

# Effects of group size and pine defence chemicals on Diprionid sawfly survival against ant predation

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**Abstract** The defence chemicals and behavioural adaptations (gregariousness and active defensive behaviour) of pine sawfly larvae may be effective against ant predation. However, previous studies have tested their defences against very few species of ants, and few experiments have explored ant predation in nature. We studied how larval group size (groups of 5 and 20 in *Neodiprion sertifer* and 10, 20 and 40 in *Diprion pini*) and variation in levels of defence chemicals in the host tree (Scots pine, *Pinus sylvestris*) affect the survival of sawfly larvae. Food preference experiments showed that ants do eat sawfly larvae, although they are not their most preferred food item. According to our results, ant predation significantly increases the mortality rate of sawfly larvae. Larval mortality was minor on pine tree branches where ant traffic was excluded. We also found that a high resin acid concentration in the host tree significantly decreased the mortality of *D. pini* larvae when ants were present. However, there was no such relationship between the chemical concentrations of the host tree and larval

mortality for *N. sertifer*. Surprisingly, grouping did not help sawfly larvae against ant predation. Mortality risk was the same for all group sizes. The results of the study seemingly contradict previous understanding of the effectiveness of defence mechanisms of pine sawfly against ant predation, and suggest that ants (*Formica exsecta* in particular) are effective predators of sawfly larvae.

**Keywords** Antipredator defence · Resin acid · Gregariousness · Formica · Diprionidae

## Introduction

Many prey species have multiple antipredator strategies that are often directed at specific phases of predation (Endler 1991; Ruxton et al. 2004; Mappes et al. 2005): crypsis is primarily effective against the predator searching phase, rapid flight against the pursuit phase, chemical defence against the capture phase, and a hard cuticle against the processing phase (Pearson 1985, 1989; Endler 1991). Different defences are not mutually exclusive; for example, herbivores can combine gregarious behaviour with unpalatability (Lawrence 1990; Boevé 1991; Codella and Raffa 1995b; Sillén-Tullberg and Hunter 1996; Sillén-Tullberg et al. 2000; Hunter 2000). This combination is likely to be beneficial, since the strength of a chemical defence increases in aggregations, and predators learn to avoid noxious prey faster when they are clumped (Endler 1991; Alatalo and Mappes 1996; Hunter 2000). Moreover, the per capita attack rate is usually lower in larger groups than in smaller ones (Lawrence 1990; Codella and Raffa 1995a; Hunter 2000; Riipi et al. 2001).

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Pine sawfly (Diprionidae) larvae exhibit multicomponent defensive repertoires against bird and ant predation: they are cryptic, gregarious and unpalatable for most predators (Larsson et al. 1986; Björkman and Larsson 1991; Codella and Raffa 1995a, 1995b, 1996, Larsson et al. 2000). After the first instar, larvae have also defensive movements, such as rearing of the front end and emission of a droplet of resin fluid when disturbed by a predator (Eisner et al. 1974; Kalin and Knerer 1977; Larsson et al. 1986; Björkman and Larsson 1991; Codella and Raffa 1995b, 1996; Hunter 2000). The chemical defence of pine sawfly larvae originates from their ability to exploit the chemical defences of pine trees (Ikeda et al. 1977; Codella and Raffa 1995b, 1996; Larsson et al. 2000). The higher the resin acid concentration of their diet, the better their defence against ants (Larsson et al. 1986; Björkman and Larsson 1991). However, the advantages of this defensive behaviour conflict with developmental requirements. High resin-acid concentration reduces growth. Thus, there is a trade-off between fast development and defence against predators (Larsson et al. 1986; Björkman and Larsson 1991; Codella and Raffa 1995b).

According to previous studies, aggregation and chemical defence reinforced by the threat displays of the pine sawfly larvae should significantly decrease the risk of ant predation (Larsson et al. 1986; Björkman and Larsson 1991; Codella and Raffa 1995a, 1995b, 1996; Larsson et al. 2000). Increased advertisement and group defence behaviour may further reduce the predation risk: although groups are more easily detected, warning signals, defensive movements and regurgitation may decrease the rate of successive attacks, increasing an individual's protection (Codella and Raffa 1995a; Hunter 2000). It is also possible that the effectiveness of a prey's defence mechanisms against predators varies between predator species and also in time and space (Endler and Mappes 2004; Mappes et al. 2005). Thus, it is important to test the effectiveness of a prey's defensive mechanisms against different type of predators.

