Neurosciences / *Neurosciences*

A new case of jumping behaviour in ants, as part of the foraging strategy

Un nouveau cas de comportement de saut intégré à la récolte alimentaire chez les fourmis

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Abstract — We demonstrated for the first time in this laboratory study that the tree-dwelling ant *Polyrhachis laboriosa* can jump down beyond any context of escape or predation. When it is necessary to jump to reach an isolated food supply or explore a larger territory, workers of *P. laboriosa* jump down from a height of 5–100 cm. The characteristics of this active jumping display are described here. During foraging or exploratory conditions, the workers learnt to jump and integrated this behaviour into their strategy of exploitation of the 3D-environment. Under laboratory conditions, they began to jump earlier and more frequently as a function of their motivation during successive tests. © Académie des Sciences / Elsevier, Paris

Formicidae / Polyrhachis / jumping / visual orientation / learning

Résumé — Ce travail constitue la première étude en laboratoire du saut chez une fourmi arboricole en dehors de tout contexte de fuite ou de prédation. Lorsque la structure du milieu lui impose de sauter pour accéder à une source de nourriture ou explorer un territoire plus grand, *Polyrhachis laboriosa* saute activement dans le vide d'une hauteur de 5 à 100 cm. Les caractéristiques de ce comportement de saut sont décrites. Cette étude met ainsi en évidence chez P. *laboriosa* l'intégration du comportement de saut dans le système d'exploitation du milieu en trois dimensions et suggère des capacités d'orientation visuelle et d'apprentissage, les ouvrières sautant d'autant plus rapidement et fréquemment qu'elles sont motivées. © Académie des Sciences / Elsevier, Paris

Formicidae / Polyrhachis / saut / orientation visuelle / apprentissage

Version abrégée

Les rares études réalisées sur le saut chez les fourmis ont montré que certaines espèces ont intégré ce comportement dans leur stratégie de prédation ou de fuite. C'est le cas notamment de l'espèce *Harpegnathos saltator*, qui pratique jusqu'à trois types de sauts différents pour capturer des proies ou pour fuir. Ce sont des sauts actifs horizontaux qui s'effectuent au sol. D'autres espèces comme *Myrmecia varians* sautent du haut de l'arbre dans lequel elles ont capturé une proie et retournent plus rapidement au nid. Les « pluies» de *Formica aquilonia* dans les forêts européennes sont provoquées par la fuite des ouvrières lors de l'arrivée d'oiseaux dans les arbres.

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L'espèce tropicale arboricole *Polyrhachis laboriosa* saute aussi des branches lorsqu'elle fuit. Mais elle est aussi capable d'incorporer ce comportement à sa stratégie d'exploitation des ressources de la canopée, en dehors de tout contexte de fuite ou de prédation. Bien qu'elle chasse très bien, cette espèce n'utilise jamais le saut pour capturer ses proies. À l'inverse des fourmis qui capturent leurs proies en sautant, elle ne présente d'ailleurs aucune adaptation morphologique particulière à la détection visuelle ou à la chasse (yeux et mandibules fortement développés). Chez cette espèce, le saut apparaît s'il est nécessaire à l'exploitation d'une source de nourriture ou à l'exploration d'un nouveau territoire plus vaste. Les ouvrières se placent face au vide, sautent en l'air et retombent sur leurs pattes, cinq à cent centimètres plus bas.

En laboratoire, le saut semble déclenché par le confinement des ouvrières sur un territoire réduit. Il apparaît d'autant plus rapidement que les ouvrières sont motivées par la recherche de nourriture. De même, il devient de plus en plus fréquent lorsque les ouvrières sont confrontées de manière répétitive à une situation dans laquelle le saut constitue la seule alternative pour accéder à une source de nourriture ou à un nouveau territoire. Ce comportement spontané et reproductible à volonté, est le fruit d'un apprentissage individuel et témoigne de la capacité des ouvrières à mémoriser la structure du milieu lors de leurs déplacements.

