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Deforestation reduces nest mound size and decreases the production of sexual offspring in the wood ant *Formica aquilonia*

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Little is known about how anthropogenic changes in nature affect reproduction in social insects such as ants. We studied the effects of clear-cutting on the production of sexual offspring and on the mound size in *Formica aquilonia*, using neighbouring uncut forests as controls. Nest mounds were smaller in clear-cuts, apparently because they tended to be new bud nests. The basal area of nest mounds decreased towards forest edges. The production of sexual offspring increased with nest mound size. Clear-cutting reduced the production of sexual offspring also when the effect of nest mound size had been factored out. Our results show that anthropogenic changes do have the potential to modify the production of sexual offspring in social insect.

Introduction

The current rate of forest loss and the fragmentation of natural habitats are considered to be a potential threat to the persistence of animal populations (Barbault & Sastrapadja 1995, Fahrig 1999). The main forest renewal method is clear-cutting where all or most of the trees are harvested from the renewal area. In Finland clear-cuts are normally planted with single tree species monoculture and are re-harvested approximately at 100-year intervals (Virkkala & Toivonen 1999). This kind of effective forest harvesting is likely to have reflections in animal populations through food shortage (Zanette *et al.* 2000) and changes in species composition (Punttila *et al.* 1991, Esseen *et al.* 1997).

Many social insects, such as termites, wasps, bees and ants, live in colonies and exploit local resources. Among them, ants and termites are excellent study organisms for studies on the effects of habitat structure change, because their colonies are perennial and due to wingless workers they are using resources on a very local scale. Workers can be either females or males in termites, but in Hymenoptera all workers are females (Wilson 1971). Whether a female develops into a worker or a queen is determined in Hymenoptera by environmental factors such as quality or quantity of food (Wilson 1971, Oster & Wilson 1978, Brian 1983, Bourke & Franks 1995), by worker behaviour (Brian 1973), or by genetic factors (Volny & Gordon 2002). Workers care for queens and offspring, so a sufficient number of workers are needed before sexual offspring (i.e. reproductive offspring) can be reared (Oster & Wilson 1978, Hölldobler & Wilson 1990, Bourke & Franks 1995). Virtually nothing is known about the effects of anthropogenic changes on sexual and worker offspring production in social insects. Especially in the boreal region forest management may have a major impact on the ant fauna dependent on mature old-growth forests.

Wood ants of the *Formica rufa* group are dominant ants in boreal coniferous forests. They have ecological effects that extend over several trophic levels, and hence the study of the association between man-made habitat alteration and the breeding success of colonies is important. In terms of resource and interference competition and predation, wood ants affect arthropod species composition (Adlung 1966, Niemelä *et al.* 1992, Punttila *et al.* 2004) and thus, also the breeding success of some insectivorous birds (Aho *et al.* 1999). Further, they affect the distribution and abundance of other ant species by their competitive superiority (Savolainen & Vepsäläinen 1988, 1989, Savolainen *et al.* 1989). Nest mounds are shared with numerous other arthropod species, so-called myrmecophiles (Päivinen *et al.* 2004) as well as earthworms (Laakso & Setälä 1997). Wood ants spread seeds of many plants (Gorb & Gorb 1995, 1999, Gorb *et al.* 2000) and influence the growth of trees due to aphid tending (Rosengren & Sundström 1991).

As in other ants, colony kin structure varies among wood ant species. A colony can have single egg-laying queen (monogyny) or multiple queens (polygyny). In the latter case colonies can also comprise multiple nests (polydomy, Rosengren & Pamilo 1983, Hölldobler & Wilson 1990, Bourke & Franks 1995). The most common wood ant in boreal forests is the highly polygynous and polydomous *Formica aquilonia* (Collingwood 1979, Rosengren *et al.* 1979). A large nest mound may contain a million workers and hundreds of queens (Pamilo 1982, Rosengren *et al.* 1987).

