# Site Fidelity of *Formica rufa*: Micro-Scaled and Persistent Despite Disturbance (Hymenoptera: Formicidae)[1]

by

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## ABSTRACT

Long-term site fidelity or Ortstreue is an individual foraging strategy typical of ants exploiting stable and predictable food sources in space and time. Red wood ant workers (*Formica* s. str.) are central-place foragers feeding on honeydew secreted by stable aphid populations. In this field study, temporal site fidelity of *Formica rufa* honeydew tenders was investigated on a micro-scaled level for a period of time. Additionally, the effect of exchanging honeydew workers between two trees on site fidelity was examined. Site fidelity of the honeydew tenders was very high and they returned repeatedly to particular micro-sites (branches, set of leaves) on a tree. The transfer to a new feeding site apparently did not influence site fidelity as honeydew tenders mainly return to their initial tree. Small-scale site fidelity decreased with time and was not so rigid as larger-scale fidelity. We discuss how site fidelity on one hand and flexibility in foraging and recruiting on the other hand promote foraging efficiency of the colony.

Keywords: site fidelity; Ortstreue; foraging behavior; ant; *Formica rufa*.

## INTRODUCTION

Red wood ants of the *Formica rufa* group are dominant central-place foragers with trails radiating in different directions from the nest (Rosengren 1971; Rosengren & Fortelius 1986). These routes lead the foragers to stable aphid colonies and hunting grounds and can persist for several years (Rosengren 1971). It is well known that a worker of the *Formica rufa* group prefers

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particular trails and even returns repeatedly to the same foraging site along that route (Rosengren 1971; Rosengren 1977a). This trail and or site fidelity (Ortsteue) has also been demonstrated in many other ant taxa (Ebbers & Barrows 1980; Hölldobler & Wilson 1990; Quinet & Pasteels 1996; Salo & Rosengren 2001; Mody & Linsenmair 2003; Beverly *et al.* 2009). Long-term Ortstreue (weeks-months even after hibernation) is typically associated with the monopolization of food sources that are predictable in space and time such as aphid colonies and extrafloral nectaries (Herbers 1977; Rosengren & Fortelius 1986; Tilles & Wood 1986; Quinet & Pasteels 1996; Mody & Linsenmair 2003). Studies on *Lasius fuliginosus* (Quinet & Pasteels 1996) and on *Camponotus sericeus* (Mody & Linsenmair 2003) demonstrated a pronounced fidelity of foragers not only to individual plants but even to small parts of these plants (branches, leaves). It is not known if honeydew tenders of the *F. rufa* group show such micro-scaled fidelity on plants.

Besides an efficient competitive monopolization, Ortstreue is assumed to promote colony efficiency in avoiding any form of time- and energy-consuming competition among fellow colony members (references in Mody & Linsenmair 2003). However site fidelity is not rigid as ant workers can flexible shift from a poor site to another more rewarding site where they can acquire site fidelity again (Lamb & Ollason 1994a; Quinet & Pasteels 1996). This flexibility allows a colony to distribute their workers according to the theory of Ideal Free Distribution. This theory predicts that animals distribute themselves among patches proportionally to the amount of resources available (Fretwell & Lucas 1970). Considering site fidelity on one hand and flexibility on the other hand, we are interested whether experimentally transferred workers to other rich feeding sites will flexibly return to these new sites or either preserve their primary site fidelity.

This paper examines the site fidelity in *Formica rufa* (Linnaeus 1758) in more detail than hitherto. The first aim of this study is to explore whether honeydew tenders of *F. rufa* exhibit micro-site fidelity in visiting persistently particular branches or even small set of leaves of a tree. Secondly we report how transferring honeydew tenders to other aphid groups affects site fidelity.

# MATERIAL AND METHODS

## Study area

The study was conducted in "de Duinbossen van De Haan" in the summer of 2009. This area is a highly fragmented dune forest of 150 Ha near the Belgian coast (Loose *et al.* 2007).

