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ORIGINAL PAPER

Combined effects of overwintering temperature and habitat degradation on the survival of boreal wood ant

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Abstract The survival of insects during diapause may be affected by overwintering temperature and other environmental stress, such as anthropogenic habitat degradation. We experimentally studied the effects of overwintering temperature (+1 and +7°C) and commercial forest clear-cutting on the overwintering survival of the forest-dwelling wood ant *Formica aquilonia*. We found that both the higher overwintering temperature and clear-cutting lowered the overwintering survival and body fat resources of *Formica aquilonia*. The survival and body fat resources were highest in lower temperature treatment forest nests and lowest in higher temperature treatment clear-cut nests. The overall survival of ants increased with higher body fat resources. It is possible that both forest clear-cutting and higher winter temperature due to possible climate warming may increase the wintertime mortality of wood ants and other forest-dwelling ants.

Keywords Ants · Climate change · Dormancy · Forestry · *Formica aquilonia*

Introduction

Winter is a time of low food availability in temperate and boreal zones. Many organisms, such as insects, have evolved to cope with this by using winter dormancy to save energy by lowered metabolic activity (Tauber et al. 1986; Danks 1987; Leather et al. 1993; Guppy and Withers 1999). Energetic costs may become higher due to increased cellular metabolic activity if the temperature during dormancy period is elevated. Therefore, energy resources (especially body fat) may be consumed at a faster rate, limiting the resources that should otherwise be allocated to reproduction. In addition, the loss of energy resources may lower the survival of individual ants.

Overwintering temperature may be higher than normal if the insect overwinters in a warmer habitat or even due to possible climate warming caused by increased atmospheric CO_2 and/or other greenhouse gases. According to the scenarios of the Intergovernmental Panel on Climate Change (IPCC), the annual mean temperature will increase 2–7°C and precipitation 5–40% in Finland by the year 2080 (Jylhä et al. 2004); especially, the winter temperatures are going to rise. In the worst-case scenario, the mean temperature in December could be 9°C higher than at present, and even in the more conservative scenarios the estimated increase is at least 4°C. Elevated overwintering temperature may have harmful effects on insects that are locally adapted to the temperature of the habitat they live in.

Man-made habitat degradation cause other kinds of environmental stress that can influence the populations of social insects such as ants (e.g. Punttila et al. 1991; Punttila 1996; McGeoch 1998; Andersen and Majer 2004), but the explicit reasons why certain species start to decline in changed environments has only rarely been studied (e.g. Sorvari and Hakkarainen 2005; Sorvari et al. 2008). For example, it is not known whether anthropogenic environmental stress affects the overwintering survival of social insects. In addition, almost nothing is known about the effects of overwintering temperature on the populations of social insects (but see Beekman et al. 1998). These

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questions are especially important in the case of social insects, because they are often dominant animals in their environments, and despite their large worker populations, the effective population sizes (i.e., the number of reproductive individuals) are relatively small and thus, the risk of population extinction may be higher than expected (see Chapman and Bourke 2001; Mäki-Petäys and Breen 2007; Seppä 2008). Changes or even extinctions in these dominant insect populations may have wide ranging effects on both local and global ecosystems.

Ants, especially the wood ants of the *Formica rufa* group, are important generalist predators of arthropods in boreal forests. Their ecological effects extend over several trophic levels, and hence, the study of the association between large-scale environmental changes and colony success is important. Wood ants affect arthropod species composition (Koivula and Niemelä 2003; Punttila et al. 2004) and the foraging ecology, breeding success, and growth of some insectivorous birds (Haemig 1996; Aho et al. 1999; Jäntti et al. 2007) through resource/interference competition. Further, they affect the distribution and abundance of other ant species by their competitive superiority (Savolainen et al. 1989; Väänänen et al. 2010). Nest mounds are shared with numerous other arthropod species, so called myrmecophiles (Päivinen et al. 2004), as well as earthworms (Laakso and Setälä 1997). Wood ants spread the seeds of many plants (Gorb et al. 2000) and may enhance the growth of trees and shrubs by preventing folivory (Mahdi and Whittaker 1993; Atlegrim 2005), but also decrease the growth of some trees due to aphid tending (Rosengren and Sundström 1991; Kilpeläinen et al. 2009).