Previous studies that have gathered useful information about ant predatory behaviour have been carried out on only a few species of ants (Björkman and Larsson 1991; Codella and Raffa 1995b; 1996). Furthermore, previous studies have not investigated possible among-colony variation in predatory behaviour (Björkman and Larsson 1991; Codella and Raffa 1995a). Since levels of aggressiveness can vary remarkably among colonies and over the breeding season, it is crucial to repeat the experiment with different colonies at different times during the growth period (Hölldobler and Wilson 1990; Rosengren and Sundström 1991;

Kumpulainen 2004). In this study, we evaluate the importance of ant predation on sawflies in a natural setting. We used *Formica exsecta* ants as a new predator species and repeated the experiments with several ant colonies. The specific objectives of the study were: (1) to explore the ants' (*F. exsecta*) readiness to prey on sawflies (*N. sertifer* and *D. pini*) and the effect of ant predation on larval mortality rates; (2) to examine the influence of larval aggregation size on larval survival; and (3) to measure whether the chemical concentration of the host tree, measured as a needle resin-acid concentration, influences the defences of sawfly larvae against ants.

## Material and methods

### Study organisms

#### *Pine sawflies*

The studies were carried out using two sawfly species, *N. sertifer* and *D. pini* (Hymenoptera, Diprionidae). These univoltine species are the most common forest pests in northern European coniferous forests and are characterized by eruptive population dynamics. Pine branches supporting *N. sertifer* eggs collected from Kerimäki and Puumala in eastern Finland were taken to the laboratory and sawfly eggs were allowed to hatch. Pupae of *D. pini* were collected from four field sites in western (Lestijärvi) and eastern Finland (Ilo-mantsi, Kiihtelysvaara and Kaavi) and reared to adulthood in the laboratory. Freshly emerged *D. pini* adult pairs were moved to the field and introduced onto pine (*Pinus sylvestris*) branches which were then enclosed within mesh bags. Branches supporting *D. pini* eggs were taken from the pines to the laboratory and sawfly eggs were allowed to hatch. These F1-generation larvae were used in field experiments in the summer of 2002. *D. pini* larvae used the next summer, 2003, were reared from this F1-generation in the same way, except that adults were mated randomly on pine branches in the laboratory. Both sawfly species were reared in 10-l plastic containers covered with nylon netting. Larvae were fed twice a week with fresh pine branches supporting current and one-year-old needles. The temperature in the laboratory reflected the temperature outdoors.

#### *Ants*

The main predator species used in our study was *F. exsecta*. It is an active, aggressive species that builds

mounds from leaf litter in open woodland, moorland and rough pasture. *F. exsecta* is mainly aphidicolous, tending aphids on *Juniperus*, *Picea* and other trees, but it is also predaceous (Collingwood 1979). It was the most common species foraging on *Pinus sylvestris* in our study area. One of the experimental nests (see below) belonged to the *Formica suecica* species. The behaviour of the *F. suecica* colony did not differ statistically from that of the *F. exsecta* colonies, and thus all of the ant nests were pooled for statistical analysis and are called Formica nests.

### Experimental design

#### *The relative palatability of pine sawfly larvae to ants*

To confirm that ants kill sawfly larvae for food and not only to protect aphids (Rosengren and Sundström 1991; Sloggett and Majerus 2000; Sipura 2002; Weeks 2003), we explored how desirable larvae were to ants as prey items. In this prey preference trial, we had 13 Formica nests in our study site in central Finland (62°N, 26°E). In the vicinity of each nest ( $n=13$ ), we chose a spot on an ant trail where the traffic was about 2–4 ant workers per minute. We offered dead adult Diptera (an attractive prey item), dead sawfly larvae (II–III instar larvae killed by freezing) and a fresh green pine needle (an unattractive item) to ants. Dead diptera and sawfly larvae were about the same size, but the needles were slightly larger. We were thus able to simultaneously compare ant reactions toward sawflies, and toward highly attractive and unattractive potential prey.