All colonies of *F. aquilonia* do not normally produce sexual offspring every year, possibly due to the age of colony and/or the availability of resources (Pamilo & Rosengren 1983, Rosengren & Pamilo 1986). Colonies are normally specialized for producing mainly queens or males and the average sex ratio across colonies is usually female biased (Pamilo & Rosengren 1983, Rosengren & Pamilo 1986). New sexual offspring are raised mainly from late April to late May, before worker progeny. Winged males and gynes (young queens) can be observed on the nest mound or in the vicinity of nests from late May to early June when mating takes place. *F. rufa* group wood ants rear sexual offspring early in the spring by using food resources collected the previous season and stored by young workers called repletes (Rosengren *et al.* 1987, Gösswald 1989). Sexual offspring are reared with lipids and glandular nutrients stored by repletes in fat-bodies. The utilization of these lipid reserves may initiate metabolic heating of a nest (Martin 1980), which also seems to be needed for sexual offspring production (Rosengren *et al.* 1987).

Clear-cutting likely reduces the food resources of wood ants, because the majority of their food comprises honeydew, aphids and other arthropods collected from trees (Rosengren & Sundström 1987, 1991, Whittaker 1991, Punttila *et al.* 2004). Lenoir (2003) found that when excluded experimentally from trees, wood ants search for new trees further away instead of increasing predation on the forest floor. In *F. aquilonia*, new colonies are frequently established by budding in clear-cuts, which alters the age and size distribution of nests (Rosengren & Pamilo 1978, Rosengren *et al.* 1979). An abrupt change in habitat structure in conjunction with decreased nest sizes may alter the probability of sexual offspring production. We suggest that an increase in colony size increases the colony's potential of producing sexual offspring and that deforestation has a negative effect on sexual offspring production by reducing nest sizes and food resources. Several studies have found that production of sexual offspring increases with an increase of colony size (Oster & Wilson 1978, Nonacs 1986, Tschinkel 1993, Deslippe & Savolainen 1995, Wagner & Gordon 1999), but to our knowledge there are no published studies on the effects of clear-cutting on the production of sexual offspring in ants of the *Formica rufa* group. We studied this by measuring nest mounds and collecting information on the production of sexual offspring in polydomous *F. aquilonia* in clear-cuts and forest interiors. Our goal in this study was to examine whether the size distributions of nest mounds differ between clear-cuts and forests, and whether nest mound size, habitat type and year-to-year variation affects the production of sexual offspring.

Materials and methods

Study area

The study was conducted in the coniferous boreal zone in central Finland, near the town of Jyväskylä (62°15´N, 25°45´E) in 2000–2001. We used two types of study areas of different habitat quality, forest interior areas ($n = 13$) and clear-cuts ($n = 18$). Forest interior areas and clear-cuts were chosen from the same region and were initially similar *Vaccinum myrtillus* growth mature forests dominated by Norway spruce (*Picea abies*) located 3.8 ± 0.3 km (mean ± S.E.) apart. Clear-cuts varied from 0.3 to 4.0 ha (mean ± S.E. = 1.5 ± 0.2 ha). Nine of the clear-cuts were cleared in the winter 1998–1999 and the remaining nine in the winter 1999–2000. The data were collected during spring in 2000 and 2001. Nest mounds situated in clear-cuts and in their managed surroundings (< 5 m away from cleared area) were treated as clear-cut nests. Forest interior nests were defined as being well inside forests (more than 50 m away from clear-cuts and plantations).

Field methods

We determined whether each nest produced sexual offspring or not by monitoring nests repeatedly within five-day intervals during May 2000 and 2001. The nests were considered to have produced sexual offspring if large (about 10 × 5 mm) pupae or eclosed winged sexuals were found. We tried to avoid causing permanent and visible damage while sampling nest mounds. We used all nests of *F. aquilonia* found in the study areas and we used same colonies in both study years.

The basal area of nest mound has been shown to correlate positively with the number of worker ants in other *Formica* species (Deslippe & Savolainen 1994, Liautard *et al*. 2003). In this study, the basal area of the nest mound was used as a rough estimate of worker population. The basal was measured from the part of the mound not covered by plants. In our study species, the shape of the nest mound base is normally circular, hence we used a common equation for circular area (πr^2) to calculate the basal area of the nest mound. We also measured the distance from each nest to the nearest forest edge.

