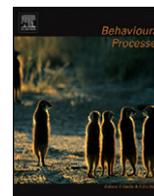




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Behavioral differentiation during collective building in wild mice *Mus spicilegus*

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ARTICLE INFO

Article history:

Received 30 June 2011

Received in revised form

10 November 2011

Accepted 11 December 2011

Keywords:

Collective building

Behavioral differentiation

RFID technique

Mus spicilegus

Self-organization

ABSTRACT

Although well documented in social insects, the possibility of behavioral differentiation during collective building has been poorly studied in mammals. In this context, the mound-building mouse *Mus spicilegus* is an interesting model. Under natural conditions, juveniles from different litters gather vegetal material and build a sophisticated structure, the mound, under which the mice will spend winter. The first steps of this complex building process may be elicited under laboratory conditions by offering cotton balls as building material. Spatio-temporal distribution of both animals and cotton balls was automatically recorded by RFID (Radio-Frequency Identification Device) technique. Our results revealed a behavioral differentiation during a collective building task. In a group of six individuals, only two mice (called carriers) transported 80% of the building material whereas the contribution of the remaining mice was weak or even non-existent. The proportion of carriers was constant in all of the six groups studied. This behavioral differentiation was implemented immediately after the building material was made available and remained stable during the 4 days of experiment. The high contribution level of carriers did not result from resource monopolization, nor did it depend on the gender or parental origin of the mice.

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1. Introduction

Collective behaviors are one of the most fascinating areas of ethology, as they can explain a multitude of complex phenomenon such as dynamics of human crowds, pelagic fish schools or ungulate herds (Ballerini et al., 2008). Animal societies are characterized by numerous communal activities sometimes governed by a task allocation. Indeed, a task allocation with animals specialized in specific activities is considered to be more efficient than a sequential activity performed by unspecialized individuals (Gordon, 1989) since there is no need to reassign the tasks to the members of the community which may cost time and requires a complex communication network (but see Dornhaus, 2008 for discussion).

Various studies have illustrated the existence of such a phenomenon in social insects and this is thought to be determinant in their ecological success (reviewed in Robinson, 1992). Social animals are involved in diversified tasks such as foraging (Arnold et al., 2005), tunnel excavation (Ebensperger and Bozinovic, 2000), or nest guarding (Clutton-Brock et al., 2003). To explain this behavioral heterogeneity, different theoretical models have been developed (Beshers and Fewell, 2001; Traniello and Rosengaus, 1997). Among others, response threshold models postulate that

individuals have internal threshold to respond specifically to stimulus associated with task (Robinson, 1992; Beshers and Fewell, 2001). The variation in response thresholds may be explained by differences in genetics and epigenetic factors such as morphology, age, developmental state and experience (Beshers et al., 1999; Jeanson et al., 2008; Robinson et al., 2009). This behavioral flexibility is a key feature to enable the colony to grow, develop and ultimately reproduce.

In mammals, only a few studies have investigated the possible role repartition during collective behavior. In the lion (*Panthera leo*), during collective hunting some females circle a prey toward others hidden in the centre waiting for the prey (Stander, 1992). Similarly in bottle-nosed dolphins (*Tursiops truncatus*), Gazda et al. (2005) illustrated a behavioral differentiation during group hunting: one individual was the “driver” herding the fishes in a circle toward the remaining “barrier” dolphins. In these two examples, animals show group behavior for achieving a common goal.

Under laboratory conditions, Colin and Desor (1986) demonstrated the existence of a behavioral differentiation in Wistar rats. They exposed groups of six animals to an experimental design in which access to the feeder was made difficult by progressively immersing the only way of access with water. In this foraging task, two rats dived and brought back food pellets to the cage (divers) while the four others (non-divers) stayed in the home cage and obtained food only by stealing it from the divers. Identically, Nejdí et al. (1996) demonstrated

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the emergence of behavioral differentiation in groups of mice C57BL/6J exposed to the same water tank social interaction test. In contrast to what was observed in lions and dolphins, the behavioral differentiation in these rodents took place as a result of individual strategies.

