

## Recruiter or recruit: who boosts the recruitment in starved nests in mass foraging ants?

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### ARTICLE INFO

#### Article history:

Received 1 April 2009

Initial acceptance 18 May 2009

Final acceptance 17 September 2009

Available online 7 November 2009

MS. number: 09-00212R

#### Keywords:

ant  
foraging  
*Lasius niger*  
starvation  
sugar transfer  
threshold

In social insects, each behavioural group holds information that may be crucial for the colony's functioning and regulation. We investigated which behavioural group plays the key role in the regulation of recruitment and how it manages to tune the foraging effort according to the level of starvation in the colony. We focused on recruiters and recruits: Recruiters hold information concerning the characteristics of the food source whereas domestics and potential recruits may be better informed about the colony's needs because of the constant contact that they have with their recruits and/or larvae. We imposed different starvation levels on nest-workers and recruiters and observed their interactions. The level of starvation did not alter the behaviour of the recruiters. However, we observed a change in the recruits' response to the recruiter's signal if the starvation level increased. This induced more recruits and thus more workers foraging in starved colonies. In nonstarved colonies, recruits did not respond to the recruitment signal and no recruitment occurred. Our results suggest that the recruits' response is the major key to the regulation of the recruitment process. This study has deciphered how individuals assess the colony's needs and integrate all the information to build up an optimal food exploitation strategy adjusted to starvation.

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For animals foraging in groups, making decisions such as leaving the group to forage and/or to recruit other foragers to a food source often depends on social interactions among group members. In social insects, these decisions to forage or recruit may be taken by individuals that exhibit preferential behaviours according to the fragmentary information they hold. The information may concern the characteristics of the food source such as its location (Hölldobler 1971; Taylor 1978), the quality and quantity of food (Von Frisch 1967; Seeley 1995; Conrath & Roper 2003), the presence of predators in the vicinity of the food source (Nonacs & Dill 1990) or the group's nutritional needs (Hölldobler 1971; Howard & Tschinkel 1980). Some of the questions that arise are: which and how many individuals have pertinent information, how do they take decisions and how do the other members of the group identify which individuals possess this information?

In this study we examined how one behavioural group could play the role of informant during starvation periods. We focused on two behavioural groups: recruiters and recruits (Depickère et al. 2008). After a long starvation period, ant colonies mobilize more

foragers (Wallis 1964; Mailleux 2001). In a previous paper (Mailleux et al. 2000), we showed that recruiters deposit a chemical signal at the nest entrance once they have discovered a food source. This signal stimulates the departure of recruits located around these recruiters and is thus partly responsible for the mobilization of foragers. The recruiting efficiency of this signal increases when the colony is starved. We have two hypotheses to explain this particular phenomenon. The first implies that recruiters play a key role in adjusting food exploitation. In this first case, the signal emitted by the recruiters at the nest entrance might be stronger when the group is starved. One could imagine that recruiters lay a stronger chemical trail in such situations. Indeed, in *Lasius niger* and many other species recruiting via chemical trails, recruiters are able to adapt their chemical trail-laying behaviour in accordance with environmental characteristics: they can communicate to recruits the availability, the location and the quality of the resources they have discovered (reviewed in Hölldobler & Wilson 1990; Detrain et al. 1999). Recruiters can fill that role effectively because they have knowledge of the characteristics of the food source and its environment. In our second hypothesis, recruits have a key role in adjusting the intensity of food exploitation. In this case, they are the informants. The higher mobilization of foragers after long starvation periods might be based on the recruits' increased perception of the signal emitted by the recruiters. An alternative

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explanation could be that the recruits' motivation could be higher after a long starvation period. Indeed, recruits are best able to assess all the parameters that characterize the nutritional needs of the colony (state of nutrition, size of brood; Cassill & Tschinkel 1999) as they are inside the colony and constantly exchange information with recruits, larvae and the queen.

