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The use of native and non-native tree species for foraging and nesting habitat by the wood-ant *Formica lugubris* (Hymenoptera: Formicidae)

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Abstract

Woodland management strategies are increasingly focused on reducing non-native plant species. However, changing the species profile of a habitat can have highly disruptive effects on local ecosystems. An isolated woodland containing a population of the northern wood-ant *Formica lugubris* ZETTERSTEDT, 1838 was used as a case study to predict the effects on the ants of proposed woodland management focussed on reducing non-native tree species. A habitat survey of the woodlands showed that increased light and presence of the native species oak (*Quercus* spp.) and birch (*Betula* spp.) were positive factors for ant presence. In addition a survey of foraging throughout the warm season showed that native oak, birch, pine (*Pinus sylvestris*) and non-native larch (*Larix decidua*) and spruce (*Picea abies*) were heavily used for foraging; mostly in the form of honeydew from aphids. Native beech (*Fagus sylvatica*) was not used for foraging nor provided suitable nesting habitat. Analysis of the results showed that the ants are not reliant on the non-native species and that light is important to them. The openings in the canopy formed during selective felling could be beneficial for the establishment of new nests.

Key words: Introduced species, non-native species, wood-ant, foraging, *Formica lugubris*, woodland management, habitat.

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Introduction

The northern wood-ant, *Formica lugubris* ZETTERSTEDT, 1838 (Hymenoptera: Formicidae) is found in the boreal forest zone throughout Eurasia. It is native to Britain and can be found from the Highlands of Scotland through upland areas of northern England as far south as mid Wales (EDWARDS & TELFER 2002). Its range is threatened by loss of suitable woodland habitat due to agricultural clearance, urban or industrial development and inappropriate woodland management, e.g., through changes in traditional practices, intensive growth of conifers or destructive felling operations. A further problem is the loss of sunny woodland rides and clearings due to overgrowth and scrub invasion. *Formica lugubris* has been classified by the International Union for Conservation of Nature and Natural Resources (IUCN) as globally Near Threatened (SOCIAL-INSECTS-SPECIALIST-GROUP 2006).

Formica lugubris is found in woodlands, usually along rides and clearings. It excavates underground nest chambers and builds a mound of soil with a thatch of vegetation fragments on top. In Britain, *F. lugubris* is polydomous, with nest mounds connected by active trails forming large supercolonies (CHERIX 1980). Where it occurs, *F. lugubris* is a dominant predator of other invertebrates. It is also a scavenger and collects honeydew from aphids (WAY 1963). In Britain, *F. lugubris* forages on both native and non-native species of tree (SUDD & al. 1977).

Biological invasions by non-native plant species are widely recognised as a significant component of global environmental change. Over 900 non-native plant taxa are established in the United Kingdom, of which at least 200 are widespread (HILL & al. 2005). While some high-profile species such as the harmful giant hogweed get plenty of attention (DAWSON & HOLLAND 1999, WADSWORTH & al. 2000), non-native species often have other negative effects, particularly on biodiversity (MANCHESTER & BULLOCK 2000, MASKELL & al. 2006). For example, of 13 tree species covered in this study, the 10 native species are known to support an average of 151 insect species, whereas the three introduced tree species only support an average of 50 insect species (KENNEDY & SOUTHWOOD 1984). The definition of "native tree" is species which colonised the British Isles after the last ice age and before they were cut off from the rest of Europe by the rising sea levels. Conservation effort is increasingly conscious of the issue of controlling non-native species (PETERKEN 2001, LOWE & al. 2004).

Management of woodlands for conservation of native species often requires felling non-native trees such as sycamore and larch, but what if native ants such as *F. lugubris* are foraging on the sycamore and using larch needles for their nests? Tree felling can have a dramatic effect on wood-ant populations, for example by disrupting the foraging route system (ROSENGREN & PAMILO 1978). Clear-cutting of forest areas can completely destroy wood-ant populations in the short term, probably due to loss of food resources (PUNTTILA & al. 1991). In the long-term, tree-felling affects mounds sizes (SUDD & al. 1977, DOMISCH & al. 2005, SORVARI & HAKKARAINEN 2005), alate production (SORVARI & HAKKARAINEN 2005), sex ratio (SORVARI & HAKKARAINEN 2007) and aggression (SORVARI & HAKKARAINEN 2004). Ant community composition changes during the regeneration period (PUNTTILA & al. 1996), and anything which affects such a dominant predator in an ecosystem as the wood-ant will have far-reaching effects on other species (SUDD & LODHI 1981, LAAKSO & SETALA 2000, PUNTTILA & al. 2004).

