

# The influence of red light on the aggregation of two castes of the ant, *Lasius niger*

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## Abstract

Insects are generally described as essentially blind to red wavelengths but sensitive to ultraviolet. Therefore, ants are generally reared in nests where “obscurity” is obtained by the use of a red filter. Yet, no study has been done in order to confirm this idea and to verify whether ants behave differently with or without red light. We performed aggregation experiments with the ant *Lasius niger* under red light and in total darkness to control the sensitivity of workers. Aggregation is a basic behavior associated with the origin of sociality and with the spatial organization of the colony. We demonstrate that *L. niger* is sensitive to red wavelengths. Moreover, we show that workers behave differently depending on their ethological caste: foragers aggregate well in total darkness but show low assembly under red light, whereas brood-tenders aggregate well in both conditions. For the first time, a link between vision, social organization and spatial patterns is revealed. The results are discussed relative to their adaptive value and relative to the physiology of the workers. Hypotheses are formulated concerning the acquisition of this change of behavior between castes.

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## 1. Introduction

In social insects, especially ants and bees, vision is mainly used for orientation of individuals and in the search for food. Their navigational performances include piloting by landmarks (Wehner and Flatt, 1972; Wehner and Räber, 1979; Wehner et al., 1996) and compass-orientation based on celestial cues, such as the sun and polarized skylight (for reviews, see Wehner, 1984; Rossel and Wehner, 1984). Vision is particularly important in honeybees for choosing food sources, based on colors of flowers (Hill et al., 2001). Beyond the question of orientation, the influence of vision on social organization was never studied, in particular the effects of vision on aggregation behavior. Aggregation mediated by inter-attraction is an important behavior at the base of social and spatial organiza-

tion of the colony (Jaisson, 1987; Depickère et al., 2004a,b) and nest moving (Jeanson et al., 2004).

Vision is well developed in honeybees and was the subject of numerous studies (see for example von Frisch, 1914; Srinivasan and Lehrer, 1988; Menzel and Backhaus, 1991; Giurfa et al., 1996). In ants, vision differs drastically among species, from a total blindness in the workers of some subterranean species to an *Apis*-like acuity in certain large-eyed, epigaeic forms. In this last category, for example, Marak and Wolken (1965) found that *Solenopsis saevissima* has a spectral sensitivity similar to that of the honeybee, ranging from below 350 to 650 nm. It is generally accepted that ants, like *Apis mellifera* workers, are essentially blind to reds but sensitive to ultraviolet. In fact, visual acuity depends on the number of ommatidia in the compound eye of the worker caste, which is correlated with their life habit (Wilson, 1971). The workers of most ant species have from tens to a few hundreds of ommatidia per compound eye; the number is roughly correlated with the amount of time spent foraging above ground.

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For instance, the workers of species in the *Formica rufa* group, which forage almost exclusively above ground, have approximately 600 ommatidia per eye (Wilson, 1971).

Vision, used for foraging and orientation, influences individual behavior. Do all the workers of a colony have the same visual sensitivity? Is there a difference between castes due to the polyethism? In the nest, foragers are familiar with the light parameter because of their function in searching for food. By contrast, brood-tenders, implicated in the care of the brood, do not go outside. Authors, in general, assume that insects are blind to red and that a red filter above a laboratory ant nest is sufficient to create “natural conditions of obscurity”. Surprisingly, no studies appear to verify this. This assumption comes from studies done at the beginning of the last century. In Wheeler (1910), we can read: “Miss Fielde (1902) summarizes her results, which agree with those of Lubbock (1882) and Forel (1886–1888, 1900–1901), in the following words: “The ants manifested no liking for any of the rays of light. If obligated to stay in light rays of some sort, the rays of longer wave-lengths are preferred to those of shorter wave-lengths. Dividing the spectrum, as we know it, into red, green and violet, we may say that to the ants’ eyes red and green are most like the darkness that they prefer and that violet is to them most luminous [...]”. Wheeler (1910) also summarizes various artificial nests employed to rear and study the ants. Some are covered with glass plates and in part also with opaque covers (Janet, 1897, in Wheeler, 1910). Another uses a “glass cover which may be of a red or orange tint [...] where ants will behave as if in the darkness where they habitually live” (Fielde, 1904, in Wheeler, 1910). This solution, red glass or red filter paper, seems to solve the methodological problem of observing the ants, respecting the need of darkness for the ants as well. Many analyses of ant behavior inside the nest have been conducted using these conditions, and the use of a red filter was never questioned. In this paper, we investigated the influence of the light conditions (total darkness versus red light) on the aggregative behavior of *Lasius niger*. Previous studies have characterized aggregation in *Lasius niger* and showed that aggregation is based on individual resting time in the cluster, which increases with the size of the cluster (Depickère et al., 2004a). Moreover, these studies showed a difference in aggregation between brood-tenders and foragers under red light: brood-tenders assembled in a big and stable cluster whereas foragers showed a low level of aggregation gathering in small and unstable clusters (Depickère et al., 2004b). This difference between the two castes is based on individual resting times, which are 10 times longer for brood-tenders than for foragers (Depickère et al., 2004b).