Three prey—one of each prey type—were offered simultaneously to ants on a dead brownish or greyish leaf which was placed on the ant trail. The assay was repeated three times per ant nest at the same spot, and the position of prey items on the leaf (and thus the order in which they would be encountered) was changed each time and the order in which ants chose prey items recorded. Choice was defined as taking the prey item to the nest. Each assay lasted 10 min or less if all prey items were removed. Prey choice trials were done with both *N. sertifer* (21–25.5 2002) and *D. pini* (30–31.7 2002) in the afternoon in sunny and warm weather (temperature >20 °C).

#### *Predation of pine sawfly larvae by ants*

To test the effectiveness of sawfly defence against Formica ant predation, we conducted predation experiments with *N. sertifer* and *D. pini* in the summer of 2002 in the same area where the prey preference exper-

iments were conducted. In the vicinity of every nest, we selected one pine (height 2–4 m) on which ants were foraging. The heights of the experimental trees varied between 2 and 4 m. Two branches with ant traffic on them were chosen from each tree. The intensity of the ant traffic was calculated three times before the start of the experiment by counting all ant workers on the whole branch from the base to the apex. Then one branch was randomly chosen as control (ant branch) and the other one as the experimental branch where ants were excluded (non-ant branch). On the non-ant branches, we blocked ant traffic by using square-shaped barriers made from transparencies. The barriers were covered with liquid Teflon or liquid silicon.

After the ant traffic had been manipulated, the sawfly larvae were moved onto the pine branches in the laboratory (20 larvae/branch) 24 h before transfer to the experimental trees so that they had enough time to reaggregate. The detached branches supporting larvae were fastened to both the “ant traffic” and “non-ant traffic” branches with wire. Ants were temporarily removed from the ant traffic branches before the transfer to avoid attracting too much attention to the larvae during the fastening process. After the transfer, the larvae moved to the branches of the experimental tree during the first 24 h.

The number of larvae surviving and the number of ant workers present on each branch were recorded (moving or touching of the branches was avoided) once a day during the first two weeks of the experiment and every second day thereafter until most of the larvae on the ant branches had disappeared. Recording was conducted at different times of the day to get reliable measurements of ant activity at the field site. Depending on the killing rate of larvae, the experiments lasted for 7–18 days. The experiment was replicated three times with *N. sertifer* from 7 May to 11 June 2002 (first trial: I–II instar larvae, ant nests  $n=6$ , second trial: II–III instar larvae,  $n=9$ , and third trial: III–V instar larvae,  $n=10$ ), and two times with *D. pini* from 17 July–7 August 2002 (first trial: II–III instar larvae,  $n=10$  and second trial: III–V instar larvae,  $n=10$ ).

#### *The number of resin ducts and larval survival*

In *P. sylvestris*, more and larger resin ducts in needles may reflect the higher resin acid concentrations of the needles (Björkman et al. 1991). As the chemical concentration in the host plants affects the chemical defence of sawfly (Codella and Raffa 1995b), we tested whether larval survival in predation experiments correlates positively with the number of resin ducts in needles of the host tree. We took random needle samples

(20 needles/tree) from branches with and without larvae from different parts of the experimental trees. The number of resin ducts was counted from thin slices of each needle under a microscope.

#### *The effect of larval aggregation size on the predation efficiency of ants*

To determine whether larval group size affected the predation success of ant workers, we compared the larval survival rates in groups of different sizes. The experiment conducted with *N. sertifer* took place in June 2002 and the ant nests ( $n=10$ ) used were the same as in the predation experiment. The experimental procedure was identical to the predation experiments except that there were four experimental branches on each tree: two ant branches with sawfly larvae in groups of 5 and 20, and two non-ant branches (ants excluded) with larval groups of 5 and 20 III–V instar larvae. This corresponds to naturally occurring larval feeding group sizes (Codella and Raffa 1995a). We recorded the number of larvae remaining and the numbers of ant workers present once a day until the end of the experiment (seven days).

Studies of the effects of *D. pini* gregarious behaviour on ant predation were conducted in July 2003. Results from the predation experiment in summer 2002 revealed that larval group sizes of 5 and 20 were not effective against ant predation, so we increased the larval group sizes used in this experiment to assess any possible increase in survival rate against ant predation exhibited by larger larval groups. There were no ant exclusions in this experiment because the results of predation- and group-size experiments conducted in summer 2002 showed that ant predation was the main cause of death on branches where ants actively patrol. The study area included six *F. exsecta* nests with six foraging trees (*P. sylvestris*). Three branches with ant traffic were chosen on each experimental tree and the number of ants present was recorded three times before placing sawfly larvae onto the branches. Groups of 10, 20 and 40 (II–III instar) larvae were placed on the branches (one group per one branch). Larval mortality was checked once a day for the first six days of the experiment and every second day thereafter. The duration of the experiment was three weeks.

