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# Cues for shelter use in a phytophagous insect

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**Suggested running head:** Cues for shelter use in a phytophagous insect

# ABSTRACT

Many insects spend a large proportion of their life inactive, often hiding in shelters. The presence of shelters may, therefore, influence where insects feed. This study examines stimuli affecting the use of shelters by adults of the pine weevil, *Hylobius abietis* (L.) (Coleoptera, Curculionidae). This species is an economically important forest pest in Europe since the adults feed on the stem bark of newly planted conifer seedlings. When there are hiding or burrowing places present in close proximity to a seedling, pine weevils may hide there and repeatedly return to feed on the same seedling. Experiments were conducted in a laboratory arena with above-ground or below-ground shelters and in the presence or absence of wind. Pine weevils were highly attracted to shelters both above and below ground. Weevils in shelters were often observed assuming a characteristic “resting” posture. Experiments with opaque and transparent shelters showed that visual stimuli are used for orientation towards shelters and also increase the probability of an individual remaining in a shelter. The presence of wind increased the weevils’ propensity to use shelters both above and below ground. The present study indicates that shelters have a major influence on the behavior of the pine weevil and possible implications of the results are discussed.

**KEY WORDS:** *Hylobius abietis*; orientation; posture; resting; visual stimuli; wind.

# INTRODUCTION

To feed is necessary but dangerous. Feeding adult insects are often visually exposed, and odors released from the newly damaged host plant may attract natural enemies (Vet and Dicke, 1992). For most insects, the risk of predation is probably higher whilst feeding than when they are in shelter resting (Bernays, 1997; Chapman, 2002). Shelter can provide protection against both natural enemies and physical factors (Danks, 2002) and insects are inactive for large proportions of their lives (Lockwood and Story, 1985; Raubenheimer and Bernays, 1993; Wright *et al.*, 1999). Rest in insects can also be in a sleep-like state (Kaiser 1988). Phytophagous insects, like most other animals, feed in discrete meals, between which they often leave the immediate area of feeding and search for shelter (Bernays, 1980; Chapman and Beerling, 1990; Wright *et al.*, 1999; Chapman, 2002). Some species construct their own shelters, *e.g.,* by curling leaves or digging in soil (Danks, 2002). The presence of shelters may influence where an insect stays, on a local scale, and thereby where it feeds.

Visual orientation towards simple black figures (*e.g.,* black and white striped patterns) has been interpreted as orientation towards hiding places for some ground beetles (Coleoptera, Carabidae) (Bathon, 1973; Bathon, 1974) and for the house cricket, *Acheta domesticus* (L.) (Kieruzel and Chmurzynski, 1982). The use of shelters has been investigated for house crickets, which were found more often in dark places enclosed by walls than in open and illuminated places (Kieruzel, 1976). Further, the influence of tactile stimuli on the use of shelters has been demonstrated experimentally for species of *Bembidion* (Carabidae), which were found more often in types of shelter similar to those present in their natural habitats in a study by Andersen (1985). Species naturally differ in the degree to which they use shelters. Some ground beetles, such as *Bembidion lampros* (Herbst), “seek” bare ground whereas others, such as *Trechus quadristriatus* (Schrank), “seek” shaded ground, although even those that seek bare ground do sometimes use shelters (Mitchell, 1963).

Wind affects processes such as heat transfer and evaporation, and wind speed is always greatly reduced within vegetation (Stoutjesdijk and Barkman, 1992). Numerous studies have investigated insect activity in windbreaks, i.e. trees or shrubs serving to reduce the force of wind (Dix and Leatherman, 1988). Many insect species are attracted to the shelter and food provided by windbreaks (Pasek, 1988), *e.g.,* the white pine weevil, *Pissodes strobi* (Peck), causes more damage in Norway spruce plantations located near shelterbelts than in plantations located in open fields (Archambault *et al.*, 1993; Lavallée *et al.*, 1996). On a smaller scale, ground vegetation, stones and crevices may provide shelter from wind, but this has not been investigated to the same extent. However, as early as 1939, John S. Kennedy observed that basking individuals of the desert locust (*Schistocerca gregaria* (Forsk.)) were confined to limited areas with low speed air movement, measured with the help of smoke-trails from a cigarette (Kennedy, 1939). It has also been shown that, for the Colorado potato beetle, *Leptinotarsa decemlineata* Say (Coleoptera, Chrysomelidae), there is a positive correlation between wind speed and hiding in weeds (Jermy *et al.*, 1988), and that arthropods are more often found on the leeward side of grass tussocks (Bossenbroek *et al.*, 1977). A wind tunnel experiment has shown that walking Colorado potato beetles respond to a clean airflow by increasing their speed and reducing the number of pauses (Thiéry and Visser, 1995); this might be a way of escaping exposure to wind.

