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# From where are insects recruited? A new model to interpret catches of attractive traps

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- Abstract**
- 1 Two new concepts describing the origin of insects caught in an attractive trap are presented.
  - 2 Male European pine sawflies *Neodiprion sertifer* Geoffroy (Hymenoptera: Diprionidae) were marked and released from 50, 100, 200, 400 and 800 m in the four cardinal directions around a centrally placed pheromone trap.
  - 3 Based on linear regression of transformed data, we calculated the seasonal sampling range ( $r_s$ ) as 1040 m.
  - 4 We estimated the previously defined ‘effective sampling area’ ( $\alpha$ ) at 4.9 ha, assuming that the insects are evenly distributed around the trap and that they are attracted from a circular area around it. This is the area from which all insects originate if the trap is 100% effective within the area but captures nothing outside of it. The effective sampling area reveals nothing about the origin of the insects caught. We defined the Cumulative Proportional Catch (CPC) that gives the proportion of the trap catch that originates from an area within a distance  $r$  from the trap. At  $r = r_s$ ,  $CPC = 1$ , and in our study 50% of the captured insects originated up to 450 m from the trap. Thus, for the trap used in this study, a relatively large proportion of the catch originates some distance from the trap.
  - 5 We also defined the Catch Concentration (CC), which is the ratio of the radius of the effective sampling area ( $r_\alpha$ ) to  $r_s$ . For our data,  $CC = 0.12$ , which is intermediate to high compared to the few other studies that we have extracted information from. If  $r_\alpha$  is considerably lower than  $r_s$ , then only a small proportion of the insects caught originate from close proximity to the trap. When  $r_\alpha$  is close to  $r_s$ , the catch adequately mirrors the population within most of its sampling range.
  - 6 By using these two new concepts, we will better understand why monitoring traps mirror the local population in some cases but not in others. This will help in designing more reliable monitoring programmes.

**Keywords** effective sampling area, sampling range, wind direction, mark-release-recapture, sex pheromone, *Neodiprion sertifer*, Diprionidae.

## Introduction

The ability to predict the occurrence and abundance of insect pests is an essential part of pest management. Moni-

toring methodologies vary between different species, but always include sampling of one or several life stages or measurements of damage. As the sampling units used for estimating population density or damage are usually very temporally and spatially restricted, a large number of samples need to be collected in order to obtain reliable data, especially when the distribution of the species is aggregated. One way to overcome this problem would be to use a method that ‘automatically’ averages the density over a larger area. The deployment of attractive traps is such a

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method. Many of these traps use the (sex) pheromone of the target species as the attractive agent (Howse *et al.*, 1998; Jones, 1998). The success of this method depends on how well the trap can mirror the density of the pest population and thereby enable prediction of its future development. Achieving these aims can be divided in two parts: (i) the trap catch should reliably estimate adult population density within a given area and (ii) adult density should correspond to density of larvae of the next generation or future damage. In this study, we focus on the first issue: where do the insects caught in a pheromone trap come from?

Common to all studies that focus on the origin of insects in an attractive trap is the use of mark–release–recapture techniques, usually with release points at several distances from the trap. The result usually obtained is a probability function relating the proportion of insects,  $P(r)$ , originating from distance  $r$  from the trap. The intercept with the  $x$ -axis gives the maximum distance from which an insect can reach the trap within a given time period. This distance, usually called the sampling range ( $r_s$ ) (Wall & Perry, 1987), is time dependent and increases towards a maximum determined by the flight ability of the insect, its longevity and the degree of wind transportation (Östrand *et al.*, 2001). The sampling range has been determined for both coleopteran and lepidopteran species (Mason *et al.*, 1990; Schlyter, 1992; Zhang & Schlyter, 1996). Another concept is the attraction range, defined by Wall & Perry (1987) as ‘the maximum distance from which an insect can show directed movements to an odour source’. Hence, attraction range is time-independent and records ‘instant’ attraction whereas sampling range includes both attraction range and any movement by the insect before entering the attraction range and, thus, will increase with time.

The sampling range is one-dimensional and does not give a quantitative description of the origin of individuals caught in the trap. It is necessary to account for the fact that the recruitment area increases with distance ( $r$ ) from the trap (Hartstack *et al.*, 1971; Turchin & Odendaal, 1996). If we assume that the recruitment area (around the trap) is circular and that the insect density ( $B$ ) is homogeneous within this area, the trap catch ( $T$ ) is determined by:

$$T = \int_0^{r_s} 2\pi r P(r) B dr \quad (1)$$

Turchin & Odendaal (1996) defined the ratio between  $T$  and  $B$  as the effective sampling area  $\alpha$ :

$$\alpha = T/B = \int_0^{r_s} 2\pi r P(r) dr \quad (2)$$

This can be regarded as the area around the trap from which all captured insects originate if the trap catches 100% of the insects within the area and no insects from outside it. If  $\alpha$  is known the population density ( $B$ ) can be estimated based on trap catch ( $T$ ). The effective sampling area can also give an indication of the trap density required

in mass trapping programmes (used for population suppression), but does not reveal much about the origin of the insects trapped.

