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Specialist and Hyperspecialist Workers of Leaf-cutting Ants during Nest Digging

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Abstract **– As Specialists are workers that repeatedly perform a certain taskand so have a high frequency of acts in this activity when compared to all workers at the colony. Within these workers, there are some others who will perform the task in a frequency even higher and were more recently denominated as hyperspecialists. Using soil pellets transport activity as a model, the present study investigated whether the level of activity of *Acromyrmex subterraneus* Hymenoptera: Formicidae) workers in a certain task differs as a function of other available tasks (brood and symbiotic fungus transport). The hypothesis was that a larger number of available tasks promotes changes in the proportion of specialist and/or hyperspecialist workers engaged in a certain task. With this purpose, we evaluated the soil pellets transport activity of individual workers exposed to conditions where there was just the soil to dig, soil with brood and fungus, soil only with fungus andsoil only with brood. The individual frequency of activity (transport of a soil pellet) was recorded for 16 mini-colonies submitted to the different treatments during 24 hours and 10 minutes of each recording hour were sampled. Data indicate that the distribution of soil pellets transport activity across workers was skewed for all tested conditions, with a large number of workers being inactive, while few workers repeatedly perform the task of soil pellets transport. The percentage of inactive, non-specialists, specialists or hyperspecialist workers did not differ between treatments, indicating that specialist and hyperspecialist workers exist during soil pellets transport and they represent a fixed worker force to this task. We conclude that there is specialization for the soil pellets transport with specialist and hyperspecialist worker proportion maintenance even when a larger number of tasks is available.**

Keywords **– Digging behavior, Division of labor, Formicidae, Specialization.**

I. Introduction

The most important behavioral attributes of social insects are adaptations associated with their ability to organize themselves (Hölldobler and Wilson 1990). The social organization of leaf-cutting ants (genera *Atta* and *Acromyrmex*) is one of the most complex within ants, with workers divided in physicalcastes which permit the collective execution of different and concomitant tasks (Della Lucia 2011). Individuals of a given morphological type are more predisposed to perform a task based on their physical attributes (Wilson 1971, 1980; Wetterer 1995) making them more efficient due their specialization (Wilson 1983; Tofts 1993) or not (Dornhaus, 2008). Actually, in *Acromyrmex subterraneus brunneus*, the tasks of foraging and cultivation of the fungus garden show a strong alloethic correlation indicating a gradual change in frequency of performing tasks related to body size of the workers (Forti et al. 2004, Camargo et al. 2007).

On the other hand, when the external stimulus is too strong workers of different castes can undertake almost any task (Theraulaz et al. 1998; Beshers and Fewell 2001; Evison and Ratnieks 2007; Waddington and Hughes 2010). This behavioral flexibility of the workers is driven by the changing needs of the colony, so workers can perform tasks not previously seen in their repertoires or switch between tasks (Robinson 1992; Gordon and Kulig1996). In contrast, workers are able to dynamically adjust to demand/task availability as occurred in *Pogonomyrmex badius* (Kwapich and Tschinkel, 2013).

Individual task performance is affected by both internal (genetic, neural, hormonal factors and experience) and external factors (environment stimuli and worker-worker contact) (Beshers and Fewell 2001).

A genetic effect mediated by the polyandrous mating system in *A. subterraneus* influences the individual foraging performance of workers, irrespective of age and size class affecting the propensity of individuals to execute tasks (Oldroyd and Fewell 2007; Waddington and Hughes 2010; Constant et al. 2012). Also this propensity may be associated with variation in the response thresholds among workers to perform different tasks, resulting in an uneven distribution of labor (Jaissonet al. 1988; Retana and Cerdá 1991; Gordon et al. 2005; Dornhauset al. 2008, 2009; Beverly et al. 2009). According to this response threshold model (Theraulaz et al. 1998; Beshers and Fewell 2001), some individuals seem to contribute a disproportionate amount of work compared to less active individuals. These key individuals act to increase the activity level of other group members and are called specialists (Robson and Traniello 1999).

