# Foraging efficiency of red wood ants, *Formica aquilonia* (Hymenoptera: Formicidae) in relation to tree characteristics and stand age

Heloise Gibb, Jon Andersson, Therese Johansson

**Background.** Optimal foraging theory states that organisms forage to maximise their energy intake per unit time. Ants are central-place foragers, so are expected to harvest greater loads from more distant and higher quality resources. We first tested this prediction at a small scale and second, at larger scales, we asked if forest successional stage affected the optimisation of worker foraging loads. **Methods.** First, we performed a fine-scale study examining the effect of distance and resource quality (tree diameter and species) on harvesting of honeydew by red wood ants, *Formica aquilonia*, in terms of crop load per worker ant and numbers of workers walking up and down each tree (ant activity) (experiment 1). Second, we calculated what the combination of load and worker number responses meant for colony-level optimisation of foraging efforts. Third, at a larger scale, we tested whether the relationship between worker load and resource quality and distance depends on stand age (experiment 2). **Results.** The first study revealed that seventy percent of ants descending trees carried honeydew, and the percentage of workers that were honeydew harvesters did not depend on tree species or diameter, but was weakly related to distance. Consistent with predictions from optimal foraging theory, distance positively affected load in both large- and small-scale experiments. Diameter had weak negative effects on load, which experiment 2 showed were dependent on stand age. **Discussion.** Stand age thus did not affect the optimal foraging relationship, beyond effects due to tree diameter and distance. Because ant activity declines with increasing distance to resources the net result at fine scales was that very little honeydew was harvested from more distant trees if they were small, but that harvesting from larger trees was relatively constant within the range of distances sampled. Although forestry alters the activity and foraging success of red wood ants, it thus does not alter the fundamental rules determining allocation of foraging effort.

1 **Foraging efficiency of red wood ants, *Formica aquilonia* (Hymenoptera:**

2 **Formicidae) in relation to tree characteristics and stand age**

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26    worker foraging loads.

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28    quality (tree diameter and species) on harvesting of honeydew by red wood ants, *Formica*

29    *aquilonia*, in terms of crop load per worker ant and numbers of workers walking up and down

30    each tree (ant activity) (experiment 1). Second, we calculated what the combination of load and

31    worker number responses meant for colony-level optimisation of foraging efforts. Third, at a

32    larger scale, we tested whether the relationship between worker load and resource quality and

33    distance depends on stand age (experiment 2).

34    **Results.** The first study revealed that seventy percent of ants descending trees carried

35    honeydew, and the percentage of workers that were honeydew harvesters did not depend on tree

36    species or diameter, but was weakly related to distance. Consistent with predictions from

37    optimal foraging theory, distance positively affected load in both large- and small-scale

38    experiments. Diameter had weak negative effects on load, which experiment 2 showed were

39    dependent on stand age.

40   **Discussion.** Stand age thus did not affect the optimal foraging relationship, beyond effects due

41   to tree diameter and distance. Because ant activity declines with increasing distance to resources

42   the net result at fine scales was that very little honeydew was harvested from more distant trees if

43   they were small, but that harvesting from larger trees was relatively constant within the range of

44   distances sampled. Although forestry alters the activity and foraging success of red wood ants, it

45   thus does not alter the fundamental rules determining allocation of foraging effort.

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## Introduction

48  Optimal foraging theory states that organisms forage to maximise their energy intake per unit

49  time (MacArthur & Pianka 1966). More specifically, central place foraging theory (Orians &

50  Pearson 1979) considers the case where animals return to a central place (e.g., a nest). It predicts

51  that more valuable resources or larger loads will be harvested at greater distances from the

52  central place. This is because the energy expenditure of foragers is proportional to the distance

53  travelled. Load-distance relationships have previously been observed in a range of taxa that act

54  as central place foragers (Giraldeau & Kramer 1982; Kacelnik et al. 1986; Kaspari 1991;

55  Mellgren et al. 1984).

56  As central place foragers, ants commonly show load-distance relationships (Bonser et al. 1998;

57  but see Holder & Polis 1987; Wright et al. 2000). Even in only moderately polymorphic or

58  monomorphic species, larger ants travel greater distances to forage and they are more efficient,

59  i.e., they are able to carry a greater load relative to their body weight (Herbers & Cunningham

60  1983; McIver 1991; McIver & Loomis 1993; Rosengren & Sundström 1987; Wright et al. 2000),

61  but see Rissing & Pollock (1984). In addition to distance, the harvesting efficiency of ants is

62  affected by a range of other factors, including resource quality, such as sucrose concentration,

63  carbohydrate:protein ratio, resource quantity, temperature or crowding (Bonser et al. 1998; Cerda

64  et al. 1998; Detrain et al. 2000; Dreisig 1988; Kay 2002; Segev et al. 2014).

65  Habitat structure plays a key role in determining the success of species (e.g., Cushman 2006;

66  Petren & Case 1998; Stephens et al. 2004), particularly ants (Gibb & Parr 2010; Lassau &

67  Hochuli 2004; Sarty et al. 2006; Sorvari & Hakkarainen 2004). For example, larger ants are more

68  successful competitors in structurally simple habitats, probably because they are faster to

69    discover and exploit resources (Gibb & Parr 2010). Anthropogenic disturbances, including

70    urbanisation, agriculture and forestry, transform landscapes, significantly altering habitat

71    structure (Gibb & Hochuli 2002; Harrison & Bruna 1999).  For example, forestry practices in

72    mid-boreal Sweden have resulted in a disproportionately large area of relatively young and dense

73    stands, with structure differing substantially from old growth stands (Linder & Östlund 1998).