In order to be able to estimate the area over which the trap catch can be considered a reliable estimate of the population density, we propose the use of two novel concepts. The first simply makes use of the fact that the effective sampling area,  $\alpha$ , also can be regarded as an area  $\times$  probability volume. Distributing this volume over the area within the sampling range,  $r_s$ , from the trap, and using the probability dimension determined by  $P(r)$ , one can estimate how large a proportion of this volume is within a certain distance from the trap. By calculating this proportion for distances from zero to  $r_s$ , a function is produced for the Cumulative Proportional Catch (CPC) of insects originating from distances up to  $r$ , and when  $r = r_s$  the CPC equals 1:

$$\text{CPC}(r) = \alpha^{-1} \int_0^r 2\pi r P(r) dr \quad (3)$$

The second concept compares the size of the sampling range,  $r_s$ , to that of the effective sampling area,  $\alpha$ . In order to get the same dimensions and units for both estimates we use the radius of  $\alpha$  [i.e.  $r_\alpha = \sqrt{(\alpha/\pi)}$ ]. If  $r_\alpha$  is nearly as large as  $r_s$ , it means that the origin of the catch is very concentrated in space, and the trap is adequately monitoring the population within most of its sampling range. If, however,  $r_\alpha < r_s$ , only a small fraction of the catch comes from the immediate vicinity of the trap. We suggest that this ratio be called Catch Concentration (CC) because it describes the concentration of the trapped individuals' origin:

$$\text{CC} = r_\alpha/r_s \quad (4)$$

Pine sawflies (Hymenoptera: Diprionidae) are among the most important pine defoliators in Europe (Austarå *et al.*, 1987; Day & Leather, 1997). The European pine sawfly *Neodiprion sertifer* Geoffroy occurs in the northern hemisphere from Europe to eastern Asia and has been introduced into North America (Kolomiets *et al.*, 1979). Adult females attract males with the aid of a sex pheromone (the acetate or propionate ester of (1S,2S,6S)-1,2,6-trimethyl-tetradecanol (diprionol)) and synthetic pheromone stimulates male antennae (Hansson *et al.*, 1991) and attracts males in the field (Anderbrant *et al.*, 1992b).

It has been shown that *N. sertifer* males respond to synthetic pheromone from 200 m away (Östrand *et al.*, 2000). In a related study, we estimated the sampling range of our pheromone traps to be approximately 400 m after 24 hours of sampling, with a 95% confidence interval (CI) of 140–1600 m (Östrand *et al.*, 2001).

The present experiment was performed to determine the effective sampling area, the cumulative proportional catch (CPC) and the catch concentration (CC) of a monitoring trap for *N. sertifer*. By using different colour markings at different release points and occasions, we recorded the temporal and spatial history of the recaptures. The influence of weather conditions, especially wind direction, was also recorded and, based on the catch of unmarked males, the local population density  $B$  was estimated.

## Materials and methods

### Study site

The study was performed from 15 August to 21 October 2000 in a 15–20-m tall plantation of Scots pine *Pinus sylvestris* L. The 1400-ha plantation is situated 24 km east of Lund, southern Sweden. It is quite homogeneous with approximately 80% Scots pine, 10% Norway spruce *Picea abies* (L) and small stands or scattered individuals of birch *Betula pendula* Roth, oak *Quercus robur* L., or European larch *Larix decidua* Mill. The plantation is dominated by older trees, with the youngest age classes, 0–9 years and 10–19 years, covering only 2% and 7% of the area, respectively.

### Experimental set-up

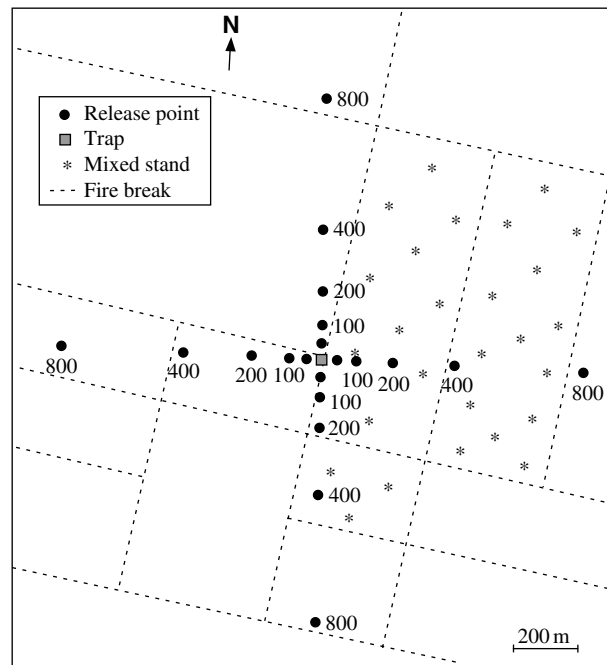
A Lund–I sticky trap (Anderbrant *et al.*, 1989) was hung in a pine about 2 m above ground close to the centre of the plantation. Approximately 2 mg of the pure pheromone, acetate of (1*S*,2*S*,6*S*)-1,2,6-trimethyl-tetradecanol, >99% stereochemically pure (Högberg *et al.*, 1990; Anderbrant *et al.*, 1992a), synthesized at the Mid Sweden University, Sundsvall, were loaded into a polyethylene vial (Kartell, #730, Noviglio, Italy), 6 mm inner diameter, 32 mm high, which was positioned underneath the roof of the trap. This dispenser releases approximately 10 µg of pheromone per day (Johansson *et al.*, 2001).

