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To be or not to be faithful: flexible fidelity to foraging trails in the leaf-cutting ant *Acromyrmex lobicornis*

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Abstract. 1. Ants using trails to forage have to select between two alternative routes at bifurcations, using two, potentially conflicting, sources of information to make their decision: individual experience to return to a previous successful foraging site (i.e. fidelity) and ant traffic. In the field, we investigated which of these two types of information individuals of the leaf-cutting ant *Acromyrmex lobicornis* Emery use to decide which foraging route to take.

2. We measured the proportion of foraging ants returning to each trail of bifurcations the following day, and for 4–7 consecutive days. We then experimentally increased ant traffic on one trail of the bifurcation by adding additional food sources to examine the effect of increased ant traffic on the decision that ants make.

3. Binomial tests showed that for 62% of the trails, ant fidelity was relatively more important than ant traffic in deciding which bifurcation to follow, suggesting the importance of previous experience.

4. When information conflict was generated by experimentally increasing ant traffic along the trail with less foraging activity, most ants relied on ant traffic to decide. However, in 33% of these bifurcations, ants were still faithful to their trail. Thus, there is some degree of flexibility in the decisions that *A. lobicornis* make to access food resources.

5. This flexible fidelity results in individual variation in the response of workers to different levels of ant traffic, and allows the colony to simultaneously exploit both established and recently discovered food patches, aiding efficient food gathering.

Key words. Ant traffic, bifurcation, decision-making, experience, foraging trail network, U-turn.

Introduction

Fidelity to foraging sites entails benefits and costs. Returning to sites with resources of known quality reduces searching time and increases the probability of acquiring food (Jakob *et al.*, 2001; Bradshaw *et al.*, 2004; Laca, 2008; Janmaat *et al.*, 2009). In addition, site familiarity reduces predation risk and increases travel efficiency (Clarke *et al.*, 1993; Stamps, 1995; Brown, 2001). However, fidelity to foraging sites may reduce the chance of encountering new resources (Fewell, 1990; Singleton & van Schaik, 2001; Schoonhoven *et al.*, 2005). Therefore, fidelity to foraging sites should be more or less flexible depending on the balance between these costs and benefits.

Leaf-cutting ants are good models for examining the fidelity of organisms to foraging sites. These ants forage on plant tissue from surrounding vegetation and carry this material back to their nest, where the plant fragments are used as substrate for a symbiotic fungus that they cultivate in underground chambers (Hölldobler & Wilson, 1990). The growth of the symbiotic fungus depends on the quantity and quality of leaf fragments collected by the ants (Camargo *et al.*, 2008). Therefore, leaf-cutting ant workers harvest large quantities of vegetation, but are also permanently searching for new plants or transient resources such as flowers and new leaves (Rockwood & Hubbell, 1987; Howard, 1990). To do this, leaf-cutting ants use a network of persistent dendritic trails radiating out from the nest to the food sources. This trail system directs foragers to known resources but also determines the area to explore for new ones (Shepherd, 1982; Farji-Brener & Sierra, 1998), with a typical mature leaf-cutting ant nest having up to 10 main trails and more than 50 branching points (Kost *et al.*, 2005).

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As a main trail has multiple branching points and each path directs foragers to different plant sources, ants frequently have to decide whether or not to use the route of its previous trip; in other words, to be or not to be faithful to its previous foraging site.

Different types of information may influence orientation of the path taken by ants to and from resources, and thus the decision to be or not to be faithful to a particular foraging route (Aron *et al*., 1993; Czaczkes *et al*., 2011). Leaf-cutting ants use information generated by nestmates through chemical pheromone trails and physical contact among foragers that pass information about foraging sources (Jaffé & Howse, 1979; Farji-Brener *et al*., 2010). In addition, these ants orientate visually (Vilela *et al*., 1987; Guajara *et al*., 1990) or by magnetic cues (Riveros & Srygley, 2008), which may allow them to use their experience to return to the same foraging sites. Branching points along foraging trails are crucial areas, because ants must decide which trail to follow. Conflicts of information may arise at these bifurcations if an ant has previously visited one trail and hence associates it with a good food resource, while nestmate traffic is higher towards the other trail. In these situations, some ant species preferentially rely more on their previous experience while others use pheromone concentration or ant traffic to decide which trail to follow (Rosengren & Fortelius, 1986; Harrison *et al*., 1989; Aron *et al*., 1993; Grüter *et al*., 2010). Under laboratory conditions, isolated leaf-cutting ant foragers without previous foraging experience chose the trail with higher pheromone concentration (Morgan *et al*., 2006). However, in situations where ants had previously foraged successfully along one other trail, it is possible they may decide to return to that trail, even if chemical and physical information from nestmates is stronger towards the other trail.