Wood ants of the *Formica rufa* group are the dominant ants in European and Asian boreal forests (e.g. Rosengren and Pamilo 1983). However, they are classed by the World Conservation Union (IUCN) as globally Near Threatened species (IUCN 2010) due to the loss or degradation of suitable forest habitats. During the recent years, the wood ants have become active earlier in the spring in boreal forests (Lappalainen et al. 2008) and wood ant workers have been observed moving on the nest mound surface even in mid-winter (December to February), when they should be in winter dormancy (Sorvari, unpublished observation). This kind of activity should reduce energy reserves since the main food source of wood ants, aphids and their honey-dew, is not available during winter.

Formica aquilonia, a member of the *F. rufa* group, is the most common wood ant in Finnish coniferous forests. Studying the possible effects of habitat degradation and climate change (in terms of higher overwintering temperature) on the survival of *F. aquilonia* is important, because changes in the populations of this keystone species may have a large impact on the whole boreal forest ecosystem. Our aim was to study the effects of (1) overwintering temperature and (2) commercial forest clear-cutting and (3) their combined effects on the overwintering survival and body fat resources of the workers of *F. aquilonia*.

Materials and methods

Study system

Ants were collected from 25 field nest mounds located in South-Western Finland during one sampling day in October 2008. During that time the workers were already congregated into hibernation clusters in the bottom of the nest mound. We took worker samples from the interior part of nest mounds always in the same way to get a comparable random mixture of workers of different ages and tasks (foragers, inside workers, etc.). Fifteen nests originated from two commercial forest clear-cuts and 10 nests from two forest interior areas were sampled for the experiment. Nests from the same study area may be members of the same polydomous colony (i.e. multi-nest coalition). However, workers of neighbouring nests may not be closely related, because each nest may contain hundreds of unrelated queens causing low level of worker to worker relatedness already within nest (Pamilo et al. 2005). Before the removal of trees the clear-cuts were originally similar Norway spruce (*Picea abies*) dominated forests than the forest interior areas. Approximately 200 workers from each sampled nest mound were divided within the sampling day into two plastic boxes (10 × 8 × 10 cm) containing moist vermiculite to maintain high relative humidity. Walls of the nest boxes were lined with fluon (PTFE) to prevent escapes. One box from each nest was kept over winter in +7°C ± 1.0 and the other in +1°C ± 1.0. The normal winter temperature of the interior of wood ant mound is less than +5°C in Finland (Rosengren et al. 1987). After the overwintering period (20 October 2008 to 1 April 2009; i.e. 162 days) living and deceased ants were counted.

Estimation of body fat resources

The nutritional status of individual insects can be quantified by measuring their body fat content (e.g. Sundström 1995; Hahn 2006; Sorvari and Hakkarainen 2009). Fat was extracted from both of the groups after the overwintering period. Before winter the fat reserves are expected to be similar in ants from the same original nests. Thus, differences in fat contents are expected to be caused by a different consumption rate during the winter period. Only the survived ants were used in fat extraction. The fat extraction method was modified after Sundström (1995). About 20 worker ants per nest box were dried (48 h at 55°C) and weighed with Mettler Toledo MX5 balance (to the nearest

0.001 mg) for dry weight 1 (d.w. 1) and extracted in 90 ml of petroleum ether (boiling point 60–90°C) for 48 h in a water bath of 60°C. New petroleum ether was added when needed during the extraction. After extraction the ants were dried (48 h at 55°C) and weighed again (d.w. 2). The weight difference (d.w. 1 to d.w. 2) represents the amount of remaining body fat in the colony. In the analyses we used the proportion of fat from d.w 1. In one nest from clear-cuts the ants of higher temperature nest box were all deceased. Thus, that nest box and its counterpart nest box of cooler temperature were excluded from the fat analyses.

