Out of sight but not out of mind: modulation of recruitment according to home range marking in ants

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Animals can acquire a global knowledge about their environment that exceeds their individual capacities by estimating the local density and activity of nestmates in an area. In ants, home range marking can indicate the density and activity of nestmates, allowing scouts to assess the potential interest of the area as a foraging site. We investigated how home range marking through footprints influences the foraging behaviour of Lasius niger scouts at a sugary food source (1 M, 1.5 ml). Over a marked apparatus the discovery time of food sources decreased while the probability of scouts recruiting nestmates and of continuing to lay a trail increased. For ants making U turns on their return to the nest, home range marking helped them to resume laying a trail after the U turn and delayed the occurrence of the U turn. As a result, the trail intensity and the rate at which information about food was conveyed by scouts to nestmates depended on home range marking. Such modulation of information reduces the number of foragers mobilized to less frequented areas that are potentially dangerous and promotes recruitment and exploitation of food sources to better known sites.

In nature, animals should be able to adjust their foraging behaviour to focus on areas that contain the most valuable food patches with low associated risks of predation or competition. Hence, animals have to acquire a good knowledge of their environment: this includes information about the distribution and quality of available resources, memory of renewing food sources and use of environmental cues that indicate the potential benefits and risks of foraging. Foragers have access to such information through their own experience but also, in group foragers, through paying attention to the behaviour of their companions. This has been demonstrated for vertebrates (mainly in bats, birds and fish) in which the success (or failure) of congeners in food discovery and exploitation can influence the foraging decisions of the individual (Valone 1989; Valone & Giraldeau 1993; Templeton & Giraldeau 1995a; Valone & Templeton 2002). This shared use of ‘public information’ can be facilitated by the existence of information centres (Ward & Zahavi 1973). For instance, one of the advantages of flocking is that it permits a group member to share information with congeners and to locate profitable food sites by keeping track of the movements of the other individuals (e.g. cliff swallow, Hirundo pyrrhonota: Brown 1988; bat, Nycticeius humeralis: Wilkinson 1992; starling, Sturnus vulgaris: Templeton & Giraldeau 1995a, b, 1996). In most cases, the visual perception of companions in a given location provides information about the potential interest of this place as a foraging area and drives group foraging choices (Nicol 1995; guppy, Poecilia reticulata: Swaney et al. 2001; sheep, Ovies aries: Scott et al. 1995, 1996; rat, Rattus norvegicus: Galef 1993).

Insect societies are well known as examples of social integration of information. Their elaborate communication system and their high level of cooperation improve the foraging efficiency of the colony. In this respect, the level of occupancy of a location by nestmates could be, as for gregarious vertebrates, important for estimating the quality of the environment. In ants, the density of nestmates can be assessed through physical contact and interaction (Gordon et al. 1993) but the physical presence of congeners is not always required. Indeed, during their exploration of nest surroundings, many ant species lay home range marks which reflect the spatial distribution of the ants. These chemical marks are laid by nestmates either actively (e.g. through the abdominal glands’ secretions) or passively (e.g. through footprint hydrocarbons; reviewed in Levings & Traniello 1981; Hölldobler &
During the exploration of new areas (Devigne & Detrain 2002), Lasius niger marking occurs to home range marking in the aphid-tending ant. Over a previously explored area, one can thus expect an increase in the efficiency of food searching and food retrieval at the individual level. However, whether home range marking acts upon the global foraging dynamics, the information transfer between nestmates and the level of cooperation in food exploitation is still unknown.

We investigated the modulation of recruitment according to home range marking in the aphid-tending ant Lasius niger. In this species, home range marking occurs during the exploration of new areas (Devigne & Detrain 2002). As L. niger scouts never lay their gaster tip over the substrate during their exploratory trips (personal observation), home range marks most probably originate from footprint hydrocarbons laid passively by walking ants (Yamaoka & Akino 1994). The intensity of home range marking is thus directly related to the density of workers and to the local activity level. We investigated whether the perception of such home range marks allows scouts to assess the potential interest of explored sites as foraging areas and thus to influence their foraging behaviour and their decision to recruit nestmates.