The existence of trail fidelity in leaf-cutting ants and the mechanisms involved are still poorly studied, despite some evidence for fidelity to the main foraging trails in these ants (Shepherd, 1982; Sousa-Souto *et al*., 2005). How ants distribute on trails of bifurcations is important in understanding their traffic organisation (Shepherd, 1982; Burd *et al*., 2002). Here, we investigate fidelity to foraging trails of the leaf-cutting ant *Acromyrmex lobicornis* Emery (Hymenoptera: Formicidae: Attini), and explore the effect of previous experience and ant traffic on foraging trail fidelity. Specifically, we first evaluated under natural field conditions whether foragers return to the trail in a bifurcation where they had previously foraged, and related their choices with ant traffic. We then generated a conflict of information by experimentally increasing ant traffic along one trail, and investigated whether ants returned to the same trail.

Methods

Fidelity to trails of ants foraging under natural conditions

We collected data from field nests of *Acromyrmex lobicornis* near Alicurá, Rio Negro, Argentina (40°39′15″S, 70°49′57″W), from November 2009 to March 2010, during daylight hours. Nests were selected based on similar mound size (60–140 cm in diameter) and with three to seven foraging trails. To evaluate whether ants choose the same trail they used previously at a branching point, we selected the first bifurcation along 1 trail for each of 16 nests. Bifurcations chosen were at least 4 m from the nest and had trails of similar width (mean relative width difference of 16%). For each trail, 2 m after the bifurcation point, we marked 100 ants with a different colour for each trail, by painting a small dot of enamel (Umbrol) on the gaster using a toothpick. We only marked ants that were returning to the nest with loads, to ensure they were successful foragers. We held the ants while painting and replaced them immediately afterwards at the same place on the foraging trail to reduce disturbance. We confirmed that painting did not affect ant survivorship by keeping marked and unmarked (control) ants under lab condition for 3 months (45 ± 27 and 47 ± 26 mean ± SD days survivorship for marked vs. unmarked, respectively, $t_{397} = 0.83$, $P = 0.41$). We also did not observe any removal of paint marks during this period.

Ants were considered faithful when they were detected on the same trail they were marked on, or unfaithful if they were detected on the other trail (Fig. 1). Counts were performed during 30 min the day after ants were marked. We chose this sampling interval as a compromise between recording as many marked ants as possible and reducing the chances of counting the same ant more than once, as well as reducing variation in trail pheromone concentration. During the 30-min observation period at a bifurcation, we recorded the proportion of faithful ants passing each trail (Fig. 1). The return of ants to trails in bifurcations was thus measured as a group response, without individually identifying marked ants (Rosengren & Fortelius, 1986; Quinet & Pasteels, 1996; Evison *et al*., 2008b; Fig. 1).

We also recorded ant traffic along the trails of a bifurcation because this is a good proxy for pheromone concentration (Jaffé & Howse, 1979), and may in itself be used as a cue (Devigne & Detrain, 2006). We counted the number of ants crossing each trail for 1 min, before and after recording the