Among the huge variety of collective behaviors, the ability to build sophisticated nests is fascinating for scientists. Nests provide protection against predators (Schradin, 2005; Ebensperger and Blumstein, 2006) and shelter against harsh environmental conditions (Hansell, 1993; Deacon, 2006; Hölzl et al., 2009); moreover nests are often a central place for the exchange of information between members of a social group. Collective building is found in various taxa but asymmetrically around the animal spectrum (Hansell, 1984). It is particularly well represented in social insects with extraordinary examples of architectural complexity found in termites, ants, wasps and bees (reviewed by Théraulaz et al., 1998a) and also birds (Hansell and Overhill, 2005). Commonly, social insects show a behavioral differentiation during the building of their sophisticated nests that can go from a simple difference in the level of participation (O'Donnell, 1998) to some more complex phenomena (Franks and Deneubourg, 1997).

In mammals, the ability to build nests occurs more sporadically and is limited to some orders like rodents (e.g. Jones, 1984; Ebensperger and Cofré, 2001; Layne, 1969; Rosell et al., 2005), lagomorphs (Deutsch, 1957), and carnivores (e.g. Neal and Cheeseman, 1996) which are often good burrowers, and to some primates with nest building by apes (Bolwig, 1959; Goodall, 1962; Casimir, 1966; Harrison, 1969; Fossey, 1974). A particular exception concerns humans whose building capacities led to the beginning of sedentarization and played a remarkable role in the conquest of new territories (Finlayson et al., 2011). In rodents, one of the most documented examples of collective building is found in the atypical naked mole rat *Heterocephalus glaber* whose social system resembles those of eusocial insects. This mammal lives in large colonies structured around a unique breeding female. As described previously in other types of collective behaviors and in addition to their reproduction skew, the naked mole rat is also characterized by the existence of a behavioral differentiation (Sherman et al., 1992; Burda et al., 2000). During the collective building task, three categories of individuals have been characterized: “frequent workers” specialized in foraging and nest building, “infrequent workers” performing the same task as “frequent workers” but at less than half the rate, and the “non-workers” which very rarely dig or carry materials (Jarvis, 1981). As a eusocial species the naked mole rat seems to be rather unique and there is no other work mentioning behavioral specialization in mammalian collective building.

In this regard, the non-eusocial wild mouse *Mus spicilegus* is an extremely interesting model to explore the characteristics of collective building behavior. At the beginning of autumn, juveniles from several parental units gather and start building a voluminous and rather sophisticated mound in a very precise temporal sequence (Festetics, 1961; Orsini et al., 1983; Garza et al., 1997; Hölzl et al., 2009). First, they collect plant materials, pile them up in a selected place and cover the vegetal pile with soil. Hölzl et al. (2009) demonstrated that they select mainly *Amaranthus* spp., *Chenopodium* spp. and *Setaria* spp. as building materials, with a positive relationship between their availability within 3 m and mound size. Then they dig a set of tunnels below this mound and push the excavated soil out of on the mound. On top of the mound they deposit clay tiles which are extracted from so-called mines located in the surroundings (Bihari, 2004). Finally, the tunnel network is completed with one or two nest chambers. The mice remain inside the mound during winter without reproducing (Gouat et al., 2003a) and get out of it to disperse in spring (Gouat et al., 2003b). The mechanism by which individuals congregate to build mounds is kin-based since mothers of juveniles found inside the mounds are more related than

if they had been chosen at random from the population (Garza et al., 1997; Poteaux et al., 2008). This collective behavior can be triggered under laboratory conditions by mimicking autumn conditions and by offering cotton balls as building materials to groups of juvenile mice from different parental origins. We used an original Radio-Frequency Identification system which records automatically in real time the localization of both animals and building materials.

Festetics (1961) suggested that only “two to six mice may be responsible of the construction” whereas up to 25 juveniles animals can be found inside a mound (Poteaux et al., 2008). The aim of our study was to test whether a behavioral differentiation occurred during the construction of the mound by the mouse *M. spicilegus*. We hypothesized that some individuals may specialize in carrying building materials whereas others would be poorly or not involved at all. This potential difference could reveal for the first time the existence of a task distribution during collective building work in a non eusocial mammalian species.

