Recapture of dispersing bark beetle *Ips typographus* L. (Col., Scolytidae) in pheromone-baited traps: regression models

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Abstract: Parent (re-emerged) spruce bark beetles (*Ips typographus* L., Col.; Scolytidae) beginning a second host-seeking flight were collected in pheromone-baited traps. These beetles were marked with fluorescent powder of different colors and released from a point source (9–16 June 1989) within a spruce, *Picea abies* L., forest (Jurbarkas forest district, Lithuania). Some of the marked beetles were recaptured with pheromone-baited traps in two experiments: (1) traps at 10 m and (2) traps 30, 60, 90, and 120m distances from the release point. Of 5920 and 5030 beetles that took flight in the two experiments, average recapture rates were $5.64 \pm 1.17\%$ ($\pm$ SEM) on traps at 10 m distance, and 1.62 ± 0.21, 0.88 ± 0.23, 0.27 ± 0.08, and $0.03 \pm 0.03\%$ on traps at the respective distances from 30 to 120 m. Parameters of several regression models were fitted with the Simplex algorithm (SYSTAT statistical software) to recapture data. The best fitting models were those of power, and an exponential form. A discussion of the biological meaning of certain coefficients in the equations is presented with regard to bark beetle dispersal.

1 Introduction

One of the most common methods for studying insect dispersal is the recapture of marked members of a population released from a single point in space and time. Quantitative information concerning dispersal plays an essential role in the evaluation of pest control (JOYCE, 1976). The dynamics of bark beetle infestations and damage in forest stands are largely dependant on short-range movements of beetles under the canopy (BOTTERWEG, 1982; ANDERBRANT, 1985; SANDERS, 1984, 1987; GRIES, 1985; ZUMR, 1990, 1992). The dispersal of spruce bark beetle (*Ips typographus* L.) is of interest since it is a major pest of Norway spruce, *Picea abies* L., in Europe (VITÉ, 1989). In this paper dispersal of *I. typographus* after release from a point source in the forest is analysed with several regression models.

2 Materials and methods

Two experiments were conducted during the flight period of 'parent' (re-emerged) spruce beetles in the Jurbarkas forest district (9–16 June 1989, western Lithuania). Weather conditions on the test days were favorable for beetle flight (above 22°C and wind less than 1.5 m/s). Beetles used in the experiments were collected from cross-barrier traps baited with 'Ipslure' dispensers (Celamerck, Germany). The trap was made of two sheets of polyethylene plastic (0.5 mm × 26 cm × 40 cm), inserted between an upper and lower cross-brace of steel wires to form four vanes that were placed over a plastic funnel (26 cm diameter) and collection vial. The traps were suspended at 1.7 m height by a pole driven diagonally into the ground. The 'Ipslure' dispenser consisted of a polyethylene bag containing pheromone components that was as efficient in attracting beetles as baits known to release approximately 50 mg of 2-methyl-3-buten-2-ol, 1 mg of (*S*)-*cis*-verbenol and 0.1 mg ipsdienol per day as measured by weight loss (unpubl. results).

In the first experiment, beetles were released 10 m from one cross-barrier trap baited with pheromone (in order to avoid trap interaction) in a stand of spruce about 75–80 years of age. The direction from the release point to the trap was chosen in one of four cardinal directions at random for each test day. Beetles collected earlier in the day were dusted with fluorescent powder (at 14.00 each day with a different color) and then released in the test area from a small wooden platform, 0.5 m above the ground. Trapped beetles were collected the following day in the afternoon before releasing the next batch of beetles. Marked individuals were counted in the laboratory where they were clearly distinguishable from unmarked beetles under normal fluorescent room lighting. A total of 5030 marked spruce bark beetles took flight from the platform over six 1-day tests.

In the second experiment at another site about 200 m away during the same period, 16 cross-barrier pheromone traps baited with 'Ipslure' dispensers were placed among four cardinal directions at 30, 60, 90 and 120 m away from the release point. Marking and collections were as in the first experiment. A total of 5920 beetles flew away from the release platform during four 1-day tests.