Males were released from 20 release points around the centrally placed trap. In each of the four cardinal directions males were released from five distances: 50, 100, 200, 400 and 800 m (Fig. 1). The trap was placed close to an intersection between three fire breaks, which were approximately 3 m wide. The fire breaks ran close to N–S and E–W, and most of the release points were easily accessible.

### Insects

About 100 000 larvae of *N. sertifer* were collected in June 2000 close to Valdemarsvik, Östergötland, Sweden. They were reared in cardboard boxes, standing outdoors in a sun- and rain-protected place, given water daily and fresh pine twigs when needed. After having spun cocoons the sexes were separated. Males were stored in plastic jars (5.5 × 5.5 × 9 cm).

Males emerged indoors and were kept individually in test tubes at 5 °C until use. The plastic test tubes (Kebo lub, Lund, Sweden), inner diameter 9.5 mm × 55 mm, contained a piece of soft moistened paper, and perforated corks allowed for air exchange. All males were colour marked before release. By dividing the pronotum into three fields and painting one or two dots from a total of eight different water based and water-resistant colours (Herdins, Falun Sweden and LeFranc & Bourgeois, Le Mans France), we achieved 216 different combinations. With four additional combinations of three colour dots on the pronotum, there were 220 different colour markings in total (i.e. enough combinations for 11 release experiments with differently marked males at each of the 20 release points). After the males had



**Figure 1** The study area illustrating the different forest stands. Unmarked stands were dominated by mature pine trees.

been marked, they were returned into their test tubes. As *N. sertifer* males live on average 12 days in the field (Östrand *et al.*, 2001) and males could not be released on 11 consecutive days, due to unsuitable weather, there was little risk of older males with the same marking being alive when others were released. The maximum recorded elapsed time from release to recapture was 15 days. The time lag between release experiments with males having identical marking was at least 15 days. Tubes with males were stacked vertically in plastic jars (inner diameter 6.4 × 8 cm). On the experimental days, males were kept in a cool box (insulated bag) until release. Males were usually released on the day after emergence, and were never older than 3 days. No differences in recapture rates of 0–4-day-old males were found in our earlier experiments (Östrand *et al.*, 2001). In order to increase the probability of recapturing males from the most distant release points, the number of released males was increased with distance. The minimum number of released males per occasion at 50 m was four (one from each direction) and the number of released males at the remaining distances were doubled for every distance. Thus, the minimum number of males for one release day was 124, with 4 + 8 + 16 + 32 + 64 at the five distances (from 50–800 m). Occasionally, somewhat fewer males were released.

### Experimental procedure

For the most part, males were released between 10.00 hours and 12.00 hours. (daylight saving time), and never later than 13.00 hours. The plastic jars containing the test tubes with the males were placed at the release points, the corks were removed and males were allowed to crawl up from the test tubes. Because it took approximately 1 hour to visit all the

release points, the order of release was changed every time, both between cardinal directions as well as the order within each 'spoke'.

All the release points were visited after approximately 24 hours to count the number of males that had left their test tubes or could be seen in close proximity to the jar. Approximately 5–15% of the males never left the release point. Presumably, these males were too weak to fly. This is supported by our observations of males remaining at the release points several days later. These males were left in the vegetation, as were males that were still in the test tubes after 24 hours. Recapture rates were based on the number of males that had left the release points (the difference between number of released males and males remaining) after 24 hours, unless the weather was bad on the day of release. In these cases (two occasions when it rained from 15 August to 30 September and during the five last experiments when the temperature was low), the recapture was based on the number of males having left the test tubes after 24 hours. Very few males left their release points during these times. The recapture rates after the first 24 hours were either zero or very low on these occasions.

Before the males were released the trap was checked, and the sticky bottom was exchanged if any *N. sertifer* had been caught. Usually, the trap was checked every day between 10.00 hours and 11.00 hours, and at the latest by 12.00 hours. All the captured males were considered to have been caught on the previous day. This is justified because 87% of the catch in a pheromone trap occurs between 11.00 hours and 17.00 hours (calculated from Jönsson & Anderbrant, 1993). Mostly, the colour markings of the recaptured males were visible to the naked eye. However, all sticky bottoms containing *N. sertifer* males were taken into the laboratory and examined under a microscope for their colour marking. The last release was done on 6 October, and the experiment was finished on 21 October. The temperature barely exceeded the flight threshold of about 11 °C (Jönsson & Anderbrant, 1993) and no *N. sertifer* had been caught during the previous 2 days.