Statistical analyses

Statistical analyses were made with statistical software SAS version 9.2 (SAS Institute, Cary, NC, USA). We used a generalized linear mixed model (GLMM using procedure GLIMMIX) with Kenward-Roger approximation of the degrees of freedom. The nest of origin was used as a random factor (nested within temperature treatment in the analyses of survival and fat content). The number of surviving ants was used as the dependent variable (events) with the number of all individuals (living and deceased) as the denominator (trials). Binomial error term with a logit link function was used in the analyses of survival, and normal error term was used in the analyses of body fat proportion.

Results

Overwintering survival

Both the overwintering temperature and nest habitat affected the overwintering survival significantly (overwintering temperature: $F_{1,43.55} = 7.27$, $P = 0.01$; nest habitat: $F_{1,43.65} = 5.04$, $P = 0.03$; nest habitat x overwintering temperature $F_{1,42.73} = 0.001$, $P = 0.97$). Fewer workers survived over winter in the higher (+7°C) temperature treatment than in the lower (+1°C). In addition, the survival was lower in workers from nests originating from commercial forest clear-cuts compared to the forest interior nests (Fig. 1). The survival was lowest among the ants from higher temperature treatment clear-cut nests (Fig. 1).

Body fat resources

After overwintering, workers in the higher temperature treatment had less body fat resources than workers in the lower temperature treatment. Also workers from nests originated from clear-cuts had less body fat resources than workers from forest interiors after overwintering (overwintering temperature: $F_{1,46} = 5.68$, $P = 0.02$; nest habitat: $F_{1,46} = 72.70$, $P < 0.0001$; nest habitat × overwintering temperature $F_{1,45} = 0.16$, $P = 0.69$; Fig. 2). The amount of body fat after overwintering was lowest in the workers from higher temperature treatment clear-cut nests (Fig. 2). The probability of survival was higher in nests whose workers had a higher amount of body fat after overwintering ($F_{1,47} = 229.47$, $P < 0.0001$; Fig. 3).

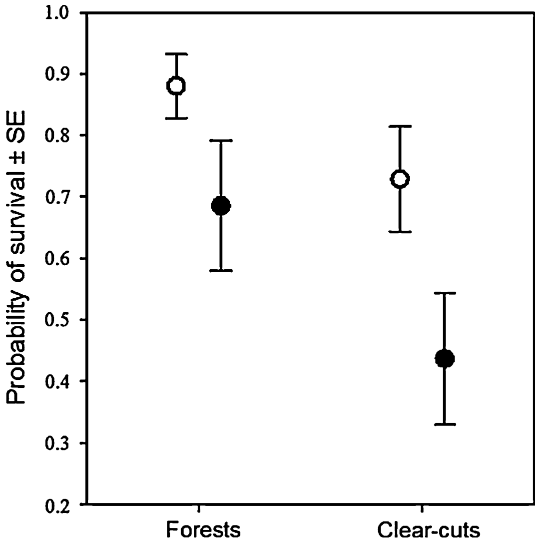

Fig. 1 Mean probability of overwintering survival of worker ants in two different temperatures (*open circles* +1°C; *filled circles* +7°C) originated from forest interiors and commercial forest clear-cuttings

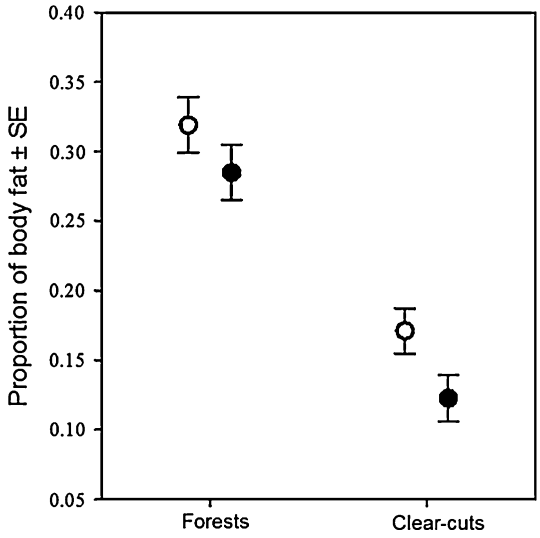

Fig. 2 Mean proportion of body fat of worker ants overwintered in two different temperatures (*open circles* +1°C; *filled circles* +7°C) originated from forest interiors and commercial forest clear-cuttings