The catches of marked beetles at various distances from the release point were fit empirically (SYSTAT statistical software, WILKINSON, 1990) to several non-linear equation forms, including logarithmic, reciprocal, power and others, that have been proposed as suitable for dispersal analysis (ITO and MIYASHITA, 1965; HARTSTACK, 1971; HARTSTACK and WITZ, 1981; FINCH and SKINNER, 1975; FREEMAN, 1977; INOUE, 1978; TAYLOR, 1978, 1980; SAFRANYIK et al., 1992; PLANT and CUNNINGHAM, 1991). Regression coefficients were calculated using a Simplex algorithm that employs an iterative direct search procedure (WILKINSON, 1990).

3 Results

Almost all marked beetles recaptured were caught within the first collection period (by the next day after they were released). In the first experiment, a few indi-
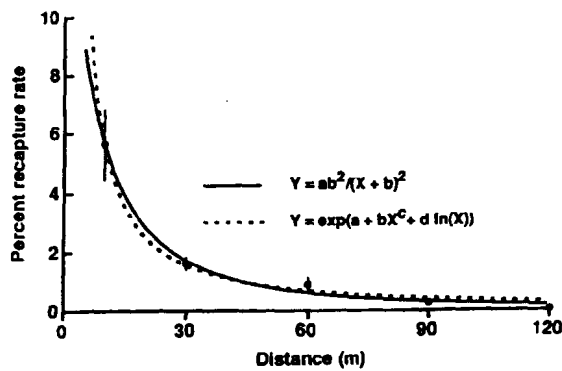
Relationship of percentage recapture of marked bark beetles, Ips typographus, with distance of pheromone-baited trap from release site in a Norway spruce forest (9–16 June 1989, Jurbarkas forest district, Lithuania). Bars represent ± SEM. Solid line corresponds to equation of model 1, dashed line to model 3 (see table)

Coefficient values and fit (R²) of the regression model of recapture rate

Data source	a	b	c	R^2
Model 1 (HARTSTACK and WITZ, 1981): $y = ab^2/(x+b)^{2}$*				
Experiment II	8.427	23.831		0.940
Pooled data	15.936	14.659		0.995
ZUMR, 1989[a]	19.388	65.220		0.989
ZUMR, 1990[a]	14.268	95.867		0.980
SAFRANYIK, 1982[b]	62.603	9.649		0.998
SAFRANYIK, 1983[b]	—	—		—
Model 2: $y = bx^c$				
Experiment II		187.085	−1.139	0.924
Pooled data		84.597	−1.177	0.993
ZUMR, 1989[a]		555.820	−1.147	0.992
ZUMR, 1990[a]		281.547	−0.974	0.996
SAFRANYIK, 1982[b]		288.158	−1.281	1.000
SAFRANYIK, 1983[b]		101945.701	−2.858	1.000
Model 3 (TAYLOR, 1978): $y = a\exp(a+bx^c)$				
Experiment II	0.693	−5e−05	2.634	1.000
Pooled data	5.111	−1.789	0.276	0.996
ZUMR, 1989[a]	10.708	−5.555	0.120	0.992
ZUMR, 1990[a]	20.701	−15.616	0.049	0.992
SAFRANYIK, 1982[b]	4.971	−5.246	0.129	0.740
SAFRANYIK, 1983[b]	30.917	−25.922	0.080	0.560

[a] Data from ZUMR, 1992
[b] Data from SAFRANYIK et al., 1992
*x = distance from release point in meters $(3 < x < 130)$; y = recapture ratio of marked beetles in percent.

viduals (less than 1% of all recaptured beetles) were caught in the traps at 10 m distance during the second day (collection period), but after this none were trapped. These few beetles were excluded from further analysis. In the second experiment, no beetles were caught at any of the four distances (30–120 m) after the first collection interval.

Recapture ratio data were averaged over all releases in both experiments. On average $8.4 \pm 1.61\%$ ($\pm$ SEM) of the marked beetles were recaptured for each 1-day release period. To check for radial symmetry of recapture rates, data were grouped by angular position form the release point into four groups, and Chi-square statistics computed to test for randomness. The distribution of catches showed no significant differences between catches in different directions (P = 0.9), indicating that beetles dispersed randomly. On average 5.64 ± 1.17, 1.62 ± 0.21, 0.88 ± 0.23, 0.27 ± 0.08 and $0.03 \pm 0.03\%$ of marked bark beetles were recaptured per trap at 10, 30, 60, 90 and 120 m distances from the release point, respectively (fig.).