Two *F. rufa* colonies were used for the experiments, further called nest 1 and 2. The two colonies foraged in open dune vegetation dominated by a pioneer vegetation of poplar saplings (*Populus alba*). The gaster of honeydew tenders visiting those saplings were marked with a dot enamel paint (Humbrol). By using small saplings (not taller than 1 meter), we could observe and follow marked ants quite easily.

## Experimental design

The first experiment (exp. 1) was designed to investigate whether honeydew tenders returned to specific regions of a tree. A heavily visited *Populus alba* sapling at 60 cm from the nest mound of nest 1 was selected. During three hours all workers were marked. Workers were released on the same spot after drying (10-15 sec.) of the paint. No impact on ant behavior was observed after painting. The sapling used for this experiment had three main branches. Workers of each branch were marked differently (green-orange-yellow). The leaves of the different branches were far apart from one another so that workers could not get from a leaf from one branch to a leaf from another and therefore the branches could be considered as distinct localities on the tree. Initially 206 workers were marked yellow on the first branch, 34 workers green on the second branch and 32 workers orange on the third branch. The succeeding four weeks at six control moments, we counted all marked and non-marked workers and we noted if they were still tending aphids on their initial branch. Additionally surrounding saplings and other plants were screened for marked honeydew tenders.

A second experiment (exp. 2) was designed to explore site fidelity on a smaller scale, i.e. leaf level. Honeydew tenders per leaf of a *Populus alba* sapling were differentially marked. The sapling (2 metres from nest 2) had four distant branches with 20 leaves and correspondingly 20 unique two-color combinations were used to mark a total of 74 workers (min. 2, max. 8 colored workers per leaf). After marking, leaf fidelity was determined during a period of nine days. We looked whether workers were observed on the same leaf ('identical') or near the original leaf ('near' = on the same branch and max. three leafs separated) or returned to more distant leaves of the sapling. In addition we checked whether surrounding saplings attract some of the marked honeydew tenders. As workers often visit a number of adjacent leaves in one excursion (pers. observation), workers found on "near" leaves can be considered as showing leaf fidelity.

A third experiment (exp. 3) was designed to examine if experimental exchange of workers between trees influenced their site fidelity. Two *Populus alba* saplings (different from exp. 1 and exp. 2) were selected near nest 2. The nest mound was built against the first tree, the second tree was located at 1.70 m from the nest. Workers tending on the closest sapling ("green" sapling) were marked green, those on the more distant sapling ("white" sapling) white. Workers were transferred by hand to the other sapling after marking. Marking and transferring was done by two persons so that the exchange between the two saplings occurred simultaneously. 125 green workers and 125 white workers were marked and transferred. Hence, after transfer 125 green workers were foraging on the white sapling, and 125 white workers on the green sapling (Fig. 3 'start'). Workers were often in threat posture due to disturbance. After a while, though, they explored the new sapling and resumed aphid tending. This experiment should elucidate whether transferred workers prefer to return to their initial food source or not. The origin of the honeydew tenders on the two saplings was checked five times in a ten-day period.

## Statistical analysis (Johnson *et al.* 2005)

Data of exp. 1 and 3 were analysed with the use of the hypergeometric distribution. This discrete probability distribution describes the number of successes in a sequence of n draws from a finite population without replacement. The probability to draw y individuals with a particular character state in a sample (size = n) from a finite population (size = N) with s individuals with the character of interest is given by the formula:

$$P(X=y)=\binom{s}{y}\binom{(N-s)}{(n-y)}\Big/\binom{N}{n}$$

P-value to find a certain number of successes is calculated by the exact probability to find this number of successes summated with the probabilities to find even more extreme number of successes.

The marked workers were initially in the proportion of 206 yellow/ 34 green/ 32 orange for the first experiment. This implies that if workers return to the sapling without preference for a particular branch, all three branches should have marked workers in a proportion not significant different from the initial proportion. Suppose that yellow workers tend to return to their initial branch ("yellow" branch), the proportion yellow workers will consequently be significant larger than 206/(206+34+32).