METHODS

Rearing of Ant Colonies

Ten queenless L. niger colonies of about 500–1000 individuals were collected in Brussels, Belgium, in 1998 and reared in the laboratory within plaster nests (20×20 cm). Nests were placed in plastic trays (48×34 cm and 7.5 cm high) with sides coated with Fluon to prevent ants’ escape. The nest plaster was moistened twice a week. Room temperature was kept at 23 ± 2°C. Colonies were fed with dead cockroaches, Periplaneta americana, once a week and had permanent access to sugar solution (1 M) and water.

Experimental Procedure

Colonies deprived of food for 4 days were connected by a cardboard bridge (30 cm long, 1 cm wide) to a foraging platform (13×13 cm). A food source (1.5 ml of 1-M sucrose solution) was then placed in the middle of the foraging platform. A drawbridge system placed at the beginning of the bridge allowed only one scout at a time to reach the foraging platform. We observed this scout during its whole foraging cycle from its arrival over the bridge until its departure from the bridge after it had drunk at the food source. Before the ant reached the nest we gently removed it from the experimental set-up and kept it in a ‘waiting box’. Since recruitment of nestmates was then prevented, we quantified the behaviours of scouts only. Furthermore, to avoid testing the same individuals several times we left the scout in the waiting box throughout each experimental day and we replicated the treatments on a large number of colonies (10) instead of on the same colony. At most, six scouts were observed within the same experiment. To prevent orientation bias from the use of visual cues (Gérard 1987; Aron et al. 1993), we surrounded the whole experimental set-up with a 50-cm-high opaque enclosure.

To investigate how area marking influences their foraging behaviour, we tested scouts on the following two experimental set-ups.

1. Unmarked Set-up (US). Ants were not allowed to explore and chemically mark through footprints either the bridge or the platform area before we added the food. Furthermore, while the scout was drinking at the discovered food source, the bridge, which might have been marked during the scout’s outgoing trip, was replaced by a fresh one. Between successive observations of scouts, the bridge and the area were systematically changed.

2. Marked Set-up (MS). On the third day of food deprivation, we placed the platform area ‘in situ’ and connected it to the nest by the bridge. Ants were allowed to explore, to mark through footprints and to familiarize themselves with the experimental set-up for 20 h before we added the food. However, ants may perceive this marked set-up as familiar either because they were able to detect home range marking or because they had already visited the bridge and the area in previous exploratory trips. To answer this question, we carried out an additional control experiment in which the set-up could be explored and footprint marked by ants from the third day of food deprivation but was not placed ‘in situ’. Instead, the bridge and the area were placed in the nest tray parallel to the front edge of the nest to prevent the ants from familiarizing themselves with the set-up placed ‘in situ’ before the experiment. This control experiment allowed us to confirm the prevailing influence of home range marking in the familiarization process (see Results).

For each scout, we quantified the following parameters.

1. The time taken to discover the foraging platform started when the scout climbed on to the bridge and ended when it reached the foraging platform.

2. The time taken to discover the food source started when the scout reached the platform area and ended when it began to drink.

3. The total time spent drinking: successive drinking times were summed when the ant spontaneously interrupted food ingestion.

4. The time spent before leaving the platform area started when the ant stopped drinking and ended when it left the foraging platform.

5. The return time started when the scout left the platform area and ended when it reached the end of the bridge.

6. The length of the whole foraging cycle was the sum of the above time parameters for each scout.

7. The number of U turns made by the scout during its outgoing and return trips over the bridge: an ant was considered to make a U turn as soon as it half-turned on the bridge and walked at least 1 cm in the opposite direction.

For each scout, we also quantified the intensity of its trail laying by counting the number of marks deposited on the platform area as well as on each bridge section. A scout was considered to be laying a trail when its gaster touched the substrate. The number of trail marks was equal to the
number of times the gaster touched the substrate. We then calculated the global marking of the set-up, which was the average number of trail marks laid by foragers on the area and over each 10-cm section of the bridge. The flat part of the bridge was divided into three 10-cm sections: A, B and C, section A being the nearest to the platform.