### Weather recording

Weather data were collected from a stationary climate station, situated approximately 22 km north of the trap (Anonymous, 2000). We collected data on wind speed and direction, temperature and precipitation as these are the main parameters that had earlier been shown to affect flight by *N. sertifer* males (Jönsson & Anderbrant, 1993; Wedding *et al.*, 1995; Östrand *et al.*, 2000; Östrand *et al.*, 2001). The wind speed and direction data were correlated (e.g. wind-speed:  $r^2 = 0.77$ ,  $P < 0.001$ ,  $n = 37$ ) to those recorded in a climate station placed 20 km south of our experimental plot, or 40 km from the other climate station. Thus, even though the distance between our plot and the climate station may seem far, we feel it is justified to use these data because the landscape in this part of Sweden is dominated by agricultural lands and the correlation mentioned above suggests that a climate station placed at our site would probably have generated comparable data.

### Statistical analysis

Linear regression analyses were used for evaluating the relationship between recapture and climatic factors or distance, and confidence intervals were calculated following Sokal & Rohlf (1995). The *G*-test was used for comparing recapture from different directions around the trap within the first 24 hours, as well as temporal differences between recapture rates from different distances.

The total recapture rate from each of the 20 release points was used as a data point when calculating the maximum sampling range, the cumulative proportional catch and the catch concentration. When correlating climatic factors to recaptures, the recapture rate after 24 hours from each of the release occasions ( $n = 37$ ) was used as separate data points.

## Results

### Recaptures: distance, direction and sampling time

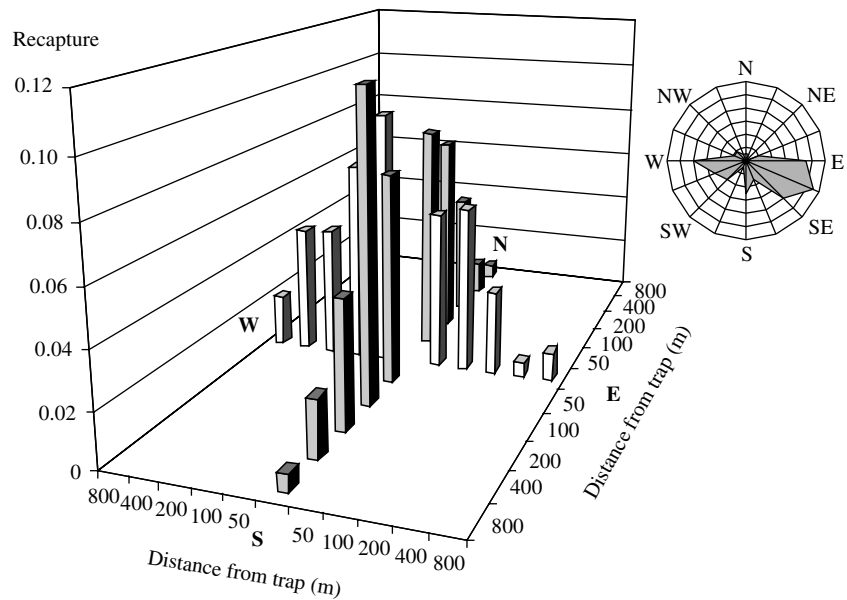
In total, 9869 males were released on 37 occasions. The number of released males on each occasion varied between 116 and 397. The proportion of males that had taken off after 24 hours was between 61% and 95%, with a total take off around 88.2% (8707). The total recapture on each of the release occasions varied between 0.4% and 7.6%, and in total 216 (2.5%) of the marked males were recaptured. Generally, it was easy to record the colour marking on the recaptured males. The definite colour marking could not be determined only on three occasions.

Males were recaptured from all 20 release points. Recapture rates decreased with distance, although recapture rates of males released from 50 m and 100 m did not differ (Figs 2 and 3). Recapture rates from each of the three shortest distances were quite similar for the four cardinal directions, but a lower proportion of males were recaptured from the eastern release points (at 50–100 m) than from the remaining directions ( $t_6 = 2.46$ ,  $P < 0.05$ , (Fig. 2). At 400 m and 800 m, recaptures from the western release points were significantly higher than those from the other three directions (Fig. 2) ( $G_3 = 29.6$ ,  $P < 0.001$ ,  $n = 95$ ; data pooled for 400 m and 800 m due to few observations).

Most males were recaptured on the day of release or the day after (43% and 22%, respectively, Fig. 4). However, more than one-third of the catch occurred after the first 2 days. The maximum time elapsed between release and recapture was 15 days (one male). A larger proportion of 'late-comers' was recorded from the 400–800-m release points compared to the 50–200-m release points (Fig. 4). For example, 90% of the total catch occurred 4 and 8 days following release for 50–200 m and 400–800 m, respectively.