74    Previous studies suggest that stand age (a measure of time since disturbance or successional

75    stage) and the associated structural differences have significant effects on the abundance and

76    behaviour of ants (Gibb & Johansson 2010; Punttila 1996; Sorvari & Hakkarainen 2004) and on

77    resource quality (Johansson & Gibb 2012).  However, no previous study has tested whether

78    successional stage affects the optimal foraging relationship for ants.  We might expect effects

79    because successional stage alters not only resource quality (Guariguata & Ostertag 2001;

80    Johansson & Gibb 2012), but also affects the biotic environment of boreal forest ants, increasing

81    competition (Gibb 2011) and altering predation risk (Niemelä et al. 1996).

82    Although most studies of central place foraging in ants focus on individual workers (e.g., Bonser

83    et al. 1998; Holder & Polis 1987; Wright et al. 2000), the aim of workers should be to optimise

84    the foraging of the colony as a whole by altering both individual loads and number of foragers

85    active.  This is because the evolution of eusocial organisms is expected to operate at the level of

86    the colony as workers of most species are sterile.  Here, we use northern red wood ants, *Formica*

87    *aquilonia* (Yarrow, 1955), in boreal forests to test, first whether individual workers adjust their

88    crop loads (mass gain) with respect to resource distance and quality (experiment 1).  Second, we

89    use activity data from a previous study to model how colony-level mass gain is affected by

90    resource distance and quality.  Third, we test whether the relationship between worker load and

91    resource quality and distance depends on forest succession (experiment 2).

## Materials and Methods

*Ethics statement*

This study complies with the current laws of Sweden. Permissions for use of the insecticide were obtained from the relevant local authority, Länsstyrelsen Västerbotten.  The forestry companies Holmen Skog AB, Sveaskog AB, SCA and Scaninge gave permission to use their land.

*Study sites and species*

This study was conducted in boreal forests in northern Sweden between the latitudes of 63.6°N and 64.5°N and longitudes of 19.7°E and 20.7°E.  The forest was dominated by Norway spruce, *Picea abies* (70-100%), while birches, *Betula pubescens* and *Betula pendula*, and Scots pine, *Pinus silvestris,* also occurred in significant numbers.  The field layer consisted mainly of dwarf shrubs (*Vaccinium spp*.) and soils were moist and of the sandy moraine type.  A detailed study of optimal foraging theory was first conducted in a single mature production forest (experiment 1). The effect of stand age on optimal foraging was then examined using a further twelve stands (experiment 2): mature stands (n=4, tree age 80–100 years, non-sapling mean basal diameter (BD) = 30.3 ± 1.6 cm, mean height (H) = 17.9 ± 0.6 m), middle aged stands (n=4, 30–40 years, BD = 13.8 ± 0.9 cm, H = 8.1 ± 0.3 m) and clear cuts with 5–10 retention trees per ha (n=4, 1–4 years, BD = 4.8 ± 0.7 cm, H = 2.1 ± 0.3 m). Further details on site characteristics are provided in Table S1.  Measures of basal diameter included all trees > 1 cm BD. Basal diameter was used in preference to diameter at breast height so that seedlings, which may be shorter than 1.3 m in height, but also provide a food source to ants, could be included.  Stands of different ages were geographically interspersed and each study plot supported several nests of the northern red wood ant, *Formica aquilonia*.  Mean ± SE stand separation was 17.5 ± 1.0 km.

114    *F. aquilonia* belongs to the *F. rufa* group, which consists of territorially dominant ant species

115    that have been reported to structure ant communities (Gibb 2011; Gibb & Johansson 2011;

116    Savolainen & Vepsalainen 1989).  It has polygynous and polydomous colonies throughout its

117    range (Pamilo 1982) and is the most common *F. rufa* group species in the central boreal region

118    of Fennoscandia (Collingwood 1979).  In the study area, *F. aquilonia* is commonly observed

119    climbing trees, where it tends the aphids *Cinara pruinosa* and *C. piceicola* (Johansson & Gibb

120    2012) (aphids identified by R. Danielsson, University of Lund and Nils Ericson, Umeå).  A

121    previous study showed that honeydew  makes up approximately 80% of the diet of *F. aquilonia*

122    in Finland, with the remainder consisting of invertebrate prey (Domisch et al. 2009).

123    *Experiment 1: Do ants adjust their foraging based on resource quality and distance?*

124    Our aim here was to determine if the quantity of honeydew harvested from a mature tree per

125    forager was affected by resource quality (tree species and basal diameter) or distance from the

126    nest.  For this reason, we selected a mature forest, where variation in stem basal diameter was

127    greater than younger stands.  Tree species affects the quality of aphid honeydew (Douglas 1993)

128    and, within tree species, honeydew quality is affected by diameter through changes in the

129    concentrations of some sugars (Johansson & Gibb 2012) and secondary metabolites (Price 1991;

130    Whitham 1978).  Unpublished data from our study sites suggests that the composition of sugars

131    and amino acids differs among honeydew samples collected from *P. abies*, *P. sylvestris* and

132    *Betula spp.*  Sampling was performed once at each site on fine days in July 2007.  We selected

133    10 nests of *F. aquilonia* in mature forest and located two spruce, one birch and one pine tree with

134    high levels of ant activity within 20 m of each nest (thousands of workers active on and around

135    the nest), with clear trails originating from the target nest.  The distance from the nest and the

136    basal diameter of each tree was measured and ambient temperatures were recorded for each tree

137     at the time sampling commenced. Nests contained multiple entrance holes, so distances were

138     measured from the centre of the nest.