## 2. Materials and methods

Two colonies of *Lasius niger*, collected in Brussels, were constituted by 500–1000 workers and brood. They were reared under laboratory conditions at  $23 \pm 2$  °C and a daily photoperiod of 12 h of light. Ants were installed in 5–10 tube nests (10 cm length, 1.5 cm in diameter) covered with red filter papers (Lee Filters<sup>®</sup>, Ref. 106, absorption spectrum: 550–850 nm, with a maximum at 625–850 nm, Lee Filters Firm, pers. comm.). These tubes were placed in a rearing box (47 × 30 cm) with food; the edges of the box were coated with Fluon<sup>®</sup> to prevent escape. Colonies were fed with special food (Bhatkar and Whitcomb, 1970) three times a week and *Tenebrio molitor* larvae one time a week. Water was always available.

*L. niger* is characterized by a typical age polyethism: young ants are brood-tenders while old individuals are mainly foragers (Lenoir and Mardon, 1978; Lenoir, 1979; Lenoir and Ataya, 1983). In our experiments, we used these two extreme castes: brood-tenders were taken inside the nest near the brood, whereas foragers were picked up out of the nest, inside the rearing box near the food.

The experimental setup was an arena made up of a PVC ring of 2 cm height and 19.8 cm in diameter, placed on a black paper sheet. The inside edge was coated with Fluon. A dark cylinder surrounding wall and a dark cover (30 cm above the arena) closed the setup in order to avoid any visual signals. A hole in the center of the cover was used to illuminate the arena, using a black chamber bulb (PF712E, 15W, 5 Lux, spectrum emission: 625–700 nm, see Jensen, 2003). A second hole, not centered, was used for the digital camera. Twenty ants were placed in the center of the arena at the beginning of the experiments. Six experiments were conducted for each caste and for each environmental condition (red light or total darkness).

### 2.1. Experiments under red light

Ant activity was recorded for 90 min. Snapshots, taken from the video at 30 s, 15, 30, 45, 60, 75 and 90 min, allowed us to analyze the ant positions inside the arena and characterize the aggregation pattern.

### 2.2. Experiments in total darkness

These experiments were divided into two parts: 90 min under total darkness followed by 90 min under red light in order to see the ants’ sensitivity between the two conditions by observing changes in behavior: (1) The first 90 minutes, where ants were in total darkness (same setup, the red light was just switched off). To monitor changes in aggregation and record ant activity, the red light was switched on during the first

minute and then, 15 s at 30 and 60 min. (2) At 90 min, the red light was switched on and remained on for an additional 90 min. A snapshot was recorded at 90 min, just after switching on the red light, and then every 15 min until 180 min.

### 2.3. Characterization of the aggregation pattern

As in previous experiments where we studied the aggregation dynamics (see Introduction), ants were considered aggregated when they had at least one neighbor at a distance (thorax to thorax) of less than 1 cm (Depickère et al. 2004a,b). From the snapshots, the Cartesian position of ants was recorded. Processing programs allowed us to calculate:

- (1) The radial distribution of ants in the arena, that was divided into five rings of 2 cm. The density for each ring was calculated (the “central ring” is a circle of 2 cm in radius).
- (2) The fraction of aggregated ants, i.e. the number of aggregated ants/total number of ants in the arena.
- (3) The size of the clusters, i.e. the number of ants involved in each cluster. For every time and each experiment, the clusters were ranked in decreased order and mean size was then calculated.
- (4) The spatial stability of the biggest cluster: the distance between the centroid of the biggest cluster at  $t - 1$  and the centroid of the biggest cluster at  $t$  was calculated. A mean distance was then found for each time.