Néanmoins, le saut est beaucoup moins fréquent en milieu naturel. Les ouvrières de *P. laboriosa* ne sautent que lorsqu'elles sont physiquement confinées et n'ont pas d'autre solution pour en sortir. Or, une telle situation est naturellement rare et ne se présente que si l'axe reliant la source au substrat est inaccessible (obstacle, prédateur ou compétiteur). De plus, la structure tridimensionnelle très complexe du feuillage (qui multiplie les choix dans les déplacements) et l'abondance de sources plus faciles à exploiter, diminuent la probabilité des ouvrières d'accéder spontanément à une source en sautant.

1. Introduction

Many insects have developed the capacity to jump, thanks to different mechanisms. In ants, we distinguish active jumping from passive falling, such as in *Formica aquilonia* [1]. Active jumping has always been anecdotally reported, except for *Harpegnathos saltator* [2–5]. In most of the cases, jumps were observed as escape reactions or for catching prey. [1, 2, 4, 5].

Arboreal ants move in a very complex environment (three-dimensional and cut up substrate). Different theoretic models of arboreal search in ants have been developed, to try to explain how ants optimise their foraging strategy to the structural constraints of the substrate [6–9]. On the other hand, numerous studies undertaken on visual orientation in ants, have demonstrated ant capacities to learn and memorise visuals landmarks [10–12].

Nevertheless it was not considered that jumping behaviour could be used by arboreal ants as an integral part of their strategy of exploitation of the canopy. As *Polyrhachis laboriosa* F. Smith forages mainly solitarily and spontaneously jumps, we decided to study the characteristics of jumping behaviour in this species.

2. Materials and methods

2.1. The ant species

P. laboriosa is a diurnal polydomous tree-dwelling Formicinae of the equatorial African forest, mainly recorded along forest edges, the banks of rivers, the sides of paths and in orchards (i.e. citrus, mango, cacao) [13–16]. The nests are attached to the undersides of several leaves thanks to a mixture of vegetable fragments held together with saliva and spider silk [17]. Workers forage solitarily, grazing on algae and epiphyls on leaf surfaces and exploiting individually small extrafloral nectaries. Larger sugary food sources (i.e. ripened fruits fallen on the ground) can also be exploited thanks to a group recruitment. Different kinds of prey can be caught, including large, non-transportable items that are cut up on the spot by recruited workers [18–20].

Fourteen colonies of *P. laboriosa* were collected in Cameroon (Kala, Ebodjié, Ndupé, Nkolbisson, Ebogo). Each of them contained 300–600 workers and brood and were queenless, which corresponds to the most frequent structure of a nest in nature. They were reared in plaster nests under laboratory conditions (temperature = 25 ± 2 °C; humidity rate = 65–85 %; photoperiod = 12 h).

2.2. Experimental setup

2.2.1. Device

2.2.1.1. Spontaneous jumps during simple exploratory and foraging conditions

Spontaneous jumps were studied using a simple experimental device (*figure 1*). Workers were allowed to go from the foraging arena (A) of the nest to another foraging arena (B) by walking on a wooden bridge (60 × 3 × 20 cm) connecting both arenas. Workers did not have to jump to reach all the areas of the device or to forage for the food source. Nevertheless, they could spontaneously jump from the bridge. All these jumps were noted and some of them were recorded on video to be analysed in detail. All the experiments realised using this simple device were carried out under 'simple conditions' (*table I*). Five different colonies were tested during ten successive periods of 15 min, under both simple exploratory and foraging conditions.

2.2.1.2. Forced jumps during modified exploratory and foraging conditions

Forced jumps were provoked using a modified version of the first experimental device. The nest of the colony

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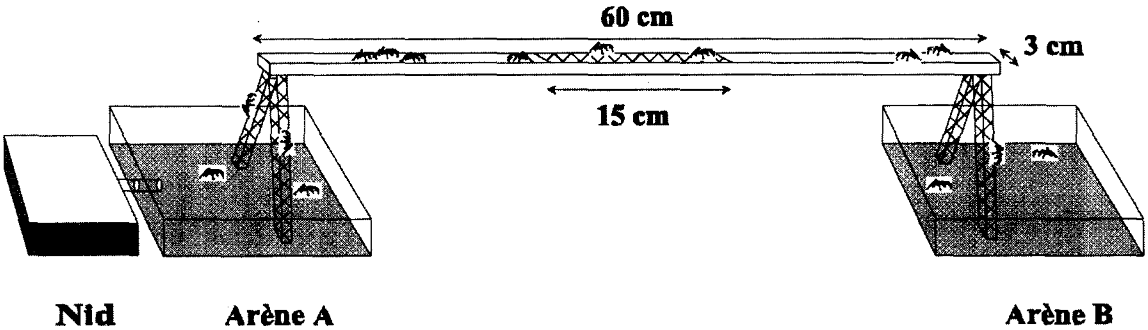