139     We used modified battery-driven vacuum cleaners with aspirators attached to collect 20 ants

140     walking up and 20 ants walking down each of the trees (a total of 40 ants x 10 nests x 4 trees =

141     1600 ants). This method was selected as ants proved less likely to squirt formic acid (and

142     therefore lose weight) when removed using an aspirator than by forceps. The forty ants were

143     collected from each tree in quick succession, irrespective of the tasks they were performing. For

144     collected individuals, we recorded whether the ant was carrying anything (needles or leaves or

145     arthropod prey) and its liquid feeding status. Liquid feeding status was assessed by examining

146     the gaster of individuals and allocating them to the following classes: 1) full: arthrodial

147     membrane stretched, such that the length of arthrodial membrane visible along the mid-line of

148     the gaster was at least half of that of the sclerites; 2) half full: some stretching of the arthrodial

149     membrane, but with the visible length less than half that of the sclerites; 3) empty: no visible

150     stretching of the arthrodial membrane.

151     Ants were killed or subdued using ether in the field and were later frozen for 3 days at -20ºC.

152     They were weighed in groups of twenty ants travelling in the same direction on the same tree.

153     Any needles or prey items were removed before weighing. The total mass of ants was divided

154     by twenty to obtain a mean mass per ant and the mean mass of the "Up" ants was subtracted

155     from that of the "Down" ants to determine the average mass gain of ants on each tree.

156     *Experiment 2: Is optimal foraging of individuals affected by stand age?*

157     To compare the mass of honeydew collected by individual ants in different stand ages, we

158     collected ants moving up and down trees on fine days in July 2008 using the methods described

159     above. Ten spruce trees were selected at each site between 0.5 and 35 m from a central nest (this

160  distance range was necessary to include sufficient trees on clear-cuts). Trees with high *F.*

161  *aquilonia* activity were preferred in order to reduce collection times.  We collected five ants

162  moving up and five ants moving down each of the ten trees at four sites belonging to each of the

163  three stand ages for a total of 1200 ants. We did not specifically select ants with laden and non-

164  laden gasters because we aimed to compare harvesting efficiency per ant.  Ants were placed in a

165  cold box (approximately 5°C) in the field and were later frozen for 3 days at -20°C to ensure that

166  they were killed. Ants were weighed individually in the lab using a Mettler AE166 balance

167  (sensitive to ± 0.1 mg) and maximum head width was measured using an eyepiece micrometer

168  on a Leica MS5 microscope.  Any needles or prey items were removed before weighing.

169  *Statistical analyses*

170  For experiment 1, a paired t-test on JMP (SAS-Institute 2007) was used to compare the mean

171  mass of ants walking up and down per tree.  We used a general linear mixed model to test the

172  effects of the fixed predictors temperature, tree species, diameter, $\log_{10}$distance and their

173  interactions and the random predictor nest, on: 1) the mean mass gain per ant; and 2) the

174  exponential-transformed percentage of individuals carrying discernible liquid loads.  Distance

175  was $\log_{10}$-transformed to improve model fit.  We tested all possible models on MuMin(Barton

176  2011) in R (R Development Core Team 2013) and, because there was no clear best model, we

177  performed model averaging of models within 2 AICc of the best model to determine the relative

178  importance of variables in the set of best models (Burnham & Anderson 2002).  We present the

179  coefficients from the model-averaged model with shrinkage, the importance of each variable

180  among the set of best models and p-values. A z-test was used to compare the slopes of the ant

181  mass (mean per tree) - distance from nest relationship for: 1) ants walking up and; 2) ants

182  walking down a tree.

183    We modelled the effect of distance from a nest and tree diameter on harvesting rates at the

184    colony level using the parameters from the model-averaged model predicting mean mass gain

185    per ant from experiment 1 (described above) and the best model predicting ant activity per

186    minute from a previous study (Gibb & Johansson 2010).  To illustrate responses across a

187    distribution of diameters typical of mature stands, we present results for trees of basal diameter

188    10 cm, 25 cm and 40 cm.  We used set values of 18.9°C for temperature (the mean value during

189    surveys) and spruce for tree species (the most commonly occurring tree species) for the modelled

190    data.

191    Finally, for data from experiment 2, a general linear mixed model with head width as a covariate

192    and site as a (random) blocking factor, was used to test the effect of temperature, stand age,

193    distance ($\log_{10}$-transformed), diameter and their interactions on the mass of ants walking down

194    trees.  We again tested all possible models on MuMin and performed model averaging of models

195    within 2 AICc of the best model to determine the relative importance of variables in the set of

196    best models. We present the coefficients from the model-averaged model with shrinkage.  We

197    report both marginal (fixed effects; $R^2_{GLMM(m)}$) and conditional (fixed + random effects;

198    $R^2_{GLMM(c)}$) $R^2$ values (Nakagawa 2013), calculated using the package MuMIn.  We also used

199    ANOVA on JMP to test the effect of stand age on microsite temperature.

200    **Results**

201    *Overview of ant loads*

202    On average, ants walking up a tree weighed significantly less than those walking down ($t_{(1, 39)}$ = -

203    9.766, $p < 0.0001$), gaining 2.11 ± 0.19 mg (Mean ± SE) in mass, or approximately 33% of the

204    average mass of an ant walking up the tree (up ants: 6.42 ± 0.17 mg; down ants: 8.53  ± 0.27

205    mg).  Observations of the loads carried by ants suggested that most ants walking down a tree

206    were carrying a discernible honeydew load (full or half full) (70.4 ± 4.9 %).  Although the mean

207    weight gain for ants was 33%, not all ants carried honeydew loads, indicating that ants with loads

208    carried around 47% of their body weight.  8.0 ± 4.0 % of ants carried nest material from trees,

209    i.e. needles (birch leaves were never taken) and 3.5 ± 1.7 % carried arthropod prey (mainly

210    aphids and spiders) (Figure 1).