2. Material and methods

2.1. Animals and housing conditions

Thirty-six experimental animals were obtained from nine wild mound-building pairs derived from a stock caught in Hungary in October 1999 and reared for 11 generations under laboratory conditions ($20 \pm 1^\circ\text{C}$) with a 14:10 h light: dark cycle. The young were housed with their mother and father until 35 days of age in standard polycarbonate cages (28 cm \times 41.5 cm and 15 cm high) with sawdust (Special Diet Services, Witham, Essex, UK) and cotton balls as nest material. Food (type M20, Special Diet Services, Witham, Essex, UK) and water were supplied ad libitum. When 35 days old, mice were weaned and transferred into new cages in a climatic chamber with a 14:h:0 h light:dark cycle (dark phase begun at 11 am) and a room temperature progressively lowered to 14°C to stimulate building activity and social cohesion. Indeed, the decrease in temperature allowed a more efficient social bonding within mixed litters groups, with a higher level of tolerance between animals as shown by unpublished experiments (Mala and Gouat, unpublished data). At 42 ± 2.2 days of age, the mice were allocated to six groups composed of six individuals. Each group was made of three pairs, i.e. one male and one female, originating from three different litters. They were placed in the experimental device 10 days before the beginning of the testing period.

2.2. RFID technique

Recording movements of animals in a complex environment, even under laboratory conditions, has always been a challenge in the study of behavior. Video recording is frequently used for this purpose but automation, even with modern techniques based on digital image analysis, remains difficult to implement when several animals are concerned or when conditions are not ideal for observations (during dark cycle for instance). By contrast, Radio-Frequency Identification (RFID) is a technique which allows recording automatically in real time and during a long period the localization of each animal or objecting. A typical RFID system consists of the following units: (i) a tag or transponder, attached to the item which will be tracked, (ii) a reception antenna, (iii) a data processing system to record the data. The RFID Anti-Collision System developed by SpaceCode (Verrières-le-Buisson, France) uses small passive glass tags (length: 12 mm; diameter: 1.5 mm), which have unlimited lifespan and contain no battery. A magnetic antenna detects the presence of each tag, and several tags may be detected at the same time thanks to the anti-collision system. This antenna is connected to a computer through an electronic device. The identification

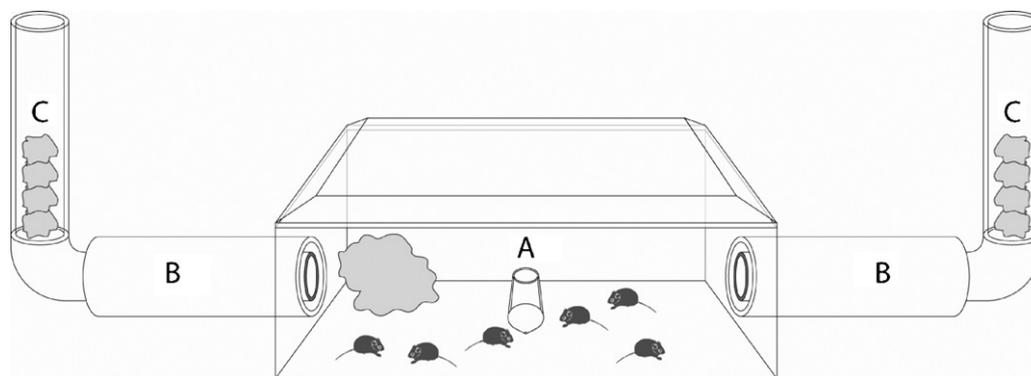


Fig. 1. Mound building device. A large cage (A) was connected to two dispensers containing tagged cotton balls (C) through tunnels (B) circled by RFID antennas (two for each tunnel).

number of the tag and the exact time of detection were recorded. There is no limitation in the number of tags (individuals or objects) or in the duration of the recording. The data are thus collected for the requested time span, pre-processed and saved in a database for further analysis. Kritzler et al. (2006) showed that the use of RFID technology does not alter social behavior and the outward appearance of laboratory mice.

For the experiment, each individual was identified by a small tag which was directly implanted by dorsal subcutaneous injection. Moreover, each cotton ball, used as building material, was identified by sticking a tag inside it. The processing system could thus record all the movements of both mice and building items.

2.3. Testing apparatus

The testing apparatus consisted of (A) a plastic cage (28 cm × 41.5 cm and 15 cm high) with sawdust and twelve cotton balls to initiate the building process (food and water were provided ad libitum) (B) two plastic tunnels (diameter 4 cm, length 50 cm) leading to (C) two vertical dispensers of cotton balls (Fig. 1). Each tunnel was encircled by a double RFID antenna: one near the cotton ball dispenser and one near the plastic cage. This made possible to detect the moving direction of the RFID tag.