The present study examines factors that may influence the use of small shelters by adults of the pine weevil, *Hylobius abietis* (L.) (Coleoptera, Curculionidae). This is an economically important forest pest in Europe since the adults feed on the stem bark of newly planted conifer seedlings (Day and Leather, 1997; Day *et al.*, 2004; Långström and Day, 2004). Soil scarification, which reduces competing vegetation and usually exposes mineral soil, is a widely used method in forest regeneration to create a good environment for seedling establishment (Örlander *et al.*, 1990; Örlander *et al.*, 1998). Scarification also decreases the damage caused by pine weevils (Lindström *et al.*, 1986; Sydow, 1997; Örlander and Nilsson, 1999; Thorsén *et al.*, 2001). Several hypotheses have been tested to determine why seedlings planted in mineral soil are less often attacked by pine weevils than seedlings planted in humus, but the reasons are still not fully understood (Kindvall *et al.*, 2000; Nordlander *et al.*, 2000; Björklund *et al.*, 2003). A critical factor may be that, as proposed by Björklund *et al.* (2003), mineral soil provides no shelter close to the seedlings. When shelters are provided in the form of good hiding or burrowing places, *e.g.*, on untreated ground surface, pine weevils may hide in close vicinity of the seedling and repeatedly return to the same seedling to feed (Björklund *et al.*, 2003). This hypothesis is supported by studies showing that the presence of litter (Nordlander *et al.*, 2000) and establishment of field vegetation on scarified areas increase pine weevil damage (Petersson and Örlander, 2003; Örlander and Nordlander, 2004; Petersson *et al.*, 2006). However, more precise knowledge is needed regarding the use of shelters and the weevils' orientation towards them.

In this study the following questions were investigated experimentally. Firstly, are shelters attractive to the pine weevil? Secondly, do visual stimuli affect the probability that a shelter is used? Thirdly, do visual stimuli affect the time that pine weevils remain in shelters? Fourthly, does wind affect the weevils' propensity to use shelters above or below ground?

# MATERIALS AND METHODS

Adult pine weevils used for the experiments were collected in the field. The weevils were stored in the dark, in a cold-storage room (+10 °C) and two weeks before the experiments started the weevils were moved to the laboratory to acclimatize to the temperature, light regime and humidity (+20 °C; L18:D6; 65% relative humidity). Between experimental days, the weevils were supplied with an abundance of food and water. All experiments were conducted in a 132×132-cm laboratory arena covered with sand. The 15-cm high walls of transparent plastic surrounding the arena were coated with a layer of Fluon to prevent the weevils from climbing them. Before each experimental day the sand was moistened to obtain a high and relative uniform humidity level.

As artificial shelters for the pine weevils, six acrylic plates (9×9 cm) were placed with one edge buried to a depth of 2 cm into the sand at an angle of approximately 30°. A weevil was considered to be in the shelter when it was within the 6×9-cm projection area covered by the plate. The plates were placed in a row at equal distances with at least 10 cm between the plates and the closest edge of the arena. Six control zones in a row in front of the row of shelters and six zones behind them were used to obtain an estimate of the probability that a weevil is recorded within an area of the same size, as the projection area covered by a plate, but without shelter (Figure 1). Each control zone had the same area (6×9 cm) as the projection area of the plates, and the margins were marked with white sand.

## Visual Orientation to Shelter

To find out whether visual stimuli affect the probability that a shelter is used an experiment was set up with alternating black (opaque) and clear (transparent) plates. Fifty weevils of the same sex were released at the centre of the arena at the start of each experimental trial (the chosen weevil density was not anticipated to cause an unnaturally stressful environment since aggregations of weevils occur in the field (Tilles *et al.*, 1986)). Two experimental trials were performed with each sex, thus in total 200 weevils were used. The number of shelters with weevils underneath, and control zones with weevils, were recorded once every ten minutes for nine hours. Individuals, once recorded underneath shelters or on control zones, were removed from the arena. The removal, using a 30-cm long pair of tweezers, did not have any observable disturbance effect on the remaining weevils. The data obtained reflect a combined effect of orientation towards the shelters and their tendency to remain in the shelter (e.g. a stronger tendency to remain under a certain shelter type increases the probability that the weevil is still there during the next sampling occasion). An additional experiment was performed to make it possible to separate the influence of these factors (see below).