### 2.4. Temperature measurement

We measured the increase of the temperature associated with the red lamp at the surface of the arena during 180 min. We used an electronic captor (LM 135 SGS Thomson Microelectronics,  $3 \times 5 \times 2$  mm), which gave us a precision of  $10^{-2}$  C.

## 3. Results

### 3.1. Radial distribution

After 90 min under red light, as in total darkness, a peak density was observed in the external ring (Fig. 1) for both castes. Nevertheless, the brood-tenders were a little more distributed in the center of the arena in total darkness than under red light. After 180 min (90 min in total darkness followed by 90 min under red light), the radial distribution was similar to the radial distribution found in reference experiments under red light (Fig. 1).

### 3.2. Fraction of aggregated ants

For the brood-tenders in red light, the fraction of aggregated ants increased during the experimental time and reached a plateau where 90% of the population was aggregated (Fig. 2). In total darkness, the same was observed: the level of aggregation at 90 min was similar between the two conditions (Fig. 2). When the red light was switched on continuously after 90 min of total darkness, the fraction of aggregated brood-tenders decreased to 40%. Then, with time, the fraction of aggregated ants increased and at 180 min was not different from the fraction observed at 90 min under red light (Fig. 2; Mann–Whitney  $U$  test:  $U = 14$ ,  $N = 6$ , NS).

For the foragers, the fraction of aggregated ants under red light was almost constant during the entire experiment: 40% of the population was aggregated (Fig. 2). In total darkness, the fraction of aggregated foragers increased to reach a plateau where 80% of the population was aggregated (Fig. 2). Then, when the red light was switched on at 90 min, the fraction of aggregated foragers decreased drastically: only 40% of the population was aggregated at 105 min, and this fraction remained constant until 180 min (Fig. 2). The

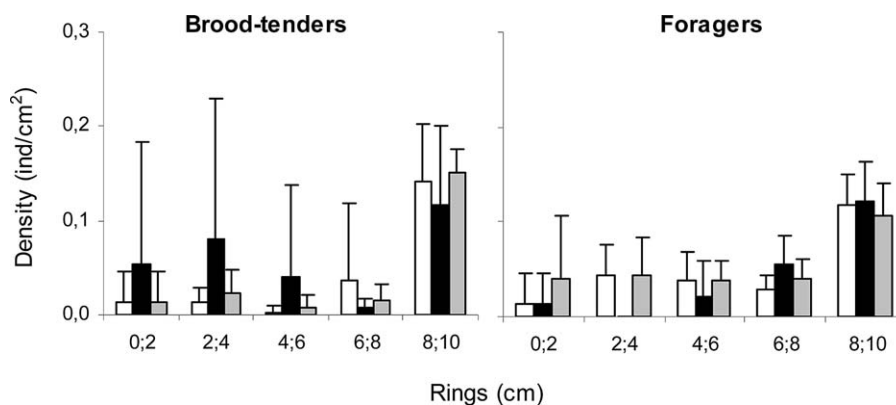


Fig. 1. Radial distribution of ants: density of workers (mean  $\pm$  S.D.) in the five rings (0 represents the center of the arena) for brood-tenders and foragers under red light at 90 min (white); in total darkness at 90 min (black) and at 180 min (grey: 90 min of total darkness + 90 min of red light).