Figure 1. Basic experimental device used for the study of spontaneous jumps during exploration and foraging in *P. laboriosa*.

tested and its foraging arena (A) were 'connected' to the second foraging arena (B) with two suspension bridges (*figure 2*). Both bridges were placed head to tail between (A) and (B), the basis of each bridge being placed in one or the other foraging arena. The workers were thus forced to jump down from the first bridge to explore or forage in the arena (B) and from the second bridge to go back to their nest. All the experiments realised using this modified device were carried out under 'jumping conditions' (*table I*).

– Three fed colonies were tested under jumping exploratory conditions.

– Six colonies were tested under jumping foraging conditions. Three of them were tested with a 0.1 M sucrose solution (not attractive at a distance), and the three others with a sweet-smelling mixture of honey and apple (more attractive at a distance).

Each test lasted 30 min, during which we noted the latency of the first jump and the number of jumps performed by the ants from each bridge. The test was repeated three times per colony (T1 to T3), 2 days separating each repetition in order to recover the same degree of starvation.

Table I. Characteristics of the different experimental conditions.

Condition	Device	Kind of food	Colonies	Kind of jump
Simple exploratory conditions	simple device (*figure 1*)	apple–honey in arena A	5	spontaneous
Simple foraging conditions		apple–honey in arena B		spontaneous
Jumping exploratory conditions	modified device (*figure 2*)	apple–honey in arena A	3	forced
Jumping foraging conditions	modified device (*figure 2*)	apple–honey in arena B	3	forced
		0.1 M sucrose in arena B	3	forced

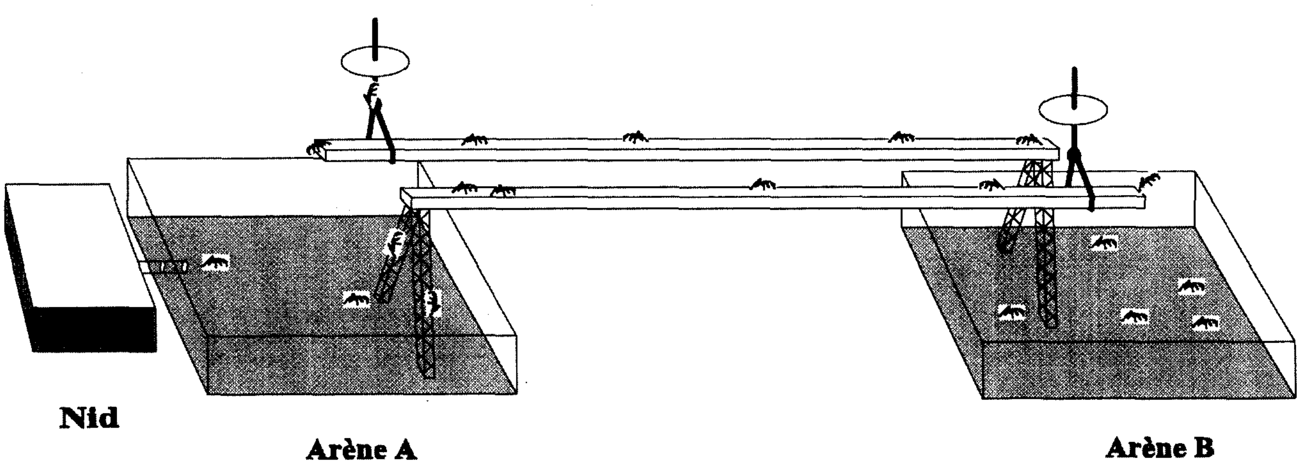

Figure 2. Experimental device used for the study of jumps during jumping exploration and foraging conditions in *P. laboriosa*.

2.2.2. Conditions

2.2.2.1. Exploratory conditions

Each tested colony was fed 1 day prior to the beginning of the experiment. The food was placed in the arena (A) and left throughout the experiment. The arena (B) was empty.