211

212    *Do ants adjust their foraging based on resource quality and distance?*

213    Analysis of the effects of quality (tree species and basal diameter) and distance of the tree from a

214    nest on mass gain revealed a reasonable fit with little contribution of random effects ($R^2_{GLMM(m)}$

215    = 0.41, $R^2_{GLMM(c)}$ = 0.41) (Table 1).  Mass gain was negatively related to tree diameter,

216    suggesting individual ants gained less on larger trees (Figure 2). Consistent with predictions,

217    mass gain was positively related to distance to nest, with ants travelling further carrying heavier

218    loads (Figure 2).  The model showed weaker predictive power for the percentage of workers

219    carrying observable honeydew loads, with the random factor 'nest' contributing most to model

220    fit ($R^2_{GLMM(m)}$ = 0.11, $R^2_{GLMM(c)}$ = 0.49).  The percentage of liquid bearers responded only weakly

221    to distance, while tree species and diameter did not appear in any of the best models.

222    The relationship between distance and mean mass of ants was significant only for ants walking

223    down trees.  Slopes for the relationship between distance and mass were significantly different

224    ($Z$ = 3.37, $p$ < 0.0005) (Figure 3).  This suggests that the distance a worker travels was not

225    determined by its size, but that ants walking further acquired a larger load.

226    The model incorporating the mass of honeydew harvested per ant and ant activity per tree

227    suggests that the effect of distance from the colony on the mass gained by the colony at each tree

228    depends on tree basal diameter (Figure 4).  Trees with larger diameters (40 cm) made relatively

229    consistent contributions to mass gain, independent of distance (within 20 m from a colony),

230    while the contribution of honeydew from smaller trees (diameter = 10 cm) decreased with

231    increasing distance from a colony.  This is because mass gain increased, while activity decreased

232    with distance and activity increased, while mass gain decreased with diameter.

233    *Is optimal foraging by individuals affected by stand age?*

234    The best model testing the effects of head width, temperature, stand age, tree diameter, distance

235    and their interactions on mass gain of ants was a good fit to the data ($R^2_{GLMM(m)}$ = 0.62, $R^2_{GLMM(c)}$

236    = 0.66). There were no significant interactions between stand age and distance, although

237    interactions with diameter were included in the best models, indicating that stand age had a

238    minimal influence on the optimal foraging relationship (Table 2).  The covariate 'head width'

239    was an important predictor of worker mass, as expected.  Consistent with detailed surveys in the

240    mature stand, distance was positively related to load. Microsite temperatures measured during

241    the surveys were not significantly higher at clear-cuts (mean ± SE: 19.2 ± 2.1) than mature (16.2

242    ± 0.5) or middle-aged stands (18.5 ± 2.0) (ANOVA: $F_{(2,9)}$ = 0.87, p = 0.451).

## Discussion

*Resource harvesting*

245    A high percentage of ants walking down trees (approximately 70%) appeared to be carrying

246    honeydew in their gasters, suggesting that this was their main task in climbing trees. This is as

247    expected as honeydew constitutes 78-92 % of the diet of wood ants (Domisch et al. 2009). Of the

248    30% of ants for which no discernible stretching of the gaster was observed, it is possible that

249    many were involved in other activities, such as guarding resources, or that they had collected

250    much smaller volumes of honeydew.  Smaller percentages of ants returning from trees collected

251    arthropod prey and nest material.  While it might appear opportune to collect arthropod prey if

252    encountered in the canopy, the collection of nest material from such a height and in trees up to

253    14 m from the nest was unexpected.  Ants collecting needles from pine or spruce canopies in

254    older forests travel considerably further than would appear necessary, given that needles are

255    abundant on the forest floor.  A possible explanation is that needle quality is better if needles are

256    removed directly from the tree, perhaps because micro-organism activity is lower on such

257    needles.  The lower Carbon to Nitrogen ratio of needles found on ant mounds, relative to those

258    found on the forest floor (Kilpeläinen et al. 2007), suggests that harvesting of needles from the

259    canopy may be common practice for *F. aquilonia*.  However, further sampling is required to

260    properly address this supposition.

261    *Do ants adjust their foraging based on distance?*

262    In accordance with central place foraging theory (MacArthur & Pianka 1966; Orians & Pearson

263    1979), the distance travelled positively affected the load collected by ants.  In contrast to

264    previous studies, which showed that larger ants travel greater distances to forage because they

265    are able to carry a greater load relative to their body weight (e.g., Herbers & Cunningham 1983;

266    McIver & Loomis 1993; Rosengren & Sundström 1987; Wright et al. 2000), size did not

267    determine distance travelled: we found a significant relationship between mass and distance for

268    ants walking down trees but not for ants walking up trees.  This suggests that, within the range of

269    distances examined in this study, there is no distinct division of labour depending on worker size,

270    but that individual workers recognize that they have travelled further and must therefore collect

271    more honeydew.

272    An alternative explanation for the observed positive load-distance relationship is that high

273    activity of ants on trees near mounds might lead to crowding and faster turnover of workers,

274    resulting in smaller loads as a consequence of reduced time spent harvesting (Grüter et al. 2012;

275    Wright et al. 2000). Such a density-dependent response could also explain our finding that,

276    although ants were more active on large-diameter trees, they harvested less honeydew. This is

277    consistent with the suggestion that greater recruitment may involve some defence of the resource

278    (Sundström 1993). This proposition is further supported by the appearance of distance as an

279    important predictor of the percentage of individuals with liquid loads among the best models

280    (Table 1), indicating more workers engaged in tasks other than harvesting at trees closer to the

281    nest.