The air temperatures were measured during six periods using data loggers (Gemini Data Loggers, Tinytalk with an external sensor, accuracy ± 0.6 °C at 20 °C). There was no difference between the air temperature, a few mm above the sand surface, beneath the transparent shelters and on control zones. The mean air temperature was 0.5 °C (SE = ±0.1) lower beneath the opaque shelters than beneath the transparent shelters.

## Time Spent Sheltering

Another experiment was carried out to measure the length of time that weevils remained in opaque and transparent shelters. In this experiment, an extra opaque plate was laid on the upper side of both the opaque and transparent plates, i.e. they were assembled as two-layered sandwiches.. This was done to provide both treatments with similar visual stimuli during the weevils approach phase. Fifty weevils of the same sex were released in the middle of the arena at the start of each experimental trial and they were kept under constant observation. Weevils were observed entering a shelter, and if they remained there for 30 seconds the extra opaque plate was removed. The total time it remained in shelter was recorded. Departures made within 5 min were excluded to avoid the influence of an imaginable startle response. If the weevil had not left after 30 min the time was recorded as >30 min. Individuals that had been recorded in shelters were removed from the arena (*N*=134). Weevils that approached shelters that were already occupied were moved back to the middle of the arena. Control zones were not used in this experiment.

## Effect of Wind

The effect of wind on the propensity of weevils to seek shelter was studied in two experiments, one with above-ground shelters and one with below-ground shelters. A fan was used to create a light breeze across the arena (1.5-3 m/s in the area around the shelters) in the wind treatment. The wind speed was chosen to simulate the upper range of wind speeds naturally occurring 5-mm off ground on a bare exposed mineral soil surface (Kennedy, 1939). In the wind-free treatment the fan was directed away from the arena (<0.1 m/s in the area around the shelters). Fifty weevils of the same sex were released in the middle of the arena at the start of each experimental trial (*N*=12 for each experiment). Each group of weevils was exposed to both treatments on two successive days (comprising a single experimental ‘Run’) and the sequence of treatments was varied between groups. Thus, in total 300 weevils participated. The order of the treatments for female and male groups was randomized. Each weevil group was exposed to each treatment for nine h. To avoid carryover effects (Díaz-Uriarte, 2002) there was a period of at least 15 h between the treatments. The number of weevils in shelters and weevils within control zones (Figure 1) were recorded once every ten min. Weevils that were recorded in shelters or within control zones were removed from the arena.

### 1) Wind and above-ground shelter experiment

Weevil responses to above-ground shelters with and without wind exposure were measured using black opaque acrylic plates (9×9 cm) as shelters (Figure 1).

### 2) Wind and below-ground shelter experiment

The response to below-ground shelters with and without wind exposure was studied in a similar experiment in which the plates were replaced by 10 glass tubes (1 cm ∅, 5 cm long) buried vertically in the sand, so that their rims were level with the sand surface. The tubes were placed in a row, evenly spaced, with at least 10 cm between the tubes and the closest margin of the arena. The mean air temperature in the tubes, measured during four periods, was 0.5 °C (SE = ±0.2) lower than the air temperature a few mm above the sand surface.

## Statistics

A Nominal Logistic model was used in the *Visual orientation to shelter* experiment to test for the differences between the total number of opaque and transparent shelters recorded with weevils underneath (procedure GENMOD, SAS Institute 1998). Occupied (yes or no) was used as the response variable, and Shelter Type (transparent or opaque), Sex (male or female), and Run (1 or 2) were the Xs (predictor variables).

In the *Time spent sheltering* experiment, the significance of the difference between the two independent proportions of weevils that left opaque and transparent shelters was tested by a

Survival Analysis, with values above 30 min as right censored values (proc. LIFEREG, SAS Inst.).

The influence of time spent in opaque and transparent shelters on the results of the *Visual orientation to shelter* experiment, where individuals underneath shelters were removed from the arena every ten min**,** was simulated using a first order Markov process (Karlin, 1966), assuming that the probability to use and leave a shelter was independent of the time since the beginning of the experiment and of the time spent in a particular state. The estimated average resting times in opaque and transparent shelters from the *Time spent sheltering* experiment were used as parameters.