Discussion

Higher overwintering temperatures are shown to increase metabolic costs and decrease survival in the gall fly

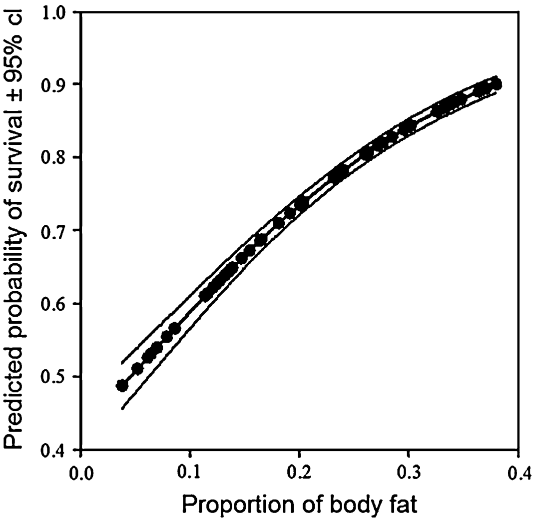

Fig. 3 Predicted probability of survival (± 95% CL) related to proportion of body fat. For simplicity the predicted values of the model for this figure are generated by generalized linear mixed model without nest of origin as a random factor. The results remained similar to that of original model ($F_{1,47} = 459.6$, $P < 0.0001$)

Eurosta solidaginis (Irwin and Lee 2000; Irwin and Lee 2003), and in the rose galling wasp *Diplolepis spinosa* (Williams et al. 2003). On the other hand, increased overwintering temperatures did not affect the overwintering survival of the bumblebee *Bombus terrestris* queens (Beekman et al. 1998). In our study, higher overwintering temperature decreased the survival of ant workers and seemed to increase metabolic costs i.e., the consumption of energy reserves (body fat content). An additional harmful effect of the higher consumption of body fat resources in worker ants is that it may suppress the production of reproductive individuals, because in wood ants the body fat resources (especially those of storage workers, so called repletes) are used in rearing a new generation of sexual offspring in spring (Bier 1958; Gösswald 1989).

Forest clear-cutting decreases the abundance of aphids, the main food resources of wood ants (Rosengren and Sundström 1991). The loss of food resources may be behind the decrease in fat resources of ant workers living in clear-cut areas observed in this and in an earlier study (Sorvari and Hakkarainen 2009). The low amount of body fat in ants originated from clear-cuts may also be linked with their lower survival compared to ants from forest interiors.

Ants may adapt locally into the winter temperatures of their habitat, as shown in the ant *Leptothorax acervorum* (Heinze et al. 1998). *F. aquilonia* has limited dispersal ability (Pamilo et al. 2005) and thus, its populations may be adapted into their local winter temperature. Due to its poor dispersal ability, this species may be unable to avoid the negative effects of climate change by migrating northwards fast enough to follow suitable overwintering conditions. The reproduction and colony survival of *F. aquilonia* may have already been severely damaged by forest logging (Sorvari and Hakkarainen 2005, 2007) and the additional harmful effect of climate warming might be detrimental. Other forest-dwelling ants are also likely to suffer from the synergy between climate change and non-climatic anthropogenic stress factors, because systems that are under multiple stresses may behave unpredictably and the sum of the stresses may push them past an extinction threshold more quickly than would a single stressor.

With the current actions, climate warming may not be reduced fast enough to avoid costs of higher overwintering temperature in wood ants. However, the ability of wood ants to resist the harmful effects of climate change may be maintained by easing other man-made stress factors for example by protecting a sufficient amount of the habitats of these important keystone species.

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