Since trail marks possibly laid by a returning scout could influence the behaviour of the following ants, we allowed at least 15 min between the removal of the last observed ant and the replacement of the bridge for the next observation. As the next observed scout always took some time before climbing on to the bridge, two successive observations were on average 25 min apart. Beckers et al. (1993) estimated the duration of a trail laid collectively at about 40 min, beyond which L. niger ants could no longer discriminate between an old trail and a fresh path on a Y-shaped bridge. However, the situation differed in our experiments, because the measured behaviours were not simple choices and the trail was laid by only one individual scout. The time interval of 15 min was chosen as a compromise between limiting the evaporation of home range marks between the testing of the first and the last scout and allowing the evaporation of most of the trail pheromone laid by a returning scout before the next observation.

We also checked for the potential influence of one scout and its trail laying on the behaviour of following ones by comparing, with the Friedman's test (Zar 1996), time parameters and number of trail marks of the first, second, third, fourth, fifth and sixth observed scout. As we did not find any significant differences for any of these parameters (all values of F, with an associated probability P > 0.17), this confirms that a 15-min time interval between two observations was sufficient for the behaviour of scouts to be independent of each other. All 10 colonies were allocated at least once to the two treatments. The experiment lasted 3–4 h. The maximal duration was fixed at 4 h or as soon as the sixth scout was observed. Some ants accidentally fell from the bridge before reaching the nest, especially in the unmarked set-up because of their meandering path (see Results). Since we did not get all time parameters or trail-laying behaviour for these ants, we removed them from the analysis.

Data Analysis

In most cases, the conditions of normality (checked with a Kolmogorov–Smirnov test) or homoscedasticity (checked with Levene's test) were not met; data were then statistically compared using nonparametric tests.

For each of the two set-ups, the evolution of global marking along successive bridge sections was compared with the Friedman’s test and the Dunn’s test for multiple comparisons. Between set-ups, analyses of global marking and time data were carried out with a Mann–Whitney test.

Changes along the bridge in the percentage of trail-laying ants were tested with a Cochran’s test followed, if significant, by multiple comparisons as described in Zar (1996). Between set-ups comparisons were made with Fisher’s exact test for the percentage of trail-laying ants. As their data distribution was normal, individual intensities of trail laying were compared with a Student’s t test with a Welch correction. We used two-tailed statistical tests.

RESULTS

Foraging Time Parameters

Home range marking significantly influenced the discovery time of the platform area: scouts took twice as long to discover the area on an unmarked than on a marked set-up (Table 1). On the unmarked set-up, they walked more sinuously from one side to the other of the bridge and seemed to walk more slowly with more U turns (X ± SD = 1.12 ± 2.25, NUS = 51) than over a marked set-up (0.64 ± 1.67, NMUS = 87; Mann–Whitney U test: Z = −2.382, P < 0.05). In the control experiment, the time taken to discover the platform area (23.2 ± 31.1 s) was similar to that on the marked set-up (35.1 ± 52.1 s; Dunn’s test: NS), indicating that previous exploratory trips and familiarization with the environment in which the set-up was placed had no significant influence compared to that of home range marking on the behaviour of scouts.

The total time ants spent on the platform area was similar for both set-ups (unmarked: X ± SD = 228 ± 115 s; marked: 227 ± 114 s; Mann–Whitney U test: Z = −0.093, NUS = 56, NMUS = 97, NS) but it was allocated differently between the drinking and the exploratory activities. On the unmarked set-up, scouts drank for a shorter period than on the marked one (Table 1). Thereafter, they spent longer exploring the foraging platform before leaving it, although this difference was not statistically significant (Table 1). Indeed, ants ‘looked for’ the platform exit more frequently on the unmarked set-up, moving around, their antennae upwards, when arriving at its edge.

<table>
<thead>
<tr>
<th>Table 1. Duration of foraging activities (s) of scouts on unmarked (N = 56) and marked (N = 97) experimental set-ups</th>
</tr>
</thead>
<tbody>
<tr>
<td>Unmarked</td>
</tr>
<tr>
<td>Time to discover area</td>
</tr>
<tr>
<td>Time to discover food source</td>
</tr>
<tr>
<td>Drinking time</td>
</tr>
<tr>
<td>Time to leave area</td>
</tr>
<tr>
<td>Time to return to nest</td>
</tr>
<tr>
<td>Duration of foraging cycle</td>
</tr>
</tbody>
</table>

Medians are given with quartiles in parentheses.