We carried out a survey of an isolated woodland population of approximately 100 *F. lugubris* nests. Active woodland management was to commence to reduce non-native species such as sycamore, larch and rhododendron, while encouraging regeneration of native species such as oak and pine. We investigated the ecological requirements of *F. lugubris* colonies, in terms of both foraging and nesting habitat. This detailed case study of a wood-ant population provides conservation advice which can be applied to this area and to other *F. lugubris* populations in similar woodlands.

Materials and methods

The study was performed in the Upper Dearne Woodlands in Yorkshire, United Kingdom (53° 34' N, 2° 41' W). These are primarily mixed-deciduous woodlands with some pine, larch and spruce, a typical species composition for woodlands in this region and further south; there are also areas of beech (*Fagus sylvatica*) typical of more southerly woodlands (RODWELL 1991). Ant identification was by key (SKINNER & ALLEN 1996) and confirmed by C. Collingwood (pers. comm.).

Habitat survey: The Ordinance Survey (OS) grid was used to divide the woodlands into 68 squares of 250 m × 250 m. For each square, wood-ant presence and seven other variables were recorded.

1. Nests. Ant-nests in the woodlands were located by combing the woodlands in transects 10 m apart. When possible, each nest location was recorded by Global Positioning System (GPS). GPS readings and transect records were used to allocate nests to squares.

2. Foraging. As ants might forage in squares where there were no nests, presence or absence of foragers was scored for each square. Foragers were considered present if 20 or more *F. lugubris* workers were immediately visible from the centre point of the square.

3. Light. For each square, three digital photographs (focal length 24 mm; aperture 4.5) were taken of the canopy, one at the centre of the square, and the other two approximately 10 m north and south of the centre. These photographs were converted to black and white, and the white pixels were counted using the histogram function in Adobe Photoshop, Version 7.0. The white pixel count was taken as an estimate of the area of sky visible from the woodland floor. Canopy area was used rather than a direct measure of brightness, as light conditions varied during the days photographs were taken.

4. Edge. As our division of the woodlands into squares was based on the OS grid, some squares overlapped the woodland boundary. All squares of which more than a quarter fell inside the woodlands were included in the survey. Excluding all incomplete squares could have concealed potentially significant edge effects (SUDD & al. 1977, SORVARI & HAKKARAINEN 2005). Each square was scored for presence or absence of edge.

5. Slope. A clinometer was used to record the inclination of the ground at the central point of each square, to within 5°, and a compass was used to find alignment of slope, to within 5°.

6. Path. Several recreational footpaths pass through the woodlands. To investigate the possible effect of disturbance by people, the presence or absence of a path was recorded.

7. Trees. The genus and size of trees were recorded. Throughout most of the woodland the trees were mature, reaching the canopy, so tree height could be taken as constant. Tree diameter 1 m from ground level was used as an estimate of size. All living trees which reached the canopy within a 20 m radius of the centre of the square were recorded, after preliminary studies had indicated that this gave a representative sample of the trees occurring in a square. The trees recorded belonged to the following genera: ash (*Fraxinus excelsior*), birch (*Betula pubescens*, *B. pendula*), beech (*Fagus sylvatica*), European larch (*Larix decidua*), hazel (*Corylus avellana*), Norway spruce (*Picea abies*), oak (*Quercus petraea*, *Q. robur*), rowan (*Sorbus aucuparia*), Scots pine (*Pinus sylvestris*), and sycamore (*Acer pseudoplatanus*).

8. Scrub. Woody vegetation which did not reach the canopy, e.g., bushes and young trees, was defined as scrub. Presence or absence of the following genera were recorded: ash, birch, beech, elder (*Sambucus nigra*), common fir (*Abies alba*), hawthorn (*Crataegus monogyna*), hazel, hornbeam (*Carpinus betulus*), holly (*Ilex aquifolium*), oak, rhododendron (*Rhododendron ponticum*), rowan, sycamore, yew (*Taxus baccata*).