### Sampling range, effective sampling area, cumulative proportional catch and catch concentration

The relationship between  $P(r)$  and  $r$  was analysed with different linear regression models using untransformed or transformed data. By log-transforming  $r$  (base 10) we



**Figure 2** The total recapture rate from each of the 20 release points. Note the logarithmic scale. The wind directions recorded from 15 August to 18 October at the stationary climate station are also shown ( $n=63$ ). Values are daily mean wind directions (out of 16 possible) from one measure each at 11.00 hours, 14.00 hours and 17.00 hours, and each ring represents two days recordings. Two days were excluded due to shifting wind direction.

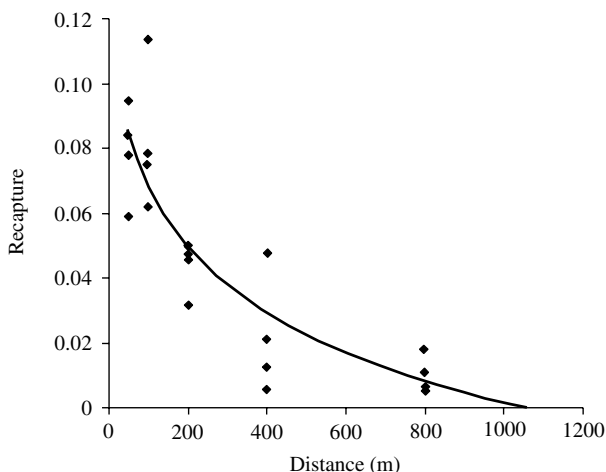
obtained an  $r^2$  value of 0.764 (Fig. 3), which was higher than for the double-transformed models  $\log P(r) - \log r$  ( $r^2=0.731$ ) or  $\log P(r) - \sqrt{r}$  ( $r^2=0.761$ ):

$$P(r) = 0.198 - 0.0656 \log r \quad (5)$$

The use of this regression model was further justified as no significant relationship between the mean and variance of  $P(r)$ , the dependent variable, was found. Solving this equation for  $P(r)=0$ , we obtained a seasonal sampling range of 1040 m with a confidence interval (95%) of 630–3300 m (Sokal & Rohlf, 1995). The corresponding equation for the catch after 24 hours was:

$$P(r) = 0.144 - 0.0510 \log r \quad (6)$$

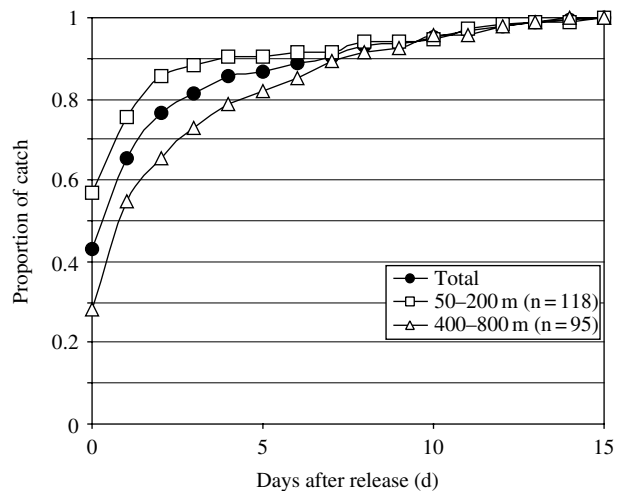
with a sampling range of 670 m (300–1900 m, 95% confidence interval).



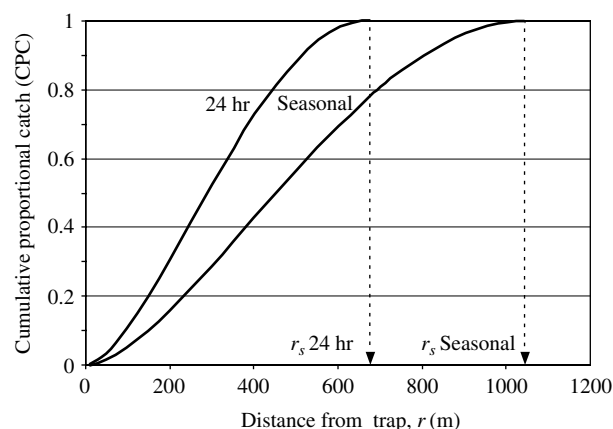
**Figure 3** Recapture rates from each of the 20 release points with regression curve from equation 5.

From equation 2, and using  $P(r)$  from equation 5, we obtained an effective sampling area  $\alpha$  of 48 705 m<sup>2</sup> or about 4.9 ha. This circular area has a radius  $r_\alpha$  of 125 m and, from this, we can calculate the catch concentration, CC, to 0.12 (125/1040 m) (equation 4).

Application of equation 3, using  $\alpha$  from above, yields a cumulative proportional catch CPC as shown in Fig. 5. From this curve it can be seen that, for example, 50% of the catch comes from beyond 450 m and that 10% of the captured insects originate  $\geq 800$  m from the trap. Similarly, the CPC for the first 24 hours can be calculated using regression equation 6 and corresponding  $r_s$  (Fig. 5), of about 300 and 450 m for the same catch proportions.