2.4. Testing procedure

Ten days before the beginning of the testing period, the six groups of mice were placed in the experimental device but had no access to the tunnels. In field conditions, Szenczi et al. (2011) analyzed *M. spicilegus* feces which revealed that the plants used as building materials are not represented in their actual diet. In laboratory conditions, cotton balls were thus chosen because of their non-edible characteristics, their small weight and their easiness to be dilacerated. Moreover, cotton balls placed on the surroundings of mounds during the piling of vegetal material can be collected by mice in the field and inserted into the mound (Hurtado, Herraira and Gouat, unpublished data). Twelve cotton balls were placed inside their cage so that they could initiate the building process. By the end of this period of socialization with alien partners, all the groups had begun mound building. On day 1 of the testing period, three tagged cotton balls were delivered in each of the two dispensers (the six mice could thus carry six cotton balls). Access to the tunnels was allowed by opening the entries. On day 2, three new tagged cotton balls were delivered in each of the two dispensers. The same procedure was continued on day 3 and on day 4. The activity of the mice was recorded continuously from day 1 to day 4. Since there were constraints associated with the cotton dispensers themselves and the available space

inside the central cage, the number of cotton balls provided was restricted.

Under laboratory observations, the maximum activity of mice is estimated at 1 h after the passage to red light and goes on average for a period of 2 h (Boucart and Gouat, unpublished data). In field conditions, above-ground activity is usually performed at dawn and throughout the night according to video monitoring (unpublished results in Hölzl et al., 2011). Tests were thus performed at 2.00 pm (3 h after the beginning of the dark cycle), corresponding to this maximal activity period. The test ended when all the cotton balls were collected, but the data recording was continuous during the whole experiment period.

Transport of a cotton ball was attributed to a mouse when the tag was detected moving inside a tunnel from the dispenser to the cage. When two mice were detected at the same time with a cotton ball, they were each considered as transporting 0.5 cotton ball.

2.5. Behavioral observations and statistical analysis

Due to the sample size, non parametric statistical analyses were performed using the exact procedure (Mundry and Fischer, 1998). All the statistical analyses were performed using StatXact-8 (Cytel Inc., Cambridge, MA 02139, USA). Data are given as mean ± SEM.

2.5.1. Characteristics of cotton balls transport

2.5.1.1. Time spent to collect the cotton balls. The time spent to collect the cotton balls was measured from the first to the last detection of a cotton ball in a tunnel for each day of test. A test of Friedman was used to determine if mice improved their performance during the 4 days of the experiment.

2.5.1.2. Individual contribution to the transport of cotton balls. To determine whether mice differed in their contribution to the transport of cotton balls, animals were ranked inside each group according to the number of cotton balls they transported during the 4-day period of the experiment. Rank #1 was attributed to the individual with the highest contribution to the transport. Mice tend to manipulate roughly the cotton balls during transport and some tags detached from the cotton balls and could not be detected. As a result the number of transported balls may slightly differ between groups (4–6 for each day; mean ± SEM: 5.5 ± 0.2). We then compared the performance of the mice, according to their ranks, to the average performance of each group using a permutation test for paired data. Average performance corresponded to the number of cotton balls detected divided by six, the number of mice within a group. Individuals with a contribution

rate higher than the average value of the group were then called carriers.

To test the stability of individual relative contributions we analyzed the performance of the mice with a day-by-day analysis using a test of Friedman. Performances were also compared between carriers of different ranks and between carriers and non-carriers using permutation tests for independent samples using group as a stratum.

2.5.2. Alternation between the two dispensers

Mice collected cotton balls either by alternating between the two dispensers or by emptying one dispenser after the other or by a combination of these two strategies. To describe the strategy used we calculated the number of changes from one dispenser to the other. This value varied from 1 up to 5. To determine if a strategy was more common than others, we compared the observed frequency of each type of strategy to the theoretical probability obtained by chance (respectively, 1 or 5 changes $p = 1/10$; 2 and 4 changes $p = 2/10$; 3 changes $p = 4/10$). Because the mice were inexperienced at performing the task on the first day of the experiment we tested whether a global change of strategy occurred during the 4 days of experiment using a test of Friedman.

2.5.3. Behavioral characteristics of the carrier and the non-carrier mice

Mice movements were recorded continuously during the full 4 days of the experimental period since access to dispensers was possible. The time spent in each part of the apparatus by each animal could be deduced from our data. We then compared the time spent in each part of the apparatus between mice according to their rank using a permutation test for independent samples and group as a stratum. The analysis was performed for the complete period of observation, and then to the limited period when cotton balls were available from the dispensers.