The parameters in the formula represent :

**N** = total number of marked workers = 272 = 206 yellow + 34 greens + 32 orange workers

**n** = total number of marked workers on a particular branch on a particular day

**s** = 206 for yellow workers

34 for green workers

32 for orange workers

**y** = for the yellow branch = the number of yellow workers on the yellow branch

for the green branch = the number of green workers on the green branch

for the orange branch = the number of orange workers on the orange branch

The number of successes were calculated per branch per day. We illustrate with an example. On the yellow branch we found 48 yellow workers and 3 non-yellow marked workers on 07-21, and thus N = 272, n = 51, S = 206, y = 48. The associated P-value is calculated by the exact probability to find 48 successes summated with the probabilities to find even more extreme number of successes: $P = P(X = 48) + P(X = 49) + P(X = 50) + P(X = 51)$.

During the third experiment we examined whether honeydew tenders returned preferentially to their original sapling. If there is no preference, it can be expected that after some time both saplings will have even proportions of green and white marked workers (random distribution). Data were analysed with the characteristics of the hypergeometric distribution, described above, with N = 250, n = number of marked workers on a sapling on a particular day, s = 125, y = number green marked workers on green sapling or number of white workers on white sapling.

All analyses were done in SAS 9.2.

## RESULTS

### Experiment 1

No marked workers were observed on the surrounding saplings, trails to other trees or on the nest mound. Marked workers were only found on their original sapling. Apparently workers tended to return to the same sapling over time (Fig. 1). Site fidelity took place even on a smaller scale as workers had clear preferences to return to the branch where they were initially tending aphids. The proportion of the different marked workers differed in most cases significantly from the initial proportion (206/34/32) (Table 1). Proportions on the yellow branch from 16 days after the start to the end of the experiment were not significant different from the random initial proportion.

### Experiment 2

Leaf fidelity (identical and near) is extremely high one day after marking (Fig. 2). Thereafter fidelity gradually decreases, but is still 50 percent after five days. After seven days, 22 % of the marked honeydew tenders were observed on the identical leaf of marking.

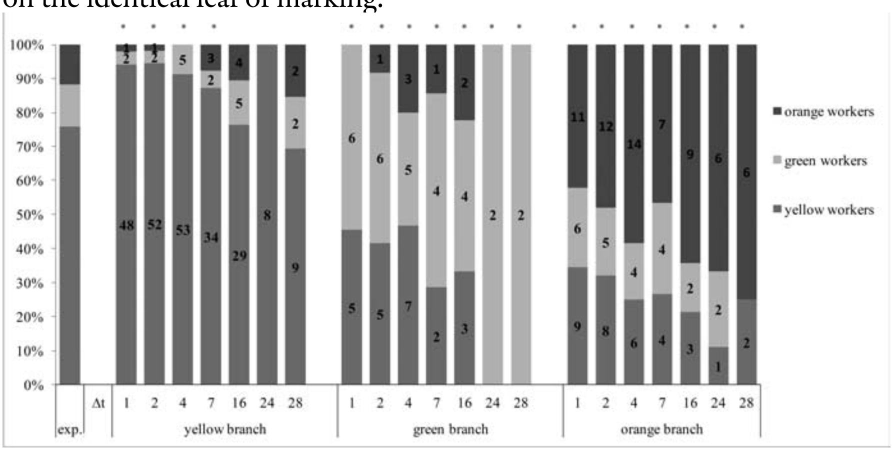


Fig. 1. Exp. 1. Proportion marked workers over time (days after start marking of samples indicated below bars (Δt)). Exp.= expected proportion marked workers under null hypothesis = proportions without worker branch preference (206 yellow workers / 34 green workers / 32 orange workers). Number of marked workers per color indicated in bars. Proportions significant different (5%-level) from expected proportion indicated with (*) above bars.

