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Forest clear-cutting causes small workers in the polydomous wood ant *Formica aquilonia*

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We examined whether the body size of mound building wood ant *Formica aquilonia* workers is affected by forest clear-cutting in a before-after logging field study. Clear-cutting is expected to decrease the availability of tree-living aphids, the main food resource of wood ants. Worker size decreased from one year to the next in clear-cuts but not in forest stands, indicating food limitation in the clear-cuts. Worker size increased with nest size in forest interiors, but not in clear-cuts, which further indicates food limitation in the clear-cuts. In addition, lower body-fat contents in ant workers in the clear-cuts supports previous suggestions of lower food resources after forest logging. Nests were cooler in the clear-cuts, which suggest that they may be poor habitats for forest-dwelling wood ants. Food resource limitation may have an effect on the ability of wood ants to regulate nest temperatures.

Introduction

Human induced habitat degradation may decrease food resource levels and create unfavourable abiotic conditions for forest-dwelling species (e.g. Zanette *et al*. 2000). For instance, for some forest-dwelling ants, clear-cutting may cause a loss of food resources and change the microclimate in suitable forest types (Punttila *et al*. 1991). About 90% of the wood ant's (*Formica rufa* group) diet consists of honeydew produced by tree-living aphids (Rosengren & Sundström 1991). Trees are also important sources of arthropod prey including large amounts of butchered aphids (Punttila *et al*. 2004) and therefore, when forests are clear-cut, wood ants may suffer from the loss of food resources. Recent studies have shown that forest clear-cutting caused lower reproduction, disturbed immune defence, and lowered colony survival in the wood ant *Formica aquilonia* (Sorvari & Hakkarainen 2005, 2007a, Sorvari *et al*. 2008).

The effects of clear-cutting may materialise via the loss of food resources. In ants, protein-rich food (e.g. insect prey) is used for egg formation and larval growth (Brian 1983), whereas carbohydrates (e.g. honeydew of aphids) are used as an energy source for adult workers. Thus, carbohydrates may have an indirect, but important role in the production of offspring (Porter 1989). Food resources are involved with caste determination and size variation within castes in social insects (reviewed in Wilson 1971, Oster & Wilson 1978, Hölldobler & Wilson 1990). The quantity of food resources in the larval growth period is likely to be associated with the size of an adult worker ant:

poor food resources may result in a small body size. In addition, large workers have defensive or specialised foraging tasks in many species of ants (e.g. Evison & Ratnieks 2007). Size variation is probably mostly beneficial for ants, although there are also many small sized and monomorphic species (e.g. Hölldobler & Wilson 1990).

Worker size may vary with habitat quality in some species. Workers of *Formica podzolica* from colonies located in a resource-rich environment (forest edge) are larger than workers from colonies located in a resource-poor environment (overgrazed meadow) (Deslippe & Savolainen 1995). On the other hand, *Formica obscuripes* colonies excluded from food resources do not show a decrease in worker size but, instead, a decrease in the variation of body size (Herbers 1980). Worker size can also be associated with the foraging ability of the colony. As compared with small ant colonies, large colonies may have a better ability to exploit food resources due to a larger available worker population (Oster & Wilson 1978, Nonacs 1986, Wagner & Gordon 1999, Sorvari & Hakkarainen 2007b), which may result in larger body sizes in workers (Clémencet & Doums 2007). Large colonies, however, may need more food than smaller ones and thus, worker sizes may not increase in large colonies if food becomes limited. Finally, offspring development can be retarded by unstable temperature conditions in the nest. Internal nest temperatures may vary more in clearings as compared with those in forest interiors in *F. aquilonia* (Rosengren *et al.* 1979). Habitat-related nest temperatures which vary more in open habitats as compared with shaded forest habitats have also been recorded in *Formica polyctena,* a closely related species to *F. aquilonia* (Frouz 2000).