Specialist workers seem to have a lower response threshold to certain tasks, contributing to work more effectively (Robson and Traniello 1999). Indeed extreme variations in individual behavior performance are registered, including nest building task (Pinter-Wollman et al. 2012) and when workers are more active and persistent in performing their tasks they are defined as “elite workers” or hyperspecialists (Rocha et al. 2014).

Another hypothesis which tries to explain the existence of specialist workers is proposed by Sendova-Franks and Franks (1993). Their foraging-for-work hypothesis suggests the occurrence of a temporal polyethism generated by the influx of young workers which actively seek for work in the central area of the nest (where they emerged). So they drive older workers to move centrifugally to find tasks, promoting the rotation of roles that are not completely occupied. As these older workers die, a decline in execution rates of some tasks occurs and there is an allocation of other workers who are near this site (Tofts 1993). In this way, age polyethism may progress from a simple algorithm to individual task performance which is not causally related to the size or age of the worker ant. Obviously, not all workers that find an opportunity to perform a task will respond equally (Beshers and Fewell 2001).

Studies indicate that ant workers are inactive most of the time, with coupled pulses of activity between nestmates, a phenomenon that promotes social facilitation (Franks and Bryant 1987). Some workers are active throughout their whole life (Chen 1937; Jaisson et al. 1988; Dornhaus 2008), while others remain inactive (Gordon 2002; Gordon et al. 2005), with 50 to 70% of the workers being inactive all the time (Charboneau and Dornhaus 2015).

Nest digging is an event that operates without any type of central control and emerges from a complex system of interactions between workers (Franks and Deneubourg 1997) which will collectively make the transport of soil pellets to the soil surface (Camargo et al. 2013a, b).Occurrence of specialist and even hyperspecialists workers during soil pellets transport is highly probable as it constitutes a high energy consuming activity (Camargo et al. 2013a, b) and of high risk, due the cuticular abrasion when the soil pellets are carried through tunnels to the surface which increases desiccation risk (Johnson 2000). Thus we can expect that some individualswill transport soil pellets at a higher frequency than that of other workers engaged at the same activity. But what will happen when other tasks are available? Will the number of specialists and even hyperspecialists workers alter due different associated risks of tasks? Tasks involved in nest construction and brood care do not carry equal cost or risk (Jeanson and Fewell 2008). When risky activities are unequally distributed within individuals, the avoidance of risky activities by some members is ultimately beneficial to risk takers (Kukuk 1998).

Thus, using soil pellets transport activity as a model, the present study investigated how *A. subterraneus* worker activity is distributed within this task and whether the availability of other tasks with different associated risks shapes task allocation. Testing the tasks simultaneously, we expected that ants working in one task might not be available to work in another (Tofts 1993).

II. Material and Methods

Sixteen *A. subterraneus* queenright colonies maintained since 2012 in the Laboratory of Myrmecology, Universidade Federal de Juiz de Fora (UFJF), were used for the evaluation of excavated soil pellets transport behavior and division of tasks. The colonies had been collected in the same municipality and maintained in a closed system consisting of three compartments interconnected by transparent plastic tubing, which corresponded to the fungus chamber, foraging arena and waste chamber. The colonies were kept under controlled conditions of temperature (26ºC) and relative humidity (70%) and received *Acalypha* daily. At the time of the experiment they had about 3L of symbiont fungus and from 5000 to 6000 workers.

For the experiment, workers were selected randomly and collected inside the fungus garden chamber from each colony. All workers belonged to the medium size class characterized by a head width of 1.6 to 2.0 mm. The pronotum of all individuals was marked with different color combinations so that each worker could be individually identified. Edding® markers were used because of their excellent adhesion, rapid drying, and good visibility (Camargo et al. 2007). The workers were placed in plastic boxes whose borders were covered with neutral talcum to prevent their escape until the dye had dried where they remained until the time of filming.

Additionally, portions of the symbiotic fungus were collected from the same colonies, removing all small or largeworkers. A fungal mass of 5 g was used per excavation tube. The larvae and pupae used in the experiment were removed from the same colonies; thus, the excavation tubes contained elements (workers, symbiotic fungus, and brood) of the same colony.