In the wind experiments, Fisher exact tests (proc. FREQ, SAS Inst.) were used to test whether there was a tendency for weevils to be more attracted to shelters already occupied than to unoccupied shelters. This was done to evaluate if it was justified to use the total number of weevils under shelter instead of the number of occupied shelters in the following analyses. To measure the power of the Fisher exact test, the effect of aggregation was modeled using an increased probability of aggregation to shelters already occupied. The power was determined by 100 computer simulations for each step of 0.5 times the basic shelter use intensity.

The time until weevils were recorded in a shelter in the wind experiments was assumed to follow an exponential distribution. Its intensity parameter (i.e. 1/average time), henceforth called "hiding propensity parameter", including a standard error was estimated by the maximum likelihood method. The estimated hiding propensity parameters for the 12 days of each experiment were analyzed in two different ways. Model A required that the pure random variation between days could be explained by the standard errors obtained for the separate hiding propensity estimates. The hiding propensity estimates, properly weighted by the inverse of their standard error, were used as input data for the analysis of variance. Since the estimates, normalized by their standard errors, are approximately normally distributed with variance 1, it follows that the error sum of squares in the analysis of variance is approximately $\chi^2$ distributed, cf. Box et al (1978, p 118). Whether this model could be used was checked by a $\chi^2$-test for the error sum of squares, i.e. if the error sum of squares based on the weighted data is larger than the tabulated $\chi^2$ –value the model could be used. Hence, instead of using the error term of the model the more efficient $\chi^2$-tests were used to calculate *P*-values. Model B was used when additional random variation was present between days for the weighted hiding propensity parameter (Error >tabulated $\chi^2$). A non-weighted hiding propensity parameter was then used as the response variable in a standard ANOVA with *F*-tests (proc. GLM, SAS Inst.).

The following factors were included in the analyses: Sex, Sequence (a trial with wind followed by a wind-free trial or the other way around), Run (Sex × Sequence) (wind and wind-free treatment), Treatment (wind or wind-free), Period (temporal treatment order), and Treatment × Sex.

Sign tests was used to test for the difference between the median number of weevils recorded within shelters and within control zones each day both in the *Wind and above-ground shelter experiment* and the *Wind and below-ground shelter experiment* (proc. UNIVARIATE, SAS Institute 1998).

# RESULTS

## General Observations

Pine weevils released in the middle of the arena usually started to move within a few min. There was a concentration of weevils close to the walls of the arena and they were frequently observed walking alongside the walls. Weevils were repeatedly observed passing by the shelters without using them.

Weevils that used the above-ground shelters were often observed placing themselves close to the plate in a characteristic "resting" posture (Figure 2). Weevils in this posture almost always remained in it for more than 30 min.

## Visual Orientation to Shelter

Opaque shelters were occupied on average six times more often than transparent shelters (d.f.=1, $\chi^2$ =45.53, P<0.0001) and males were more inclined than females to occupy shelters (d.f.=1, $\chi^2$ =3.95, P<0.05). There was no significant effect of *Run* (d.f.=1, $\chi^2$ =0.54, P=0.46). Transparent shelters were on average occupied about twice as often as control zones (Figure 3). Weevils were often observed to repeatedly bump into the transparent shelters, as if they did not see them.

In total, 89% (110 out of 124) of the weevils recorded using shelters were in the opaque ones. If differences in resting time are accounted for, 87% of the weevils in the shelters should have been in opaque shelters, according to a simulation based on a Markov process (using data from the *Time spent sheltering* experiment). Thus, the influence of differences in resting time is small when recordings are made once every ten min and it can, therefore, be concluded that visual stimuli strongly affect the weevils' orientation to shelters.

## Time Spent Sheltering

Pine weevils remained in opaque shelters for longer periods of time than in transparent shelters (Survival Analysis: N=111 (opaque shelters N=60, transparent shelters N= 51) Right Censored Values=84, d.f.=1, P= 0.004). The proportion of weevils that stayed for more than 30 min in opaque and transparent shelters were 79 and 46% respectively.