282    *Do ants adjust their foraging based on resource quality?*

283    Optimal foraging theory suggests that animals allocate more effort to harvesting resources of

284    higher quality (MacArthur & Pianka 1966). Individual honeydew load did not differ between

285    tree species, despite differences in sugar composition (Johansson *unpublished*). In contrast, ants

286    responded to trees differing in diameter as though they differed in quality. Differences between

287    small- and large-diameter trees in the mature forest may reflect differences in the quality of

288    honeydew as a result of changes in tree defence against aphid herbivory with age. Vigorous

289    and/or fast growing plants usually have fewer secondary metabolites and are therefore often

290    preferred by herbivores, including aphids (Price 1991; Price et al. 1987; Whitham 1978).

291    However, Johansson & Gibb (2012) showed that spruce trees in mature forest, which tend to be

292    of larger diameter, have a greater concentration of some sugars attractive to ants than young trees

293    regenerating in clear-cuts.  This suggests that sugar quality may actually be higher in large-

294    diameter trees, so resource quality is unlikely to be a driver of this difference.

295    Despite the smaller individual loads harvested from larger trees, colonies allocated more workers

296    to large trees.  Models showed that the net result of opposing allocation of worker activity and

297    individual loads was that, close to the nest, a similar mass of honeydew was harvested from

298    small and large trees (Figure 4).  However, further from the nest, larger honeydew loads from

299    smaller trees did not compensate for the greater activity on larger trees.  Thus, the colony-level

300    mass gain from large trees remained relatively constant with distance, while the mass gain from

301    smaller trees declined rapidly.

302    At the colony level, a decline in selection of smaller trees with distance from the nest is

303    consistent with optimal foraging as small trees can be considered to act as small resource

304    patches. This is in agreement with previous studies that have shown greater recruitment to better

305    quality (or larger) resource patches (Nonacs & Dill 1991; Taylor 1977).  However, another

306    possible explanation for the rapid decline in use of small trees with distance may be related to the

307    limitations of ant navigation, which, for *Formica spp.*, is largely dependent on memorising the

308    location of landmarks (Fukushi & Wehner 2004; Graham & Collett 2002).  Larger trees may

309    therefore present a clearer image for visual memory, although the panorama, rather than

310    individual features, may be critical for navigation (Collett 2009).  Alternatively, foraging paths

311    can be costly to maintain in complex habitats (Shepherd 1982), so resources available from

312    smaller trees may fall below the threshold under which maintenance is efficient.

313    *Is optimal foraging affected by stand age?*

314    Although the total quantity of honeydew harvested per hectare differs between stands of different

315    ages (Gibb & Johansson 2010), we detected no change in the foraging responses of individual

316    ants. While the interaction between diameter and stand age appeared amongst the best models for

317    mass gain, this relationship was of low importance.  The basic rules that determine the behaviour

318    of individuals were minimally altered by anthropogenic disturbance alone.  However tree

319    diameter and distance, which vary with stand age, were important predictors in the set of best

320    models.  This suggests that other factors that vary with stand age, such as time since disturbance,

321    competition or predation are not important in modifying the optimal foraging relationship.

322    Previous studies suggest foraging behaviours of ants and other species are often affected by

323    anthropogenic disturbances (Goverde et al. 2002; Mahan & Yahner 1999; Sorvari &

324    Hakkarainen 2004). However, changes in behaviour may reflect attempts by individuals to

325    optimise foraging in the new environment, so may not alter this fundamental relationship.

326    *Conclusions*

327    Our findings suggest that most *F. aquilonia* workers observed on trees are engaged in honeydew

328    harvesting.  The clear effect of distance on worker loads is consistent with predictions from

329    optimal foraging theory.  However, for both distance and diameter, activity declined as loads

330    increased, indicating a role for crowding in reducing colony-level efficiency (Dreisig 1988;

331    Grüter et al. 2012).  Load-distance relationships were consistent across stands of different ages,

332    suggesting no effect of stand age on this fundamental response, despite effects of stand age on

333    activity and honeydew quality (Gibb & Johansson 2010; Johansson & Gibb 2012).  This is in

334    contrast to findings suggesting effects of anthropogenic disturbances on a range of behavioural

335    responses.  However, changes in behaviour may often occur to optimise foraging or nesting

336    success.  Behavioural changes in response to disturbance may thus tend to be consistent with

337    optimal foraging if they are within the evolutionary experience of a species.

338 **Supporting information**

339 **Table S1:** Available background data on the study sites, including head width, nest volume and

340 activity of *Formica aquilonia* (Gibb & Johansson 2010), temperature on days of sampling for

341 experiment 2, numbers of aphids on three branches taken from five spruce trees and aphids per

342 needle collected in arboreal surveys (Gibb & Johansson 2010), and sucrose levels in honeydew

343 collected from the crops of *F. aquilonia* workers (Johansson & Gibb 2012).

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346 field.

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490 **Figure captions:**

491 **Figure 1:** Mean ± SE percentage of total trips (n = 1598) that ants collected honeydew, needles,

492 arthropod prey or nothing apparent for birch, pine and spruce.