2.6. Ethical note

Animal care and experimental procedures were approved by an Ethic committee (Regional Ethics Committee in Animal Experiment No. 3 of Ile-de-France: p3/2007/023). The number of mice used was strictly restricted to the minimum needed for statistical analysis. Subcutaneous injection of the tag was performed 3 days before constituting the groups of six mice by an animal keeper specifically trained in order to limit stress of individuals. Mice were taken from their cage very carefully and the injection which lasted only a few seconds was realized as gently as possible. Their behavior was systematically observed 24 h after the procedure. Young mice behaved normally and did not seem to be affected by the injection.

After the experimental period, mice were placed in familiar groups of the same sex to avoid aggression when reaching sexual maturity. Since these animals were already identified with RFID tags, they were kept and used to adjust subsequent protocols involving the RFID technique.

3. Results

3.1. Characteristics of cotton balls transport

3.1.1. Time spent to collect the cotton balls

On the first day of the test mice investigated the tunnels very quickly and adopted different strategies to cross the tunnels with their load. They could either push or pull the cotton balls using their mouth as well as their forelegs. Mice spent 15.8 ± 1.7 min to collect and transport six cotton balls (range: 4.2–36.2 min). The time spent for collecting six cotton balls varied day after day for each group, but no significant decrease was revealed (respectively from D1 to

D4: 17.2 ± 4.9 min; 20.6 ± 3.6 min; 13.7 ± 2.0 min; 11.6 ± 1.7 min; Friedman ANOVA, $\chi^2 = 3.8$, $p = 0.32$).

3.1.2. Individual contribution to the transport of cotton balls

Inside each group, mice could be ranked according to the number of cotton balls they collected during the 4-day experiment. Mice ranking first and second transported $79.5 \pm 5.4\%$ (range: 67.3–98.1%) of the cotton balls. This observed contribution was significantly higher than the theoretical value for an equal contribution of each rank (Fig. 2); whereas contribution of mice from rank three to six was significantly lower than the theoretical value ($p = 0.031$ for each rank, permutation tests for paired samples; Fig. 2).

Over the 4 days of the experiment, in each group two mice transported clearly more cottons than the average (range for respectively rank # 1: 38.5–58.5%; rank # 2: 23.1–46.2%) and behaved as carriers whereas the overall contribution of the other four mice in each group was always lower than the average (range: 0–13.5%). Of the twelve carriers identified, five were females and seven were males, originating from eight of the nine reproductive pairs used in the experiment. In five of the six groups, carriers were originating from two different litters.

A day-by-day analysis confirmed these results (Fig. 3). In this analysis the rank was attributed to each mouse of a group according to its performance on the first day. Although the two carrier mice may shift rank from 1 day to the next, they did not differ from each other in their contribution to cotton ball collection (p respectively day 1: $p = 0.06$; day 2: $p = 0.25$, and $p > 0.93$ for days 3 and 4) but they always differed significantly from the non-carrier mice ($p = 0.03$ for each day; Fig. 3). The contribution of each individual remained stable during the 4-day period and no significant change was observed over time (Friedman ANOVA, $\chi^2 = 1.032$, $p = 0.79$).

3.2. Alternation between the two dispensers

The most common strategy used by the mice was to empty a dispenser and then to collect cotton balls from the other dispenser (Fig. 4) even though it did not differ significantly from theoretical frequency (permutation test for paired data: $p = 0.063$, $N = 6$). Though being the most expected by chance, three changes of dispenser was far from common (permutation test for paired data: $p = 0.063$, $N = 6$). A systematic alternation between dispensers was

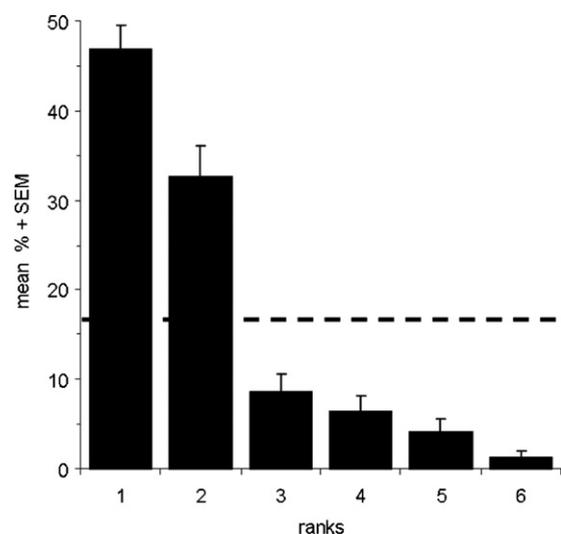


Fig. 2. Individual contribution to the global cotton ball transport. The observed contribution (in percentage of the total cotton balls) for each rank was compared to the expected equal contributions of each group represented by the black line.