#### *Statistical methods*

To test whether ants kill pine sawfly larvae in significant numbers, we used a repeated measure ANOVA that takes into account the dependent structure of the

data. Since ant branches and non-ant branches were tested simultaneously on the same tree, the larval mortality rate in different ant manipulations (ants vs. non-ants) was used as a within-subject factor in the model. The different trees where ant manipulations were conducted and the replicates (three replicates) were used as between-subject factors. When testing the effect of group size on the mortality risk of *N. sertifer* larvae, the larval mortality rate in the different ant manipulations was used as a within-subject factor and the group size and the experimental tree were used as between-subject factors in the model. In the group size experiment with *D. pini*, the larval mortality risk, calculated from the first, the third and the sixth experimental days, was used as a within-subject factor and the group size and the experimental tree were used as between-subject factors. The main effects of ANOVAs were read from the models that included insignificant two-way interactions. To achieve a normal structure for the data, the larval mortality risk was transformed using the arcsine square-root transformation. For pairwise comparisons we used a Wilcoxon Signed Ranks test. All statistical analyses were performed with SPSS 12.0 (SPSS Institute Inc., Cary, NC, USA). All *P*-values are two-tailed.

## **Results**

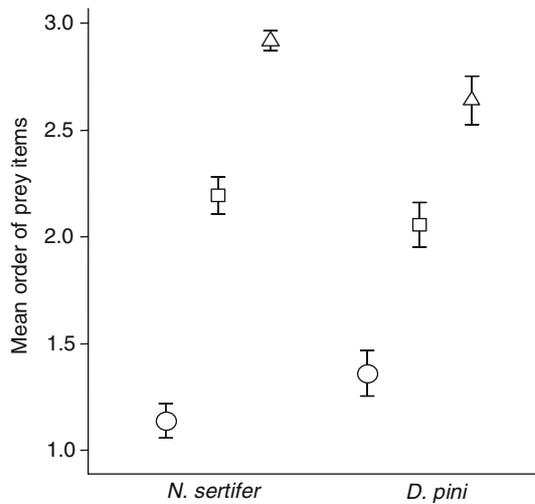
### The relative palatability of pine sawfly larvae to ants

Ants preferred Diptera to other prey items; their second choice were pine sawfly larvae and their last choice was pine needles (Diptera and *N. sertifer* larva:  $Z=-4.676$ ,  $n=36$ ,  $P<0.001$ ; *N. sertifer* larva and a needle:  $Z=-4.328$ ,  $n=36$ ,  $P<0.001$ ; and Diptera and a needle  $Z=-5.565$ ,  $n=36$ ,  $P<0.001$ ) (Diptera and *D. pini*:  $Z=-3.329$ ,  $n=36$ ,  $P=0.001$ ; *D. pini* and needle:  $Z=-2.819$ ,  $n=36$ ,  $p=0.005$ ; Diptera and needle:  $Z=-4.144$ ,  $n=36$ ,  $P<0.001$ ) (Fig. 1). These results suggest that dead Diptera are the most preferred prey item for ants. Sawfly larvae were, however, chosen immediately after Diptera. Thus, ants clearly use sawfly larvae for food, but the larvae do not seem to be their most preferred food item.

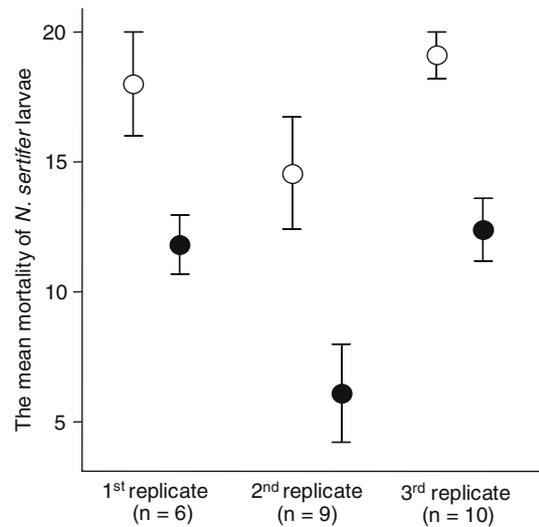
### Predation of pine sawfly larvae by ants