2.2.2.2. Foraging conditions

The tested colony was starved for 7 days (preliminary experiments showed that this was the optimal period for eliciting foraging behaviour). On the 7th day, (A) and (B) were connected by the bridge(s). Food was only placed in (B).

2.3. Statistical analysis

The results obtained with the five colonies tested under both simple exploratory and foraging conditions, were compared using a non-parametric Wilcoxon test.

Comparisons between the different modified experimental conditions were conducted using ANOVA/MANOVA for repeated measures and post-hoc Newman-Keuls and LSD tests (STATISTICA© software). Learning of jumping behaviour was analysed by comparing the results between the successive tests of each experimental condition.

3. Results

3.1. Description of the jump

Each jump is preceded by an intense exploratory period, during which the worker rears on its mid and hind legs and moves its antennas forward. When encountering the limits of the substrate, the worker bends its head forward and paddles the air with its forelegs. It can attempt to jump: while thrusting with its mid legs, the worker continues to clutch at the substrate with one or two hind legs. Then it turns back to the substrate and tries to jump again.

We observed two different kinds of jumps.

– Jumps with active thrust: when jumping, the worker violently raises up its gaster and throws itself forward with its mid legs. As a consequence, the trajectory of the ant is obviously curved. In most of the cases, the worker falls on its legs.

– Jumps without active thrust = falling down: the worker is generally on the lower side of the substrate. It grips the substrate with mid and hind legs, then progressively loses its hold and falls down. Its trajectory is vertical and it does not systematically fall on its legs. These kinds of jumps were considered as passive and were not taken into account.

3.2. Spontaneous jumps under simple exploratory and foraging conditions

The average number of spontaneous jumps is significantly greater during exploration than during foraging (6 versus 0.5/15 min, respectively; Wilcoxon test: $Z = 2.8$; $P = 0.005$) (*figure 3*). The workers jumped from one side of the bridge to one of the two arenas (61 % of the jumps), from the middle of the bridge out of the arenas (23 % of the jumps) or from one 'pile' of the bridge (16 %). No evolution as a function of time was observed.

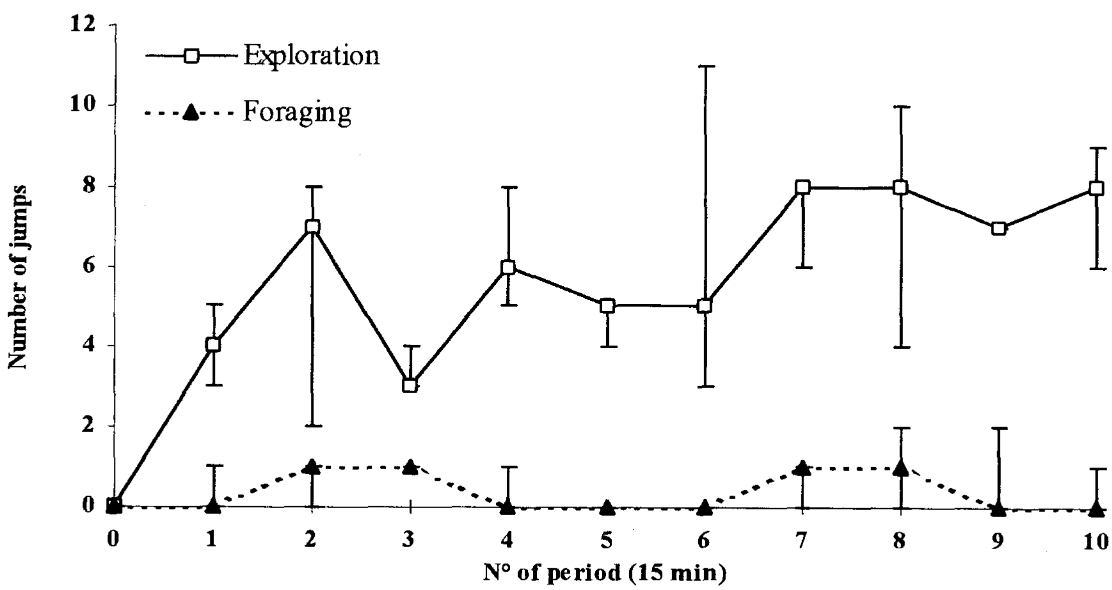

Figure 3. Median number (with quartiles) of spontaneous jumps of workers of *P. laboriosa* under simple exploratory and foraging conditions ($n = 5$).