The excavation cylinders consisted of transparent plastic bottles, each measuring 25 cm in height and 10 cm in diameter. The cylinders were filled with previously sieved latosol soil collected on the campus of UFJF at a depth of 60 cm. Considering the volume of the cylinder, the soil was weighed to obtain a density of 1.6 g/cm3and water content of 5.4 %according to Camargo et al. (2013 a, b). A 250-mL transparent plastic box was placed above each cylinder for observation. The observation box had a hole in its bottom to permit direct contact with the soil to be excavated (Fig.1). A high resolution micro camera (Pacific-Co) was positioned perpendicular to the cylinder to record the activities of workers for 24 hours. Workers (from 1.6 to 2.0 mm of head width, age from 21 to 30 days), fungus and brood were placed inside the observation box.

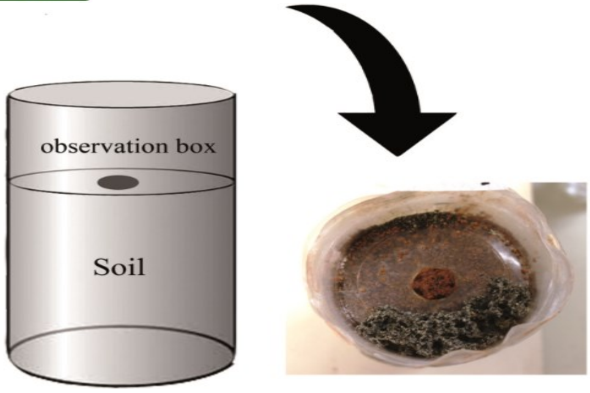

Fig. 1. The observation box had a hole in its bottom to permit direct contact with the soil to be excavated

The frequency of soil pellets transport by workers was evaluated in four experimental treatments. Each treatment was tested in four different colonies (n total = 16): treatment FB: 30 workers, 5 g of fungus garden, and 30 brood items (larvae or pupae); treatment FG: 30 workers and 5 g of fungus garden; treatment LP: 30 workers and 30 brood items (larvae or pupae); treatment WK: 30 workers without fungus garden and brood.

Observation was performed for 10 minutes per hour for each colony and respective treatment, recording the individual frequency of soil pellet transport, during 24 hours, according to Camargo and Forti, 2014. After filming the workers, the remaining fungal mass and untransported brood were returned to the colony of origin.

For each colony, we first calculated a specialization baseline (Fig. 4) arbitrarily corresponding to 1.5 times the mean number of rejections per worker. Ants that performed more rejections than the baseline were considered specialized in this particular task (see Corbara et al. 1989 and Schatz et al. 1995 for a similar treatment). The dashed lines correspond to 1.5 times the mean number of rejections per worker within the previously defined specialist group. For each colony, we first calculated a specialization baseline (Fig. 4, continuous lines) arbitrarily corresponding to 1.5 times the mean number of rejections per worker. Ants that performed more rejections than the baseline were considered specialized in this particular task (see Corbara et al. 1989 and Schatz et al. 1995 for a similar treatment). For hyperspecialists, the baseline value corresponded to more than 1.5 times the mean number of soil pellets transport per worker that performed this task (just those ones who did soil pellet transport) (Rocha et al. 2014). Thus workers that performed less soil pellets transport than the baseline value were considered non-specialists. After classification of the workers, the percentage of specialists and hyperspecialists was determined and compared among the treatments by one-way Anova. The distribution of individual soil pellets transport was computed and compared with an expected negative binomial distribution using the Kolmogorov-Smirnov test. The expected negative binomial distribution is a null modelobtained by multiplying the probability density (maximum likelihood estimate of aggregation parameter k) by the total sample size. The aggregation parameter *k* of the negative binomial distribution was also calculated. If *k* tends toward zero, the distribution is skewed; if *k* tends toward infinite, the distribution becomes random. Thus, positive values close to zero indicate a skewed arrangement and values higher than 8 indicate a random distribution (Pielou 1977; Southwood 1978). All analyses were performed using the R 3.1.1 statistical program (R Core Team, 2017).