The clear-cutting of aphid bearing forests is a common disturbance event in boreal forests (Virkkala & Toivonen 1999), and is likely to have nutrition related effects on wood ants. The aim of this study was to determine whether forest clear-cutting (before-after logging field experiment) and mound sizes affect the sizes and size variation of *Formica aquilonia* worker ants. In addition, we investigated whether forest clear-cutting is associated with lower body fat contents of wood ant workers and whether it disrupts temperature regulation of the nest mounds.

Material and methods

Study species and study area

The study species, *F. aquilonia*, is a member of the European *F. rufa* group. It builds large mound nests, often over 1.5 m high in mature forests. The species is polygynous (more than one functional egg-laying queen in the nest) and polydomous, i.e. it has multiple nests in one colony (Collingwood 1979, Seifert 1996). This species is the most common wood ant in the boreal coniferous zone and it prefers the interiors of mature spruce forests (Punttila 1996, Punttila & Kilpeläinen 2009). Because of large colony sizes, *F. aquilonia* may need large forest patches to maintain stable access into rich food resources.

Our study material was collected from central Finland in the region around the city of Jyväskylä. The study area consisted of 13 different forest stands and 9 separate forest clear-cut areas, which were logged in the winter of 1999–2000. All study stands represented similar mature spruce-dominated forests before clear-cutting. Samples of 30 worker ants were collected from the top of 13 nest mounds from the clear-cuts and 13 mounds from the forest stands in April 2000. Because workers are reared during summer, all workers collected in April 2000 were produced before the loggings. A second set of samples of 30 workers were collected from the top of the same nests a year later in June 2001, when at least the majority of workers in the clear-cuts were produced under logged conditions.

The effective foraging area of *F. aquilonia* and its relatives in the *F. rufa* group is about 50 m (Rosengren 1977, Rosengren *et al.* 1979, Rosengren & Sundström 1991, Vepsäläinen & Savolainen 1994) and the loss of trees within the foraging area is expected to reduce their food resources. Therefore, all forest stand colonies used in this study were situated more than 50 m into the forests, and clearing colonies were from clear-cut areas.

Body size measurements

Maximum head width above the eyes is commonly used as a standard measure of body size in *Formica* ants (Deslippe & Savolainen 1994, Schwander *et al*. 2005). We measured 10 ants of each sample to provide an indication of the average worker size in the nests. The ants were set between two microscope slides and the head width was measured above the compound eyes by using an Olympus SZ40 microscope with 40× magnification, and an Olympus 24-10/100 ocular micrometer. Head widths were measured from 520 individuals.

Nest size

The area of the mound base correlates positively with the number of worker ants in a *Formica* colony (Seifert 1991, Deslippe & Savolainen 1994, Liautard *et al*. 2003). In this study, the basal area of the nest mound was used as a rough estimate of the worker population. Basal area was measured from the part of the mound not covered by plants. The shape of the nest mound base is usually circular in *F. aquilonia* and thus, we used the equation for a circular area (πr^2) to calculate the basal area of the nest mound.

Fat content

The nutritional status of individual insects can be quantified by measuring their body fat content (e.g. Sundström 1995, Koskimäki *et al*. 2004). Fat content was measured from the workers of 85 nests (42 nests from 12 cleared areas; 43 nests from 10 forest areas), which included 85% of the ant nests used in the head-width measurements of workers. The fat extraction method was modified after Sundström (1995). A sample of 20 worker ants per nest were dried (48 h at 55 °C), weighed (to the nearest 0.001 mg) with a Mettler Toledo MX5 balance for dry weight 1 (d.w. 1), and extracted in 90 ml of petrol spirit (boiling point 40–60 °C) for 24 h in a water bath of 40 °C. New petrol spirit was added when needed during the extraction. After extraction the ants were again dried (48 h at 55 °C) and weighed (d.w. 2). The weight difference (d.w. 1 – d.w. 2) represented the amount of fat in the colony sample. In the analyses we used the percentage value of fat from the dry body mass before extraction.