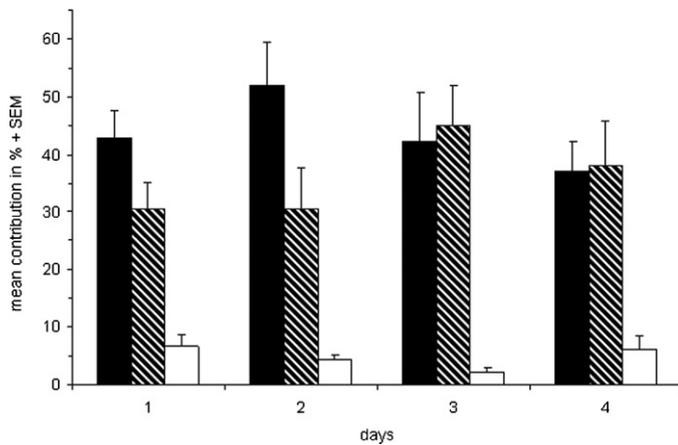


Fig. 3. Individual contribution to the cotton ball transport for each day of test. Black bars: carrier mice from rank # 1; hatched bars: carrier mice from rank # 2; white bars: non-carrier mice.

observed only once in a single group on 1 day and this result did not differ from random distribution ($p=0.22$; Fig. 4).

A day-by-day analysis did not reveal any significant global changes (Friedman ANOVA, $\chi^2=4.46$, $p=0.36$). Nevertheless each group could change strategy from 1 day to another. On day 3, four groups out of six had emptied one dispenser before fetching cotton balls in the other one (i.e. one change), and this proportion differed significantly from a random distribution ($\chi^2=21.41$, $df=5$, $p=0.0013$).

3.3. Behavioral characteristics of the carriers and the non-carriers mice

3.3.1. Time spent in the different parts of the device during the 4-day experiment

Dispensers were freely accessible during the 4 days of the experiment (mean duration of the full experiment \pm SEM: 72 h 11 min \pm 17 min). During this 4-day experiment, mice spent on average $9.1 \pm 1.3\%$ of their time inside the tunnels and the dispensers and never more than 20% except for a non-carrier female which spent 49% of its time in this part of the apparatus. The proportions of this time did not significantly differ between carriers and non-carriers (permutation test with group as stratum; $p=0.71$; Fig. 5(a)).

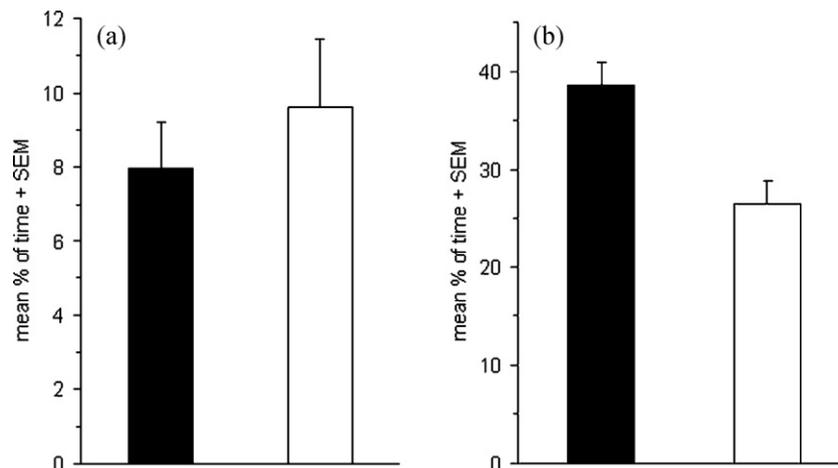


Fig. 5. Percentage of time spent (mean \pm SEM) by the carrier mice (black bar) and the non-carrier mice (white bar) of the six groups inside the tunnels and the dispensers during the 4 days of the experiment (a) and only during the limited period when cotton balls were available in the dispensers (b).