*Mann–Whitney test.
set-ups, ants returning to the nest were regularly observed turning back on the bridge and revisiting the platform for a while. These additional visits to the platform were equally frequent in both set-ups (number of revisits: unmarked: $X \pm SD = 1.64 \pm 1.05$; marked: $1.27 \pm 0.53$; Mann–Whitney $U$ test: $Z = -1.671, N_{US} = 31, N_{MS} = 52, NS$) but on their last trip back to the nest, ants returned more quickly over the unmarked bridge (Table 1).

As a whole, the foraging cycle lasted longer on the unmarked set-up (Table 1), mainly because the scouts took longer to discover the platform area.

**Trail-laying Behaviour of Individual Scouts**

A significantly lower percentage of ants laid a trail at least once when returning to the nest on the unmarked than on the marked set-up (unmarked: 73.3%, $N = 75$; marked: 89%, $N = 109$; chi-square test: $\chi^2 = 6.53$, $P < 0.05$). In most cases, these ants started laying a trail over the foraging platform as soon as they left the food source. Since $U$ turns over the bridge can alter the trail-laying behaviour of workers (Beckers 1992), we analysed separately the trail-laying behaviour of ants returning straight to the nest after having fed on the food and those making one or several $U$ turns over the bridge, for a subset of observed ants (unmarked: $N = 35$; marked: $N = 46$).

**Ants returning straight to the nest**

The ants differed in their probability of continuing to lay a trail along the bridge according to home range marking (Fig. 1a). Most recruiting ants (85%, $N = 27$) remained engaged in trail laying until the end of their homeward trip over the marked set-up (Cochran’s test: $Q = 10.5, N_{US} = 27, P < 0.05$; Fig. 1a). In contrast, over the unmarked set-up, the percentage of trail-laying ants decreased by half as soon as they left the platform area until they reached their nest (Cochran’s test: $Q = 10.5, N_{US} = 14, P < 0.05$; Fig. 1a).

This low persistence of trail laying by ants walking on the unmarked set-up led to significantly lower percentages of trail-laying individuals than on the marked set-up over the first and the last sections of the bridge (Fig. 1a). For trail-laying ants, the individual trail intensity was not influenced by home range marking, since the number of trail marks laid per ant was similar between set-ups, over each section of the bridge (Table 2).

**Ants making $U$ turns**

In both set-ups, a similar percentage of ants made $U$ turns over the bridge (unmarked: 65.3%, $N = 75$; marked: 62.4%, $N = 109$; chi-square: $\chi^2 = 0.06$, NS). $U$ turns can be related to disorientation of ants caused by the absence of visual cues in both set-ups. However, they made their first $U$ turn closer to the foraging platform when the set-up was not marked. On this set-up, ants made a first $U$ turn at a mean $\pm SD$ of 13 $\pm$ 9.4 cm, whereas over the marked set-up the first $U$ turn was made at 19.3 $\pm$ 10.4 cm (Mann–Whitney $U$ test: $Z = -2.255, N_{US} = 26, N_{MS} = 20, P < 0.05$).

As for ants returning straight to the nest, home range marking strongly influenced their probability of continuing to lay a trail. The percentage of trail-laying ants dropped significantly along the bridge for both set-ups (Cochran’s test: unmarked: $Q = 57.3, N = 37, P < 0.001$; marked: $Q = 27, N = 48, P < 0.001$; Fig. 1b), but this decrease was steeper on the unmarked one. Hence, for each bridge section, the percentages of trail-laying ants were always significantly lower over the unmarked set-up (Fig. 1b).