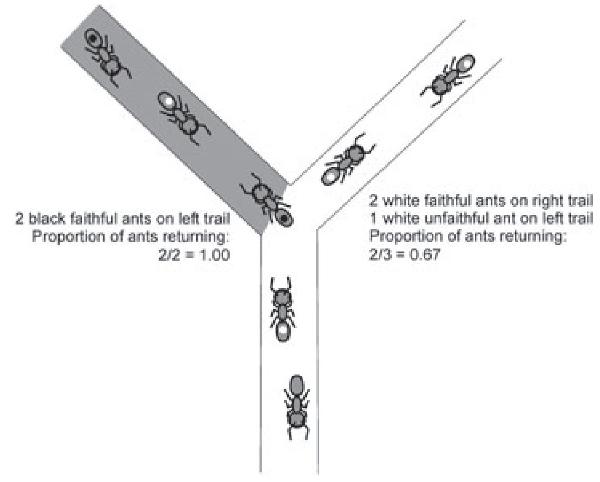

Fig. 1. Illustrative example of data gathering for ants returning to trails at a bifurcation, where the same numbers of ants (i.e. 100) were marked the previous day with white paint if they were on the right trail, and with black if on the left trail. The leaves of returning ants were not drawn for clarity.

number of marked ants on each path, and averaged these two counts to obtain a measure of ant traffic. As the return of an ant to a trail could be influenced by both the ant's previous experience and ant traffic, we evaluated whether previous foraging experience determined selection of one trail over the other by statistically accounting for the effect of ant traffic. For this, we used binomial tests to compare the proportions of ant traffic on a trail as the null hypothesis with the choices of marked ants. More ants returning to the trail than expected from the ant traffic indicates they were using information from previous successful foraging experiences to choose between the trails.

In addition, to assess whether the observed pattern in fidelity was stable through time, we measured trail choice at bifurcations over 4–7 consecutive days for a subset of six typical nests. We recorded ant traffic and presence of marked ants for each trail once or twice per day, during the morning and afternoon. We tested for a change over time in the proportion of ants returning to previously selected trails using a Kendall's rank correlation (Legendre & Legendre, 1998).

Conflict between previous foraging experience and ant traffic: a field experiment

We evaluated the influence of ant traffic on trail selection by manipulating ant traffic for 10 nests. After recording the number of ants of each colour on both trails during 30 min, as well as ant activity for 1 min at the beginning and end of the 30 min period, we placed attractive baits near the trail with lowest activity to stimulate a change in ant traffic. Baits were corn flakes and oats, which are highly attractive food sources for leaf-cutting ants (Farji-Brener, 2001), and sprigs of *Rosa eglanteria*, which are naturally foraged by the ants (Farji-Brener, 1996). These food items were offered to the ants mixed together, in a 10 × 10 cm tray placed next to the edge of the trail, approximately 2 m beyond the bifurcation. We placed the bait next to the trail of the bifurcation with less activity to increase the conflict between previous experience of foragers and ant traffic. Bait was replenished as needed. After 2–4 h of bait provision, we measured ant traffic and the number of marked ants on both trails as before.

For analyses, we only considered those cases in which there were significant changes in ant activity in the expected direction (i.e. a reduction in traffic along the trail without bait and an increase along the trail with bait), based on χ^2 tests. We evaluated the change in proportions of ants returning to trails before and after bait addition using paired Wilcoxon signed-rank tests. As before, we used binomial tests to evaluate whether ants used previous experience while accounting for the effect of ant traffic, contrasting the proportion of marked ants returning to their trail with the proportion of ant traffic towards that trail as the null hypothesis. As these analyses evaluated to what extent ants were faithful to the trail when ant traffic to the other trail was very strong, we only analysed fidelity of marked ants to the trail without bait (i.e. with less ant traffic). For example, a significant binomial test where 0.58 of marked ants return to a trail and ant relative activity towards that trail was 0.31, suggested fidelity of these ants to their trail.

U-turns after trail choice

Some ants turned 180° shortly after choosing a trail and then took the other trail of the same bifurcation (hereafter 'U-turn', Beckers *et al*., 1992). We registered the number of these U-turns and classified them as faithful turns, when the ant changed its direction to maintain fidelity (relying on its experience more than on ant traffic) or unfaithful turns, when ants changed direction towards the trail with more traffic (not relying on its experience). Thus, we evaluated whether U-turns under natural traffic conditions (i.e. without bait) were more frequent towards trails with higher ant traffic (thus suggesting that U-turns depend on ant traffic), using χ^2 tests. We compared the number of faithful U-turns performed from the trail with more traffic towards the one with less ant activity, with the number of faithful U-turns performed from the trail with low activity to that with high activity.