Statistical analyses

We used generalized linear model (Genmod) for comparing nest mound sizes, habitat types and year as fixed factors; and colony (nested within habitat type) as a repeated subject and normal error term. The relationship between the nest mound size and the distance to the forest edge in both habitat types was also analysed with a generalized linear model (Genmod), with the distance to the forest edge as a quantitative variable, and the study area as a repeated subject and normal error term. The relationships between the production of sexual offspring and several variables (basal area of nest mound, study year, habitat type, age of clear-cut) were tested with logistic regression analyses in a generalized linear model using colony (nested within habitat type or age of clear-cut) as a repeated subject in the models (no production = 0; production = 1; logit link function, binomial distribution; type 3 contrasts, Genmod). All generalized linear model analyses were performed with SAS statistical software version 8.2 (SAS Institute Inc., Cary, NC, USA). Abandoned nest mounds were excluded from all analyses. Non-parametric tests were used in distribution analyses (two-sample Kolmogorov-Smirnov test and χ^2-test) and were carried out with SPSS 11.5 statistical software (Norušis 1999).

Results

The basal area of inhabited nest mounds was larger in forest interiors as compared with that in clear-cuts (Genmod: $\chi^2 = 20.20$, df = 1, $p <$

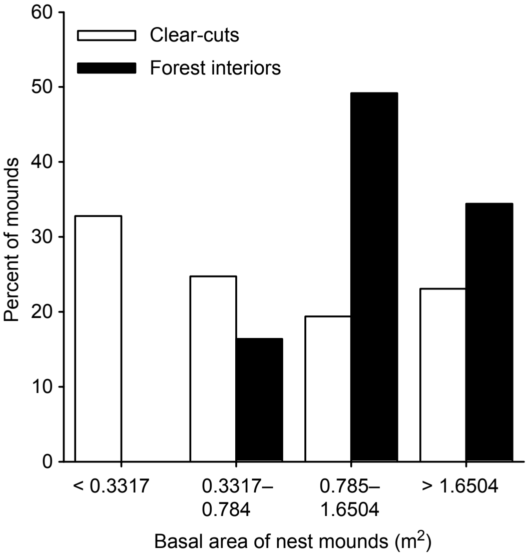

Fig. 1. Distribution of nest mound basal areas divided into four categories using quartiles of the size frequency as cut points.

0.0001; Table 1). The basal areas were similar in size between study years, and study year did not affect basal areas differently between habitat types (Genmod: Year: $\chi^2 = 1.55$, df = 1, $p = 0.214$; Year × Habitat type: $\chi^2 = 1.50$, df = 1, $p = 0.221$). We analysed the similarity of the distributions of basal areas with a two-sample Kolmogorov-Smirnov test. Inhabited nest mounds were divided into four size categories, using quartiles of the size frequency distribution as cut points ($Q_1 = 0.3317$ m^2, $Q_2 = 0.785$ m^2 and $Q_3 = 1.65038$ m^2). Nest mound size quartiles were differently distributed between habitat types being biased towards small sizes in clear-cuts, whereas in forest interiors such small nest mounds were not found (clear-cuts $N = 299$, forest interiors $N = 61$; two-sample Kolmogorov-Smirnov: $Z = 2.928$, two-tailed $p < 0.0001$; Fig. 1). In forest interiors the most frequent nest size category was the second largest category (0.785 m^2–1.65038 m^2), whereas this category was the least represented in clear-cuts (Fig. 1). In both habitat types, the basal area of nest mounds increased with increasing distance from the forest edge (Genmod: forest interiors: $\chi^2 = 6.68$, df = 1, $p = 0.010$; clear-cuts: $\chi^2 = 4.48$, df = 1, $p = 0.034$; Fig. 2).

Sexual offspring were produced more often in nests with a large basal area, than in nests with a small basal area (Table 2 and Fig. 3). Colonies located in the forest interior were more likely to produce sexual offspring than colonies located in clear-cuts (Table 2 and Fig. 4). The fraction of nests producing sexuals was higher in 2001 (87 produced whereas 208 not) than in 2000 (65 produced whereas 247 not), but the increase was similar in both habitat types (non-significant interaction term Habitat type × Year; Table 2). The basal area had a similar effect on the production of sexual offspring in both years and habitat types (Clear-cuts: 44%, Forest interiors: 41%; non-significant interaction terms Habitat type × Basal area, Basal area × Year; Table 2).