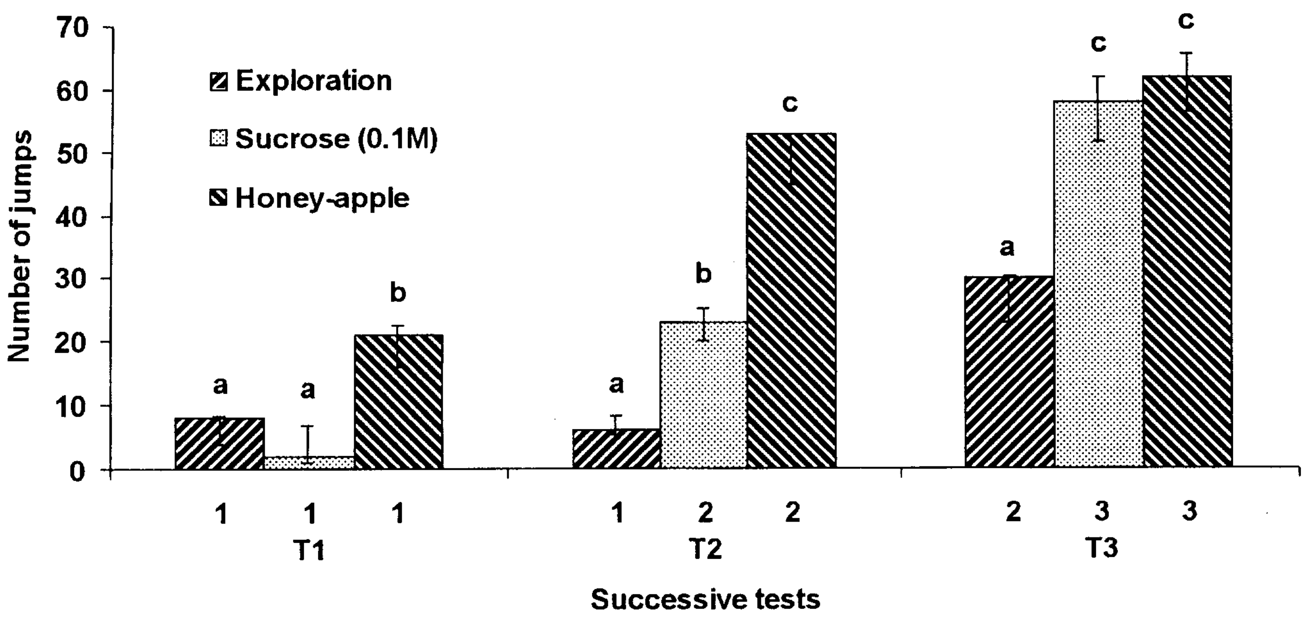

Figure 4. Median number of jumps (with quartiles) on the way to to the arena (B) by workers of *P. laboriosa* during three successive tests (T1, T2, T3; 1-day intervals) ($n = 9$). a, b, c: statistically significant differences between the three experimental conditions for each successive test (ANOVA). 1, 2, 3: statistically significant differences between the three successive tests for each experimental condition (ANOVA).

3.3. Jumping behaviour under jumping exploratory conditions

Under exploratory conditions, the well-fed workers did not exploit the food supply in the arena (A). Most of them climbed onto the suspension-bridge, explored it and tried to jump. The median latency of the first jump down to the arena (B) significantly decreased from the 1st day (T1) to the 3rd day (T3) (T1: 18'33" – quartiles: 17'41"/20'24"; T2: 15'29" – quartiles: 13'02"/16'27"; T3: 5'46" – quartiles: 5'03"/9'36"; $P < 0.05$). The mean number of jumps down to (B) and back to (A) was low during T1 (2.5/15 min) and significantly increased between T1, T2 (/15 min) and T3 (/15 min) (*figures 4* and *5*). The total average percentage of jumps down to the arena (B) and back to the arena (A) increased from 30 (T1) to 63 % (T3).