III. Results

Recording the soil pellets transport activity of workers showed that in mean 45.21% of the observed individuals were not engaged in any task (FB: 31.67%; FG: 50%; LP: 53.33%; WK: 45.84%, Total mean number = 45.21%). In fact, a few very active individuals performed most proportion of the task and many rarely active individuals performed a small proportion of the task or no task at all (Fig. 2).

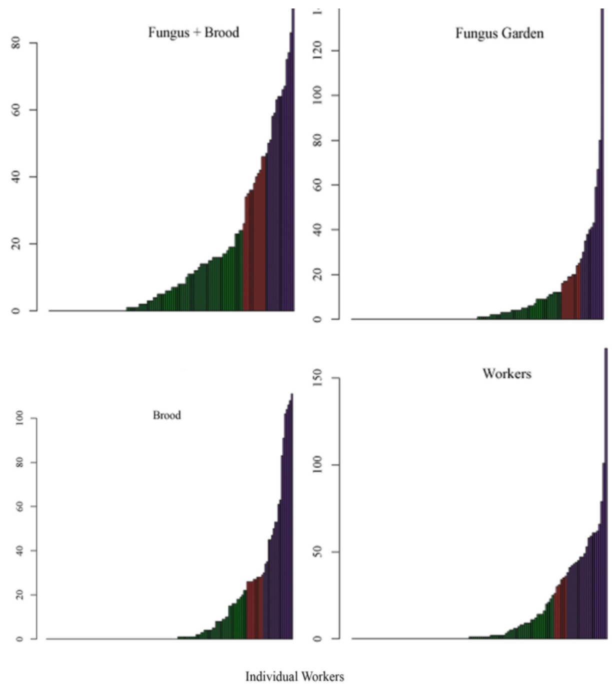

Fig. 2. Number of soil pellets transport activity individually recorded for the workers in the different treatments. Each worker is represented individually by a bar (purple bar: non-specialist worker, red bar: specialist; green bar: hyperspecialist). Note that inactive workers are also present in the graph; however, since their frequency is zero, the bars do not appear but rather result in an empty space on the left side of the white bars. Specialists baseline: FB = 23.82, FG = 19.91, LP = 12.43, WK = 9.33. Hyperspecialists baseline: FB = 34.26, FG = 31.94, LP = 23.51, WK = 18.61.

The values of aggregation parameter *k* indicated that soil pellets transport activity across workers was highly skewed (Table 1). The observed distribution fitted the negative binomial distribution when treatments include the fungus and brood (treatment FB) and only fungus (treatment FG). On the other hand, when only brood (treatment LP) or workers (WK) were present, the frequency distribution of soil pellets transport activity, although skewed, did not fit thenegative binomial distribution (Table 1, Fig. 3).

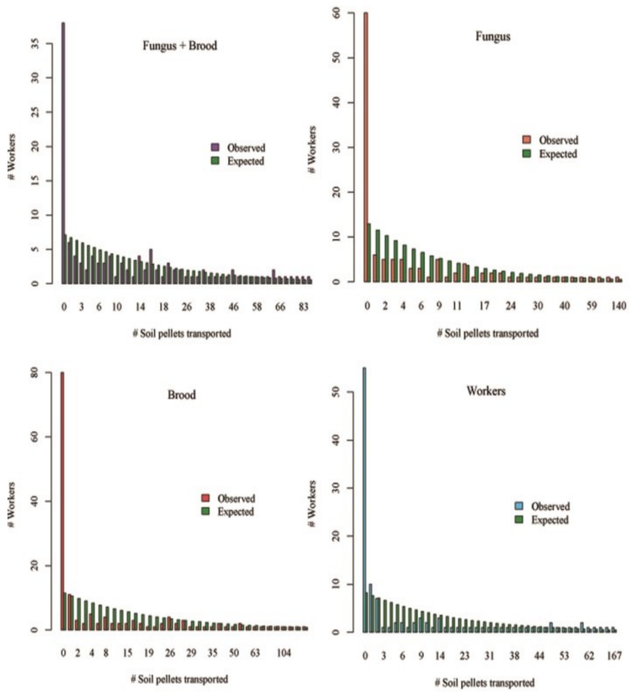

Fig. 3. Distribution of observed and expected frequencies (negative binomial distribution) of soil pellets transport activity across *Acromyrmex subterraneus* workers in treatments FB, FG, LP and WK.