**Figure 4** Relationship between cumulative proportional catch and days elapsed after release for males released at 50–200 m or 400–800 m distance from the trap as well as the total recapture rates. Males captured on the day of release = 0 days after release.



**Figure 5** Cumulative Proportional Catch (CPC) of male *N. sertifer* after 24 hours of sampling and for the whole season.

### Local population density

In total, 112 unmarked (wild) *N. sertifer* males were caught in the trap during the trapping period, which covered the entire flight period of *N. sertifer* in this area. By using  $T=112$  and  $\alpha$  calculated above, the density of wild *N. sertifer* males  $B$  can be estimated at 23 per ha. This is indeed a low value, showing that the local population was in the endemic population phase.

### Recapture and climatic factors

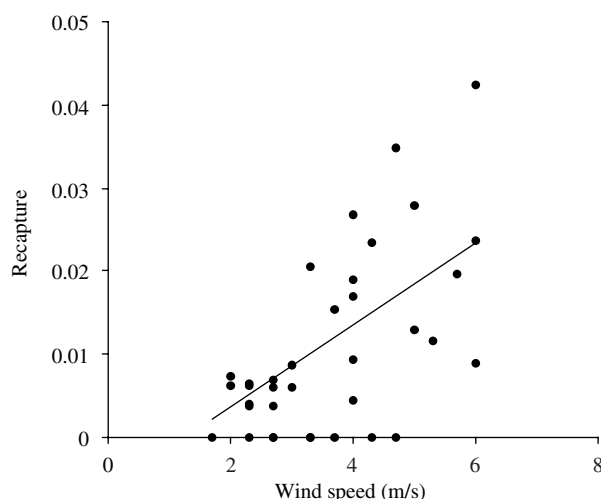
During the majority of days, the wind came either from east or west (Fig. 2). As the recaptures from the 400-m and 800-m western release points were significantly higher than from the other three cardinal directions, we investigated whether males from more distant release points (400–800 m) had been affected by wind direction, either negatively (headwinds) or positively (tailwinds). Indeed, the origin of males that were recaptured within the first 24 hours from 400 m and 800 m differed significantly from that expected if males had been recaptured irrespective of wind direction ( $G_1 = 14.4$ ,  $P < 0.001$ ,  $n = 27$ , Table 1). This was also found for males released at the shorter distances (50–200 m) ( $G_1 = 14.2$ ,  $P < 0.001$ ,  $n = 62$ ). However, there was no evidence demonstrating that males released at the greater distances had been transported to the trap by wind. That is, there was no significant difference in the proportion of downwind movements between these males and those males released at the shorter distances ( $G_1 = 3.51$ ,  $n = 89$ , NS).

The recapture rate within the first 24 hours was positively correlated with wind speed (Fig. 6). Temperature was not related to the recapture after 24 hours ( $r^2 = 0.001$ ,  $n = 37$ , NS). Nor did temperature improve the recapture-wind speed regression ( $P = 0.0078$  and  $P = 0.017$  for regression lines excluding and including the interaction between wind speed and temperature, respectively).

**Table 1** Number of males recaptured within 24 hours following release, from release points placed upwind, downwind, or crosswind from the trap

Flight to trap	50/100/200 m		400/800 m	
	Recorded	Expected	Recorded	Expected
Upwind	19	7.75	9	3.375
Downwind	7	7.75	7	3.375
Across	36	46.5	11	20.25

Mean wind directions were calculated based on recordings from 11.00 hours, 14.00 hours and 17.00 hours. Upwind and downwind flight are defined as males having flown against or with the wind with a maximum deviation of  $\pm 22.5^\circ$ . All other flights are considered across the direction of the wind. The expected values were calculated assuming that males were recaptured irrespective of the wind direction. Results from  $G$ -tests are presented in the text.



**Figure 6** Relationship between wind speed and recapture rate after 24 hours. Wind data are means calculated from values recorded at 11.00 hours, 14.00 hours and 17.00 hours. The line in the figure follows the equation  $y = 0.0046x - 0.0051$ ,  $r^2 = 0.23$ ,  $P = 0.0024$  ( $n = 37$ ).