Nest temperatures

Internal nest temperatures were measured on the 27 June 2001, which was in the middle of a dry and sunny season. The temperatures were measured from all 13 forest stand nests and all 13 clear-cut nests, and from an additional 13 nests from the clear-cut areas. The nests were measured twice, first early in the morning at 04:00–07:00 and then later at 14:00–17:30. Internal nest temperatures were measured by keeping the tip of a digital thermometer at a depth of 15 cm for one minute and ambient temperatures were measured 0.5 m outside the nests at a height of 0.5 m (temperatures were measured in the shade). The measurements were taken during dry weather conditions.

Statistical analyses

In the analyses of head width variation, habitat type, study year and their interaction were used as fixed factors. The basal area of nest mounds was used as a covariate, study stand as a random variable, and nest was used as a repeated subject in a mixed model ANOVA (proc Mixed in SAS. We used a mixed model ANOVA to evaluate differences in the fat contents of workers. We used fat percentage as a dependent variable, habitat type as a fixed factor and d.w. 2 as a covariate. Because many of the nests were sampled from the same study stand, stand was used as a random factor. Differences in temperatures were analysed with a mixed model ANOVA using nest as a repeated subject. All analyses were performed using the SAS statistical software version 9.1 (SAS Institute 2001). Means are always reported with ± SE.

Results

Body size, measured here as head width, differed between habitat types and study years. There was a statistically significant interaction between

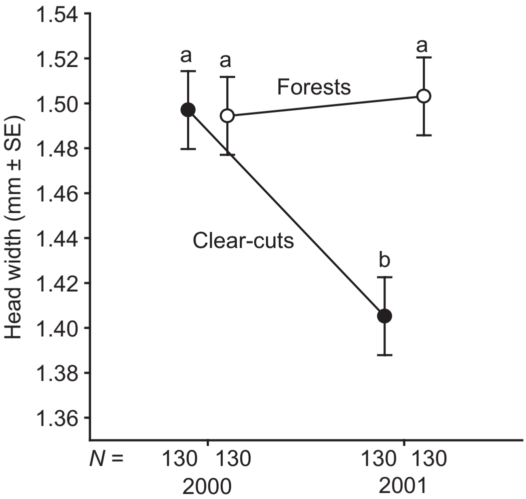

Fig. 1. Within-nest variation in head widths between years in clear-cuts (●) and forest interiors (○). Model based least-squares means are used. The same nests were used in both study years (clearing nests *N* = 13, forest nests *N* = 13; 10 workers per nest). Data are based on individual workers, with nest of origin as a nested variable in the analysis. Symbols with the same letter are not significantly different (*p* > 0.05) according to the Tukey-Kramer test following the mixed model ANOVA.

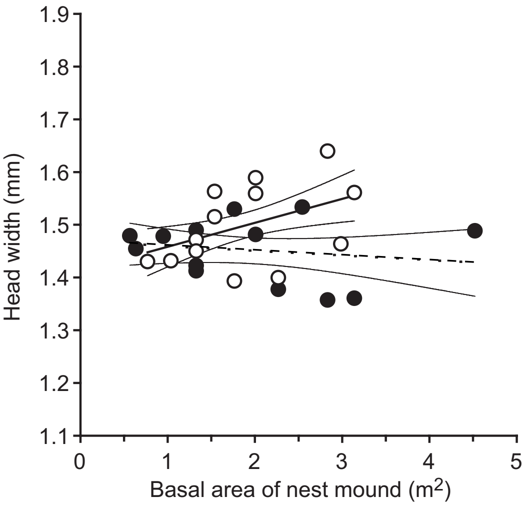

Fig. 2. Relationships between head width of workers and basal area of the nest mound in clear-cuts (●) and in forest interiors (○). The fitted model-based prediction lines (± 95% CI; dashed line for clear-cuts, solid line for forest interiors) are constructed from the original data (10 workers/year/nest) while the data points shown in the figure are colony means (pooled over two years due to non-significant interactions within habitat types).

year and habitat type: ant size decreased significantly from the first year to the next in the clear-cut nests, while ant size increased marginally in the nests located in the forests (year × habitat type: $F_{1,494} = 8.99, p = 0.0028$; Fig. 1).