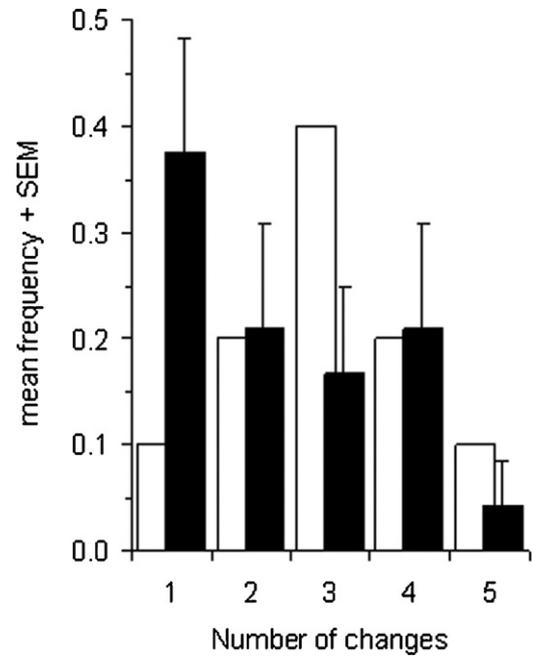


Fig. 4. Frequency of the number of changes (mean \pm SEM) of dispensers during collection of cotton balls for the 4 days of the experiment. White bars: theoretical frequencies; black bars: observed frequencies.

3.3.2. Time spent in the different parts of the device during the cotton balls' delivery

The mice spent clearly more time in the dispensers and the tunnels when cotton balls were available than during the full period of 4 days of experiment (mean \pm SEM: $30.5 \pm 2.0\%$; permutation test for paired samples: $p<0.001$, $N=36$). Carriers spent significantly more time than non-carriers inside the dispensers and tunnels when cotton balls were available (permutation test with group as a stratum: $p=0.003$; Fig. 5 (b)).

4. Discussion

The main objective of our study was to examine whether behavioral differentiation could arise in the early stages of mound construction by juvenile mice. By providing cotton balls as building materials we succeeded in recreating appropriate conditions to initiate a collective building process in groups of six mice. During the

10-day period of socialization, mice began to build the mound as soon as they had free access to cotton balls put inside their cage in all the groups observed. When the experiment started, the task was more complicated since animals had to walk through tunnels to go to the dispensers delivering cotton balls. The mice had to transport the balls from the dispensers to their cage in order to incorporate them to the mound being built. In all cases, cotton ball transportation was performed with very short delays (on average 15 min) even on the very first day, demonstrating both the attractiveness of the task and the high level of adaptability of *M. spicilegus* challenged with a new situation. The totality of the transported material was shredded and used to build the communal nest.

When analysing the individual contribution to the transport of building materials, two behavioral profiles emerged. In each group and for each day of test, two out of the six mice achieved almost 80% of the transport whereas the contribution of the four other mice was limited or even nonexistent. This behavioral differentiation was not related to gender or parental origin, since carrier mice were both females and males originating from different litters. Moreover, the emergence of behavioral differentiation was implemented as soon as the first cotton ball was available, suggesting that such behavior can appear spontaneously in the social group. Interestingly, the identity of the carriers did not change over the 4 days showing that once behavioral profiles are set, they do not change. Our result corroborates the behavioral differentiation observed during collective tunnel building in the naked mole rat (Jarvis, 1981), during group hunting in dolphins and lions (dolphin: Gazda et al., 2005; lion: Stander, 1992) and during a conflicting foraging task in laboratory rodents (Colin and Desor, 1986; Nejdí et al., 1996).

In experiments where rats had to dive to access for food (Colin and Desor, 1986; Krafft et al., 1994), it is interesting to note that within groups of six animals, the number of divers was in the same proportion as ours (2/6) even though our conditions did not impose such drastic constraint. In the conflict diving-for-food situation, it has been shown that the occurrence of non-divers was strongly influenced by group size (Thullier et al., 1992). A similar result was described in insect colonies where changes in the division of labor could be artificially induced by altering colony size (e.g. Winston and Fergusson, 1985). In our experimental conditions, we can therefore wonder to what extent the number of carriers is influenced by group size.