### Discussion

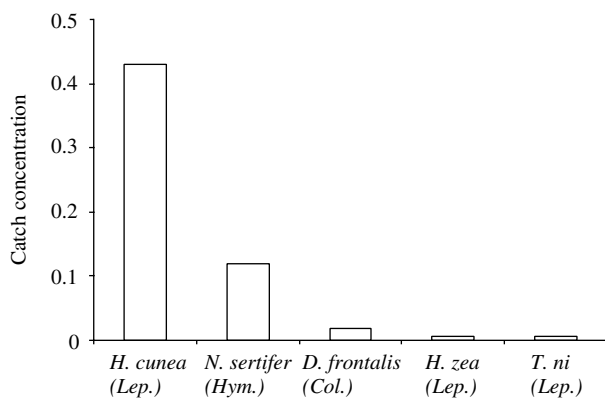
From this study, the sampling range after 24 hours (i.e. 670 m; 95% CI 300–1900 m), was comparable to that calculated for the same sampling time in a previous study (i.e. 400 m; 160–1600 m) (Östrand *et al.*, 2001). This is encouraging because several parameters differed between the two studies. In the previous study, males were released only from the downwind side of one or five pheromone trap(s), at three different distances. Furthermore, that experiment was performed in a young birch plantation and the males were released at the same height as the pheromone source(s) (1.7 m above ground). The cotton rolls used in the earlier study release approximately 45  $\mu\text{g}$  of the active pheromone during the first 24 hours (calculated from Anderbrant *et al.*, 1992b) compared to approximately 10  $\mu\text{g}$  per day (Johansson *et al.*, 2001) from the plastic vials used in this

study. However, release rates will also vary with, for example, temperature and usually differences of a factor of 10 or more are needed to considerably change the distance of response (Baker & Roelofs, 1981).

The sampling range and effective sampling area depend on insect longevity. Males of *N. sertifer* live on average 12 days (Östrand *et al.*, 2001), and in this study males were recaptured up to 15 days following release. About one-third of the males recaptured had spent >48 hours in the plantation. Zhang & Schlyter (1996) performed studies on sampling range of traps for the fall webworm moth *Hyphantria cunea*. About 90% of their recaptures of *H. cunea* occurred during the first night, with recaptures on the second and third night comprising only 9% and 0.9%, respectively, of the total number of recaptured moths. In another study, gypsy moth males were kept in a forest for up to 3 days before release (Elkinton & Cardé, 1980). The recapture rate decreased with age of 1, 2 and 3-day-old males of this moth, and 19.7%, 0.9% and 0.2%, respectively, males were recaptured. The relatively long longevity of *N. sertifer* males combined with modest flight capability (800 m within 24 hours and >2 km within up to 5 days, see below), indicate a potentially large dispersal capacity.

By developing two new quantitative concepts describing the origin of insects caught in an attractive trap, it will be easier to compare different traps, attractive agents, different pheromone blends or concentrations and possibly also the response or sensitivity of different species; a discussion of sampling range is provided elsewhere (Schlyter, 1992). In addition, and probably more importantly, it is now possible to deduce information about the distance from the trap certain proportions of the trap catch have originated from. This will aid the design and interpretation of monitoring studies using attractive traps.

Our estimated catch concentration (0.12) is intermediate compared to the few other studies that we have been able to extract information about  $\alpha$  and  $r_s$  from Fig. 7. The effective attraction area has been calculated for traps used for the



**Figure 7** Catch concentration (CC) of pheromone traps used for catching the fall webworm moth *Hyphantria cunea* (Zhang & Schlyter, 1996), the pine sawfly *N. sertifer* (this study), the southern pine beetle *Dendroctonus frontalis* (Turchin & Odendaal, 1996), the bollworm *Heliothis zea* and the cabbage looper *Trichoplusia ni* (Hartstack *et al.*, 1971).

southern pine beetle *Dendroctonus frontalis* to be approximately 0.1 ha after 12 days of sampling (Turchin & Odendaal, 1996), and for the fall web worm *H. cunea* to approximately 7 ha after 60 hours of sampling (Zhang & Schlyter, 1996). Disregarding the different sampling periods and assuming a sampling range of 340 m for *H. cunea* and 1000 m for *D. frontalis* (the maximum release distance used; sampling range not explicitly calculated), CCs of 0.43 and 0.019, respectively, can be calculated for *H. cunea* and *D. frontalis* (Fig. 7).

Hartstack *et al.* (1971) used a somewhat different approach when they investigated the trapping efficiency of bollworms *Heliothis zea* and cabbage loopers *Trichoplusia ni*. By performing a large number of release–recapture experiments and analysing the results with the least-square technique, they fitted two parameters, the ‘effective radius’ of the trap and the ‘trap efficiency’. The trap efficiency was defined as the percentage of insects caught for those insects entering the effective radius of the trap. The estimated values were about 30 m and 42.8% for *H. zea* and 25 m and 61.4% for *T. ni*. Using these figures, the effective sampling area can be calculated, and for both species it is close to 1250 m<sup>2</sup>. This will give an  $r_s$  around 20 m and values of CC of 0.006 for both moths (Fig. 7), using the assumed maximum travel distance by the moths of 2 miles per night (Hartstack *et al.*, 1971).

Lund-I traps were used for monitoring *N. sertifer* density in young pine plantations in Sweden for 10 years (Lyytikäinen-Saarenmaa *et al.*, 1999). For the most part, the correlation between trap catch and preceding larval density was poor, but higher during population increase than during population decrease. The seasonal sampling range of the Lund-I trap (i.e. 1040 m and the effective sampling area of 4.9 ha) suggest that *N. sertifer* males were attracted from an area much larger than the size of the pine plantations used by Lyytikäinen-Saarenmaa *et al.* (1999). One plausible explanation for the poor correlation between trap catch and future larval density they obtained could be the relatively flat CPC curve, which suggests that as many as 50% of the captured insects originated from >400 m away. This was one of the hypotheses proposed by Lyytikäinen-Saarenmaa *et al.* (1999). Trumble (1996) also presents other reasons why relations between trap catch and population density/damage are often poor.