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Table 1. P-values Exp. 1. Branch color Y = yellow, G = green, O = orange. N = total marked population, s = sample size, n = sample number, y = number of workers with same color as branch sampled (= successes).

| branch | day | N | s | n | y | P |
|---|---|---|---|---|---|---|
| Y | 1 | 272 | 206 | 51 | 48 | 0.00021 |
| Y | 2 | 272 | 206 | 55 | 52 | 0.00007 |
| Y | 4 | 272 | 206 | 58 | 53 | 0.00077 |
| Y | 7 | 272 | 206 | 39 | 34 | 0.04939 |
| Y | 16 | 272 | 206 | 38 | 29 | 0.55528 |
| Y | 24 | 272 | 206 | 8 | 8 | 0.10465 |
| Y | 28 | 272 | 206 | 13 | 9 | 0.81710 |
| G | 1 | 272 | 34 | 11 | 6 | 0.00073 |
| G | 2 | 272 | 34 | 12 | 6 | 0.00132 |
| G | 4 | 272 | 34 | 15 | 5 | 0.02705 |
| G | 7 | 272 | 34 | 7 | 4 | 0.00549 |
| G | 16 | 272 | 34 | 9 | 4 | 0.01641 |
| G | 24 | 272 | 34 | 2 | 2 | 0.01522 |
| G | 28 | 272 | 34 | 2 | 2 | 0.01522 |
| O | 1 | 272 | 32 | 26 | 11 | 0.00003 |
| O | 2 | 272 | 32 | 25 | 12 | 0.00000 |
| O | 4 | 272 | 32 | 24 | 14 | 0.00000 |
| O | 7 | 272 | 32 | 15 | 7 | 0.00054 |
| O | 16 | 272 | 32 | 14 | 9 | 0.00000 |
| O | 24 | 272 | 32 | 9 | 6 | 0.00011 |
| O | 28 | 272 | 32 | 8 | 6 | 0.00004 |

## Experiment 3

Workers (both green and white marked) returned preferentially to the sapling were they initially ( = before transfer) collected honeydew (Fig. 3). In all samples the proportion of faithful workers (green workers returning to the green sapling, white workers returning to the white sapling) was significantly higher than 0.5 (Table 2). Workers returned very quickly and maintained their initial fidelity during the 9-day sampling period. The total

Table 2. P-values Exp. 3. Sapling color W = white, G = green. N = total marked population, s = sample size, n = sample number, y = number of workers with same color as tree sampled (= successes). P < 0.05 significant different from random distribution.

| sapling | day | N | s | n | y | P |
|---|---|---|---|---|---|---|
| W | 1 | 250 | 125 | 72 | 68 | 0.000000 |
| W | 4 | 250 | 125 | 40 | 36 | 0.000000 |
| W | 6 | 250 | 125 | 16 | 16 | 0.000009 |
| W | 9 | 250 | 125 | 5 | 5 | 0.030003 |
| G | 1 | 250 | 125 | 39 | 35 | 0.000000 |
| G | 4 | 250 | 125 | 40 | 31 | 0.000110 |
| G | 6 | 250 | 125 | 61 | 50 | 0.000000 |
| G | 9 | 250 | 125 | 52 | 36 | 0.001416 |