Regression coefficients were calculated on two different sets of recapture data: (1) for data from the second experiment (traps 30–120 m from release point): and (2) for data pooled from both experiments (10–120 m distance). It is reasonable to pool data of both experiments as traps at each distance from the release point caught only a small proportion of the marked beetles (5.64% or less) and thus should not significantly affect the catches at other distances. Regression coefficients also were calculated on published data from similar experimental designs, such as data on *I. typographus* recapture at distances from 50 to 300 m (results from 2 years as calculated from fig. 2 in ZUMR, 1992) and from *Dendroctonus ponderosae* (2 years recapture data at distances from 10 to 250 m (table and fig. in SAFRANYIK et al., 1992). The equations with the best fit (table) were those of HARTSTACK and WITZ (1981) which can be treated as a form of power regression (model 1), power (model 2), and a type of exponential regression (TAYLOR, 1978, model 3). Regression coefficients differed among data sets from our experiments and

those of ZUMR (1992) for *I. typographus* as well as for data from SAFRANYIK et al. (1992) for *D. ponderosae* (table).

4 Discussion

Dispersal analysis can be performed by three general methods. The first uses statistical analysis to describe the insect distribution, for example, dispersal of fruit flies (BAKER et al., 1986; FLETCHER, 1974; FLETCHER and ECONOMOPOULOS, 1976; PLANT and CUNNINGHAM 1991). The second method uses empirical models of insect population dispersal and attempts to fit the data to a regression curve. For example, TAYLOR (1978) found that none of the earlier proposed models for predicting density of released individuals at various distances from a source could adequately fit dispersal data from several insect species. TAYLOR (1980) proposed a general form of power regression that was later used by other authors (SAFRANYIK et al., 1992; PLANT and CUNNINGHAM, 1991). The third methodological category, the so-called fundamental models, consists of a system of differential equations that attempts to represent assumptions about the biological properties underlying the observed behavior. These models are mathematically complex and usually are based on diffusion equations. The models have been applied to several insect species with various modifications (AIKMAN and HEWITT, 1972; OKUBO, 1980; RUDD and GAN-

DOUR, 1985; BANKS and KAREIVA, 1985; KAREIVA, 1982, 1983; HELLAND et al., 1984, 1989).

The dispersal potential of spruce bark beetles may be different at different stages of their life history. Re-emerged beetles that have already reproduced may consist of relatively poor dispersers since in our experiments few individuals of those released were trapped during the second day. However, the alternative hypothesis is that these beetles exhibited a good ability to disperse and left the test site quickly without responding to pheromones from our traps. Freshly emerged individuals might have a greater potential for flight endurance (FORSSE and SOLBRECK, 1985) than the beetles used in our experiments, but newly emerged beetles would probably show a lower response to aggregation pheromone (GRIES, 1985). Thus, pheromone trap catches may not correctly measure the flight and dispersal power of freshly emerged beetles. Beetles in our experiments had already flown and responded to pheromone (collected in traps prior to marking) and may, therefore, have been low in fat reserves and thus 'desperate' to settle on 'suitable' hosts as indicated by pheromone (cf. BYERS, 1994). This may explain why some beetles were trapped soon after and near the time and place of their release. Other mark-recapture studies also have shown that most beetles are caught shortly after their release (BOTTERWEG, 1982; HELLAND et al., 1984; LINDELÖW and WESLIEN, 1986; WESLIEN and LINDELÖW, 1990).