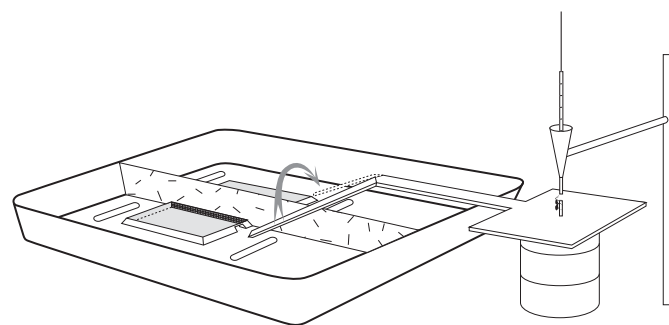
The aim of this study was to determine the relative importance of recruiters and recruits in the adjustment of signals according to the starvation level. To do this, we observed the mutual interactions between recruiters and recruits that were starved to different degrees.

## METHODS

The black garden ant, *L. niger*, is a common Palearctic species, which feeds on the honeydew of aphids such as *Tuberolachnus salignus* (Mittler 1958), *Aphis fabae* (El-Ziady & Kennedy 1956; Klingauf 1987) or *Metopeurum fuscoviride* (Völkl et al. 1999). It is a mass foraging ant species, that is, during the recruitment process, foragers returning from food to the nest deposit chemical trails that stimulate trail following and serve as a guide to orient ants rapidly to the target area (Hölldobler & Wilson 1990).

Four mature queenless colonies of *L. niger* were collected from the slopes of earth banks in Brussels. They were composed of 1100 workers on average (range 800–1400 workers) and were reared in plaster nests (20 × 20 cm and 0.5 cm high) covered by a glass plate and placed in plastic arenas (50 × 38 cm), the borders of which were coated with Fluon. Nests were regularly moistened and kept at a temperature of 22 ± 3 °C with a 12 h photoperiod. Ants were fed three times a week with brown sugar solution (0.6 M), cockroaches (*Periplaneta americana*) and maggots (*Calliphora erythrocephala*). Nests were selected so as to be as homogeneous as possible in terms of the number of recruits. Each nest was divided in half (7 × 10 cm and 0.5 cm high; Fig. 1) by a double metallic wire grid (wire mesh, opening 0.1 × 0.1 mm, each grid separated by 2 mm). Ants in the separate half-nests could have antennal contact but could not perform trophallactic exchange. The two half-nests were separately starved for 1 or 8 days.

We studied how the behaviour of recruiters and recruits was influenced by starvation at the beginning of the food recruitment phase, and the relative importance of recruiters and recruits in the adjustment of the recruitment effort to the starvation level (Howard & Tschinkel 1980; Crawford & Rissing 1983; Anderson & Bartholdi



**Figure 1.** Experimental set-up. The nest was divided into two half-nests separated by a double metallic wire grid. These two half-nests were separately starved for 1 or 8 days. The first recruiter to discover the food droplet drank from the micropipette and returned to the nest. While the recruiter was drinking at the food source, the bridge was shifted and positioned to lead to the second half-nest. The recruiter that had been starved for 1 day returned to the half-nest with recruits that had been starved for 8 days, and the recruiter that had been starved for 8 days returned to the half-nest that had been starved for 1 day.

2000). We analysed the responses of ants to 3 µl droplets of sucrose solution (0.6 M) which exceeded crop capacity (Mailloux et al. 2000). The concentration and volume of droplets were similar to those of the honeydew droplets produced by aphids (Auclair 1963). For a period of 1 h, one half-nest (further referred to as the departure half-nest) was connected by a cardboard bridge (length 20 cm, width 0.5 cm) to a small foraging area (6 × 6 cm). The ants from the departure half-nest were able to explore the foraging area freely. After this exploration phase, a food source was placed in the centre of this foraging area. The first recruiter to discover the food droplet (called the tested recruiter) drank and returned to the nest. While the tested recruiter was drinking at the food source, the bridge was shifted and positioned to lead to the second half-nest (i.e. the arrival half-nest). In a series of experiments, the tested recruiter was diverted to a half-nest that was not its initial half-nest. The tested recruiters that had been starved for 1 day returned to the half-nest with recruits that had been starved for 8 days (experiment '1 to 8'). In another series of trials, the tested recruiter that had been starved for 8 days returned to the half-nest that had been starved for 1 day (experiment '8 to 1'). The tested recruiter contacted its recruits and left the arrival half-nest to return to the food source. Immediately after this departure from the nest, this tested recruiter was permanently removed. The foraging area was also removed. In doing so, we prevented other ants reaching the food droplet and limited our study to the behaviour of only one recruiter at a time and its contact with recruits. During an experiment, three recruiters were observed. The 'diversion experiment' was repeated 20 times for each starvation period (20 times '8 to 1', 20 times '1 to 8').