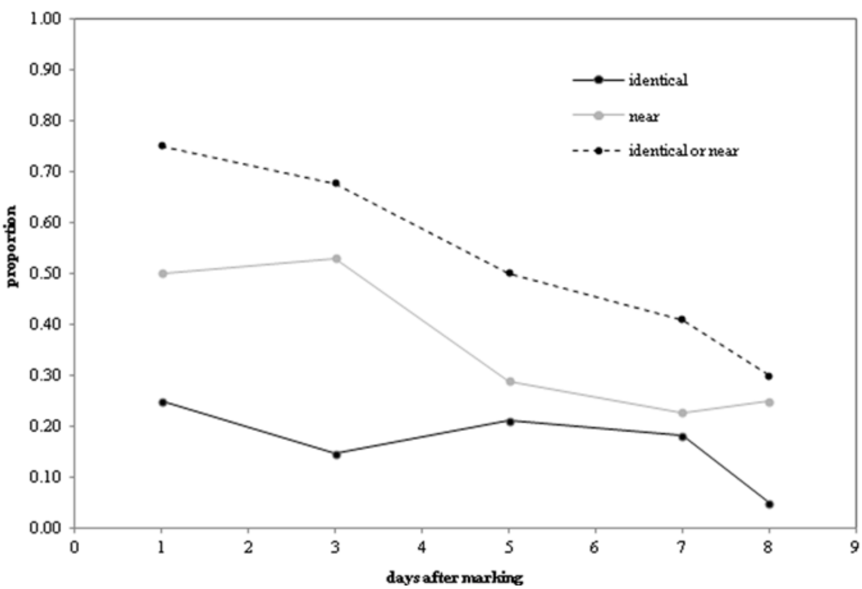
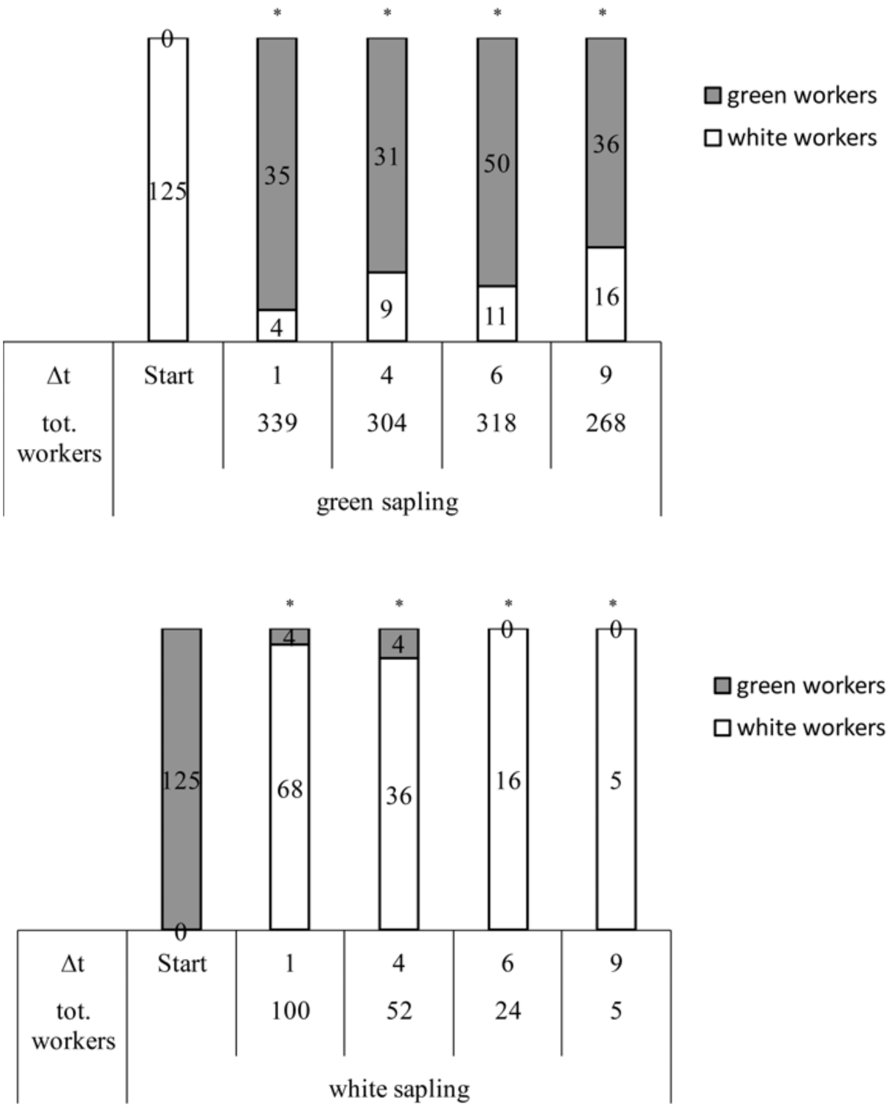



Fig. 2. Temporal variation in leaf site fidelity during exp. 2. Identical line represents workers found on the same leaf of the initial marking. Near line represents workers that tend aphids not on but near the original leaf (max. three leaves distant). Identical or near line is the cumulative proportion of identical and near workers.