The within-nest standard deviation of head widths was similar between years and between habitat types (clear-cuts 2000: 0.19 ± 0.01, 2001: 0.17 ± 0.01; forest interiors 2000: 0.19 ± 0.01, 2001: 0.19 ± 0.01; habitat type, $F_{1,49} = 0.84, p = 0.36$; year, $F_{1,49} = 1.95, p = 0.17$). In addition, the within nest standard deviations were parallel between years and habitat types (forest interiors, $F_{1,24} = 0.31, p = 0.58$; clear-cuts, $F_{1,24} = 1.83, p = 0.19$; year × habitat type: $F_{1,48} = 0.44, p = 0.51$).

Nest mound size was differently related to worker size between clearings and forests (basal area × habitat type: $F_{1,515} = 6.96$, $p = 0.0086$; Fig. 2). In forest interiors, an increase in the basal area of nest mound was associated with an increase in worker size, and the effect was similar between years (basal area: $F_{1,257} = 7.09$, $p = 0.0082$; basal area × year: $F_{1,256} = 0.02$, $p = 0.70$). In clear-cuts, however, basal area of the nest mound was not associated with worker size in either year (basal area: $F_{1,257} = 0.62$, $p = 0.43$; basal area × year: $F_{1,256} = 0.72$, $p = 0.40$). In 2000, the mound base areas of nests in both habitats were similar (clear-cuts 1.94 ± 0.26 m^2, forest stands 1.89 ± 0.26 m^2; $F_{1,24} = 0.02$, $p = 0.89$).

The percentage of fat in worker ants ranged from 0.8% to 28% (mean ± SD = 9.5% ± 5%) and was lower in clear-cuts than in forests ($F_{1,18.8} = 13.25, p = 0.0018$; Fig. 3). As a covariate, d.w. 2 (dry body mass without fat) did not have any effects on the percentage of fat in the ants ($F_{1,81.5} = 0.34, p = 0.56$).

Ambient temperatures were lower in the early mornings as compared with those in the afternoons, and lower in forest stands as compared with those in clear-cuts (time: $F_{1,75} = 653.1, p < 0.0001$; habitat type: $F_{1,75} = 5.7, p = 0.02$; interaction term time × habitat type: $F_{1,74} = 0.34, p = 0.56$; Fig. 4). Despite the lower ambient temperatures in forests, nest mounds in forest interiors were generally warmer than nest mounds in clear-cuts ($F_{1,74} = 12.57, p = 0.0007$; Fig. 4). Internal nest temperatures tended to develop

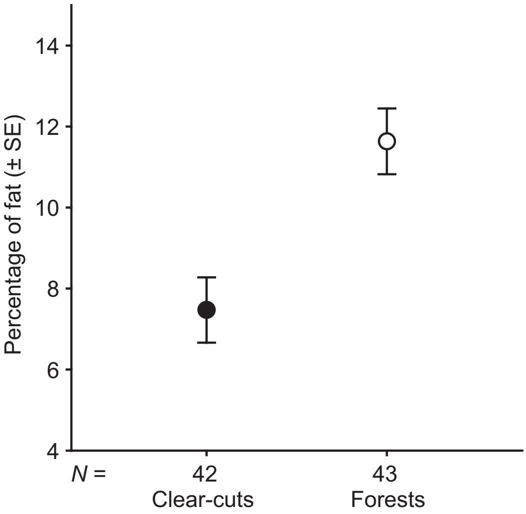

Fig. 3. Percentage of fat in workers from clear-cut (●) and forest (○) stands (model-based least-squares means). Data are based on individual workers with nest of origin as a nested variable in the analysis.