Data of SAFRANYIK et al. (1992) reported that between 86 and 93% of all recaptured *D. ponderosae* were caught within 30 m from the release point. Up to 98.5% of all marked *Scolytus multistriatus* beetles were recaptured at only 1.5 m from the release point (WOLLERMAN, 1979). However, some marked *I. typographus* that had prior flight experience were caught in traps 1200 m away from the release point (ZUMR, 1992). According to flight-mill studies by FORSSE and SOLBRECK (1985), most *I. typographus* are able to fly much farther than 1600 m in one day. Marked *I. typographus* beetles have occasionally been found in traps from 5 to 9.5 km from the nearest release sites (WESLIEN and LINDELÖW, 1990). However, many experiments with *I. typographus* have been performed with freshly emerged beetles in open areas where dispersal may be facilitated (e.g. they may be easily carried away by winds), whereas under the canopy (our experiments) these possibilities are probably reduced and there is more chance for beetles to land on a host tree rather than on a trap. Differences in suitable host-tree density can also influence the percentages of recaptured beetles, for examples SALOM and MCLEAN (1989) found that 24.9% of marked *Trypodendron lineatum* were recaptured in pheromone traps placed in areas without competing host material, while only 6% of marked beetles of this species were caught in a timber sort area with large quantities of susceptible material (SHORE and MCLEAN, 1988).

As can be seen from the results of regression analyses, power regression (model 2) estimates the dispersal distance expected for reemerged spruce bark beetles quite well. The model of HARTSTACK and WITZ (1981), which can be considered as a type of power regression, also fits the data well. The equation is based on the assumption that released beetles simply spread radially and

'dilute' in an ever increasing area (WESLIEN and LINDELÖW, 1990). Two characteristics of traps are supposed to be evaluated with this equation: coefficient a was called 'trap efficiency', and coefficient b the 'effective radius' of the trap. Trap efficiency (coefficient a) is low in *I. typographs* recapture experiments, and this corresponds to a low recapture rate and is consistent with the assumption that re-emerged beetles should have a lower dispersal potential than emerged, overwintering spruce bark beetles. Our trap efficiency corresponds well with that of ZUMR's data (15.9 and 14.3% respectively, table), since traps of similar construction were used.

The effective radius of our trap (coefficient b in the equation of HARTSTACK and WITZ, 1981) was equal to 14.7 m (table) as obtained from the pooled data and indicates that single pheromone traps uniformly influenced beetles in areas up to 135 m from the release point without either overlap or large gaps between effective trap radii. The effective trap radius was 65.2 or 95.9 m as calculated from each year of ZUMR's data (table). If the attractive radius really is 95.9 m, then there must have been an interaction between trap groups because they were placed at 100 m intervals (ZUMR, 1992). The larger attraction radius of 95.9 m calculated by ZUMR may have been larger than the 14.7 m radius we calculated because he used groups of four traps at each position compared to our single traps; also there could have been pheromonal affects of surrounding trees colonized by attracted bark beetles. Differences in the attraction radius also may be due to stand and environmental conditions. Another obvious difference is that we used re-emerged beetles (attracted to pheromone baits after the first flight period) while ZUMR (1992) used emerged beetles (reared from host logs). The effective attraction radius as calculated by regression methods above must be distinguished from the effective attraction radius obtained by comparison of trap catches on pheromone-baited and unbaited traps (BYERS et al., 1989; BYERS, 1993).

In model 3 (TAYLOR, 1978) and more complicated derivative models (TAYLOR, 1980), biological meaning was attributed to coefficient c: where $c < 2$, $c > 2$, or $c = 2$ depending on whether there is attraction, repulsion, or no interactions between dispersing insects, respectively (TAYLOR, 1978). Coefficient estimates indicate that there should be attraction between both species of dispersing bark beetles, ($c < 2$ in pooled data set, table), but it is more likely that this effect is due to the attraction of beetles to trees, not due to attraction between flying individuals as proposed by Taylor. In model 3, $c = 2.6$ as calculated from data of experiment two (table), which suggests that there is a repulsion among dispersing beetles (but this is unlikely). However, coefficient b is very close to zero, causing the equation to become a simple exponential form and the biological meaning of coefficients is thus uncertain. Interestingly, the c coefficients in models 2 and 3 are similar for both species and may represent a more general measure of dispersion for bark beetles.

More complex exponential models (TAYLOR, 1980) with more coefficients were not used because there were not enough sampling distances in our experiment to yield reliable results with the Simplex method. Fur-

thermore, the more complex the model, the more variations in coefficient values are possible that give essentially the same relationship. Also, complex regression models lead to confusion regarding biological interpretation and imply that descriptive models are of limited usefulness and unlikely to apply to a wide range of conditions (STINNER et al., 1983). For example, the models are not applicable to situations where insects do not originate from a point source.

Acknowledgement

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