3.4. Jumping behaviour under jumping foraging conditions

Whatever the experimental foraging conditions, the mean number of jumps on the way to the food supply or to return to the nest increased significantly from T1 to T2, and from T2 to T3 (*figures 4* and *5*). The mean number of jumps observed on the way to forage during T1 and T2 was significantly higher when foraging on a sweet-smelling supply than on a 0.1 M sucrose supply (*figure 4*; honey–apple versus 0.1 M sucrose; T1: $P < 0.01$; T2: $P < 0.001$). No difference was observed between these two experimental conditions during T3.

The mean number of jumps observed on the way back to the nest during T2 and T3 was significantly higher when foraging on a sweet-smelling supply than on a 0.1 M sucrose supply (*figure 5*; honey–apple versus 0.1 M sucrose; T2: $P < 0.001$; T3: $P < 0.05$). No difference was observed between these two experimental conditions during T1.

Under both foraging conditions, the median latency of the first jump into the arena B decreased significantly between T1 and T3 (honey–apple: T1: 12'25" – quartiles: 12'18"/21'12"; T2: 9'48" – quartiles: 8'35"/12'38"; T3: 4'53" – quartiles: 4'26"/7'21"; $P < 0.05$) (sucrose 0.1 M: T1: 17'02" – quartiles: 12'32"/18'25"; T2: 16'10" – quartiles: 15'34"/17'13"; T3: 5'14" – quartiles: 5'08"/6'29"; $P < 0.05$). It was not significantly different between conditions for each test.

The median latency of the first jump on the way back significantly decreased between T1 and T3 for honey–apple foraging conditions (T1: 27'02" – quartiles: 26'33"/28'31"; T2: 18'11" – quartiles: 16'13"/18'57"; T3: 12'21" – quartiles: 11'05"/15'06"; $P < 0.05$) and between T2 and T3 for 0.1 M sucrose foraging conditions (T1: 29'17" – quartiles: 26'31"/29'38"; T2: 22'18" – quartiles: 20'02"/26'09"; T3: 17'11" – quartiles: 12'45"/20'48"; $P < 0.05$). It did not vary significantly between foraging conditions.

4. Discussion

Spontaneous jumps are more numerous during simple exploratory than simple foraging conditions. On the contrary, forced jumps are more numerous during jumping foraging than jumping exploratory conditions. In fact, when foraging, workers jump only if it is necessary for them to reach the food source or to go back to their nest.