9. Undergrowth. The most widespread and vigorous ground flora were bracken (*Pteridium aquilinum*) and bramble (*Rubus pedatus*), so an estimate of the percentage ground cover of these species was made from the central point of each square, based on the area within 20 m radius of this point.

The quantitative variables (light, slope cline, slope direction, total tree number, number of trees for each genus, size of trees, undergrowth cover) were analysed using stepwise discriminant analysis followed by canonical analysis, using Statistica (version 6. StatSoft, Inc. 2001). Ash, rowan and hazel were excluded from the analysis as they were represented at a very low frequency in the woodlands. The binomial (presence or absence) data (path, edge, scrub, nests in neighbouring squares) were analysed using chi-square tests. For analysis the thinner scrub was grouped

Tab. 1: Trees included in the foraging survey for each study site.

Trees	Sites					
	1	2	3	4	5	6
Alder	0	0	0	1	0	0
Beech	3	0	1	0	0	1
Birch	0	0	5	0	0	0
Oak	1	3	5	4	2	1
Spruce	0	0	3	0	0	0
Sycamore	3	1	0	1	0	2
Hawthorn	0	0	0	1	0	0
Hornbeam	0	0	0	0	0	1
Larch	0	5	0	0	3	2
Pine	2	0	0	0	0	3
Rowan	0	0	0	0	2	0

separately from the denser species likely to cause a lot of shading below canopy level, i.e., holly, rhododendron and yew. The dependant variable in the analyses was the presence or absence of ant nests in each square.

Foraging survey: Six sites, each with a group of large ant nests, were chosen throughout the woodlands for a detailed survey of the trees used by the ants for foraging. The sites were distributed such that there was a variety of trees within the foraging range of the nest (10 - 20 m), enabling us to compare ant traffic across all the major tree genera. For each site the trees clearly within the foraging range of the ants were chosen to be included in the survey; these totalled 7 - 14 depending on the site (Tab. 1). The diameter of each tree trunk 1 m from ground level was recorded. The ant traffic on these trees was surveyed at each site at two weekly intervals throughout the ant foraging season (May - September). The trunk of each tree was observed for 1 minute and the number of ants passing down the trunk was counted. Of these ants, the number carrying prey or building materials was counted, and where possible these ants were caught and the prey identified.

An average for the whole foraging season was calculated, as different trees could be important at different times of year due to seasonal variation in ant preference for carbohydrate (honeydew) versus protein (Rosengren & Sundström 1987).

Tab. 2: Habitat survey: Effect of quantitative variables on presence or absence of wood-ant nests; results of canonical analysis. Magnitude and sign of standardised canonical coefficients indicates the strength of the relationship.

Variable	Canonical coefficients	Mean ± SE	
		Nests present	Nests absent
Slope cline (degrees)	0.371	31.21 ± 3.00	23.84 ± 2.21
Light (pixel count)	0.335	$4.60 \times 10^5 \pm 0.54 \times 10^5$	$2.53 \times 10^5 \pm 0.40 \times 10^5$
Oak (no. trees)	0.307	3.21 ± 0.40	1.52 ± 0.30
Birch (no. trees)	0.230	0.67 ± 0.13	0.023 ± 0.10
Tree size (diameter, cm)	-0.226	35.80 ± 1.24	40.65 ± 0.91
Sycamore (no. trees)	-0.380	1.167 ± 0.58	1.80 ± 0.43
Beech (no. trees)	-0.512	2.167 ± 0.58	5.64 ± 0.43

Tab. 3: Habitat survey: Correlation matrix of the quantitative variables used in discriminant function analysis. * indicates P < 0.05; ** P < 0.01; *** P < 0.001.

	Slope cline	**Slope align**	**Beech**	**Birch**	**Larch**	**Oak**	**Pine**
Light	-0.237	-0.215	-0.492***	0.363**	0.417***	0.040	-0.041
Slope cline		0.081	-0.060	0.016	0.028	0.146	-0.050
Slope align			0.178	-0.219	-0.177	-0.326**	-0.093
Beech				-0.358**	-0.532***	-0.330**	0.122
Birch					0.306*	0.213	0.000
Larch						0.256*	-0.170
Oak							0.067