The small catch of wild males during our study, indicating a very low local population density of *N. sertifer*, has other implications. For example, very few wild pheromone-emitting females were present to compete with the pheromone trap. This could be one explanation why the 24-hour sampling range in this study was similar to that from a previous study performed in a nonhost habitat. In other studies using the same trap and bait, the seasonal catch could reach 3500 males (Herz *et al.*, 2000) giving an estimated density  $B$  of around 700 males per ha. Also 700 males per ha is a very low population estimate compared to larval densities which sometimes attain two million per ha (Hanski, 1987; Lyytikäinen-Saarenmaa *et al.*, 1999). During such epidemic conditions, with a dense population of competing females, one could expect a lower  $P(r)$  curve as many



of the males end up mating (with one or several females) instead of reaching the trap. The sampling range might remain unchanged, but the effective sampling area, and therefore the catch concentration (CC) should be lower during epidemic conditions.

In this and in other published studies dealing with sampling range, the trap efficiency has been assumed to be equal in all directions. This implies that either the effect of wind is negligible, which intuitively sounds unrealistic as the pheromone is depending on wind transportation and similarly the ability of the insects to reach the source is facilitated by an anemotactic response, or that the wind direction changes, resulting in a homogeneous distribution of directions. In our study, the differences between recapture rates were generally small for different directions, despite the dominant east–west wind directions. There are two possible explanations for this. First, the flight capacity of the males may be so high that they sooner or later reach ‘the plume’ irrespective of their release point. Second, the forest habitat contributes to a more turbulent air-flow, distributing the pheromone more evenly and consequently to a less directional component of wind-flow. The significantly higher recaptures from the 400-m and 800-m western release points was probably due to a combination of mostly east–west wind directions and the release points in the west being close to the fire breaks.

The best strategy to locate an odour source when outside the attraction range would be to fly across the direction of the wind (Elkinton & Cardé, 1983). Flight direction in relation to wind direction was studied in gypsy moth males *Lymantria dispar* and the moths did not preferentially fly across the direction of the wind, upwind or downwind (Elkinton & Cardé, 1983). In contrast, the cabbage root fly *Delia radicum* flew upwind before intercepting the host odour plume (Finch & Skinner, 1982), and *Agrotis segetum* moths typically flew across the direction of the wind when outside the range of a pheromone plume (Riley *et al.*, 1998). Both these studies were performed in open habitats (e.g. pastures), where the effects of wind are certainly more pronounced. Males of *N. sertifer* took off into the wind in pheromone-free environments in a birch plantation, but this does not imply that they will fly upwind outside of the attraction range (Östrand *et al.*, 2000). It is unknown what the dispersal ‘strategy’ of *N. sertifer* males is prior to pheromone-detection, nor is it known how far they can travel during their lifetime (actively or passively). However, we have recorded net movement of *N. sertifer* males >2 km within 1–5 days (Östrand & Anderbrant, unpublished data).

A positive relationship between recapture and wind speed has been reported for *N. sertifer* (Wedding *et al.*, 1995). In that study, males were released on different sides of one to several traps, thus it is difficult to know what proportion of the catch had flown upwind vs. that that had been transported downwind. In a young birch plantation, fewer *N. sertifer* males were recaptured downwind of pheromone traps under increasing wind speeds. This effect increased with distance to the traps (Östrand *et al.*, 2001). As the plantation in the present study was quite dense, it seems reasonable that more males were recaptured at increasing

wind speeds because, at weaker wind speeds, the pheromone plume trajectories are less likely to be aligned with wind direction (David *et al.*, 1982), especially in a forest (Elkinton *et al.*, 1987).

Although a number of significant patterns with respect to the influence of wind speed or direction on trap catches have been reported by us, we regard them as indicative rather than conclusive. Complementary studies in different environments with higher resolution weather data are needed.

It is obvious that actual catches and perhaps also calculated parameters would have been different if the study had been conducted at a different site, or if weather conditions, lure strength, trap type or height of the trap had been different. For example, the density of flying *N. sertifer* males is higher at canopy level than it is closer to the ground (Simandl & Anderbrant, 1995). Hence, if the trap had been placed higher up the tree, more *N. sertifer* may have been caught. However, it is likely that the proportion originating from different distances had been the same, resulting in similar CPC and CC. Also, the ratio of marked/unmarked males probably remained the same, resulting in similar estimates of the local population density. Thus, the concepts described here are universal and robust enough to have wide application in research to better understand the function of attractive traps. It would certainly be interesting if this experiment could be repeated for other insects, allowing for comparisons and the formulation of generalities.

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