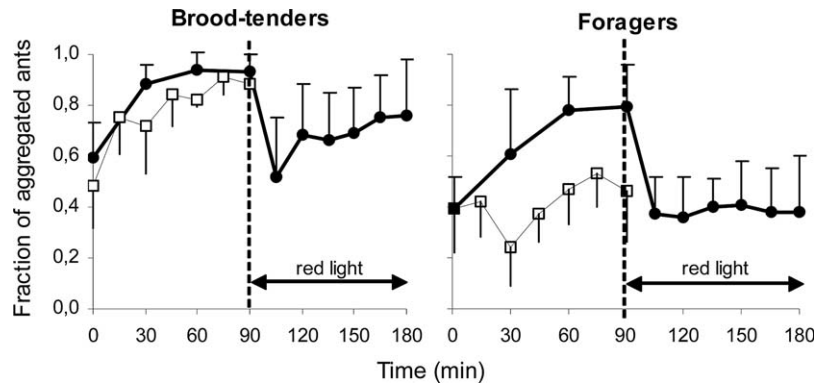


Fig. 2. Evolution of the fraction of aggregated ants (mean  $\pm$  S.D.) for the two castes under red light (white square) and total darkness (black circle).

fraction of aggregated foragers at 180 min was not different from the fraction observed at 90 min under red light (Mann–Whitney  $U$  test:  $U = 14.5$ ,  $N = 6$ , NS).

### 3.3. Pattern of aggregation

For brood-tenders, under red light, the size of the biggest cluster increased quickly at the beginning of the experiments. It then continued to rise slowly and reached 80% of the population at 90 min (presence of a main cluster). The change and population of the biggest cluster were similar in total darkness. No difference in the size of the biggest cluster at 90 min appeared between total darkness and red light (Mann–Whitney  $U$  test:  $U = 7$ ,  $N = 6$ , NS). Then, when the red light was switched on continuously at 90 min, the size of the main cluster fell to only 40% of the population at 105 min, suggesting a dispersal of this cluster. Afterwards, the size of the main cluster increased again, reaching 60% of the population at 180 min. This value is not different from the value of the size of the main cluster at 90 min in red light (Mann–Whitney  $U$  test:  $U = 9.2$ ,  $N = 6$ , NS).

For the foragers, the size of the biggest cluster in red light was almost constant and incorporated only 20% of the population (Fig. 3). The pattern consisted of several clusters of small size. In total darkness, the size of the biggest cluster increased during the entire experiment, reaching 60% of the population at 90 min (main cluster). When the red light was switched on continuously at 90 min, the size of this main cluster decreased drastically and remained constant, gathering 20% of the foragers. This value is not different from what we observed at 90 min in red light (Mann–Whitney  $U$  test:  $U = 12$ ,  $N = 6$ , NS).

### 3.4. Spatial stability of the biggest cluster

Under red light, the distance separating the centroid of the main cluster of brood-tenders between two con-

secutive times decreased with time until reaching just a few millimeters (Fig. 4). This shows the acquisition of spatial stability of the main cluster. The same qualitative and quantitative change was observed in total darkness. The main cluster was located in the external ring for all the experiments under red light, and in 4/6 of the experiments in total darkness. This result explains the radial distribution of ants in total darkness (Fig. 1) and suggests a less important wall following behavior (thigmotaxy) under total darkness. At 90 min, when the red light was switched on continuously, the distance increased until 120 min, and then decreased until reaching 20 mm on average (Fig. 4). This distance is not different from that observed at 90 min in red light (Mann–Whitney  $U$  test:  $U = 15$ ,  $N = 6$ , NS). For each experiment in total darkness, the distance between the centroid of the main cluster at 90 and the centroid of the main cluster at 180 min was measured. We observed for the four experiments where the main cluster at 90 min was in the external ring that the ants aggregated in the same place as in total darkness. This suggests a role of ground marking on the location of the main cluster without a change on the aggregation level, as described in Depickère et al. (2004c). In the two experiments where the cluster was located in the central part of the arena at 90 min (end of the total darkness) we observed that the main cluster was located at 180 min in the external ring.

For foragers under red light, no spatial stability was observed for the biggest cluster: the distance remained high (90–120 mm) during the entire experiment (Fig. 4). In total darkness, the distance decreased with time and was 30 mm at 90 min. For all the experiments, the main cluster was located at the external ring. When the red light was switched on continuously at 90 min, the distance increased and remained high until 180 min. The distance at 180 min is not different from the distance observed at 90 min under red light (Mann–Whitney  $U$  test:  $U = 15$ ,  $N = 6$ , NS). This result suggests a link between spatial stability and size of the