	Spruce	**Sycamore**	**Tree no.**	**Tree size**	**Bracken**	**Bramble**
Light	0.079	0.106	0.033	-0.220	0.432***	-0.020
Slope cline	0.148	-0.207	-0.082	-0.039	0.080	-0.211
Slope align	-0.119	-0.140	-0.295*	0.1860	-0.142	-0.002
Beech	-0.291*	-0.284*	0.001	0.441***	-0.568***	-0.202
Birch	0.542***	-0.096	0.153	-0.405***	0.473***	-0.077
Larch	0.485***	0.077	0.509***	-0.324**	0.443***	0.114
Oak	0.160	-0.037	0.477***	-0.367**	0.375**	-0.055
Pine	-0.078	-0.156	-0.023	0.110	0.055	-0.137
Spruce		-0.095	0.253*	-0.235	0.309**	0.049
Sycamore			0.481***	-0.342**	0.149	0.391***
Tree no.				-0.399***	0.249*	0.146
Tree size					-0.497***	-0.124
Bracken						-0.030

Results

Habitat survey: Ant nests were present in 24 of the 68 squares. Of the 14 variables used in the stepwise discriminant analysis, 7 variables were included in the model, and 7 excluded. The variables included in the model were oak, birch, slope cline and light as positive factors for ant nest presence and beech, sycamore and overall tree size as negative factors for nest presence (Tab. 2). The excluded variables (larch, pine, spruce, tree number, bracken cover, bramble cover, and slope alignment) are correlated with the included variables (Tab. 3) or do not contribute a significant amount of information to the discrimination. The canonical analysis of the 7 variables included in the model allowed significant discrimination of the squares with and without ant nests (R = 0.679, Wilk's Λ = 0.539,

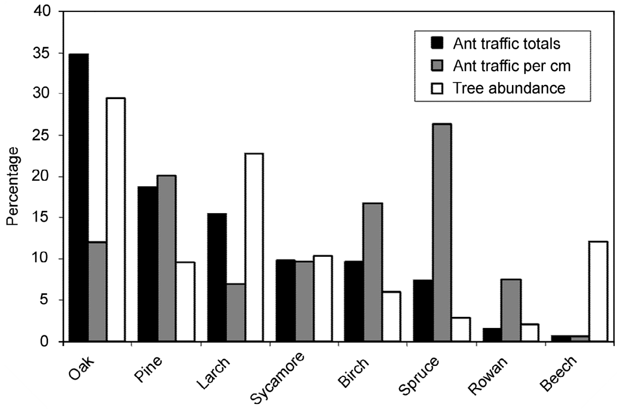

Fig. 1: Proportion of ant foraging on each type of tree in relation to tree abundance. Ant-traffic totals are ants per minute on each tree type over all sites and dates, as a percentage abundance of the total. Alder, hornbeam and hawthorn make up the remaining 4.66 % and were omitted due to low occurrence. Ant-traffic per cm takes into account the sizes of the foraging trees. Tree abundance is the percentage of tree biomass represented by each tree type, across all sites.

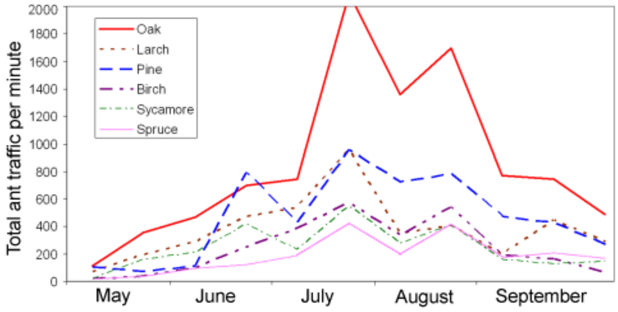

Fig. 2: Foraging activity throughout the foraging season on the six most used tree genera.

Tab. 4: Percentages of different prey types and other matter carried by foraging ants returning to the nest down the tree trunks.