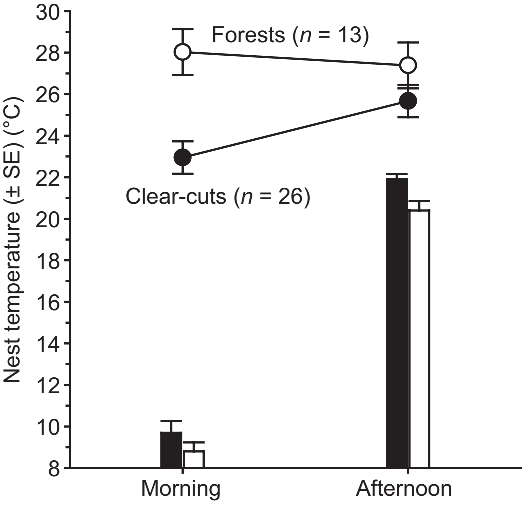

Fig. 4. Internal nest temperatures (lines) and ambient temperatures (bars) in clear-cuts (filled circles) and forest interiors (empty circles) in the morning and afternoon (model-based least-squares means).

differently between clear-cut and forest interior nests (interaction term time × habitat type: $F_{1,74} = 3.08$, $p = 0.084$). The internal temperatures of nest mounds increased significantly from early morning to the afternoon in clear-cut nests, but not in forest stand nests (clear-cuts: $F_{1,50} = 4.34$, $p = 0.042$; forest stands: $F_{1,24} = 0.93$, $p = 0.35$; Fig. 4). Temperatures inside nests increased with increasing ambient temperatures in clear-cuts, but in forest interiors ambient temperature had no observable effects on the inside temperatures of nests (clear-cuts: $F_{1,50} = 5.55$, $p = 0.022$; forest stands: $F_{1,24} = 0.77$, $p = 0.39$; Fig. 4).

Discussion

In many species of ants there is a genetic component to size, but environmental conditions are also a strong contributor of size variation and colony lifestyle. In the ant *Formica truncorum* the size of queens seems to have a strong genetic component, whereas heritable components seem to be lower among workers than in queens (Bargum *et al*. 2004). Similar to *F. truncorum* queens, the sizes of the reproductive castes of *Formica podzolica* appear to be more genetically than environmentally determined, as habitat had no effect on their head width (Deslippe & Savolainen 1994). Worker size may be more related to food availability than to the sizes of sexual. In the ant *Cataglyphis cursor*, colonies of better foraging ability had larger workers (Clémencet & Doums 2007) and the better fed first generation workers of the ant *Pogonomyrmex californicus* were larger than food deprived workers (Johnson 2002). In addition, in poor habitats, workers of *Formica podzolica* were smaller than workers from more luxurious habitats (Deslippe & Savolainen 1995). Intraspecific variations in worker size have also been shown to occur between different social structures, as workers from the colonies of a single egg-laying queen were larger than workers from the colonies of multiple egg-layers in both *Formica exsecta* (Pisarski 1981) and *Formica selysi* (Schwander *et al*. 2005), which may be a general trait among ants.

We showed that forest clear-cutting and the colony size of forest nests affected ant worker body size. Worker size was smaller in clear-cuts in the second study year than in the first, whereas in forests such a change did not appear. Forest clear-cutting had no effect on the magnitude of variation (measured here as SD) of worker head widths, in contradiction to a study on *Formica obscuripes* (Herberts 1980). The size of workers increased with an increase in nest size in forest stands, whereas such an association did not occur in clear-cuts. The fat content of workers as well as nest temperatures were lower in clear-cuts than in forests. Fat content provides information on the nutritional status of insects (e.g. Sundström 1995, Koskimäki *et al*. 2004), suggesting that limited food resources, especially aphids, in clear-cuts play a role in reducing the size of workers.