Comparison of the percentage of worker categories between treatments showed no difference for inactive workers (ANOVA: $F_{3,12} = 1.84$, $p = 0.19$), non-specialists (ANOVA: $F_{3,12} = 1.4$, $p = 0.29$), specialists (ANOVA: $F_{3,12} = 0.93$, $p = 0.45$), or hyperspecialists (ANOVA: $F_{3,12} = 0.62$, $p = 0.61$) (Fig. 4).

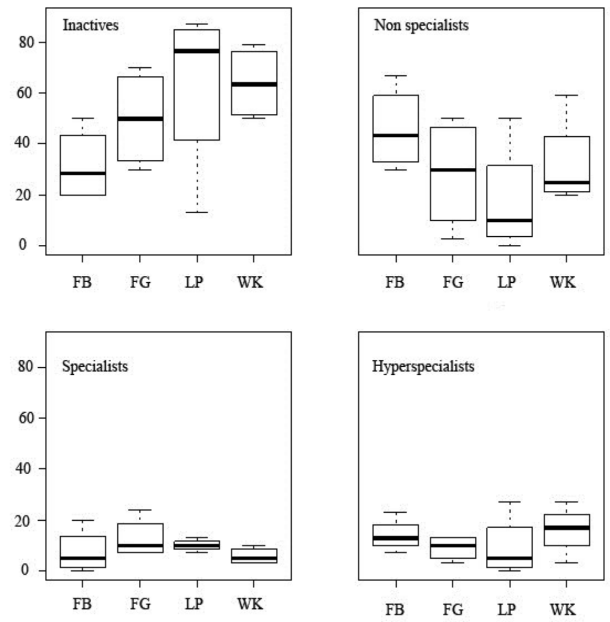

Fig. 4. Percentage of inactive workers, non-specialists, specialists and hyperspecialists in the four treatments applied to *Acromyrmex subterraneus*.

IV. Discussion

The level of activity differed between workers regardless of the number of available tasks to be executed. Usingsoil pellets transport activity as model and the main activity, since the stimulus to dig (soil) is present in all treatments, a small number of very active workers and a large number of not very active or inactive workers are observed, generating a skewed distribution of the frequency of individual activity. This skewed distribution allows denominating some workers as specialists and hyperspecialists, once their activity frequency is above baselines, confirming the existence of specialization during nest digging.

A low and similar proportion of workers engaged in soil pellets transport was maintained despite the availability of other tasks, such as brood and fungus garden transporting. Thus, the presence of a larger number of activities did not imply a homogenous division of labor among workers. This skewed pattern in the division of labor might be related to the fact that ant workers are idiosyncratic, i.e., they sense and react in a special and individual manner to the influence of different agents and their response thresholds vary according to stimulus.In this case response thresholds to varioustasks are independent from one another (Oster and Wilson 1978). Idiosyncrasy has been reported for other social insect species (O'Donnell and Foster 2001; Hurdet al. 2003; Weidenmuller 2004; Pinter-Wollmanet al, 2011), with the observation that nestmates have different response thresholds to a set of stimuli (Pinter-Wollman et al. 2011). Despite individual differences, it is expected that ant workers behave adaptively, adjusting themselves and becoming more active the greater the needs of the colony (Oster andWilson 1978), thus, in larger colonies, such as those of leaf-cutting ants, lower individual effort or even a larger number of inactive workers are expected due the great number of individuals (Oster and Wilson 1978; Herbers 1981; Houston et al. 1988; Dornhaus et al. 2008. In the other hand, there are many examples where colonies simply do not react to changes in demand or react slowly or poorly. Indeed, in one case where half of the foragers were removed from field colonies, the colony did not reallocate workers to foraging and half of the brood perished (Kwapich and Tschinkel 2013). Even in the case of Pinter-Wollman et al. 2011 removed emigration specialists are replaced, but only after a significant amount of time (hours), which would be extremely non-adaptive for colonies in the field exposed to dehydration, extreme temperatures, predators (Johnson 2003, Schmid-Hempel 1992, Charbonneau & Dornhaus 2015).