## Effect of Wind

There was no tendency for occupied above-ground shelters to be more attractive than unoccupied ones (Fisher's exact test: 12 tests, 6*54 table, P= 0.08-0.99). At the significance level 0.05 and a sample size of 50, the power 0.8 was obtained when the aggregate effect was 2.5 times the basic shelter-use hiding propensity. In the below-ground shelter experiment there were only a few observations with two or more weevils in the same shelter and hence no aggregation test was performed. Since there was no detectable aggregation effect, it was justified, in the following analyses, to use the total number of weevils under shelter instead of the number of occupied shelters.

Model B (see *Methods*) was used to analyze the calculated hiding propensity parameter (i.e. 1/ average time until weevils were recorded under shelter) of the *Wind and above-ground shelter* experiment because the error sum of squares based on weighted data was larger than the tabulated $\chi^2$-value (17.2>7.8, $\chi^2$, d.f.=3). An initial analysis showed that the factors sequence (F=0.01, d.f.=1, P=0.937), period (F=0.38, d.f.=1, P=0.580), and treatment×sex (F=0.80, d.f.=1, P=0.436) were far from having a significant effect on the hiding propensity parameter, and these factors were therefore excluded. In the reduced version of the model there was a significant effect of wind (F=7.25, d.f.=1, P=0.043) and sex (F=9.36, d.f.=1, P=0.038) on the time until above-ground shelters were used. The average time until shelters were used was shorter in the wind treatment and it was also shorter for females than for males (Figure 4a).

In the case of below-ground shelters, Model A (see *Methods*) was relevant since the error sum of squares based on weighted data was smaller than the tabulated $\chi^2$-value (2.5<7.8, $\chi^2$, d.f.=3). There was a significant effect of Wind ($\chi^2$=30.561, d.f.=1, P<0.001) on the hiding propensity parameter (i.e. 1/ average time until weevils were recorded to be in shelter). The average time until shelters were used was shorter in the wind treatment (Figure 4b). There was also a statistically significant effect of Run (Sex x Seq.) ($\chi^2$=11.152, d.f.=1, P=0.011), which was an effect of that the strength of the response to wind was more variable between the groups of females than between the groups of males (Figure 4b). However, in each case the average time until below-ground shelters was used was shorter during the wind treatment.

The weevils always climbed down into the tubes, none were observed to fall in. This was probably because they could easily walk over the tubes since the diameter of each tube was about the same as the length of the weevils.

Very few weevils were recorded in the control zones compared to the numbers recorded in either the above- or below-ground shelters, both in the wind and the wind-free treatments

(Figure 5). This demonstrates that both opaque above-ground shelters (N=12, M=-6, P<0.05) and below-ground shelters (N=12, M=-5, P<0.05) attract weevils.

# DISCUSSION

This study shows that both opaque above-ground shelters and below-ground shelters are highly attractive to *H. abietis*. Visual stimuli are evidently used in the orientation towards shelters and increase the probability of the insects remaining in a shelter for a long period. The results also show that presence of wind increases the weevils' propensity to use shelters both above and below ground.

Visual stimuli are clearly important for the use of shelters, since opaque shelters were occupied more frequently than transparent shelters. In addition the influence of the visual stimuli might be underestimated in the present study because the mean temperature was 0.5 °C lower beneath the opaque shelters than beneath the transparent shelters. The ambient temperature was 20°C and pine weevils seems to prefer warmer temperatures up to 25°C (Christiansen and Bakke, 1968; Leather *et al.*, 1994). However, the preferred temperature might be influenced by the relative humidity which probably differed between the current and previous studies. It remains to be determined whether the greater attractiveness of opaque shelters compared to transparent shelters is due to the opaque shelter per se or to the lower light intensity under the opaque shelter. There were more weevils in transparent shelters than in the control zones. This could be due to that they choose to pause in transparent shelters.

However, I believe that it is due to that the transparent shelters form a physical barrier limiting movement, since weevils were often seen repeatedly colliding with the transparent shelters.

Time spent in shelters was affected by visual stimuli, as indicated by the *Time spent sheltering* experiment: the pine weevils remained for longer periods in opaque shelters than in transparent shelters. In the *Visual orientation to shelter* experiment more than seven times as many individuals were found in the opaque shelters than in the transparent shelters. This could be an effect of both a difference in orientation towards the shelter and of the time weevils remain in the shelter. However, a simulation of the influence of resting time in opaque and transparent shelters on the results of the *Visual orientation to shelter* experiment showed that the influence of the longer resting time in opaque shelters was small when recordings were made once every ten min. Thus, it can be concluded that visual stimuli are used in the weevils' orientation towards shelters.