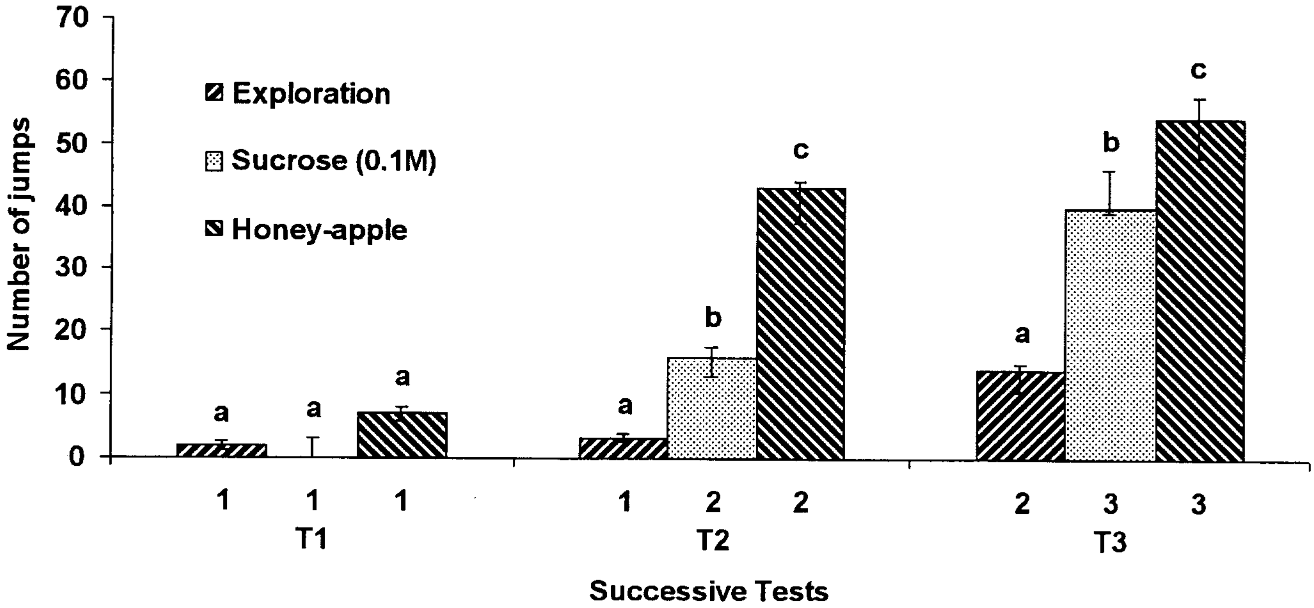

Figure 5. Median number of jumps (with quartiles) on the way back to the arena (A) by workers of *P. laboriosa* during three successive tests (T1, T2, T3; 1-day intervals) (n = 9). a, b, c: statistically significant differences between the three experimental conditions for each successive test (ANOVA). 1, 2, 3: statistically significant differences between the three successive tests for each experimental condition (ANOVA).

Observations in nature showed that jumps are less frequent than in the laboratory, because the workers prefer to find another path to reach the supply rather than jumping. The structural complexity of the foliage (which frequently permits them to find another path) and the abundance of other food sources easier to exploit (which motivates the forager more) decrease the probability that a worker will jump. Nevertheless, when well-fed or starved workers are confined on an isolated food supply, 100 % of them jump down after having explored the substrate or having foraged on the food source. This behaviour is reproducible at will: in our rearing devices, jumps from the birds' drinking trough placed in the foraging arena of each nest are very frequent.

The first study on jumping behaviour was performed in *Harpegnathos saltator* [5]. The authors distinguished three kinds of jumps thanks to physical (length and frequency distribution) and behavioural criteria: escape jumps, hunting jumps and group jumps. All these jumps are in length on a ground continuous plan and are related to the interaction between two individuals. Jumps in height have been reported in *Myrmecia varians* [4]. This terricolous species stalks flies in the trees. After having caught a fly on a bough, the workers can jump off the branch onto the ground from a height of 1 m before returning to their nest. Workers of *Formica aquilonia* increasingly actively or accidentally fall from the trees in the presence of foraging birds [1]. The author suggested different mechanisms causing ant rain in a fleeing context. In all these studies, all the jumps observed were considered as escape jumps for survival or preying jumps and thus are closely related to the 'life–dinner principle' [21]. Nevertheless, jumps in height have already been anecdotally observed without any context of escape or predation in several species belonging to the same tribe as *P. laboriosa* [3]. In *P. laboriosa*, we observed in nature foraging workers and queens escaping by jumping down from the foliage to the ground, which made their capture difficult. On the other hand, active jumping behaviour appears to be independent of any context of predation. It may be interpreted as resulting from an adaptation to the labile and complex structure of the foliage. During exploration, it may be a good alternative for the ants to escape from closed loops in which they have been caught as opposed to resorting to the outline-tracing strategy (arboreal systematic research) [6, 7]. During foraging, it may allow the foragers to return to their nest even if the path is unfortunately broken.

Furthermore, in both genera *Harpegnathos* and *Myrmecia*, jumping behaviour is associated with morphological adaptations to visual detection and hunting (powerful mandibles; very large eyes) [4, 5]. Although workers of *P. laboriosa* hunt large prey, they do not use jumping behaviour for predation [19]. As they use it only for exploration or foraging, no morphological adaptations are associated with their jumping capacity. Nevertheless, our experiments demonstrated that workers learnt to jump more speedily and memorised the path to the food supply and to return to their nest. Workers that performed spontaneous jumps under simple exploration or foraging conditions jumped again from the same place in 80 % of the cases. Under 'jumping' conditions, workers jumped down earlier and increasingly from one test to the other. They also jumped earlier and more frequently when starved and attracted to an odoriferous supply. Such results suggest that short term (during the experiment) and long term (6 d) memorisation processes do occur, reinforced by an increase in the motivation, permitting them to integrate jumping behaviour into their foraging strategy thanks to visual cues. Mercier and Lenoir also demonstrated that they modify their foraging strategy from solitary foraging to group recruitment as a function of the characteristics of the food supply [20].

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