Wood ants are wood ants: deforestation causes population declines in the polydomous wood ant *Formica aquilonia*

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**Abstract.** 1. One of the main themes in ecology is adaptation for survival in different habitats and the potential of the environment to regulate populations.
2. The effects of clear-cutting on nest-abandonment rate and local population sizes in the polydomous wood ant *Formica aquilonia* was studied, using uncut forest stands as controls.
3. The nest-abandonment rate was clearly higher in clear-cuts than in forest interiors. In clear-cuts, 39% of pre-deforestation nests and 73% of new bud-nests were abandoned 4–5 years after deforestation, whereas in forest interiors fewer than 2% of nests were abandoned at the same time period. Local population size decreased 30% in clear-cuts, but fewer than 2% in forest interiors.
4. The results demonstrate that despite modern logging practices in which mechanical harming of nest mounds is reduced, nest mounds are abandoned at high rate, and despite frequent establishment of new bud-nests, populations start to decline.
5. The likely reason for the high nest-abandonment rate in clear-cuts is a combination of changed abiotic conditions, resource limitation, and disturbed reproduction.
6. Species that are sensitive to changes in the size of habitat patch, such as *F. aquilonia*, likely are harmed by logging, even employing biodiversity oriented management practices. Hence there is a need for conservation actions that are based on the size of protection areas.

**Key words.** Colony survival, deforestation, *Formica rufa* group, habitat loss, logging, nest mortality.

**Introduction**

There is an increasing concern about the potential threat of the current rate of forest loss and the fragmentation of natural habitats to the persistence of animal populations (Barbault & Sastrapadja, 1995; Fahrig, 1999). Boreal forests are one of the last biomes where natural ecosystems have remained relatively intact and unmanaged. The highly developed forest industry, however, has resulted in the loss of the most of the natural boreal forests in northern Europe threatening the existence of several hundred species (Esseen *et al.*., 1997). The main forest harvest method in boreal region is clear-cutting in which all or most of the trees are harvested from the renewal area. In Finland, clear-cuts have generally been planted with single tree species monoculture and re-harvested at approximately 100-year intervals (Virkkala & Toivonen, 1999; Peltola, 2003). This kind of effective forest harvesting likely affects abundance and survival of forest-dwelling animal populations such as insects that live primarily in old-growth forests (e.g. Punttila *et al.*, 1991; Niemelä, 1997). Owing to this concern, more sustainable forest management practices have been developed (Anon., 1998). This includes smaller size of clear-cuts, leaving decaying wood and some trees on the cleared areas, and lighter site preparation for forest renewal. This new practice has been shown to benefit coleopterans that live on decaying wood; however, organisms such as polypore fungi that need forest microclimate (e.g. shaded conditions) have not benefited (Lindhe & Lindelöw, 2004; Lindhe *et al.*, 2004).
Mound-building wood ants of the *Formica rufa* group are among the most dominant animals in European boreal coniferous forests (Hölldobler & Wilson, 1990). They collect the majority (≥90%) of their food from trees (Rosengren & Sundström, 1987, 1991; Whittaker, 1991; Punttila et al., 2004) and thus they are expected to suffer from the loss of large part of their food resources after clear-cutting (Rosengren & Pamilo, 1978; Rosengren et al., 1979; Punttila et al., 1991). Forest clearing suppresses reproduction of *F. aquilonia*, a member of the *F. rufa* group (Sorvari & Hakkarainen, 2005, 2007a, b). Lenoir (2003) found that when excluded experimentally from trees, the wood ant *Formica rufa* search for new trees further away instead of increasing predation on the forest floor. Thus it seems likely that even though the wood ants have the possibility to widen their foraging areas, clear-cuts could have harmful effects on the colony’s economics because of the increased costs of foraging. In addition, the changed abiotic conditions due to loss of forest shade may have harmful effects on wood ants and their nests. Nest mounds are shown to be abandoned at high rate among *F. rufa* group wood ants in natural or semi-natural conditions (Klimetzek, 1981); however, it is not clear whether habitat degradation has any effect additional to natural nest turn-over in these forest-dwelling ants.

