occurs distant from it; therefore workers involved in these activities could have responded more rapidly.

Alternatively, if the low rate of task-switching from foraging to building was representative for all tasks, and the methodology was not flawed, then the alternation hypothesis of activation of reserve labour may be correct (Seeley, 1982; Kolmes, 1985; Gordon, 1989, 1996; Johnson, 2002). Inactive termites have been observed in laboratory tunnelling experiments, and these may represent a reserve force. 'Inactive' may be inaccurate; perhaps these termites are ruminating like cellulose-eating mammalian counterparts. Perhaps resting-ruminating is important after foraging and an intermittent task before engaging in another active task. The differences noted between small and large workers may have been due to different resting times, or small workers may avoid risky behaviour (note the difference in response to mound damage in the testing mound damage methodology experiment; Figure 2). If resting is the crucial behaviour through which termite workers pass before commencing another task, then how to measure it becomes an important methodological question.

This study is only a first attempt to measure task allocation in a higher termite using a disturbance to test foraging for work ideas. The many other factors that have been show to be important in affecting task allocation decisions, such as hormone levels, genetic response thresholds and communication with other individuals remain to be investigated (Robinson et al., 1989, 1994; Gordon et al., 1992; Tofts, 1993; Franks and Tofts, 1994; Jeanne, 1996; Theraulaz et al., 1998; Gordon and Mehdiabadi, 1999; Beshers and Fewell, 2001). That age-related behaviours have been observed among higher termites (McMahan, 1977; Miura and Matsumoto, 1995; Hinze and Leuthold, 1999), but not lower termites (Rosengaus and Traniello, 1993; Crosland and Traniello, 1997; Crosland et al., 1997), suggests that this trait appeared relatively late in termite evolution, and may parallel the evolution of age related behaviour in ants (Traniello, 1978) and other social Hymenoptera; but may be also associated with colony size (Oster and Wilson, 1978; Bourke, 1999; Thomas and Elgar, 2003). Therefore, as with theories that explain the evolution of social behaviour, termites appear to provide an excellent opportunity to test task-allocation theory.

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