Item carried by ants	**Percentage** (n = 1078)
Coleoptera (beetles)	0.79
Diptera (flies)	14.68
Homoptera (aphids and true bugs)	60.32
Hymenoptera (wasps)	1.98
Hymenoptera (*F. lugubris* fragments)	2.38
Larvae	3.97
Pupae	0.79
Parts of insects (unidentified)	5.56
Vegetable material	9.52

$P < 0.001$). In 15 out of the 19 squares which the discriminant function analysis predicts to contain ant nests, the prediction is correct; in 40 out of 49 predicted to contain no nests, the prediction is correct. No significant effect was found of path ($\chi^2_1 = 0.34$, $P > 0.4$), edge ($\chi^2_1 = 0.0028$, $P > 0.6$), thin scrub ($\chi^2_1 = 1.87$, $P > 0.1$) or thick scrub ($\chi^2_1 = 0.06$, $P > 0.6$). Presence of nests in neighbouring squares had a significant effect on nest presence in the focal square ($\chi^2_1 = 25.45$, $P < 0.001$). The nests were broadly distributed in two groups of several adjacent occupied squares, with only one square isolated from these groups. In addition, in seven squares ants were foraging extensively, but not nesting. These squares were on the edges of suitable nesting habitat. We recorded a total of 92 nests in August 2003. The number of nests varies considerably throughout the year, as new nests bud off when conditions are good, but may not survive long.

Foraging survey: The ant-traffic (number of ants per minute per cm of trunk diameter) differed highly significantly between different genera of tree (ANOVA: $F_{5,60} = 5.96$, $P < 0.001$) (comparing the six most abundant tree genera: beech, birch, larch, oak, pine, sycamore). This is strongly contributed to by the low use of beech. The difference between sites is also significant (ANOVA: $F_{5,60} = 4.80$, $P < 0.05$). In absolute terms, oak was clearly the most used genus of tree making up more than a third of the ant traffic (Fig. 1). Pine, larch, birch, sycamore and spruce are also well used. However, when the prevalence of the tree genera at the sites and the size of the trees are taken into account, the ant traffic between tree genera differed significantly from the expected distribution using the abundance of the genera at the sites ($\chi^2_7 = 316$, $n = 27451$, $P < 0.001$). Birch, pine and spruce are used disproportionately heavily when they do occur (Fig. 1). Beech and to a lesser extent larch and oak are used disproportionately little.

Tree-use was recorded across the full foraging season (Fig. 2). Oak was the most used genus at almost every point, with larch generally the second most used in the early part of the year, and pine in the later part. General conclusions cannot be drawn from these data as there are no data from other years to confirm the trends seen, but the data suggest that the ants do not rely heavily on particular trees for a brief period, but rather that the same trends occur across the season. Significantly more of the ants were not carrying any prey (mean = 2403, SD = 1542) than were (mean = 93, SD = 58) (t-test unequal variances: $t11 = 0.99$, $P < 0.001$). Most of the ants which were not carrying prey will have been collecting honeydew secreted by aphids as this is their primary source of carbohydrate (ROSENGREN 1977). These returning foragers could be seen to have distended abdomens due to the volume of honeydew. The proportion of ants carrying prey differed significantly between tree genera (ANOVA: $F_{5,60} = 8.47$, $P < 0.001$). A high proportion of prey was collected from sycamore trees. Levels of prey-collection did not differ between the sites (ANOVA: $F_{5,60} = 1.91$, $P = 0.11$). Adult prey was identified to the level of order (Tab. 4). Ants also collected larvae, pupae, insect-fragments which could not be identified and vegetable material.

Discussion

Oak is clearly an important foraging resource for ants in these woodlands. Although its use was lower than its abundance predicts, it still had the highest overall traffic across all sites and times of year. Birch was used for foraging disproportionately heavily compared to its occurrence in the woodlands. This matches the habitat survey results, which show that birch and oak were important positive factors for ant nest presence.

The conifers, larch, spruce and pine were all used for foraging, with spruce and pine used disproportionately heavily where they are present. Although wood-ants are often observed to use conifer needles as nest materials, the presence of nests in parts of the woodlands without conifers showed that ants also make use of other vegetable material for their nest thatches. The non-native larch is therefore not essential to the ants, so the loss of some mature larch trees is unlikely to cause problems. Encouraging regeneration of the native oak and pine should benefit the ants considerably, as oak is the genus most heavily used by the ants, and pine is used disproportionately heavily for its abundance.

Beech and sycamore were negatively associated with ant nest presence. Both these species, particularly beech, have dense canopies, but our method of light measurement by estimating canopy cover should exclude this effect from the analysis. Their negative effect may be due to their unsuitability as feeding grounds and the competition they pose to the wood-ants' forage trees. Ants almost never foraged on beech. Although the ants did use the non-native sycamore, particularly for prey gathering, its presence is clearly shown not to be essential to them in these woodlands.