The use of shelters could be affected by: orientation toward the shelter; length of time spent in the shelter once an individual arrives there; or interception by the physical barrier effect of the shelter. Earlier studies, on Carabidae beetles and crickets, have interpreted orientation towards simple black figures (*e.g.,* black and white striped patterns) as orientation towards hiding places (Bathon, 1973; Bathon, 1974; Kieruzel and Chmurzynski, 1982). These findings are supported by the present study, in which the actual use of shelters has been examined. The use of shelters has been investigated for house crickets which were found to be present more frequently in dark places enclosed by walls than in open and illuminated places (Kieruzel, 1976). In the present study the physical barrier effect of the shelter was taken into account and it was shown that the more frequent occurrence of pine weevils in opaque shelters than in control zones was due to both orientation towards shelters and weevils staying in a shelter once they arrived there.

In the present investigation, opaque and transparent shelters with the same tactile stimuli were used. To my knowledge, this is the first study on insects to demonstrate that vision *per se* influences the use of shelters. It has been shown previously that house crickets use glass tubes lined inside with black paper more frequently than glass tubes lined with transparent plastic. However, since the tactile stimuli also differed between the treatments the influence of vision could not be determined. Similarly, responses of species of *Bembidion* (Carabidae) to pieces of transparent glass and withered grass seem to be affected by tactile similarities with shelters occurring in the natural habitats of the investigated species (Andersen, 1985). That is, species that live in habitats with gravel and stones were more often found under pieces of glass than the vegetation species. Thus, the influence of vision in these studies could not be determined because the tactile stimulus was not the same in the two treatments.

It has, however, been shown that some crustaceans (*Orconectes rusticus* (Girard) and *Procambarus clarkii* (Girard)) are more often found in dark thigmotactic shelters than in clear thigmotactic shelters (Alberstadt *et al.*, 1995; Steele *et al.*, 1997). This accords with the results of the present study (Figure 3). The impact of the crustaceans' orientation towards shelters and the time spent in the shelters were not considered separately, but the study was performed in rather small aquaria (45×25×25 cm) and the influence of orientation was probably much weaker than in the present study. The use of tactile stimuli by crustaceans was also studied and found to be secondary in importance to visual stimuli in "shelter-seeking" behaviour. The importance of the shelters' tactile stimuli was not investigated in the present study but weevils under shelter were, in most cases, found close to the plate, indicating that a thigmotactic response may possibly be involved.

Wind exposure increased the use of shelters both above and below ground. The average time before above-ground shelters were used was 80% longer in the wind-free treatment than in the wind treatment; the corresponding figure for below-ground shelters was 92%. The results of the few previous studies that have investigated the effect of wind on the propensity of insects to use small shelters (see introduction) are in agreement with the results of the present study.

The response to wind may be due to that there is a correlation between being exposed to wind and exposure to solar radiation or to natural enemies. Wind speed is invariably much reduced within vegetation (Stoutjesdijk and Barkman, 1992) and vegetation could provide protection against both natural enemies, *e.g.,* birds, and the risk of overheating due to exposure of the ground to solar radiation. The lethal temperature for carabid beetles is between 47 and 52 °C (Thiele, 1977) and *Hylobius radicis* (Buchanan) and *Hylobius pales* (Herbst) go into heat stupor within two min if the ground temperature exceeds 50 °C (Corneil and Wilson, 1984; Wilson, 1968).

Both opaque above-ground shelters and below-ground shelters were highly attractive compared to the control zones. The size of a shelter probably has a huge impact on its attractiveness, and since only one size of each shelter type was used in the present study, it was not meaningful to statistically test if there are a significant difference between the above and the below ground shelters. However, the total surface area in which the weevils were considered to be in shelter was 324 cm$^2$ (6 areas of 6×9 cm) in the *Wind and above-ground* *shelter* experiment and ≈8 $\text{cm}^2$ (10 areas of $\pi \times 0.5^2$cm) in the *Wind and below-ground shelter* experiment. Further, above-ground shelters ought to be visually detectable from a longer distance than below-ground shelters. Despite the much larger surface area and the longer detection distance in the *Wind and above-ground shelter* experiment the average time until weevils were recorded within shelters was slightly shorter in the *Wind and below-ground shelter* experiment (Figure 4). This indicates that below-ground shelters are more attractive, possibly because they provide better protection against physical factors and natural enemies. Holes have been shown, previously, to be visually attractive to pine weevils (Nordlander *et al.*, 1986). The ground beetles *Bembidion argenteolum* (Ahr.) and *Bembidion lapponicum* (Zett.) excavate hiding places even when stones are available for use as shelters (Andersen, 1978).