The aim of this study was to examine whether there are differences: (i) in the nest-abandonment rate, and (ii) in the change in population size between clear-cuts employing the new forstry practice and forest interiors in the wood ant *F. aquilonia* during the period of 4 years. It was also examined whether abandonment rate is different between new bud-nests and pre-deforestation nests located in clear-cuts.

**Materials and methods**

The study species was the highly polygynous (multiple queens) and polydomous (multiple nests) *Formica aquilonia*, which is the most common member of the *F. rufa* group in northern European coniferous forests (Collingwood, 1979; Rosengren et al., 1979). The wood ants of the *F. rufa* group build large mounds from conifer needles, small branches, resin, soil, small particles, etc. (Collingwood, 1979; Hölldobler & Wilson, 1990). Mature nest mounds can be of several cubic metres in volume (e.g. Seifert, 1991), but normally they are smaller (e.g. Ecva et al., 2004; Domisch et al., 2005). The function of the nest mound is to maintain optimal temperature and humidity conditions for rearing of offspring, and especially in shaded forest environments, large nest mounds and populous colonies are needed for generating temperatures high enough for this purpose (e.g. Rosengren et al., 1987; Hölldobler & Wilson, 1990). Large nest mounds of *F. aquilonia* may contain a million workers and hundreds of queens (Rosengren et al., 1987). Colonies frequently reproduce new nests by budding. The budding behaviour is increased in clear-cuts (Rosengren & Pamilo, 1978; Rosengren et al., 1979), and sometimes the old nest is abandoned when its population moves to one or several bud-nests, and the term *nest-splitting* might be more precise. Despite high numbers of new nests in clear-cuts, however, their reproductive output and growth rate is very low because small nests do not produce sexual offspring (Sorvari & Hakkarainen, 2005). *F. aquilonia* is a threatened species in many European countries (Social Insects Specialist Group, 1996), but not in Finland, hence the association between deforestation and development of population size is possible to study in Finnish forests.

The study was conducted in the coniferous boreal zone in central Finland, near the town Jyväskylä (62°15’ N, 25°45’ E) in 2000–2003. Two types of study stands were used, forest interior areas (*n* = 13) and clear-cuts (*n* = 18). Forest interior areas and clear-cuts were initially similar *Vaccinium myrtilius* growth mature forests dominated by Norway spruce (*Picea abies*) located 3.8 ± SE 0.3 km apart. Clear-cuts varied from 0.3 to 4.0 ha (mean 1.5 ± SE 0.2 ha). Nine of the clear-cuts were cleared in the winter 1998–1999 and the remaining nine in the winter 1999–2000. Nest mounds located in clear-cuts and in their managed surroundings (<5 m away from cleared area) were treated as clear-cut nests. Forest interior nests were located well inside forests (more than 50 m away from clear-cuts and plantations).

Between the years 2000 and 2003, the nest mounds were examined every year several times between May and July. The basal diameters of nest mounds and their distance to forest edge were measured. The shape of the nest mound base is generally circular in the study species (Sorvari & Hakkarainen, 2005) and the basal diameter was used as an estimate of nest mound size. A minority of nests were visibly ellipsoid and these nests were cross-measured and the mean value was used as basal diameter. The basal diameter and thus basal area of mound has been shown to correlate with the worker population inhabiting the mound (Seifert, 1991). The summary of the basal areas of all inhabited nests from each study area was used as an estimate for the size of local population.