493 **Figure 2:** Contour plot showing the relationship between tree diameter, $\log_{10}$ distance and mean

494 mass gain per ant for the small-scale study. Black circles represent values for mass gain, ranging

495 from -0.74 mg (smallest circles) to 2.11 mg (largest circles). Contour bin width is 0.5 mg.

496 **Figure 3:** Mean mass per ant walking down (●) and up (○) each of the trees plotted against

497 ln(distance) from the nest. The slope for the relationship between weight and distance travelled

498 was significant for ants walking down trees ($F_{(1,38)}$ = 8.520, $p$ = 0.0059, $R^2$ = 0.18 ), but not those

499 walking up ($F_{(1,38)}$ = 0.403, $p$ = 0.5296, $R^2$ = 0.01).

500 **Figure 4:** Model of the relationship between the mass of honeydew gained by the colony per

501 minute and the distance of the tree from the nest at three different tree basal diameters (BD = 10,

502 25, 40). The estimate was calculated by multiplying equations for mass gain per ant (Mass

503 gain.ant$^{-1}$ = 2.87 − 0.03*18.9 + 0.52*$\log_{10}$(distance) − 0.05*Diameter) by ant activity per minute

504 (Activity.min$^{-1}$ = -6.17 + 0.34*18.9 -0.43*Ln(distance) − 0.03*Diameter). Calculations were

505 made for spruce trees in mature forests.

506

**Estimates, importance ($\Sigma w_i$) and p-values from model-averaged models for mass gain and liquid loads at the site level.**

Models tested the effects of tree species, temperature, distance, basal diameter and their interactions on the mean mass gain and the percentage of individuals bearing liquid loads in their gasters. Significant effects are presented in bold. Random effects not shown.

| Source | Mass gain | | | | % Liquid bearers | | | |
|---|---|---|---|---|---|---|---|---|
| | Estimate | (SE) | $\Sigma w_i$ | p-value | Estimate | (SE) | $\Sigma w_i$ | p-value |
| Intercept | 3.00 | (1.13) | | **0.011** | 1.64 | (0.42) | | **<0.001** |
| Tree species (pine) | 0.05 | (0.26) | 0.25 | 0.853 | | | | |
| Tree species (spruce) | -0.13 | (0.30) | | 0.661 | | | | |
| Temperature | -0.03 | (0.05) | 0.30 | 0.634 | 0.01 | (0.02) | 0.31 | 0.622 |
| $Log_{10}$(distance) | 0.52 | (0.18) | 1.00 | **0.006** | 0.07 | (0.06) | 0.75 | 0.241 |
| Basal diameter | -0.05 | (0.02) | 1.00 | **0.038** | | | | |

**Table 2**<sub>(on next page)</sub>

**Estimates, importance ($\Sigma w_i$) and p-values from model-averaged models for worker mass across stands.**

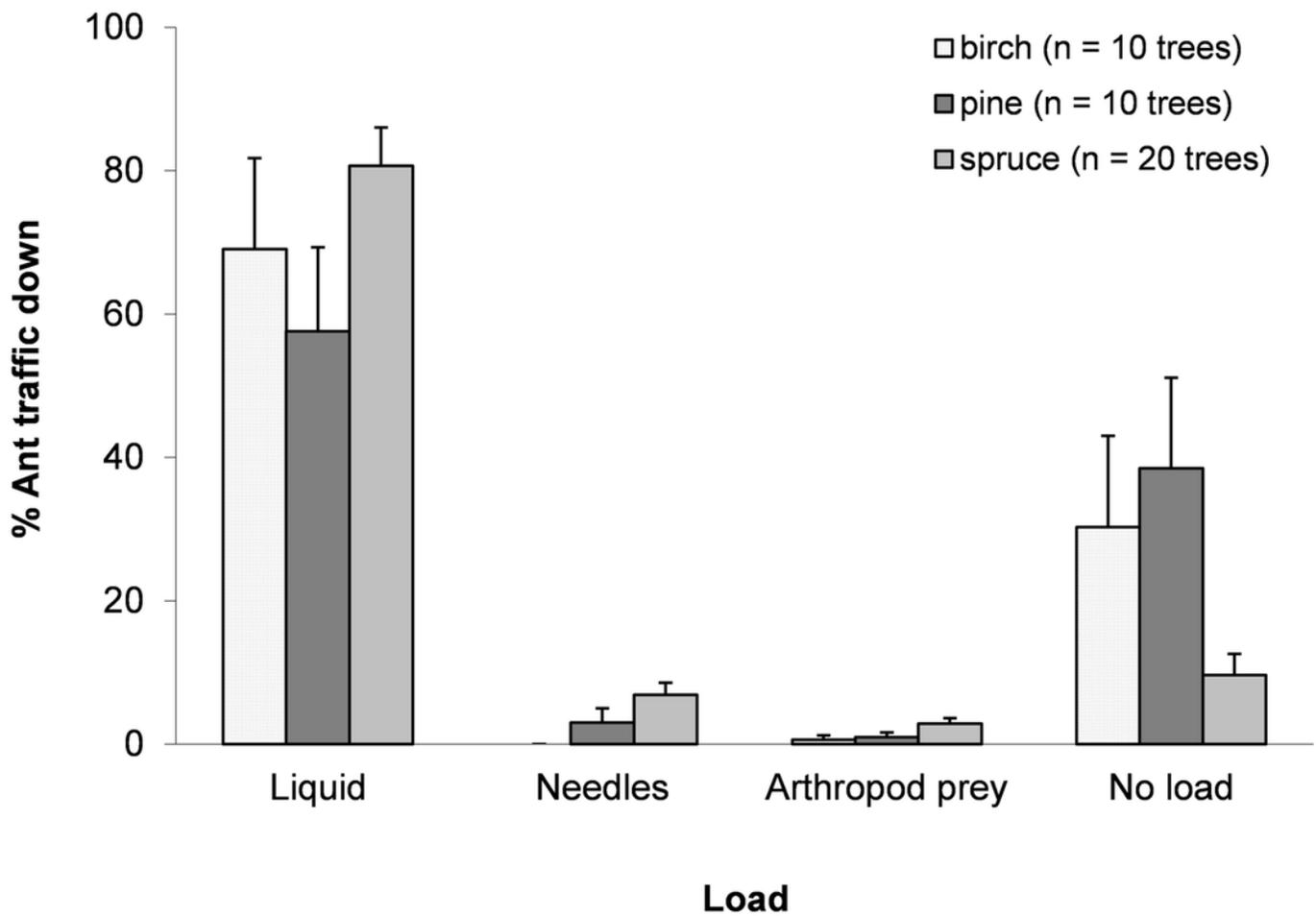
Models tested the effects of stand age, temperature, distance, basal diameter and their interactions on the mass of workers climbing down trees. Significant effects are presented in bold. Random effects are not shown.