The experimental set-up was constructed in such a way that ants did not perceive the shift of the bridge. The angle between the two positions of the bridge was less than 10 degrees. A 60 W lamp was set vertically above the departure half-nest, from which the recruiter originated. This visual cue was moved above the arrival half-nest simultaneously with the shift of the bridge. All other visual markers (tubes with water) were placed symmetrically in the two half-nests.

To test a possible influence of the nest division on ants' behaviour, we also repeated the experiment without rerouting the recruiter to another half-nest. This control experiment was also repeated 20 times (20 times '1 to 1', 20 times '8 to 8').

After each experiment, the two half-nests were fed ad libitum during a resting period of at least 1 week. Then the nests were starved again (1 day for one half-nest, 8 days for the other). Half-nests were assigned to the starvation period they had not yet undergone. Regardless of the period of starvation borne by nests (1 or 8 days), the foraging activities of ants were similar after the resting period of 1 week (Mailloux et al. 2000). The maximal starvation period (8 days) that we tested did not induce abnormal mortality (Lenoir 1979). The diversion and the control experiments were done on the same nests, at the same period.

We defined a recruiter as an individual exploring a new foraging area and searching for a food source without having prior information about its location (Biesmeijer & de Vries 2001); a recruit was an individual inside the arrival half-nest. We focused on recruits that had contact with a recruiter. This group included recruits that had performed antennal contact (called a-recruits) or trophallactic contact (t-recruits) with a recruiter.

For both recruiters and recruits, we measured the following.

(1) The probability of leaving the nest within 20 min after the entrance of the recruiter.

(2) The time elapsing before a recruit left the nest. For the recruiters, the time taken to leave the nest started once the last contact ended and lasted until the recruiter left the half-nest. For recruits, the time taken to leave the nest started at the end of the last contact with the recruiter and ended when the recruit left the nest.

(3) The number and duration of antennal and trophallactic contacts between recruiters and recruits. Preliminary observations showed that the ants that did not leave the nest within 20 min joined an aggregate and stopped moving. Hence, we considered that these ants were not involved in the initiation of foraging activity and we did not evaluate the duration or the number of contacts they had with recruits. We only measured the behavioural parameters of ants that left the nest within 20 min after the entrance of the recruiter.

Data were analysed using GraphPad InStat version 3.05 for Win95/NT (GraphPad Software 1998, Inc., San Diego, CA, U.S.A.). As most data were not normally distributed, we used nonparametric statistics. To determine the probability of leaving, we compared data using the Fisher's test. Other behavioural parameters were compared using two-tailed Mann–Whitney *U* tests.

## RESULTS

### Recruiter

For both starvation periods, all recruiters returned to the nest, unloaded their sugar freight and left the nest within 5 min (Table 1). The time taken to leave the nest was not influenced by the starvation period of recruiters or recruits but the total number of antennal contacts and the contact duration were influenced by the starvation period and decreased significantly when nest starvation was prolonged. In contrast, the number and duration of trophallactic contacts were not influenced by the starvation period of the recruiters or recruits (Table 1).

For both starvation periods and for the large majority of the recruiters, we observed one very long trophallactic contact with a recruit (*N* of trophallactic contacts: median  $\pm$  range: 8 to 1:  $1.0 \pm 4.0$ ; 1 to 8:  $1.0 \pm 3.0$ , defined as the main trophallactic contact, MT). During this MT, we observed that the recruiter's gaster decreased markedly in size while the recruit's gaster increased in size and most of the sugar solution loaded by the recruiter was probably discharged. During an MT, other recruits joined the exchange but obtained little sugar solution and their gaster volume did not change. A recruiter had a probability  $P_{MT}$  of making an MT that is described by the following mathematical relationship:

$$F_r(i) = (1 - P_{MT})^{i-1} \times P_{MT}$$

$F_r(i)$  = relative number of recruiters making an MT after *i* contacts,  
*i* = number of contacts,

$P_{MT}$  = probability of performing a main trophallactic contact, which is a constant.