**Table 2. Average number of trail marks $\pm$ SE laid per ant over each section of the bridge**

<table>
<thead>
<tr>
<th>Section</th>
<th>A</th>
<th>B</th>
<th>C</th>
</tr>
</thead>
<tbody>
<tr>
<td>Straight return</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Marked set-up</td>
<td>8.96 ± 1.27</td>
<td>7.27 ± 0.91</td>
<td>7.03 ± 0.82</td>
</tr>
<tr>
<td>Unmarked set-up</td>
<td>7 ± 2.12</td>
<td>5.57 ± 1.21</td>
<td>5.43 ± 0.87</td>
</tr>
<tr>
<td>$t^*$</td>
<td>0.79</td>
<td>1.12</td>
<td>1.35</td>
</tr>
<tr>
<td>$df$</td>
<td>30</td>
<td>27</td>
<td>28</td>
</tr>
<tr>
<td>$P$</td>
<td>0.44</td>
<td>0.28</td>
<td>0.20</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>U turn</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Marked set-up</td>
<td>8.73 ± 0.93</td>
<td>6.67 ± 0.8</td>
<td>6.19 ± 0.78</td>
</tr>
<tr>
<td>Unmarked set-up</td>
<td>7.69 ± 1.08</td>
<td>3.31 ± 0.57</td>
<td>3.35 ± 0.86</td>
</tr>
<tr>
<td>$t^*$</td>
<td>0.72</td>
<td>3.41</td>
<td>2.45</td>
</tr>
<tr>
<td>$df$</td>
<td>65</td>
<td>47</td>
<td>41</td>
</tr>
<tr>
<td>$P$</td>
<td>0.47</td>
<td>&lt;0.01</td>
<td>&lt;0.05</td>
</tr>
</tbody>
</table>

A, B, C sections are three successive 10-cm sections of the bridge from the platform area to the nest. Only ants that laid a trail over the platform were taken into account.

* Student’s $t$ test with Welch correction.
The individual intensity of trail laying also differed according to home range marking, with significantly lower values on the unmarked than on the marked set-up for the last two bridge sections (Table 2). This result from the differential impact of U turns on trail-laying intensity with respect to home range marking. After the first U turn, a significant decrease in the number of trail marks/cm laid by the ants was observed for both set-ups (unmarked set-up: before U turn: $X \pm SE = 0.44 \pm 0.11$; after U turn: $0.04 \pm 0.02$; marked set-up: before U turn: $0.57 \pm 0.11$; after U turn: $0.26 \pm 0.07$; paired t test: unmarked set-up: $t_{22} = 3.761, P < 0.005$; marked set-up: $t_{23} = 3.651, P < 0.005$), but it was more pronounced over the unmarked one (10-fold versus two-fold decrease for the unmarked and marked set-up, respectively) which resulted in fewer trail marks/cm after the first U turn ($t$ test: $t_{24} = 3.197, P < 0.005$).

**Global Trail Amount Over the Set-up**

Through its influence on the trail-laying behaviour of scouts, home range marking altered the global amount of trail pheromone laid between the food source and the nest. Whereas the average number of trail marks was similar on the foraging platform, it was significantly lower on the unmarked than on the marked set-up over each section of the bridge (Mann–Whitney $U$ test: A section: $Z = -4.163$; B section: $Z = -5.057$; C section: $Z = -6.220$; Fig. 2). Although discovered food sources were the same, the information that was conveyed globally by scouts to nestmates through trail recruitment differed greatly according to area marking.

For both set-ups, the average trail amount decreased significantly along the bridge (Friedman test: unmarked: $\chi^2 = 33.85, P < 0.001$; marked: $\chi^2 = 34.33, P < 0.001$) with more numerous trail marks laid on section A than on section C (A and C sections differed significantly for each set-up: Dunn’s test: $P < 0.001$).

**DISCUSSION**

In *Lasius niger*, home range marks are laid passively by workers walking on the substrate (Yamaoka & Akino 1994). As a result, the density of these marks over an area is directly related to its level of occupancy by the colony. Home range marking thus provides to each worker information about the distribution of nestmates over the foraging range, independently of any direct contact with them. Getting such information can be important for scouts, because the density of ants influences the efficiency of their recruitment. In mass-recruiting species, colony foraging success is closely related to the level of cooperation between nestmates, especially when large or renewable food sources are discovered. We have shown that the decision to lay a trail and hence the global dynamics of foraging are altered by these chemical indicators of the presence of nestmates. Home range marking influenced the individual behaviour of *Lasius niger* workers during their whole foraging cycle, from food discovery until their return to the nest.