Because clear-cuts were made in two successive winters, some ($N = 9$) clear-cut areas were fresh and some ($N = 9$) had already passed through one summer season at the beginning of the study. Nests in both age groups of clear-cuts produced equally often sexual offspring (Genmod: $\chi^2 = 2.20$, df = 1, $p = 0.138$). The number of productive nests varied between years, but the increase was similar in both age groups (Genmod: year: $\chi^2 = 4.32$, df = 1, $p = 0.038$; Age-group × Year: $\chi^2 = 0.11$, df = 1, $p = 0.746$). The probability of producing sexual offspring increased with increasing basal area of the nest mound (Genmod: $\chi^2 = 35.95$, df = 1, $p < 0.0001$).

Table 1. The number of study areas, number of colonies, number of colonies producing sexuals and nest mound area (± SD) of *F. aquilonia* examined in central Finland in 2000–2001.

	Productive/all colonies (%)		Area of nest mound)	
Year	2000	2001	2000	2001
Forest interiors (13)	24/60 (40%)	33/60 (55%)	1.52 ± 0.7 m^2	1.52 ± 0.7 m^2
Clear-cuts (18)	41/252 (16%)	54/235 (23%)	1.03 ± 0.9 m^2	0.99 ± 0.9 m^2

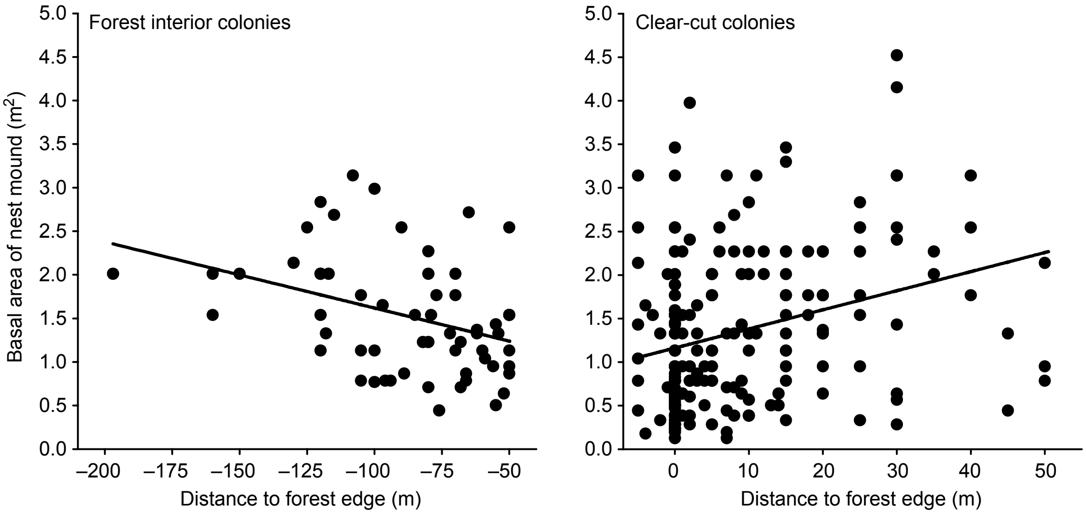

Fig. 2. Relationships between the basal area of nest mound and distance to forest edge in forest interiors and clear-cuts (with fitted regression lines). The zero point is forest edge in the X-axis and negative values indicate location inside of forest.

We also tested whether colonies located in fresh clear-cuts lose their potential for producing sexual offspring after exposure to one summer in resource poor clear-cuts. In the younger clear-cuts, 20 nests produced sexual offspring in both 2000 and 2001, whereas six nests produced sexuals only in 2000. In forest interiors, 22 nests produced sexuals in both 2000 and 2001, whereas two produced sexuals only in 2000 (Pearson χ^2 = 2.018, df = 1, two-tailed p = 0.155).