The maintenance of this skewed pattern at the division of labor within a small number of workers from the same size class could be related to the associated risk of the nest construction activity. Also we must take in account that when symbiotic fungus was provided over excavation tubes at both treatments FG and FB the frequency distribution did not fit the negative binomial what could be due to a trend of less inactive and more non-specialists workers. In fact the loss of the symbiotic fungus garden is fatal to the survival of the colony while the offspring can be replenished.

The finding that the majority of workers do not perform any activity during excavation is in line with the proposal of Gordon (2002) that some individuals execute little or any task, while others perform most of the work as observed in this study. It can be observed that active workers perform the same task repeatedly, reaching extreme values for the same task, in this case soil pellets transport. A single *Temnothorax* worker can transport 143 soil pellets (Dornhauset al. 2009), while in the present study a single *Acromyrmex* worker transported 167 soil pellets. These results suggest that some individuals may contribute a disproportionate amount of work compared to their less active nestmates (Robson and Traniello1999; Pinter-Wollmanet al. 2012; Charbonneau and Dornhaus 2015). It is interesting to note that the proportion of inactive workers registered here is similar to that of different studies, even those involving different species (Retana andCerdá, 1990; Robson and Traniello 1999; Dornhaus 2008, 2009; Pinter-Wollmanet al. 2012; Charbonneau and Dornhaus 2015).

With respect to workers involved in soil pellets transport, the mean frequency of 20% specialists and 12.5% hyperspecialists agrees with the classical study on the division of labor in polymorphic ant species conducted by Wilson (1980), which indicates the existence of generalist and specialist workers. Specialization could thus be associated with increased efficiency by reducing the costs of task switching (Jeanne 1986; Goldsbyet al. 2012) and facilitating the learning process (O'Donnell andJeanne 1992; Trumbo and Robinson 1997; Langridgeet al. 2008; Chittka and Muller 2009), since repeatedly performing a single task can alter the velocity and precision of its execution. The repeated execution of the same task can also modulates the response of an individual to the stimulus promoting the behavior, considering the contiguity and repetition of the stimuli (Jeanson and Weidenmüller 2014). The probability, intensity and threshold of the individual response are therefore subject to the effects of repetition or specialization.

There are also situations in which the variations in individual behavior seem to be extreme and which are described as elitism in processes such as nest construction and brood care. These processes depend on the behavior of these individuals referred to as elite workers (Robson and Traniello 1999). "Elite" or "leader" ants that work hardest and best when alone exert a stimulating effect on nestmates, while "follower" ants are slower and have a retarding effect (Hölldobler and Wilson 1990).

The skewed distribution of soil pellets transport activity confirms the presence of elitism in *Acromyrmex subterraneus*, with no difference in the proportion of specialists and hyperspecialists. If a change in the distribution of soil pellets transport activity occurred in the presence of more tasks, this would be evidence of the absence of elitism. This study highlighted the importance of specialization for task allocation in ant colonies and suggests that the differential propensity of individuals to execute risky activities must have some effect at the task allocation system. Further studies are needed to determine whether specialists and hyperspecialists are indeed more efficient than non-specialists and thus compensate for the activity of inactive workers and also if the multiple tasks are of same risk we will find another group of specialized workers.

Table 1. Estimated values of aggregation parameter *k* of the negative binomial distribution, Kolmogorov-Smirnov test value for comparison of observed data and expected from the negative binomial distribution, and respective p-values.

Treatment	*k* parameter	Kolmogorov-Smirnov test value	p-value
FB	0.21	D = 0.26	0.1019
FG	0.55	D= 0.34	0.0636
LP	0.25	D = 0.4	0.0073
WK	0.30	D = 0.46	0.00003

V. Conclusion

We conclude that there is specialization for the soil pellets transport with specialist and hyperspecialist worker proportion maintenance even when a larger number of tasks is available.

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