Each nest mound was characterised as abandoned if offspring production was not found in nest excavations and if less than 10 workers of the study species were found on the surface or inside of the nest mound. Foragers from neighbouring inhabited colonies can be seen on the litter as well as on the surface of abandoned nests or even inside the abandoned mound and thus may cause false-positive determination of nest as inhabited. In addition, other ant species, such as *Formica fusca*, *Lasius niger*, and several species of the genus *Myrmica* can use mounds as nest sites when the original species has disappeared (Oinonen, 1956). All nests of *F. aquilonia* found in the study stands were examined, whereas the colonies of other *F. rufa* group species were excluded as well as those abandoned nest mounds that were likely abandoned before the time of clear-cutting. The ants successfully repaired all signs of excavations in their mounds within a week.

Nests in clear-cuts were divided into two categories, pre-deforestation nests and new bud-nests. The new bud-nests are usually smaller than older nests (Sorvari & Hakkarainen, 2005), but other characteristics were used in classification; for example, the base of older nests, even that of small ones, is often covered by vegetation, whereas in new bud-nests, the nest material is piled over the ground vegetation such that the ground vegetation remains under the newly brought nest material. Some analyses of these two kinds of nest mounds were carried out separately, because of differences in their history and also functions in production of sexual offspring.
Nest mound sizes were analysed with nested mixed ANOVAS using Satterthwaite approximation of degrees of freedom (necessary in case of unbalanced designs) and study site as a nested random factor (nested within deforestation treatment). Original population sizes were compared with resulting population sizes by paired-samples t-test. In the following analyses nest mounds that were abandoned (and were not re-colonised) at the final survey in the end of June 2003 were classified as abandoned. Deforestation treatment, nest type (class variables) and basal diameter of nest mound (cm; covariate) were applied into logistic regression analyses in generalised linear models (binomial error term; inhabited = 0, abandoned = 1) using study stand as a repeated subject (nested within deforestation treatment). In another test, nest types (pre-deforestation nests and bud-nests) were analysed in a similar logistic regression analysis, but study area as a repeated subject was nested within nest type. Type 3 contrasts were used in all mixed and generalised linear model analyses. The analyses were made by using procedures TTEST, MIXED, and GENMOD in SAS 9.1 statistical software (SAS Institute, 2001).

Results

Basal diameters of nest mounds were smaller in clear-cuts than in forest interiors, but did not differ after removing the small bud-nests from the analysis (no bud-nests found in forest interiors; Table 1). Nest-abandonment rate was very low in forest interiors where only 1.6% of the nests (one of 61 studied nests) were abandoned. In clear-cuts, however, 53.6% of all nests (164 of 306) were abandoned; 39.2% (69 of 176) of the pre-deforestation nests and 73.1% (95 of 130) of the new bud-nests were abandoned. The total loss in numbers of inhabited nests was 34 in clear-cuts (originally 176, at the end 142) and 1 (originally 61, at the end 60) in forest interiors. Population size was measured here as the sum of basal areas of inhabited nest mounds in each study stand. Population size decreased 30% in clear-cuts but only 1.6% in forest interiors. In clear-cuts populations declined significantly ($t_{12} = 2.48$, one-tailed $P = 0.012$), but not in forest interiors ($t_{12} = 1.00$, one-tailed $P = 0.17$).

Location in clear-cuts as well as being a new bud-nest increased the nest mound’s propensity of abandonment (Table 2; Fig. 1), but the nest size as a covariate and all possible interactions were non-significant (Table 2; interaction nest type × deforestation was not possible as there were no bud-nests in forest interiors). When new bud-nests were excluded from the analysis, nest-abandonment was significantly positively associated with deforestation, but not with the diameter of nest mound (deforestation: $\chi^2 = 13.25$, d.f. = 1, $P = 0.0003$; diameter of nest mound: $\chi^2 = 0.25$, d.f. = 1, $P = 0.62$). The bud-nests had higher probability of being abandoned than pre-deforestation nests in clear-cuts ($\chi^2 = 11.37$, d.f. = 1, $P = 0.0007$).