Results

Fidelity to trails of ants foraging under natural conditions

Most of the marked ants returned to the trail where they had previously foraged (0.70 ± 0.19 mean ± SD proportion of ants returning, $n = 32$ trails from 16 bifurcations; Table 1a). As in nearly half of bifurcations ant traffic differed significantly between trails (binomial tests, $P < 0.05$) and proportion of fidelity was positively correlated with ant traffic ($r = 0.74$, d.f. $= 30$, $P < 0.001$), it was necessary to statistically remove the effect of ant traffic to evaluate the effect of individual experience on trail selection. After controlling for ant traffic in binomial tests (see Methods), the proportion of ants returning to the trail where they were originally marked was still significantly higher for 62% of the trails ($P < 0.05$ in 20 from 32 binomial tests with relative ant traffic, Table 1a). The return by ants to trails did not change over the course of consecutive days in most bifurcations examined (Kendall correlation $P > 0.05$, exceptions shown in Appendix S1).

Conflict between previous experience and ant traffic

The addition of baits increased ant traffic and the proportion of ants returning to trails. The number of forager ants increased on average 4.2-fold on the trail with bait and decreased 2.2-fold on the other trail. Thus, changes in ant traffic between trails were not a mere consequence of ant recruitment from the nest. Compared with traffic before bait addition, the proportion of ants returning to the trail without bait decreased 2.8-fold (Wilcoxon signed-rank test: $T = 3$, $n = 9$, $P = 0.01$) and increased 1.4-fold to the trail with bait (Wilcoxon signed-rank test: $T = 42.5$, $n = 9$, $P = 0.02$). Only 33% of the trails showed a higher proportion of ants returning to the previously used trail, compared with ant traffic on that trail ($P < 0.05$ in three of nine binomial tests accounting for ant traffic, Table 1b), a percentage significantly lower than that obtained under natural foraging conditions (${\chi_1}^2 = 2.85$, $P = 0.05$). The bifurcation from one nest was not included in the analyses, because ant activity was not affected by the addition of bait.

Table 1. Proportion of ants returning to their trail of a bifurcation, total number of ants marked on that trail that were recorded there again (N), relative ant traffic, average number of ants per minute towards each trail, and P values for binomial test results for ants foraging (a) under natural conditions, and (b) with bait addition (only results for the trail without bait).

(a)

	Right trail					Left trail				
			Ant traffic					Ant traffic		
Nest no.	Proportion returning	N	Relative	Ants/min	P value	Proportion returning	N	Relative	Ants/min	P-value
1	0.36	14	0.23	16	0.335	0.79	42	0.77	54	1
2	0.93	27	0.42	31.5	**0**	0.75	48	0.58	43	**0.019**
3	0.51	89	0.27	8	**0**	0.86	69	0.73	22	**0.02**
4	0.88	43	0.41	35.5	**0**	0.59	39	0.59	51	1
5	0.94	64	0.65	85	**0**	0.54	68	0.35	45.5	**0.001**
6	0.82	22	0.73	35	0.474	0.65	17	0.27	13	**0.001**
7	1	31	0.84	33.5	**0.006**	0.21	29	0.16	6.5	0.457
8	0.92	49	0.67	48	**0**	0.53	47	0.33	23.5	**0.005**
9	0.9	58	0.63	27.5	**0**	0.73	37	0.38	16.5	**0**
10	0.76	67	0.46	37.5	**0**	0.84	45	0.54	43.5	**0**
11	0.64	50	0.39	28.5	**0**	0.7	43	0.61	45.5	0.347
12	0.89	37	0.69	18.5	**0.007**	0.63	49	0.31	8.5	**0**
13	0.89	36	0.65	33.5	**0.002**	0.42	55	0.35	18	0.322
14	0.43	82	0.39	27	0.496	0.71	49	0.61	43	0.186
15	0.68	88	0.50	23	**0.001**	0.46	50	0.50	20	0.672
16	0.72	29	0.67	24	0.562	0.58	24	0.33	12	**0.015**

(b)