Figs. 3a &3b. Exp. 3. Number of green and white marked workers. Start experiment with 125 green workers transferred to the white sapling and 125 white workers to the green sapling. Days after start experiment indicated below bars. Tot. workers include marked and non marked workers on a sapling. (*) significant different ( 5% level) from random distribution (equal numbers of green and white marked workers).

number of marked workers decreased with time. The white sapling was gradually deserted. After 9 days, more white workers visited the green sapling than their familiar white sapling.

## DISCUSSION

Honeydew tenders of *F. rufa* showed high persistence in foraging site. In the first experiment no marked workers were observed on other saplings or on trails and in experiment 2 only a minor proportion switched to neighboring saplings. This large-scale fidelity of red wood ants is already well documented (Rosengren 1971; Rosengren 1977a). However, in this study also small-scaled site fidelity of red wood ants in the field was recorded. Workers, differentially marked in accordance with branch visit, persistently travelled to a familiar branch on the tree during four weeks. This branch fidelity was also observed in *Lasius fuliginosus* (Quinet & Pasteels 1996). Yet site-fidelity of *Formica rufa* is even organized on a smaller scale (leaf level) as found in *Camponotus sericeus* (Mody & Linsenmair 2003). However, leaf fidelity tended to decrease rapidly and was not so rigid as larger scale fidelity.

When presenting a suitable sapling alternative, workers preferred to return to their initial familiar sapling in the short-term. We do not have support that this is applicable in the long-term, because of the gradual desertion of the far sapling (white sapling). On the short-term, worker sapling choice was seemingly not affected by distance effects as for an individual worker it would be most optimal to forage on the green sapling. After 9 days, though, white workers preferred the closest sapling to their familiar white sapling. However it is not clear whether this is due to distance effects or due to flexibility of the white workers in response of a less rewarding sapling.

Long-term site fidelity can be beneficial for colonies of the *Formica rufa* group as they are typical K-strategists defending their territory (Mabelis 1979). Long-term fidelity of veteran foragers and efficient recruiting of novice workers by those veterans may have evolved to occupy all parts of the territory (Rosengren & Fortelius 1986). Long-term storage of spatial information is also useful to re-restore previous honeydew collecting sites after hibernation. Rosengren & Fortelius (1986) demonstrated that trail fidelity of workers of *F. rufa-group* is not decreasing with time and is even maintained after hibernation. Rapid returning foragers in spring can give protection to vulnerable aphid stages and allow a rapid restoration of the territory before resources become monopolized by competitors (Mabelis 1979; Rosengren & Fortelius 1986; Quinet & Pasteels 1996).

Site fidelity can also reduce time and energy consuming competition between fellow colony members (Mody & Linsenmair 2003). However, ant colonies are confronted with changes in the distribution and quality of food sources. Rigid site fidelity would hamper the colony ability to approach the Ideal Free Distribution. This distribution will only arise if individuals move among several feeding sites and eventually forage to the site that maximize their rate of feeding. However it has been demonstrated that a proportion of mobile ants can assess the quality of different patches and change their foraging in such a way that they maximize their food uptake rate rather than returning to a previous feeding site (Rosengren & Fortelius 1986; Lamb & Ollason 1994a). Additionally, efficient recruiting of wood ant workers to a high rewarding patch can accelerate the flexibility of the colony (Hörstmann 1976; Mabelis 1979; Rosengren & Fortelius 1987; Rosengren & Sundström 1987; Lamb & Ollason 1994b). In our study, indeed, we observed a rapid decrease in site fidelity on a small scale caused by flexibility and efficient recruiting.

We conclude that *F. rufa* honeydew tenders exhibit strong site fidelity even on a small scale and this fidelity is not influenced by offering comparable food rewards. This fidelity promotes an efficient occupation of the territory and minimize food search and energy and time consuming competition with colony members. However flexibility of workers and efficient recruiting allow the colony to maximize its energy uptake under changing conditions.

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