This relationship showed that an entering recruiter had a probability  $P_{MT}$  of an MT at its first contact with a recruit and this probability remained constant for the successive contacts. If the first recruit contacted refused the MT, the recruiter had a probability  $(1 - P_{MT})^{(i-1)} \times P_{MT}$  of achieving an MT at its second attempt. We observed that  $P_{MT}$  was influenced by starvation: when recruits were starved for 1 day  $P_{MT} = 0.08$  (correlation coefficient between the experimental data and the data calculated with the relationship:  $R^2 = 0.9$ ,  $N = 293$ ,  $P < 0.005$ ) and when recruits were starved for 8 days  $P_{MT} = 0.42$  ( $R^2 = 0.96$ ,  $N = 104$ ,  $P < 0.005$ ).

### Recruits

For a-recruits the only behavioural parameter affected by starvation was the probability of leaving the nest. The time taken to leave, the number of contacts and the contact duration were similar for both starvation periods. As they did not receive any sugar solution from the recruiter, these ants made no further trophallactic contact with other recruits.

For t-recruits no parameter was statistically affected by starvation, probably because of the low number of t-recruits. For t-recruits, as for recruiters, the total number and duration of antennal contacts decreased when nest starvation was prolonged (Table 1).

### Comparison between the Two Recruit Groups

Both a-recruits and t-recruits that were subjected to identical starvation periods had a similar probability of leaving the nest (Fisher's test: 1-day starvation period recruits:  $D = 0.02$ , NS; 8-day recruits:  $D = 0.02$ , NS). Unlike a-recruits, t-recruits did discharge their sugar solution before leaving the nest. Consequently, the time taken for t-recruits to leave the nest, their antennal contact number and duration, and the number of trophallactic contacts were statistically higher than those observed for a-recruits (time taken to leave the nest: 1 day:  $U = 39.5$ ,  $N = 59$ ,  $P = 0.03$ ; 8 days:  $U = 68$ ,  $N = 42$ ,  $P = 0.03$ ; number of contacts: 1 day:  $U = 7$ ,  $N = 59$ ,  $P = 0.02$ ; 8 days:  $U = 42$ ,  $N = 42$ ,  $P = 0.003$ ; duration of contact: 1 day:  $U = 0$ ,  $N = 59$ ,  $P < 0.0001$ ; 8 days:  $U = 10$ ,  $N = 42$ ,  $P < 0.0001$ ; number of trophallactic contacts: 1 day:  $U = 3$ ,  $N = 59$ ,  $P = 0.002$ ; 8 days:  $U = 39$ ,  $N = 42$ ,  $P = 0.002$ ). We observed that once the ants had received sugar, they in turn had to unload and perform trophallaxis before leaving the nest.

**Table 1**  
Results of the diversion experiments

Behavioural group	Departure half-nest to arrival nest	<i>P</i> of leaving the nest	Time taken to leave the nest (s)	<i>N</i> of antennal contacts	Duration of antennal contact (s)	Number of trophallactic interactions	Trophallactic duration (s)
Recruiter	8 to 1	1.00 (20)	55±286 (20)	11±33 (20)	10±33 (20)	1±4 (20)	32±133 (20)
	1 to 8	1.00 (20)	43±105 (20)	3±19 (20)	5±34 (20)	1±3 (20)	41±161 (20)
	Statistics		$U=142$ , NS	$U=51$ , $P<0.0001$	$U=101$ , $P<0.01$	$U=0.06$ , NS	$U=184$ , NS
a-Recruits	8 to 1	0.20 (275)a	80±647 (55)	1±14 (55)	1±28 (55)	0±1 (55)	11±5 (2)
	1 to 8	0.40 (85)b	56±651 (34)	1±17 (34)	1±28 (34)	0±1 (34)	9±4 (2)
	Statistics	$D=0.2$ , $P<0.005$	$U=788$ , NS	$U=911$ , NS	$U=920$ , NS	$U=914$ , NS	$U=1$ , NS
t-Recruits	8 to 1	0.22 (18)a	269±234 (4)	8±16 (4)	9±16 (4)	1±2 (4)	47±27 (4)
	1 to 8	0.42 (19)b	152±697 (8)	5±20(8)	6±24 (8)	1±2 (8)	47±62 (6)
	Statistics	$D=0.2$ , NS	$U=14$ , NS	$U=10$ , NS	$U=10.5$ , NS	$U=15$ , NS	$U=15$ , NS