	Trail without bait				
			Ant traffic		
Nest no.	Proportion returning	N	Relative	Ants/min	P value
4	0.68	40	0.25	47	**0**
6	0.67	9	0.48	21	0.326
8	0.38	34	0.25	52	0.075
9	0.04	102	0.03	11	0.545
10	0.23	52	0.30	36	0.363
11	0.15	40	0.15	40	1
12	0.10	52	0.11	19	1
13	0.13	68	0.04	11	**0.003**
14	0.58	40	0.31	29	**0.001**

The proportion of ants returning to their trail is the number of experienced ants marked on a trail that returned to that trail from all the ants marked with the same colour passing by the bifurcation in 30 min (N, see Fig. 1). Binomial tests include ant traffic as the null expectation to compare with the proportion of ants returning to each trail to remove the effect of traffic on trail choice by the marked ants. P values in bold show significant differences that suggest the effect of experience once ant traffic effect was controlled for (62% of trails for ants foraging under natural conditions, and 33% of trails for ants returning to trails without bait).

U-turns after trail choice

U-turns were recorded in 46% of bifurcations under natural foraging conditions, but only 2% of marked ants crossing a bifurcation U-turned. Faithful U-turns were more frequent than unfaithful ones (74 vs. 12 ants performed faithful and unfaithful U-turns, respectively; $\chi_1{}^2 = 41.9$, $P < 0.001$). A similar proportion of ants performed faithful U-turns towards trails with high or low relative ant traffic (39 ants performing U-turns towards high activity trails vs. 35 ants towards trails with low activity, $\chi_1{}^2 = 0.22$, $P = 0.64$). The number of unfaithful U-turns of ants that turned towards trails with high or low traffic was also similar (seven ants performing U-turns towards high activity trails vs. five ants towards trails with low activity). However, it was not possible to statistically evaluate the difference due to the low frequency of occurrence.

Discussion

Behavioural flexibility is a beneficial trait as it allows organisms to quickly adapt to changing situations. Our results highlight the flexible behaviour of *Acromyrmex lobicornis* during the selection of foraging routes, flexibility also demonstrated for leaf-cutting ants in other foraging contexts (Dussutour *et al*., 2009; Ribeiro *et al*., 2009). The experience of an ant forager seems to be more important than ant traffic in deciding the foraging route when ant traffic towards both trails of a bifurcation was similar. After correcting for the effect of ant traffic, ants for 62% of the trails sampled showed a significant preference for the trail they used previously. However, this dropped to 33% when ant traffic was experimentally increased towards the trail with low ant traffic. If a strong and rapid increase of ant traffic is a social cue that represents exploitation of a recently discovered food resource, a rigid fidelity to a previous foraging site may be costly for the colony. A rapid colonisation of a food resource is vital to avoid competition with other herbivores, including neighbouring leaf-cutting ant colonies, and to consume transient resources before they change in palatability (i.e. flowers or new leaves). Accordingly, most of the ants previously selecting a trail using their experience switched to use the other more active route. Notwithstanding this, a portion of ants maintained their fidelity to the previous foraging site despite abrupt changes in ant traffic. Overall, this individual variation in response to different levels of ant traffic might allow the colony to simultaneously exploit recently discovered food patches while continuing to use other known resources, thereby aiding efficient food gathering by the colony as a whole.

Two nonexclusive mechanisms could account for this flexible foraging behaviour. First, ants with more successful foraging trips along a trail in a bifurcation may be more entrained and thus show a stronger fidelity to that trail than other ants with less successful experiences. Research into other ant species showed that route fidelity often increases with experience (Buchkremer & Reinhold, 2008; Grüter *et al*., 2010). Leaf-cutting ants leave the nest to forage using the same exit hole on consecutive days (Shepherd, 1982; Sousa-Souto *et al*., 2005; for *A. lobicornis*, L. Elizalde, unpublished results), which, in addition to their fidelity to the trail of a bifurcation, increases ant experience of a particular trail. Second, ants from the same colony may have different response thresholds to ant traffic. The existence of different response thresholds among workers from the same colony has been previously reported in leaf-cutting ants (Roces, 1993; Kleineidam *et al*., 2007). These two mechanisms may act in concert, because foraging experiences that are more successful may increase the response threshold to ant traffic. In other words, ants with more successful foraging trips may need a greater increase in ant traffic to change their foraging routine than ants with fewer foraging trips.