Large colonies may have enhanced capabilities to exploit food resources due to larger worker populations (Nonacs 1986, Wagner & Gordon 1999, Clémencet & Doums 2007). In forested habitats, this might explain the larger workers in larger nests as compared with workers in smaller nests. In clear-cuts, however, the environment may not provide sufficient resources for large colonies and thus, adults and offspring may become starved. In addition, the correlation between colony size and nest mound size may disappear in clear-cuts due to the possible starvation-accelerated decrease of worker populations (ants are known to devour offspring when starved, e.g. Wilson 1971).

In addition to food resource availability, nest temperature may also have an effect on worker size. Wood ants may try to maintain a constant optimal temperature for offspring production in their nest mounds. In forest interior nests, temperature variation was low and the temperature was slightly higher in the early morning before sun rise as compared with that in the afternoon. A higher night temperature is possibly due to closed nest entrances during a less active night period. Similarly high nighttime temperatures and a slight decrease in temperature during the day in forest interior nests are also typical in the closely related ant *Formica polyctena* (Frouz 2000). In clear-cuts, however, ants seem to fail to keep an optimal temperature during the night, probably due to the drying of nest material. This may result in large variations in internal nest temperatures (higher during the day and lower at night). Nest mounds in the study area contain a lot of conifer resin. In clear-cuts, nest mounds are often very dry and hard (hardly penetrable by hand) due to a dried mixture of resin and other particles. Temperature regulation in such nests is supposedly more complicated than in normal nests. We suggest that the lower nest temperatures in clear-cuts may partly be the cause of small worker sizes.

A reduction in food resources and unfavourable nest temperatures may not be the only causes for smaller workers in clear-cuts; smaller workers in clear-cuts may also originate from the loss of large workers. Large workers have longer foraging trips than small ones in *F. aquilonia* (Rosengren & Sundström 1987), and the loss of trees used as orientation cues (Rosengren 1977) may cause orientation problems and a selective loss of large workers. They may also drift into nearby forest nests. However, increased inter-nest hostilities in clearings (Sorvari & Hakkarainen 2004) may reduce such drifting. This selective loss of large workers could be an additional reason for smaller worker sizes in clearings, but seems to be of minor importance in our study system as we did not show a decrease in size variation in ants in the clear-cuts.

The nests of polydomous colonies of *F. aquilonia* seem to split into separate colonies after forest clear-cutting, resulting in a monodomous life style (Sorvari & Hakkarainen 2004). Polydomous wood ant species usually do not need large bodied workers for colony defence because they can rely on the support from neighbouring nests. Monodomous colonies instead do not receive such support and thus need larger workers (Rosengren & Pamilo 1983). Large workers may be better than small ones in foraging and in nest defence (e.g. Rosengren & Sundström 1987, Evison & Ratnieks 2007). Therefore, smaller worker size in clear-cuts may affect the colony's foraging efficiency negatively. Smaller worker size in clear-cuts may also weaken the competitive ability of a colony, especially if reproduction also decreases (*see* Sorvari & Hakkarainen 2005). For example, *Formica aquilonia* is excluded from clear-cuts soon after logging by other ant species (*see* Punttila *et al*. 1991). In *F. aquilonia,* this is likely due to the synergetic negative effects of clear-cutting, i.e. suppression of reproduction, smaller worker size, and the decline of polydomous relationships.

In conclusion, the observed variation in body size of *F. aquilonia* in the present study can be explained in a following manner: habitat degradation in terms of commercial forest clear-cutting decreases the food resources of ants (measurable as body fat contents) and changes thermal conditions and probably also humidity as unfavourable for larval growing. Thus, the produced workers rarely reach a large body size. This may temporally weaken the foraging efficiency and competitive ability of *F. aquilonia* in heavily managed forests.

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