The two half-nests were separately starved for 1 or 8 days. Highly starved recruiters were deviated to a moderately starved half-nest (8 to 1) and vice versa (1 to 8). We compared the behaviours of the different groups (recruiters, a-recruits having antennal contact with the recruiter and t-recruits having trophallactic contact with the recruiter) after two starvation periods. Median  $\pm$  range (*N*) are given for all parameters. Numbers in parentheses indicate the sample size. In the statistics row, we compared the probabilities of leaving the nest using the Fisher's test; the other parameters were compared using the Mann–Whitney test. Data with the same superscript letters (a, b) were not statistically different ( $P > 0.05$ ).

### Comparison between Diversion and Control Experiments

The nest division had no influence on ants' behaviour (Table 2): most measured parameters were similar in the diversion and in the control experiment. In the diversion experiment 8 to 1, recruiters and recruits behaved as if they were all starved for 1 day, that is, when the starvation state of the recruit was kept low, changing the recruiter's starvation state had no effect on recruitment dynamics. Similarly, in the experiment 1 to 8, recruiters and recruits behaved as if they were starved for 8 days, that is, when the starvation state of the recruit was kept high, changing the recruiter's starvation state had no effect on recruitment dynamics (Table 2). This showed that recruiters had a minor role in the recruitment intensification after starvation, and that the recruits' response is the key to the recruitment process.

In both experiments (diversion and control), the total number of antennal contacts and the contact duration for the recruiter were influenced by the starvation period and decreased significantly when nest starvation was prolonged.

For a-recruits, the only behavioural parameter affected by starvation was the probability of leaving the nest. We observed only one difference between the diversion and the control experiments: in the diversion experiment, the time taken by the recruiter to leave the nest was similar after 1 to 8 or 8 to 1 whereas in the control experiment, this time decreased after 1 starvation day (1 day for recruiters and recruits; Mann–Whitney test:  $U = 105$ ,  $P = 0.01$ ).

## DISCUSSION

The nutritional needs of the group modulate foraging activity in social insects (Hölldobler 1971; Traniello 1977; Cosens & Toussaint 1986; Roces & Hölldobler 1994; Dussutour et al. 2009) and after a long starvation period, ant colonies mobilize more foragers (Wallis 1964). In a previous study (Mailleux et al. 2000), we showed that the increased number of recruits observed in highly starved colonies originates from recruits located near the entrance of the nest, regardless of their contact with the recruiting recruiter. We hypothesized that a recruiter returning with a load emits a signal which triggers recruitment. In this study, we found that this signal was not modified by the starvation level of the colony. Instead the response of potential recruits was higher in a starved colony (there was no increase in intensity or frequency of trail laying). The recruits are therefore the individuals that tune the workforce

allocated to the foraging task according to the colony's nutritional state.

After long starvation periods, higher mobilization is essentially based on the increased motivation of the recruits to leave the nest and forage. Our study of social interactions sheds light on the relative allocation attributed to recruiter and recruit during boosted recruitment. The recruiters' role is to transport the sugar solution to the colony and to trigger recruits' departure by emitting a signal with a certain intensity and frequency informing the colony about the source's qualities but regardless of the starvation level. Recruits receiving the chemical signal have a propensity to leave the nest that grows stronger as they become hungrier. On the other hand, recruits may or may not accept the food load offered by a recruiter, and this depends on their starvation level. Afterwards, they can decide whether to leave the nest or not.

This study also shows that a highly starved recruiter (after 8 deprivation days) returning from a food source to a moderately starved nest (1 deprivation day) does not easily find recruits to unload its freight. The loaded recruiter will have to contact a greater number of workers before finding a receiver. Conversely, a moderately starved recruiter (1 day) returning to a very hungry nest (8 days) will be able to discharge food quickly and easily. So the starvation level affects the recruits' motivation to accept trophallaxis. In honeybees, *Apis mellifera*, a forager has to unload the food it ingested at the source before leaving for another trip (Seeley et al. 1996; Anderson & Ratnieks 1999; Thom 2003). The availability of receivers thus acts as negative feedback: if no recruit accepts the recruiter's load, the latter remains inside the nest and the exploitation of the food source will diminish and finally stop. The same occurs with potential recruits that have received sugar from a forager, such that they will remain inside the nest if they cannot find receivers. However, this regulation seems more complex in honeybees. Indeed, a forager loaded with nectar, but which then experiences a long unloading delay, will perform a tremble dance to recruit additional nectar receiver bees. Our results do not highlight such additional feedbacks. In the ant *Solenopsis invicta*, the influence of starvation on foraging activity seems to be linked to the increased activity of the recruiters (Howard & Tschinkel 1980). These authors showed that a hungry recruiter diverted to a well-fed colony encounters fewer ants accepting trophallactic exchanges. As in *L. niger*, the forager's state of hunger plays an important role in regulating food distribution. In sugar-satiated nests, previously starved foragers are highly successful at passing on labelled sugar whereas previously fed foragers are not.