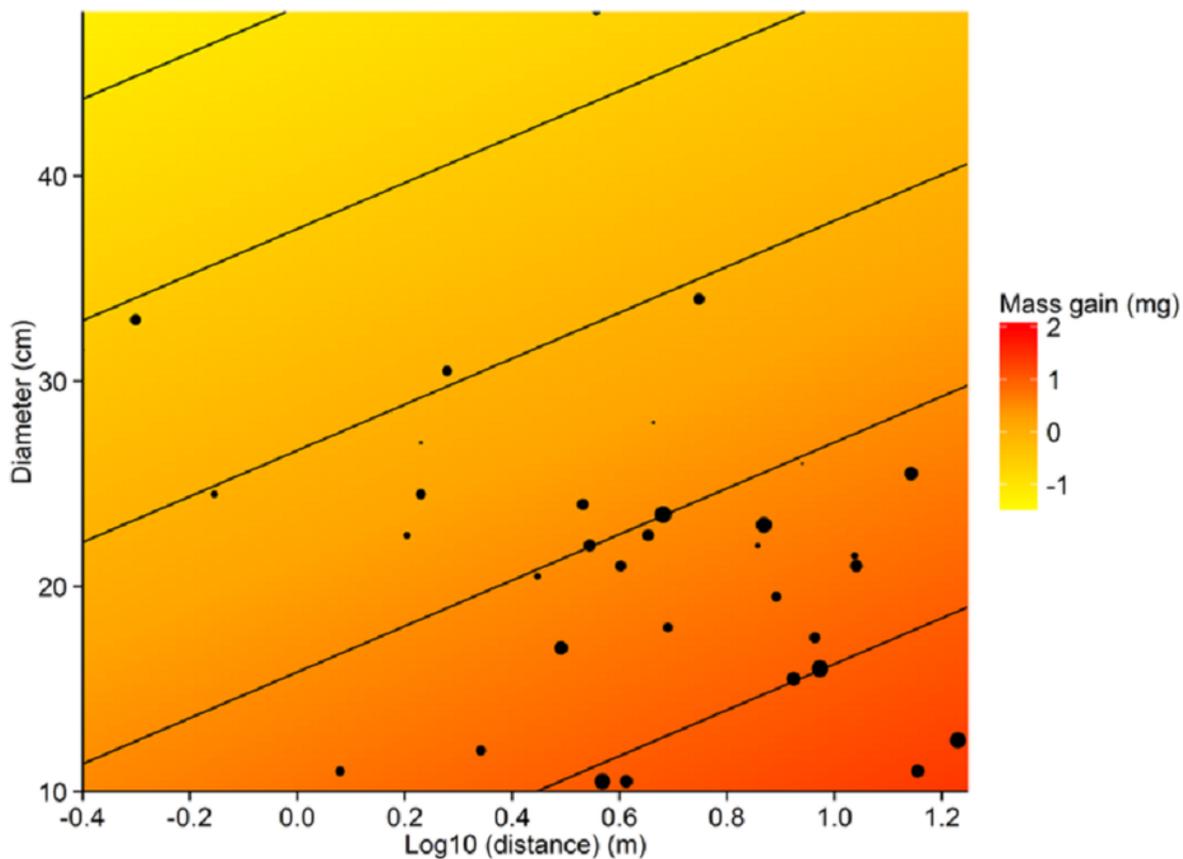
| Source | | Estimate | (SE) | $\Sigma w_i$ | p-value |
|---|---|---|---|---|---|
| (Intercept) | | -1.02E-02 | (7.78E-04) | | **<0.001** |
| Head width | | 1.17E-02 | (4.22E-04) | 1.00 | **<0.001** |
| Temperature | | -2.65E-06 | (1.45E-05) | 0.13 | 0.855 |
| Stand age | 80-100 yrs | 1.41E-04 | (4.25E-04) | 0.14 | 0.753 |
| | 30-40 yrs | 5.88E-05 | (2.72E-04) | | 0.846 |
| $Log_{10}$(Distance) | | 3.29E-04 | (1.05E-04) | 1.00 | **0.002** |
| Diameter | | 1.96E-05 | (3.34E-05) | 0.75 | 0.558 |
| Diameter*Stand age | 80-100 yrs | -1.27E-05 | (3.45E-05) | 0.14 | 0.713 |
| | 30-40 yrs | -8.05E-06 | (2.59E-05) | | 0.756 |
| Diameter*log(distance) | | 1.02E-06 | (3.91E-06) | 0.16 | 0.795 |