These results correspond well with the findings of other studies of British *F. lugubris* populations (SUDD & al. 1977, ROBINSON & WOODGATE 2004).

In our study most foraging ants were collecting honeydew rather than prey. The ants collected both honeydew and prey (mostly aphids) from a range of tree genera, showing that the ants do not depend solely on one type of tree for one type of food. In general, the larger the average tree size, the fewer ant nests. This is not due to the canopy shading, as the analysis considered light separately. Possibly the aphid colonies are simply more accessible when the trees are smaller. It should be noted that the sites chosen for the foraging studies contained several large nests, and we cannot rule out the possibility that foraging patterns are different at lower nest densities. In addition the limited number of sites used in this study means that care should be taken with drawing general conclusions. Oak was the only tree present at all sites, and the ants clearly use a variety of trees, depending on what is available, so the importance of a certain native or non-native tree species is likely to be related to the general species composition of the area.

Light level correlated positively with nest presence, probably due to the reliance of wood-ants on sunlight for heat. Small-scale thinning of non-native trees would increase the light reaching the woodland floor, which should benefit the ants, especially small newly-budded nests (SUDD & al. 1977, ROSENGREN & al. 1987). Thick scrub does not have a significant association with the ants at its present levels, so reducing area of non-native rhododendron cover is not predicted to adversely affect the ants, and pruning would increase light levels. Controlling bracken to encourage regeneration is unlikely to affect the ants, as bracken was not a significant factor in our analysis.

Slope cline was also positively correlated with nest presence, which was unexpected, as nests on steep slopes may slide down the slope or be washed away. However many flat parts of the woodlands are marshy, so there would be a risk of underground nest chambers flooding in these areas. No affect of footpaths was apparent, suggesting that the level of human activity experienced by the woodlands does not disturb the ants, or that any disturbance is very local to the region around the path. Similarly we found no edge effects, contrasting with previous findings (SUDD & al. 1977). A finer-scale study of the perimeter of the woodlands would be required to investigate this finding further.

The nests were clustered within the wood. This is to be expected from the polydomous habit of this species which spreads primarily by budding. However, out of the total 68 squares, we identified only four unoccupied squares which have habitat suitable for the ants. This suggests that at present, the suitable habitat in the woodlands is close to saturation. This wood-ant population is healthy and vigorous, and the ants use many different tree genera in the woodlands for foraging, so seem to be flexible in their requirements. It is likely that this population will be robust enough to withstand the disturbance caused by minor changes to the woodlands. The management proposals for the wood-ant areas can be expected to have either a beneficial effect or no effect on the population of *Formica lugubris* in the Upper Dearne Woodlands.

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Zusammenfassung

Schutz- und Pflegekonzepte für Waldland zielen zunehmend auf ein Zurückdrängen nicht-heimischer Pflanzenarten ab. Allerdings kann die Veränderung des Arteninventars von Lebensräumen lokal negative Auswirkungen auf das Ökosystem haben. Wir schätzen anhand einer Fallstudie in einem isolierten Waldland ab, welche Auswirkungen das Entfernen nicht-heimischer Pflanzen auf die Waldameise *Formica lugubris* ZETTERSTEDT, 1838 haben könnte. Eine Habitataufnahme des Waldes ergab, dass hohes Lichtangebot und die Anwesenheit der heimischen Bäume Eiche (*Quercus* spp.) und Birke (*Betula* spp.) positive Faktoren für die Anwesenheit der Waldameisen sind. Eine zusätzliche Untersuchung des Fouragierverhaltens in der warmen Jahreszeit ergab, dass die heimischen Bäume Eiche, Birke, Rotföhre (*Pinus sylvestris*) und die nicht-heimischen Bäume Lärche (*Larix decidua*) und Fichte (*Picea abies*) intensiv zur Suche nach Futter genutzt werden, vor allem nach dem Honigtau von Blattläusen. Die heimische Baumart Rotbuche (*Fagus sylvatica*) wurde weder zur Futtersuche genutzt noch bot sie geeignete Nistmöglichkeiten. Die Zusammenschau aller Analysen ergab, dass diese Ameisen nicht von nicht-heimischen Pflanzen abhängen, sowie, dass Licht für sie von Bedeutung ist. Lücken im Kronenschluss, die durch das selektive Fällen von Bäumen entstehen, könnten der Gründung neuer Nester förderlich sein.

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