**Table 2**  
Results of the control experiments

Behavioural group	Departure half-nest to arrival nest	<i>P</i> of leaving the nest	Time taken to leave the nest (s)	<i>N</i> of antennal contacts	Duration of antennal contact (s)	Number of trophallactic interactions	Trophallactic duration (s)
Recruiter	1 to 1	1.00 (20)	72±79 (20)	13±31 (20)	7±70 (20)	1±3 (20)	52±76 (20)
	Statistics		$U=145$ , NS	$U=187$ , NS	$U=133$ , NS	$U=153$ , NS	$U=173$ , NS
a-Recruits	8 to 8	1.00 (20)	57±77 (20)	3±16 (20)	1±13 (20)	1±3 (20)	49±70 (20)
	Statistics		$U=142$ , NS	$U=193$ , NS	$U=147$ , NS	$U=134$ , NS	$U=132$ , NS
a-Recruits	1 to 1	0.18 (227)	96±339 (41)	1±4 (41)	1±9 (41)	0±0 (41)	—
	Statistics	$D=0.02$ , NS	$U=1114$ , NS	$U=1041$ , NS	$U=1041$ , NS	—	—
t-Recruits	8 to 8	0.32 (111)	57±341 (35)	1±18 (35)	1±19 (35)	0±0 (35)	—
	Statistics	$D=0.08$ , NS	$U=572$ , NS	$U=575$ , NS	$U=540$ , NS	—	—
t-Recruits	1 to 1	0.22 (28)	218±241 (6)	10±19 (6)	6±14 (6)	2±2 (6)	48±34 (6)
	Statistics	$D=0.08$ , NS	$U=10.5$ , NS	$U=11$ , NS	$U=9$ , NS	$U=8$ , NS	$U=11.5$ , NS
t-Recruits	8 to 8	0.35 (32)	264±695 (11)	6±22 (11)	8±27 (11)	2±3 (11)	62±41 (11)
	Statistics	$D=0.08$ , NS	$U=33$ , NS	$U=34$ , NS	$U=32$ , NS	$U=23$ , NS	$U=36$ , NS

Highly starved recruiters were deviated to a highly starved half-nest (8 to 8) and starved ones to a starved half-nest (1 to 1). We compared the behaviours of the different groups (recruiter, a-recruits having antennal contact with the recruiter and t-recruits having trophallactic contact with the recruiter) after two starvation periods. Median ± range (*N*) are given for all parameters. Numbers in parentheses indicate the sample size. In the statistics row, we compared the results obtained in the control and the diversion experiments. In other words, the results obtained for '1 to 8' were compared to '8 to 8', and the results obtained for '8 to 1' were compared to '1 to 1'. The probabilities of leaving the nest were compared using the Fisher's test; the other parameters were compared using a Mann–Whitney test.

Animals must make decisions about when to feed, when to court, when to sleep, etc. in such a way that they optimize as much as possible their chances of survival and their reproductive success. For animals that forage or travel in groups, movement decisions often depend on social interactions between group members. However, in many cases, few individuals have pertinent information, for example about the location of a food source or a migratory route. The devolution of different roles as an informant between the individual recruiters and recruits seems to be related to their spatial location near the source of the information that is to be conveyed.

## Acknowledgments

A.B. is a FRIA researcher. C.D. and J.L.D. are research associates from the Belgian National Fund for Scientific Research and were financially supported by the Fund for Joint Basic Research (Grant 2.4510.01). A.C.M. is financially supported by the IRSIB (Institut d'encouragement de la Recherche Scientifique et de l'Innovation de Bruxelles).

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