#### *N. sertifer*

The mean ant traffic on ant branches was 6.4 ant workers/count and on non-ant branches 5.2 ant workers ( $T=11$ ,  $n=10$ ,  $P=0.05$ ). After exclusion of the ants,



**Fig. 1** Ant workers chose Diptera first (circles), pine sawfly larva second (squares) and pine needles third (triangles). Bars show  $\pm$ SE



**Fig. 2** Mean number of *N. sertifer* larvae killed on non-ant branches (filled circles) and ant branches (empty circles) in the different replicates. Bars show  $\pm$ SE

mean ant traffic on ant branches was 3.7 ant workers/count and on non-ant branches 0.08 ant workers/count. Thus, ant exclusion effectively created a difference in ant traffic between manipulated and control branches ( $T=0, n=10, P<0.005$ ).

There was no pronounced difference in the numbers of larvae that were killed by ants on different trees ( $F_{(9,13)}=2.38, P=0.075$ ). The larval mortality varied between replicates on ant branches ( $F_{(2,13)}=7.49, P=0.007$ ). However, no interactions between mortality and the replicates were found ( $F_{(2,13)}=0.11, P=0.897$ ) which indicates that the difference in mortality between ant and non-ant branches remained the same over the season although predation intensity changed.

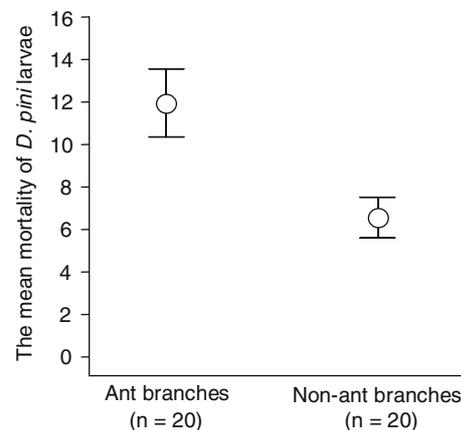
Mortality was significantly lower on the non-ant branches in all replicates ( $T=1, n=6, P=0.025$  for the first replicate;  $T=3.5, n=8, P=0.025$  for the second; and  $T=0, n=10, P<0.005$  for the third) (Fig. 2). Thus, even if the larval mortality varied between replicates, it was always higher on the ant branches. However, we did not find a direct relationship between the mortality rate of *N. sertifer* larvae and ant traffic intensity among control branches (Spearman correlation:  $r_s = 0.20, n=25, P=0.337$ ).

*D. pini*

The mean ant traffic on the ant branches (controls) and the non-ant branches did not differ before exclusion of the ants ( $T=18, n=9, P>0.10$ ). Thus, in this respect, the selected branches were similar. After exclusion of the ants, there was a significant difference in mean traffic

between the non-ant and the ant branches ( $T=0, n=10, P<0.005$ ), indicating that the manipulation was successful. There was no significant interaction between larval mortality rate and trees ( $F_{(9,9)}=2.22, p=0.125$ ), but there was a significant main effect of trees ( $F_{(1,9)}=4.91, P=0.013$ ). This suggests that although predation pressure varied between trees, it was always higher on the ant branches. There were no differences between the replicates in terms of larval mortality ( $F_{(2,13)}=0.11, P=0.897$ ) but *D. pini* larvae placed on the ant branches were always less likely to survive than larvae on the non-ant branches ( $F_{(1,13)}=51.20, P<0.001$ ) (Fig. 3).

Furthermore, on the ant branches there was a significant positive relationship between the ant traffic and larval mortality ( $r_s = 0.557, n=20, P=0.011$ ).