**Discovery of Food Resources**

In *Lasius niger*, home range marking favoured the discovery of food sources: the time taken to reach the platform area was significantly shortened as scouts seemed to walk more quickly with a less meandering path (as also shown in *Cataglyphis cursor*: Mayade et al. 1993; *Pheidole pallidula*: Cammaerts & Cammaerts 1996; *Tetramorium*: Cammaerts & Cammaerts 2000). In a competition context, the swiftness of discovery is important, as it gives the colony an advantage in food exploitation. The success of invasive species relies mainly on their opportunist strategy of rapid food discovery, often associated with active defence of foraging sites (Davidson 1998; Holway 1998).

**Exploration Versus Food Exploitation**

The residence times on the platform area (from the discovery of the food source until the departure from the platform area) were similar between the two set-ups, but the time allocated either to exploration or to exploitation of food resources differed according to the presence of home range marks. Home range marking seemed to influence the motivation of scouts to forage or to acquire information about the environment through its exploration. Over unmarked areas, scouts invested more time on exploration and familiarization with the areas surrounding the food. In contrast, on already marked areas, scouts almost exclusively devoted time to the exploitation of the discovered food sources. Similarly, barbary doves, *Streptopelia risoria*, are known to trade-off vigilance (head movements allowing information gathering) and foraging according to their familiarity with the environment (Desportes et al. 1991). In ants such as *Lasius niger*, scouts use their perception of home range marks to solve such trade-offs between exploration and foraging. Home range marking could also be perceived by scouts as indicative of the safety of an area. Over an unmarked area, ants spent less time drinking perhaps to increase their patrolling behaviour.

**Transmission of Information to Nestmates**

Like other mass-recruiting ants (reviewed by e.g. Hölldobler & Wilson 1990; Detrain et al. 1999), *Lasius niger*...
scouts convey information to nestmates about food resources by modulating their trail-laying behaviour (*L. niger*: Traniello 1983; *L. niger*: Beckers et al. 1993; Mailleux et al. 2000; Portha et al. 2002). We have shown that ants can also tune their recruitment behaviour according to environmental factors such as the home range marking of the nest surroundings. Indeed, scouts laid the same amount of trail in the vicinity of food sources but, over their journey back to the nest, their trail-laying behaviour decreased less steeply over a home range-marked substrate. Hence, even when sources are identical in every respect, the information that will reach the nest will differ: the chemical trail intensity perceived by recruited ants within the nest will be higher over a marked than over an unmarked set-up. As a result, colonies will preferentially orient their foraging towards areas that are intensively explored and that concentrate a patrolling force likely to generate quick and efficient food exploitation.

During the first steps of exploration of new areas and during homing, scouts of *L. niger* rely mainly on visual cues (Carthy 1951; Beckers 1992) but also on the perception of home range marks. In our experimental set-up devoid of any visual cues, scouts were likely to become disoriented and more than half the scouts made U turns on their way back to the nest. However, home range marking somewhat reduced disorientation among scouts besides having an impact on trail-laying behaviour. First, over a marked set-up, U turns occurred at longer distances from the platform area. Second, while nearly all the ants stopped laying a trail after a U turn over an unmarked set-up, half the trail-laying scouts continued their trail-laying behaviour when home range marks were present. Similarly, for ants returning straight to the nest, the perception of home range marks led them to maintain high levels of trail laying until they reached the nest. This supports the idea that recruitment occurs preferentially when the platform areas are well known (e.g. Van Vohis Key & Baker 1986; Mercier 1997), and decreased trail laying in disoriented ants limits the transmission of misleading information about food location.

In summary, there is a modulation of information transfer according to the knowledge of the environment. Scout ants laid trails more frequently and with a greater intensity on a marked area than on an unmarked area. At the individual level this makes sense because the cost associated with competitors from other colonies may be a constraint on individual foraging decisions in *L. niger*, and in the same way as directional fidelity in *Pogonomyrmex occidentalis* (Fewell 1990). This constraint may be compensated at the colony level by collective exploration of new areas which allows a colony rapidly to pre-empt an area and mobilize workers around newly discovered food sources (Devigne & Detrain 2002). Furthermore, although weaker and delayed, the existence of recruitment towards unknown areas can make up for the depletion of regularly exploited zones or for an increase in colony needs.

Finally, home range marks inform scouts without direct contact with nestmates about the patrolling force available to generate rapid and efficient food recruitment. Home range marking is a way for nestmates to be ‘out of sight but not out of mind’ and for scouts to make adaptive trail-laying decisions.

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