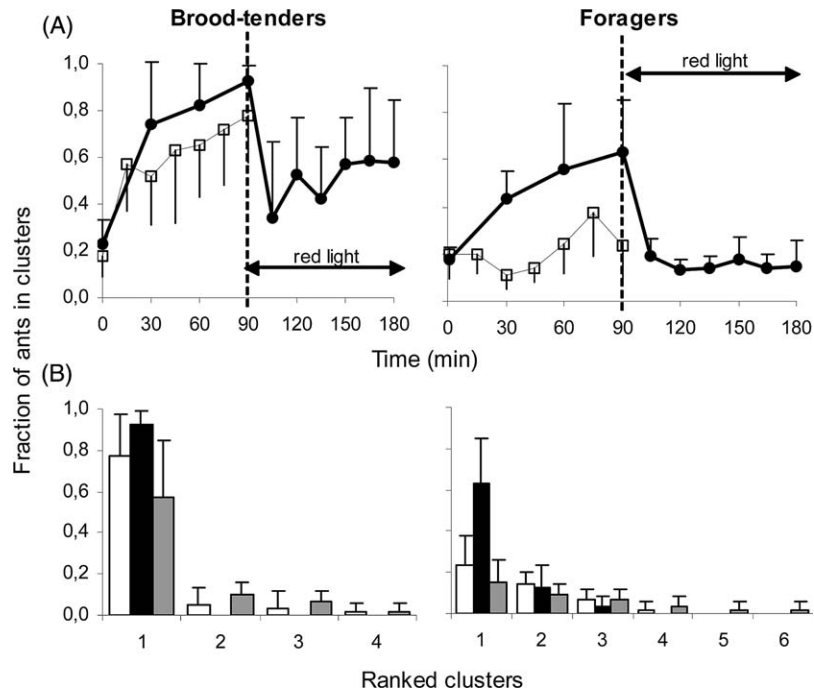


Fig. 3. Size of clusters (mean  $\pm$  S.D.). (A) Changes in size of the biggest cluster relative to the total population for both castes, under red light (white square) and in total darkness (black circle). (B) Size of clusters ranked in decreased order for both castes, under red light at 90 min (white) and total darkness at 90 min (black) and 180 min (grey: 90 min of total darkness + 90 min of red light).

cluster: the greater the cluster, the higher its spatial stability.

### 3.5. Comparison between the aggregation of foragers in total darkness and the aggregation of brood-tenders under red light at 90 min

There was no difference in either in the fraction of aggregated ants (Mann–Whitney  $U$  test:  $U = 14$ ,  $N = 6$ , NS) or in the size of the main cluster (Mann–Whitney  $U$  test:  $U = 7$ ,  $N = 6$ , NS). Only the spatial stability was lower for the foragers than for brood-tenders (Mann–Whitney  $U$  test:  $U = 14$ ,  $N = 6$ ,  $p = 0.03$ ).

### 3.6. Temperature measurement

Are the ants responding to the wavelengths of the lamp, or to the increase of temperature associated with the lamp? We measured the temperature at the surface of the arena during 180 min, and found an increase which follows an exponential law ( $T = T_m - (T_m - T_0)e^{-0.02t}$ , with  $T_m = 26.8$  °C and  $T_0 = 23.3$  °C, test of Pearson coefficient:  $r = 0.99$ ,  $N = 13$ ,  $p < 0.05$ ). A plateau was reached at 60 min (+3.5 °C). Nevertheless, ants began to disperse in the minute that followed the lighting of the red lamp. In the first minute, the increase of the temperature was less than 0.1 °C,

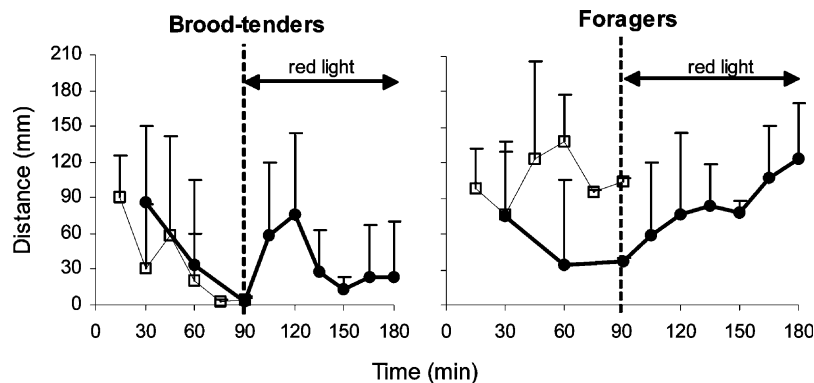


Fig. 4. Changes in the distance (mean  $\pm$  S.D.) between the centroid of the biggest cluster at  $t-1$  and the centroid of the biggest cluster at  $t$  under red light (white square) and total darkness (black circle) for both castes.

suggesting that ants are more sensitive to the wavelength than to an increase of temperature.