Discussion

The basal diameters of nest mounds were smaller in clear-cuts than in forest interiors owing to the frequent establishment of bud-nests. Accordingly, the diameters of nest mounds did not differ when those new bud-nests were excluded. Nest-abandonment rate was very low in forest interiors compared with that of clear-cuts, where both the old pre-deforestation nests and the young bud-nests were abandoned with high frequency. Despite the frequent establishment of new bud-nests, wood ant populations declined significantly in clear-cuts. Newly established bud-nests have a low survival rate, and thus cannot compensate the declining older nests. Deforestation increased the propensity of nest for abandonment and it was especially high among new bud-nests. When new bud-nests were excluded from the analyses, only deforestation affected the propensity of abandoning significantly, whereas the diameter of the nest mound did not. In clear-cuts, the bud-nests had a higher probability of being abandoned than larger and older pre-deforestation nests.

The likely reason for high nest abandonment rate in clear-cuts is the changed abiotic conditions such as over-drying of nest material (especially of large domes, own unpublished data) and wide ranging temperatures (Rosengren et al., 1979). Small nests may be more easily abandoned in ants because either (i) abandoning a small nest is less costly than abandoning a large nest (e.g. Gibb & Hochuli, 2003), or (ii) small groups (i.e. small nests) are generally more vulnerable to extinction. Among small nest mounds, herbal overgrowth (grass, fireweed, and raspberry bushes) may have additional negative effects and may explain the higher nest-abandonment rate of bud-nests compared with pre-deforestation nests. Resource limitation owing to forest fragmentation and longer foraging trips to the remaining food sources may also decrease the nest mound occupancy in clear-cuts. Because both the deforestation and small size of nest have independent negative effects on the probability of producing sexual offspring (Sorvari & Hakkarainen, 2005), the high frequency of nest abandonment in clear-cuts may also result from the disturbed production and recruitment of new queens. Owing to this suppression in the production of sexual offspring and the relative short life-span in the queens of polygynous wood ants (Keller & Genoud, 1997), the number of queens in clear-cut colonies may have become too low for the maintenance of viable colony functions.

Logging in the study sites was done by using modern logging practices; all rotten wood was left on the clear-cuts, the shape of clear-cuts simulates the shape of small wildfires, and the site

<table>
<thead>
<tr>
<th>Nest type</th>
<th>Clear-cuts, mean ± SD</th>
<th>Forest interiors, mean ± SD</th>
<th>$F$</th>
<th>d.f.</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>PDN</td>
<td>1.30 m ± 0.42</td>
<td>1.36 m ± 0.3</td>
<td>1.62</td>
<td>130.2</td>
<td>0.213</td>
</tr>
<tr>
<td>Bud nests</td>
<td>0.54 m ± 0.23</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>All nests</td>
<td>0.97 m ± 0.51</td>
<td>1.36 m ± 0.3</td>
<td>17.37</td>
<td>36.7</td>
<td>0.0002</td>
</tr>
</tbody>
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The results of nested mixed model ANOVAS of pre-deforestation nests (PDN), bud-nests and all nests.

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modern logging practices. The current practice of leaving few trees or rotten logs intact in clear-cuts may be beneficial, for example, for maintaining populations of saproxylic coleopterans (e.g. Lindhe & Lindelöw, 2004), but may not be, not enough for wood ants that use large areas of forest for foraging (radius of foraging area: ≈50 m, e.g. Savolainen & Vepsäläinen, 1988; Rosengren & Sundström, 1991) and seem to need large forest covered areas to maintain stable multi-nest colonies. The results presented here are very much in line with the recent recommendation of Tikkanen et al. (2006): in addition to biodiversity oriented forest management practices, large enough protected areas are needed to maintain species populations in the boreal forest ecosystem. Polydomous wood ants are one of the dominant forest-dwelling insects in boreal forests affecting the assemblage of other forest-dwelling invertebrates (Niemelä et al., 1992; Punttila et al., 2004); therefore, the decline of wood ant populations could have extensive effects in the boreal forest ecosystem.

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References


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