Our results also contribute to understanding the use of individual and social information by these ants to make foraging decisions. Ant traffic is a social cue that is positively correlated with trail pheromone concentration (Jaffé & Howse, 1979; Morgan *et al*., 2006), and with information exchange among foragers through head-on contacts (Farji-Brener *et al*., 2010). On the other hand, ant fidelity to a particular foraging trail is probably a consequence of individual information that the ant acquired by learning and memorising the route. We found that in leaf-cutting ants, both individual experience and social information may play a role in the process of selecting foraging routes. Specifically, we found that foragers of *A. lobicornis* often use their foraging experience to decide which trails to follow (i.e. are faithful to foraging sites). However, while some ants remain faithful, most become unfaithful and switch to an alternative foraging route when the social cue given by ant traffic was very high. This suggests that the relative importance of these two sources of information varies among workers, and illustrates the need to study in more detail the learning and memorising of foraging routes by these ants.

At least two potential limitations of the work may affect this interpretation. First, other unmeasured factors, such as the information transfer in contacts with returning nestmates from the trail with low traffic, might influence the decision of the route to follow at branching points (Farji-Brener *et al*., 2010), and/or temporal differences in overcrowding on a trail may motivate ants to choose that with lower traffic (Deneubourg *et al*., 1989; Dussutour *et al*., 2004). However, the probability of faithful and unfaithful ants contacting other ants is expected to be the same, and we did not observe instances of overcrowding at bifurcations, even when ant traffic was experimentally increased (L. Elizalde, pers. obs.). In addition, the maintenance of fidelity over consecutive days, as well as the behaviour of ants that U-turned to return to their previous trail, both support the idea that these ants returned to their trail because of their previous successful foraging experiences. In fact, the higher frequency of faithful compared to unfaithful U-turns, in addition to the lack of association between U-turn frequency and ant traffic to a trail, suggests that ant traffic was not the main cause of these U-turns in *A. lobicornis* and that they may serve to correct an erroneous decision made by disorientated ants. This behaviour was not previously reported in leaf-cutting ants, although U-turns were observed in the context of minima ants laying pheromone trails (Hughes & Goulson, 2001; Evison *et al*., 2008a). Second, because data were gathered for ants as a group and not individually, the measures of ant fidelity reported here may be underestimated because some ants may have initially been recorded when not on their normal trail. Lastly, when comparing fidelity with ant traffic, the effect of ant fidelity might be reduced because our measurement of ant traffic might have included ants that used previous experience to select a trail. This effect will be more important in cases where the difference in ant traffic between trails of a bifurcation was higher, since most ants returning to the trail with less traffic made their decision probably based on previous experience. All these issues may affect quantification of the relative contribution of each information type. However, these potential biases in the estimation of trail fidelity were probably the same in all of the colonies studied, and thus should not affect the comparative measures on which our interpretation is based.

In sum, our findings may have implications for traffic organisation and ant foraging strategies. The variation among foragers in their response to differences in ant traffic may help in regulating the distribution of ants on trails of bifurcations with different traffic flows. This individual variation may inhibit the positive feedback mechanism by which ants at bifurcations select the trail with higher pheromone concentrations or ant traffic, then depositing more pheromone while returning and thus making that trail even more attractive (Beckers *et al*., 1992). Therefore, under a situation in which faithful ants inhibit this process, the bulk of ants will distribute more or less homogeneously along all stretches of the foraging trail network where resources are in use, keeping resource flow high (Aron *et al*., 1993; Howard *et al*., 1996). Combining two foraging strategies, one that rapidly allocates foragers to ephemeral resources and another that diverts foragers to stable resources, may be important in enhancing the ability of colonies to forage efficiently on predictable and unpredictable resources simultaneously (Jaffé *et al*., 1985; Howard, 1990).

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Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference:
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Appendix S1. Results and Figures showing the proportion of ants returning to the trail over consecutive days for the bifurcations of six nests.

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