#### 4. Discussion

Two main results appear in this study: (1) Ants behave differently in total darkness and red light conditions: in total darkness, the two castes aggregate well and one main and stable cluster forms. Under red light, brood-tenders also have a high aggregation level, but foragers only aggregate in small and unstable clusters. These results under red light are similar to those obtained under the same conditions (Depickère et al., 2004b). (2) A switch of the light regime from total darkness to red light during the experiment changed the aggregation tendency. Both castes dispersed when the red light was switched on. Then, brood-tenders reaggregated in a similar level as observed in total darkness, whereas foragers only gathered in small and unstable clusters. This result demonstrates the sensitivity of both castes to red light. It is interesting to note that the same behavior under red light was observed for both castes.

Sensitivity to the wavelengths of the red lamp is interesting because its spectrum emission starts at 625 nm and peaks above 700 nm (see Jensen, 2003; Philips Group, pers. comm.). This spectrum is close to the absorption spectrum of the red filter paper used for simulating the total darkness under a laboratory nest which absorbs wavelengths between 550 and 850 nm, with a maximum at 625–850 nm (Lee Filters Ref. 106, Lee Filters Firm, pers. comm.). The few studies which deal with spectral sensitivity of insect compound eyes suggest that the majority of insects do not see red wavelengths (Diptera: 349–560 nm, Wu and Lin, 1990; Neuroptera: 350 nm, Yang et al., 1998; Hymenoptera (honeybees): 300–650 nm, Wilson, 1971). In ants, *Cataglyphis bicolor* is known to see wavelengths between 350 and 510 nm (Meyer and Domanico, 1999) and *Solenopsis saevissima* between 350 and 650 nm (Marak and Wolken, 1965). Though *L. niger* is certainly sensitive to the red light by its compound eyes, we cannot neglect other sources of detection. *L. niger* workers are known to have ocelli (A. Lenoir, pers. comm.). Ocelli are unable to form an image (Mizunami, 1995; Lazzari et al., 1998), yet they discriminate the presence of light and play a role during flight and orientation (Goodman, 1970, 1981; Wehrhahn, 1984; Mizunami, 1994, 1995). The ocelli can also mediate phototactic responses in *Triatoma infestans* (Lazzari et al., 1998). Few studies have examined the spectral sensitivity of ocelli, but Pappas and Eaton (1977) showed that it can be broad for the tobacco hornworm moths *Manduca sexta* (360–520 nm), with a higher sensitivity to 520 nm than to 360 nm. In ants, ocelli of

*Cataglyphis bicolor* are known to possess only one spectral type (UV) of receptor (Mote and Wehner, 1980; Fent and Wehner, 1985).

Our results stress the fact that some experimental conditions that have been accepted and applied regularly for a long time are not necessarily the best conditions and can lead to wrong interpretations. When the ant literature is investigated, many articles do not specify the light conditions of rearing and/or of experiments. Such information is important, especially for studies of behavioral processes relative to the aggregation inside the nest (the attractiveness of the queen, study of ant distribution inside the nest, etc.) and also for studies on the exploration or food recruitment where light could increase the activity of foragers.