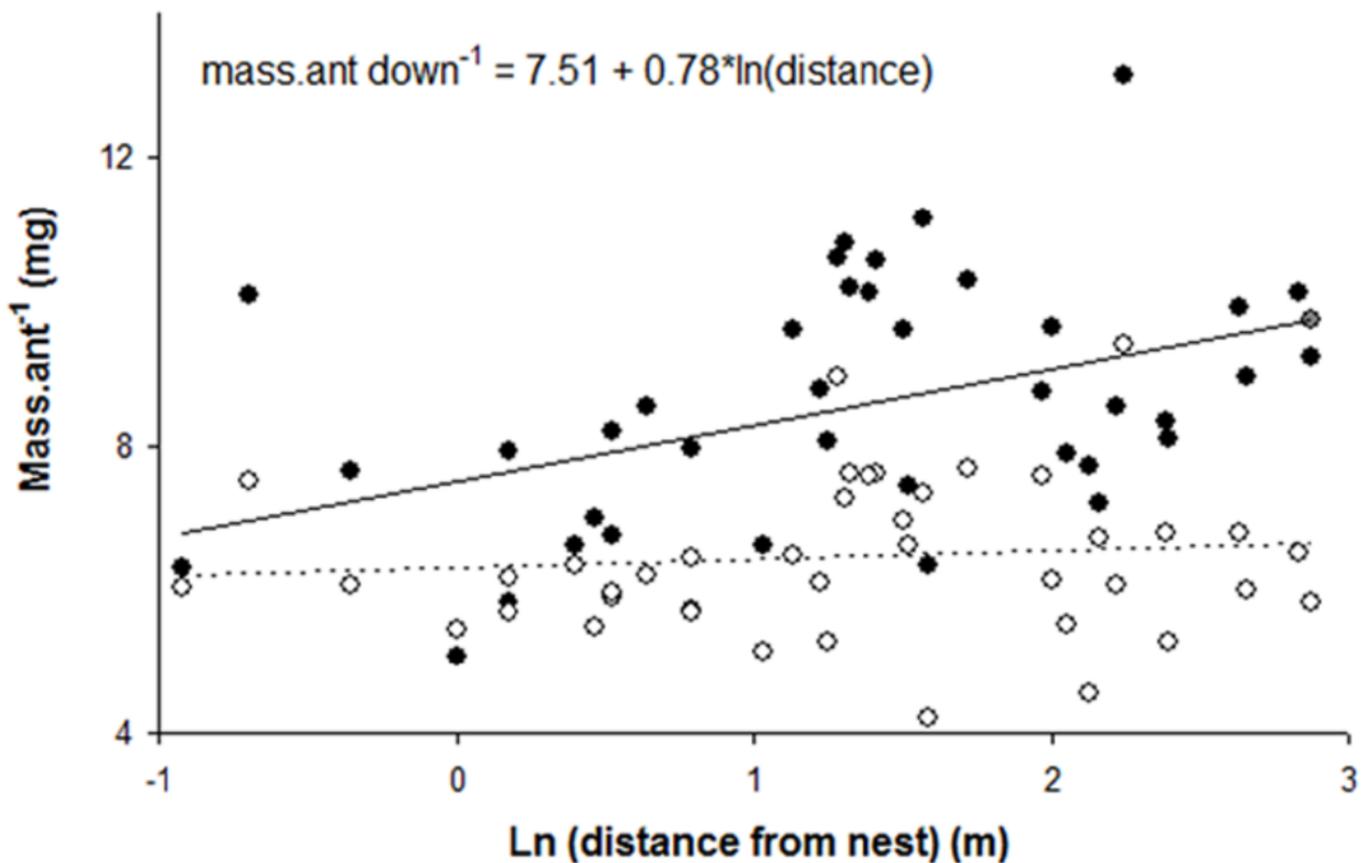
# 1

**Mean ± SE percentage of total trips for each resource collected** .

Ants collected honeydew, needles, arthropod prey or nothing apparent for birch, pine and
spruce. N = 1598 trips.

*Figure with y-axis "% Ant traffic down" (0–100) and x-axis "Load" categories: Liquid, Needles, Arthropod prey, No load. Legend: birch (n = 10 trees), pine (n = 10 trees), spruce (n = 20 trees).*

**Contour plot showing the relationship between tree diameter, log$_{10}$ distance and mean mass gain per ant for the small-scale study** .

Black circles represent values for mass gain, ranging from -0.74 mg (smallest circles) to 2.11 mg (largest circles). Contour bin width is 0.5 mg.

**Mean mass per ant walking down (●) and up (○) each of the trees plotted against ln(distance) from the nest**.

The slope for the relationship between weight and distance travelled was significant for ants walking down trees ($F_{(1,38)}$ = 8.520, $p$ = 0.0059, $R^2$ = 0.18 ) , but not those walking up ( $F_{(1,38)}$ = 0.403, $p$ = 0.5296, $R^2$ = 0.01).

**Model of the relationship between the mass of honeydew gained by the colony per minute and the distance of the tree from the nest.**

Models were produced for three different tree basal diameters (BD = 10, 25, 40). The estimate was calculated by multiplying equations for mass gain per ant (Mass gain.ant$^{-1}$ = 2.87 – 0.03*18.9 + 0.52*Log$_{10}$(distance) – 0.05*Diameter) by ant activity per minute (Activity.min$^{-1}$ = -6.17 + 0.34*18.9 -0.43*Ln(distance) – 0.03*Diameter). Calculations were made for spruce trees in mature forests.