**Fig. 3** Mean number of *D. pini* larvae killed on non-ant branches and ant branches. Bars show  $\pm$ SE

### Number of resin ducts and larval survival

Repeatability of the number of resin ducts was calculated from a one-way analysis of variance comparing the variation in the number of resin ducts among trees to the within-trees variation (e.g. Lessells and Boag 1987). The variation in the number of resin ducts among trees was 14 times higher ( $MS_{TR}=19.011$ ) than the within-trees variation ( $MS_E=1.357$ ) which represents an intermediate repeatability ( $R=0.5$ ,  $F_{(13,126)}=14.008$ ,  $n=139$ ,  $P<0.001$ ). Thus, as a measure of resin acid concentration, the number of resin ducts was quite reliable even though there was some variation at the within-trees level.

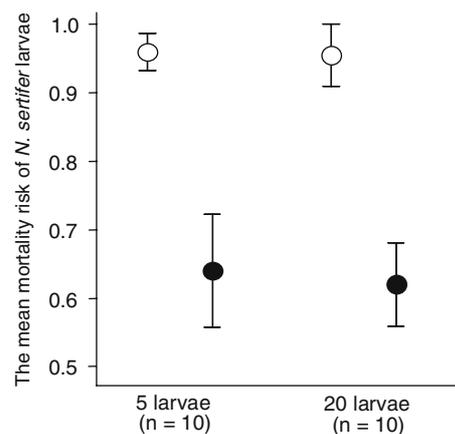
The number of resin ducts in the needles of the host plant did not affect the mortality rate of the *N. sertifer* larvae on either the non-ant or the ant branches. There was no correlation between larval mortality and the number of resin ducts ( $r_s=-0.048$ ,  $n=25$ ,  $P=0.819$  for ant branches and  $r_s=-0.158$ ,  $n=25$ ,  $P=0.450$  for non-ant branches).

For *D. pini*, the number of resin ducts in the needles of host plants had no effect on the mortality of the larvae on the non-ant branches ( $r_s=-0.094$ ,  $n=20$ ,  $P=0.693$ ). However, on the ant branches the relationship between larval mortality and the number of resin ducts ( $r_s=-0.641$ ,  $n=20$ ,  $P=0.002$ ) was negative. This indicates that a higher resin acid concentration increases larval survival in *D. pini*.

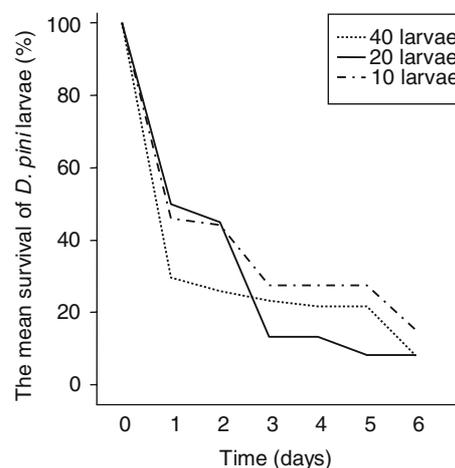
### The effect of aggregation size on larval survival

The mortality of *N. sertifer* larvae was higher on the ant than on the non-ant branches ( $F_{(1,18)}=62.2$ ,  $P<0.001$ ). Surprisingly, group size did not affect the relative mortality risk of the larvae on either non-ant or ant branches, which is indicated by the lack of significant interaction ( $F_{(1,18)}=0.57$ ,  $P=0.459$ ) (Fig. 4). This may be caused by the fact that large aggregations of larvae attracted more ants than small aggregations ( $T=3$ ,  $n=10$ ,  $P<0.005$ ).

The relative mortality risk of *D. pini* larvae was the same in all group sizes (10, 20 and 40 larvae) ( $F_{(2,10)}=1.69$ ;  $P=0.234$ ). Predation pressure was intense and most of the larvae were killed during the first experimental day. There was no significant interaction between mortality risk and group size ( $F_{(4,20)}=1.12$ ,  $P=0.374$ ). Thus, a larger group size did not increase the survival rate of *D. pini* larvae (Fig. 5). There was a marginally insignificant trend for an interaction between larval mortality rates and experimental trees ( $F_{(10,20)}=2.31$ ,  $P=0.053$ ), which indicates that predation pressure among trees potentially differs.