The modulation of the aggregation behavior as a function of light is adaptive: in total darkness inside a nest, individuals aggregate while the presence of light leads to dispersal of individuals specialized in food search. An ant nest can be seen as an aggregation of cooperating individuals. Brood is clustered by workers in specific places depending on the parameters of the environment (humidity, temperature, etc.) and requirements of the brood. Ants specialized in the care of the brood are therefore more prevalent near larvae and thus have high aggregation behavior. On the contrary, foragers disperse under light to find food sources. In total darkness, as inside the nest, foragers have no task to perform: the aggregation allows them to decrease their consumption of energy and facilitates their recruitment for some tasks when needed. Our results suggest that a weak light source is sufficient to disperse and to lead to foraging in ants. This amount of light may be available from the moon (Santschi, 1923; Jander, 1957). Why does red light lead to a change of the behavior in one caste but not in the other? In *L. niger*, the polyethism is mainly based on the age of the workers: the youngest ants are brood-tenders and the oldest are foragers. We assume that a physiological change occurs with age, decreasing the level of aggregation. An increase of phototaxis with the age may also be involved, as was shown in honeybees (Ben-Shalal et al., 2003). Therefore, a scenario can be proposed: at the beginning of their life, ants stay inside the nest, have a high level of aggregation and care for the brood. The oldest individuals could be found nearest to the entrance of the nest due to their higher phototaxis. When needed, the individuals with the lowest level of aggregation, i.e. the oldest, begin to leave the nest to forage. The outside light would strongly decrease their tendency to aggregate. This behavior may be reinforced by learning, since ants could associate the presence of the light with the need to disperse and search for food.