Pine weevils cause serious damage to newly planted conifer seedlings (Örlander and Nilsson, 1999). Planting of seedlings is commonly done after soil scarification, which removes the ground vegetation and often exposes mineral soil. Even though approximately the same number of weevils approach seedlings on mineral soil compared to humus (Björklund *et al.*, 2003) the seedlings planted in mineral soil usually display less than half the level of weevil-induced mortality as those planted in undisturbed humus (Örlander and Nilsson, 1999; Thorsén *et al.*, 2001; Björklund *et al.*, 2003; Petersson and Örlander, 2003). Undisturbed humus has an abundance of suitable hiding places, and burrowing is more frequent in humus than in mineral soil (Nordlander *et al.*, 2005). It was proposed by Björklund *et al.* (2003) that the difference in attack rate on seedlings in undisturbed humus and mineral soil may be due to pine weevils using shelters close to the seedling on undisturbed humus and repeatedly returning to the same seedling to feed. The present study demonstrates that shelters, both above and below ground, are attractive to pine weevils and they often remain in a shelter for long periods. Wind speed is increased on scarified plots since the vegetation is removed (Stoutjesdijk and Barkman, 1992) and the present study shows that wind influences the use of shelters. During field conditions pine weevils orientate towards the olfactory and visual stimuli from conifer seedlings (Björklund *et al*. 2005) but the lack of hiding or burrowing places around the seedlings on wind-exposed mineral soil spots may cause the pine weevils to move away from these areas. In order to prevent damage, I suggest that attention should be paid to minimizing shelter opportunities close to coniferous seedlings. Thus, planting should be avoided in locations where accumulation of litter occurs and in substrates preferred for burrowing. This may also be relevant for other situations where phytophagous insects cause damage to commercial plants.

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# FIGURE-CAPTION LIST

**Figure 1.** The arena with six acrylic plates (9×9 cm) used as artificial shelters, 12 control zones and a fan.

**Figure 2.** Typical resting posture of *H. abietis* characterized by: resting hind end of the abdomen and apex of the snout (rostrum) against the ground, the first antennal segment (scape) held tightly against the snout, and legs lifted, not stretched, with the tarsi pointing upwards.

**Figure 3.** Mean number of observations of shelters with *H. abietis* beneath them during the four experimental trials, in the *Visual orientation to shelter* experiment, divided by the number of shelters of each type on the arena (3), and weevils within control zones divided by the number of control zones (12).

**Figure 4.** Average time in h until (a) above-ground shelter, and (b) below-ground shelter was used by a *H. abietis* individual, with and without wind exposure, for six weevil groups. Numbers on the *x*-axis correspond to the temporal order in which the experimental trials were carried out (i.e. Run).

**Figure 5.** Total number of observations of *H. abietis* in shelters divided by the number of shelters in the arena (6 or 10), and observations within control zones divided by the number of control zones (12). In the *Wind and above-ground shelter* experiment six opaque shelters were used and in the *Wind and below-ground experiment* 10 tubes (1 cm ∅) were used. Note that the area of a control zone is more than 60 times as large as the surface area of a tube.

Figure 1.

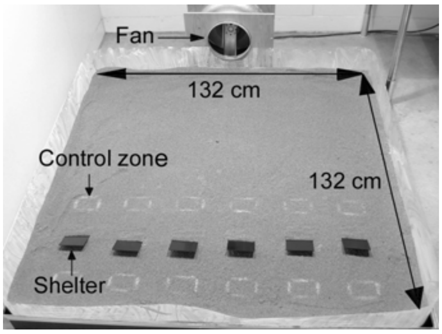


Figure 2.

Figure 3.

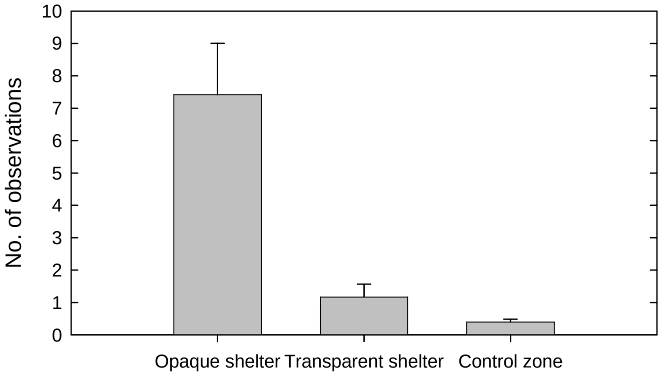

No. of observations
0
1
2
3
4
5
6
7
8
9
10
Opaque shelter
Transparent shelter
Control zone

Figure 4.