Discussion

Our results demonstrate that nest mounds were smaller in clear-cuts as compared with those in forest interiors and that the basal area of nest mounds decreased towards forest edges. Large nests were more likely to produce sexual offspring, probably because of a greater number of workers. Small colonies may need to invest more in worker production to finally reach the mature stage, whereas large nests probably were already in mature stage and hence were more likely to produce sexual offspring (Oster & Wilson 1978). The actual correlation between the colony size and the basal area of nest mound, however, may need further study. Clear-cutting had a negative effect on the production of sexual offspring, also when the effect of nest mound size had been factored out. The number of colonies producing sexual offspring was higher in the second study year, but the increase was similar in both habitat types. The production of sexual offspring was equally frequent in the younger and older age-classes of clear-cuts.

A likely reason for the observed bias towards small nests in clear-cuts is an increase in nest budding (Rosengren & Pamilo 1978, Rosengren *et al.* 1979). The spatial distribution of nest mounds of different sizes seemed to indicate migration towards forest edges leading to

Table 2. The effect of the basal area, habitat type and year on production of sexual offspring (logistic regression analysis in Genmod). Non-significant interaction terms were excluded one by one from the final model containing only the main effects of basal area, habitat type and year (Backward conditional method).

	χ^2	df	p
Basal area	33.37	1	< 0.0001
Habitat type	11.54	1	0.0007
Year	14.37	1	0.0002
Basal area × Year	1.05	1	0.306
Habitat type × Basal area	0.49	1	0.482
Habitat type × Year	0.14	1	0.713

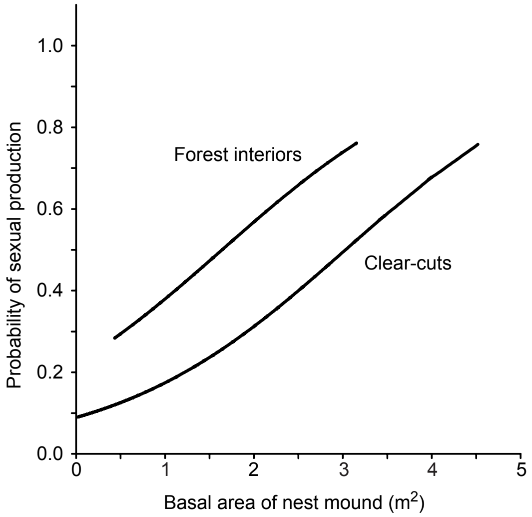

Fig. 3. Relationships between the sexual offspring production and the basal area of nest mound. Fitted logistic regression curves of both the habitat types.

smaller nest mound sizes in forest edge zones. In clear-cuts, this could also be an artefact as new daughter nests are close to a forest edge in small clear-cuts even if they are located at the centre of the cleared area. However, using study area as a repeated subject is likely to reduce the impact of this artefact. In clear-cuts, ants are likely to move closer to the food resources whereas in forests migration is towards sunny patches suitable for new nests. Colony movement towards food resources is known to be typical especially in army ants (Schneirla 1971, Wilson 1971, Franks & Fletcher 1983, Bourke & Franks 1995), and moving towards better nest sites is common in ant species adapted to unstable environmental conditions (Hölldobler & Wilson 1990), such as *Linepithema humile* (Passera 1994) and *Leptothorax albipennis* (Dornhaus *et al.* 2004). *F. aquilonia* seems to prefer sunny patches for new nests whenever available and it has been suggested that the reason is a need for solar radiation for nest warming, because small nests may have poor thermoregulation (Rosengren *et al.* 1987).