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## References

- Ben-Shalar, Y., Leung, H.-T., Pak, W.L., Sokolowski, M.B., Robinson, G.E., 2003. cGMP-dependent changes in phototaxis: a possible role for the *foraging* gene in honey bee division of labor. *Journal of Experimental Biology* 206, 2507–2515.
- Bhatkar, A.P., Whitcomb, W.H., 1970. Artificial diet for rearing various species of ants. *Florida Entomologist* 53, 29–232.
- Depickère, S., Fresneau, D., Deneubourg, J.-L., 2004a. A basis for spatial and social patterns in ant species: dynamics and mechanisms of aggregation. *Journal of Insect Behavior* 17, 81–98.
- Depickère, S., Fresneau, D., Deneubourg, J.-L., 2004b. Dynamics of aggregation in *Lasius niger* (Formicidae): influence of polyethism. *Insectes Sociaux* 51, 81–90.
- Depickère, S., Fresneau, D., Detrain, C., Deneubourg, J.-L., 2004c. Marking as a decision factor in the choice of a new resting site in *Lasius niger*. *Insectes Sociaux* 51 (in press).
- Fent, K., Wehner, R., 1985. Ocelli: a celestial compass in the desert ant *Cataglyphis*. *Science* 228, 192–194.
- Giurfá, M., Vorobyev, M., Kevan, P., Menzel, R., 1996. Detection of coloured stimuli by honeybees: the role of chromatic and achromatic contrast. *Journal of Comparative Physiology, A* 178, 699–709.
- Goodman, L.J., 1970. The structure and function of the insect dorsal ocellus. *Advances in Insect Physiology* 7, 97–195.
- Goodman, L.J., 1981. Organisation and physiology of the insect dorsal ocellar system. In: Autrum, H. (Ed.), *Handbook of Sensory Physiology*, vol. VII/6C. Springer-Verlag, Berlin, Heidelberg and New York, pp. 201–286.
- Hill, P.S.M., Hollis, J., Wells, H., 2001. Foraging decisions in nectarivores: unexpected interactions between flower constancy and energetic rewards. *Animal Behaviour* 62, 729–737.
- Jaisson, P., 1987. The construction of fellowship between nestmates in social Hymenoptera. *Experientia Supplementum (Behavior in Social Insects)* 54, 313–331.
- Jander, R., 1957. Die optische Richtungsorientierung der Roten Waldameise (*Formica rufa* L.). *Zeitschrift für Vergleichende Physiologie* 40, 162–238.
- Jeanson, R., Deneubourg, J.-L., Grimal, A., Theraulaz, G., 2004. Collective decision-making during refuge site selection by the ant *Messor barbarus*. *Behavioral Ecology and Sociobiology* 55, 388–394.
- Jensen, J.J., 2003. Available from [http://www.durst-pro-usa.com/quality\\_of\\_light.htm](http://www.durst-pro-usa.com/quality_of_light.htm).
- Lazzari, C.R., Reiseman, C.E., Insausti, T.C., 1998. The role of the ocelli in the phototactic behaviour of the haematophagous bug *Triatoma infestans*. *Journal of Insect Physiology* 44, 1159–1162.
- Lenoir, A., 1979. Le comportement alimentaire et la division du travail chez la fourmi *Lasius niger* (L.). *Bulletin Biologique de la France et de la Belgique CXIII (2–3)*, 1–314.
- Lenoir, A., Ataya, H., 1983. Polyéthisme et répartition des niveaux d'activité chez la fourmi *Lasius niger* L. *Zeitschrift für Tierpsychologie* 63, 213–232.
- Lenoir, A., Mardon, J.-C., 1978. Note sur l'application de l'analyse des correspondances à la division du travail chez les fourmis. *Compte Rendu de l'Académie des Sciences de Paris* 287, 555–558.
- Marak, G.E., Wolken, J.J., 1965. An action spectrum for the fire ant (*Solenopsis saevissima*). *Nature* 205, 1328–1329.
- Menzel, R., Backhaus, W., 1991. Colour vision in insects. In: Gouras, P. (Ed.), *Vision and Visual Dysfunction. The Perception of Colour*. Macmillan Press, London, pp. 262–288.
- Meyer, E.P., Domanico, V., 1999. Microvillar orientation in the photoreceptors of the ant *Cataglyphis bicolor*. *Cell Tissue Research* 295, 355–361.
- Mizunami, M., 1994. Information processing in the insect ocellar system: comparative approaches to the evolution of visual processing and neural circuits. *Advances in Insect Physiology* 25, 151–265.
- Mizunami, M., 1995. Functional diversity of neural organization in insect ocellar systems. *Vision Research* 35, 443–452.
- Mote, M.I., Wehner, R., 1980. Functional characteristics of photoreceptors in the compound eye and ocellus of the desert ant, *Cataglyphis bicolor*. *Journal of Comparative Physiology* 137, 63–71.
- Pappas, L.G., Eaton, J.L., 1977. The internal ocellus of *Manduca sexta*: electroretinogram and spectral sensitivity. *Journal of Insect Physiology* 23, 11–12.
- Rossel, S., Wehner, R., 1984. Celestial orientation in bees: the use of spectral cues. *Journal of Comparative Physiology, A* 155, 605–613.
- Santschi, F., 1923. L'orientation sidérale des fourmis, et quelques considérations sur leurs différentes possibilités d'orientation. *Mémoires de la Société Vaudoise des Sciences Naturelles* 1, 137–176.
- Srinivasan, M.V., Lehrer, M., 1988. Spatial acuity of honeybee vision and its spectral properties. *Journal of Comparative Physiology, A* 162, 159–172.
- von Frisch, K., 1914. Der Farbensinn und Formensinn der Biene. *Zoologische Jahrbücher (Physiology)* 35, 1–188.
- Wehner, R., 1984. Astronavigation in insects. *Annual Review of Entomology* 29, 277–298.
- Wehner, R., Flatt, I., 1972. The visual orientation of desert ants, *Cataglyphis bicolor*, by means of terrestrial cues. In: Wehner, R. (Ed.), *Information Processing in the Visual Systems of Arthropods*. Springer, Berlin, Heidelberg, New York, pp. 295–302.
- Wehner, R., Räber, F.W., 1979. Visual spatial memory in desert ants, *Cataglyphis bicolor* (Hymenoptera, Formicidae). *Experientia* 35, 1569–1571.
- Wehner, R., Michel, B., Antonsen, P., 1996. Visual navigation in insects: coupling of egocentric and geocentric information. *Journal of Experimental Biology* 199, 129–140.
- Wehrhahn, C., 1984. Ocellar vision and orientation in flies. *Proceedings of the Royal Society of London B* 222, 409–411.
- Wheeler, W.M., 1910. *Ants: Their Structure, Development and Behavior*. Columbia University Press, New York.
- Wilson, E.O., 1971. *The Insect Societies*. The Belknap Press of Harvard University Press, Cambridge, MA.
- Wu, C.Y., Lin, J.T., 1990. Spectral sensitivity of the compound eye of moth (*Heliothis armigera*). *Chinese Journal of Entomology* 10, 151–158.
- Yang, I.F., Lin, J.T., Wu, C.Y., 1998. Spectral sensitivity of the compound eye in the green lacewing, *Mallada basalis* (Neuroptera: Chrysopidae). *Chinese Journal of Entomology* 18, 117–126.