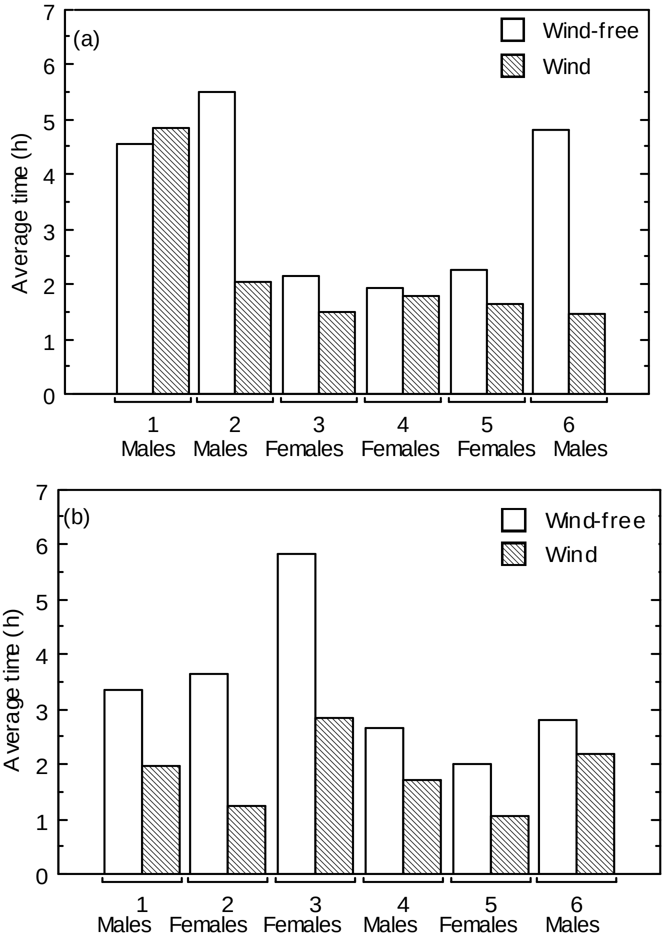
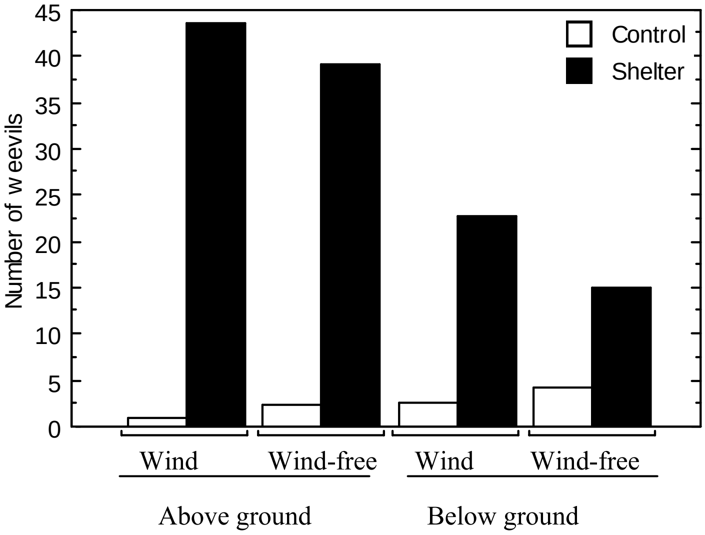

(a)
Average time (h)
0
1
2
3
4
5
6
7
☐ Wind-free
▨ Wind
1 Males
2 Males
3 Females
4 Females
5 Females
6 Males
(b)
Average time (h)
0
1
2
3
4
5
6
7
☐ Wind-free
▨ Wind
1 Males
2 Females
3 Females
4 Males
5 Females
6 Males

Figure 5.


45
40
35
30
25
20
15
10
5
0
Number of weevils
Control
Shelter
Wind
Wind-free
Wind
Wind-free
Above ground
Below ground