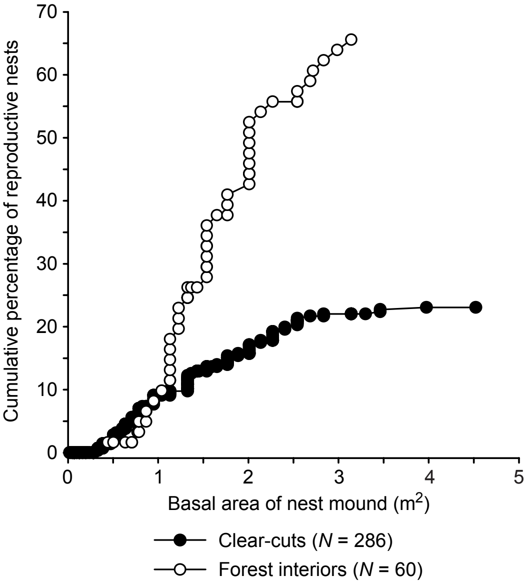

Fig. 4. The cumulative percentage of reproductive nests and basal area of nest mounds in both habitat types. A nest is classified as reproductive if it produced sexual offspring in one or both of the study years. Each nest is used only once.

Several possible reasons for an increased formation of bud nests observed in clear-cuts were listed by Rosengren and Pamilo (1978); those included (1) changes in the visual environment, (2) harmful changes in the microclimate and increased exposure of nests, (3) food deficit due to collapse of route system, and (4) uneven distribution of worker population around the nest. In addition to those, a reason for budding may be the rapid increase of sunny patches around nest mounds. This reaction may be an adaptation to natural forest succession, especially self-thinning in ancient forests (sporadic openings in canopy). Because small nests may have limited survival in shady forests (Rosengren *et al.* 1987), new nests may be established in disturbed patches, where solar radiation is used for nest heating. This, however, may be maladaptive in clear-cuts, because nests are exposed to food resource limitation at the same time if the nests are not established near the forest edge. Daughter nests located far away from the forest edge may have a short life-span (J. Sorvari & H. Hakkarainen unpubl. data), whereas, new nests that are established near to the food resources at forest edges might survive and start re-colonisation of growing seedling areas.

Clear-cutting lowered the production of sexual offspring possibly due to food shortage caused by destruction of foraging areas. In the

F. rufa group, sexual offspring are reared early in spring using food resources of the previous season stored in replete-workers (Rosengren *et al*. 1987, Gösswald 1989). Therefore, nests from younger clear-cuts should be more capable of producing sexual offspring than nests from older clear-cuts, but we did not find any support for this. However, *F. aquilonia* seems to produce sexual offspring about two weeks later than sympatric *F. polyctena* colonies (Sorvari 2005 in press), at a time when forests are mostly free from snow and arthropod prey is already available. It is thus possible that *F. aquilonia* uses stored food resources only at the beginning of sexual brood rearing and arthropod prey during the later stages of sexual production. In support of this, we observed that plenty of arthropod prey is brought into some forest interior nests that had large sexual larvae inside.

The reason for lowered production in clear-cuts may also result from a failure in rearing sexual offspring due to abiotic conditions, or to a lower worker density in clear-cuts as compared with that in forest interiors. Rosengren *et al*. (1979) showed that temperatures inside the nest mound may vary more in clear-cuts than in spruce stands. Because temperature regulation seems to be an important factor for the production of sexual offspring (Rosengren *et al*. 1987), extensive variation in inside nest temperatures may be deleterious for growing larvae. Nest splitting is likely to lead to lower worker densities in clear-cuts because workers are distributed over a greater number of nests. Therefore, the number of storage workers and other workers may not reach the possible threshold for sexual offspring production.

Polydomy and colony budding is often associated with scattered stable habitats such as forest patches or meadows but also so called Tramp-species are usually living in polydomous colonies and are using budding dispersal (Hölldobler & Wilson 1990). Tramp-species such as *Linepithema humile*, *Monomorium pharaonis*, *Pheidole megacephala* and *Wasmannia auropunctata* are distributed by human commerce and thrive in human disturbed environments (Höldobler & Wilson 1990, Brandão & Paiva 1994, Passera 1994). Pest species *M. pharaonis* and *L. humile* readily develop new bud-nests when the colony is disturbed, which is one of the reasons why the species are difficult to eradicate from infected areas (Smith & Whitman 1992, Passera 1994). *F. aquilonia* seems to have a similar strategy when faced with disturbance in terms of clear-cutting. This seems to be, however, maladaptive due to the loss of colony fitness as the production of sexual offspring decreases.

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