Our data revealed that in each group, two mice transported most of the cotton balls suggesting that task distribution may have resulted from the monopolization of the resource by the two carriers. With two dispensers available, one may hypothesize that only two individuals could monopolize them, each mouse choosing a specific dispenser that they could empty and in which they would spend the majority of their time. In fact our results showed that this was not the case, the most common strategy being to empty one dispenser and then the other which precludes any resource monopolization by specific mice. Moreover, when we analyzed the behavioral characteristics of the carriers and the non-carriers, whatever their rank in the transport of cotton balls all the mice spent equivalent amounts of time in the different parts of the device (the two dispensers, the two tunnels and the cage), rejecting the resource monopolization hypothesis. Nevertheless, during cotton balls deliveries, carriers spent more time in the tunnels and the dispensers than non-carriers, indicating a renewed attractiveness for this part of the device only when building materials were available. These data corroborate the demonstration of a real behavioral differentiation illustrated for the first time during a collective building process in a non-eusocial mammal. The question of the potential role of non-carrier mice, which could be dedicated to other kind of activities in the building process, remains to be investigated by additional laboratory observations. Furthermore, future studies would be necessary to determine the possible costs and benefits of

individual involvement in mound building. One may hypothesize that this task allocation achieves an energy saving since only carrier mice are exposed to the energetic costs of harvesting and transport. It also reduces the exposure of the non-carrier mice to predators in the field.

The emergence of such a behavioral differentiation, with a ratio of carriers being constant between groups and stable over the time, remains to be explained and is yet a subject of debate. The self-organization concept states that complex patterns can emerge spontaneously by means of simple and local interactions among the animals (Camazine et al., 2001). According to Bonabeau et al. (1997) highly structured collective behaviors do not rely on individual complexity. Based on this assumption, researchers have developed theoretical models for studying self-organizing systems. In insect societies, the phenomenon of task distribution has been modeled by a mechanism called response thresholds (Théraulaz et al., 1998b; Bonabeau et al., 1999) which explains the genesis of specialization in a group of homogeneous individuals. In mammals, only one mathematical model has been developed to simulate rat collective behaviors in a foraging situation (diving-for-food situation: Colin and Desor, 1986): the Hamelin theoretical model created by Thomas et al. (2004). By merging two models (adaptive response thresholds and dominance relationships), the Hamelin simulation system managed to reproduce the behavioral differentiation observed by biologists in groups of rats confronted to an increasing difficulty to reach food. This simulation (i) enables to explore the influence of numerous factors (number of animals, external conditions) on task performances and (ii) illustrates the way local rules (dominance hierarchies and hunger of the rats) can explain the emergence of the two behavioral profiles (the divers and non-divers rats) without requiring a high degree of complexity at the individual level. This theoretical model highlights the importance of local rules, responsible for the emergence of behavioral differentiation in rats considered like homogeneous agents without social recognition. Nevertheless, one cannot exclude that these local rules might interact with individual complexity to explain the task distribution observed in vivo. In collective mound building by *M. spicilegus*, could the emergence of carriers within a group have also resulted from an intrinsic predisposition of some individuals to explore new environments or novel objects (e.g. being less fearful or more curious) and carry materials? In rats, it has been reported that early behavioral features can predict behavioral profiles of adults in the difficult food supply situation (Deviterne et al., 1993). Similarly in mice placed in the same feeding experimental challenge, it has been found that major divers have a tendency to be less anxious than non-divers (Nejdí et al., 1996) which suggests a relationship between individual characteristics and task repartition. In this way, further research characterizing body weight, level of anxiety, degree of affinity with the building materials, general activity and novelty seeking behavior, should be undertaken in order to evaluate the possible connection between carriers' behavioral profiles and morphological traits. In addition, others studies investigating in what extent the size of the group and the availability of the building materials could have an influence on the ratio of carrier and non-carrier mice may be undertaken. Indeed, in insect societies, Gautrais et al. (2002) found that increasing the overall work demand while keeping the colony size constant causes an increase in the differentiation among individuals in their activity levels. In the same way, increasing colony size while keeping the demand proportional to the colony conducts to a similar result.

5. Conclusions

Life history traits of mice *M. spicilegus* gave us the opportunity to demonstrate that behavioral differentiation during collective

building is not limited to eusocial species. The stability of the proportion observed during specialization (two carrier mice and four non-carriers) remains a fascinating area to explore in regards to intrinsic characteristics of animals and self-organization.

Acknowledgments

This project was funded by an ANR (“Agence Nationale de la Recherche”) grant (05-BLAN-017701). We thank Simone Demouron for investing her time and for her efficiency in taking care of the animals.

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