**Fig. 4** Mean mortality risk of groups of 5 and 20 *N. sertifer* larvae. Filled circles denote non-ant branches and empty circles denote ant branches. Bars show  $\pm$ SE



**Fig. 5** Mean percentage of surviving *D. pini* larvae in each group size from the first to the sixth day of the experiment

### Discussion

Our results suggest that ants are significant predators of sawfly larvae. The mortality of larvae was always higher on ant branches than on branches where ants were excluded. Ant predation was the primary reason for larval mortality, since manipulation excluded only ants and not, for example, bird predation from the experimental branches. Thus, if there had been other significant predation sources, the mortality rates would have been higher on the non-ant branches. The palatability experiment also showed that ants do prey upon sawflies, although they are not the most desirable prey items for them.

At the end of the aggregation size experiments with *N. sertifer* and *D. pini*, larval survival was the same in all group sizes. Thus, there was no dilution of mortality

risk in larger groups. When ants were excluded, the larval survival rate was better, but larvae in larger groups did not have a diminished risk of being killed. The most probable explanation for the ineffectiveness of larval aggregations against ant predation is that ants are density-dependent foragers, responding quickly to any increase in prey numbers in their foraging territory and recruiting other workers to patches abundant with prey (Carroll and Janzen 1973; Dejean 1991; Hölldobler and Wilson 1990, Robson et al. 1997). This density-dependent predation pressure was observed in the aggregation size experiment with *N. sertifer*, where large aggregations attracted more ant workers than small aggregations. However, the same comparison was not possible with *D. pini* because most of the larvae were killed during the first day of the experiment and thus meaningful analysis of ant traffic between large and small aggregations was not possible.

Our results seemingly contradict previous results which suggested that the defence mechanisms of sawfly larvae are effective against ant predation (Larsson et al. 1986, Björkman and Larsson 1991; Codella and Raffa 1995a, 1995b, 1996; Larsson et al. 2000). However, the results are not necessarily contradictory, since predator–prey interactions are complicated in nature. For example, availability of alternative prey and predators' hunger level affects prey-type preferences and foraging behaviour (Koh and Li 2003; Jacob 2004). Hungry predators can be more prepared to attack distasteful prey than well-fed ones (Sherrat et al. 2003). In addition, in our study, the main predator species (*F. exsecta*) is known to be an aggressive species (Collingwood 1979). The high foraging activity and aggressiveness of workers are essential factors in increasing the success of ants against defensive prey (Codella and Raffa 1995a, 1996) and aggressively attacking ant workers attract recruits more rapidly than ants that first examine a defending prey individual (Codella and Raffa 1996). This socially facilitated foraging behaviour of ants may also turn the larvae's own defensive movements against them. Ant species with large eyes are known to have excellent vision and they are very good at detecting moving objects (Hölldobler and Wilson 1990). Thus, defensive movements may arouse the attention of other ant workers and further escalate the predation activity by making larvae more conspicuous. This increased conspicuousness to ants could explain the slightly higher mortality risk of larvae in large aggregations (Fig. 5).

According to our results on the effects of the number of resin ducts in host tree needles on larval survival, the mortality of *D. pini* larvae on ant branches decreased on trees with high resin acid concentrations.

Thus, it seems that the high resin acid concentrations of host tree pine needles increase the defence capability of *D. pini* larvae against ant predation. This is consistent with previous studies (Björkman and Larsson 1991; Codella and Raffa 1995b). In addition, there were significant differences in the mortality of *D. pini* larvae on ant-branches between trees. The explanation for the differences in larval mortality between trees could be the variation in resin acid concentration of the experimental trees. In contrast to earlier findings by Björkman and Larsson (1991) and Codella and Raffa (1995b), resin concentrations did not affect the mortality of *N. sertifer*. If *N. sertifer* are less sensitive to the resin acid concentrations of needles than *D. pini*, the resin duct number may not be accurate enough to observe the possible effect of resin acid concentration on the survival of *N. sertifer* larvae.

Our results show, in contrast to many other studies about ant–sawfly interactions, that the defensive mechanisms of sawfly larvae are not particularly effective against *F. exsecta* ants. This suggests that the effectiveness of defence mechanisms in sawfly larvae (grouping and defensive chemicals) varies depending on the predator species and their behaviour. Pine sawflies are the most common pests of pine trees. At present, outbreaks of *N. sertifer* are controlled biologically with the aid of viruses, but only chemical pesticides are available for use against *D. pini*. This study encourages further examination of the possibilities of using ants as a biological control agent against pine sawflies. It is arguable that, at least on a local scale, ant predation is significant and could prevent sawfly populations from reaching outbreak levels.

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