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An encounter rate model of bark beetle populations searching at random for susceptible host trees

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Abstract

Iterative equations were developed that predict the encounter rate between a population of moving animals and a population of stationary objects, where the animals cease to search upon finding an object. The encounter rate through time depends on the number of searching animals (bark beetles), number of stationary objects (host trees), average speed of the animals, average radius of the object, and area of the search arena. The iterative equations were used in a computer program to vary these parameters with regard to flight dispersal of the bark beetle *Ips typographus* (Coleoptera: Scolytidae) during their search for susceptible host trees of Norway spruce (*Picea abies*). Realistic parameters of flight speed, numbers of beetles and susceptible host trees, tree diameters, density of healthy trees, search area, and time searching were held constant while certain of these parameters were varied in computer model runs. In most cases, significant proportions of the modeled bark beetle population (of which individuals fly forward with a random component) found the relatively few susceptible host trees suitable for colonization. Only at very low effective flight speeds (due to longer stays on trees) or with widely distributed hosts of smaller diameter, did relatively few beetles find suitable hosts. Once the 'pioneer' beetles find susceptible hosts, release of aggregation pheromone would greatly increase the effective radius of the host and allow rapid concentration of the population on these trees. The model suggests that primary attraction to host tree volatiles is not mandatory for host finding and selection in many species of bark beetle. Evolution of an olfactory response to host volatiles is more probable in species with low population densities or widely dispersed host plants, or both. Also, there would be little selection pressure on a bark beetle species to evolve aggregation pheromones if they can respond over some meters to plant volatiles that reveal the location of a susceptible host.

Keywords: Bark beetle; Dispersion; Host–parasite interaction; Search strategies; Spruce

1. Introduction

Bark beetles (Coleoptera: Scolytidae) emerge from forest litter or brood trees and begin a dispersal flight where they seek suitable host trees in which to reproduce. The dispersal and host-finding phase of their life cycle is known to be risky, with only 15–25% of the adults successful in finding a host, boring into the bark, and reproducing in the phloem–cambium layers (as indicated from ratios of exit holes of brood emergence to entrance holes of attack, Struble and Hall, 1955; Miller and Keen, 1960). In a forest of conifer trees of one or a few species it might seem easy for bark beetles to find a host. However, healthy trees when injured produce

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resin that can be toxic and physically impede and entrap beetles (Smith, 1961; Hodges et al., 1985; Byers, 1995). Usually, only a small fraction of trees in a forest area are unhealthy, weakened by diseases and insects, or of old age such that they are susceptible to attack by bark beetles. Unhealthy or injured trees release higher amounts of volatile chemicals than healthy trees, and these volatiles may serve as kairomone signals attractive to some species of bark beetles (Graham, 1968; Moeck, 1970, 1981; Gara et al., 1984; Byers et al., 1985). For example, ethanol from microbial activity in decaying tissue, and monoterpenes from wound resin, are well known to be attractive to a number of species (reviews: Byers, 1992, 1995).

On the other hand, species that attack living trees and use aggregation pheromones are usually weakly, if at all, attracted to host log odors or monoterpenes and ethanol (Moeck et al., 1981; Klimetzek et al., 1986; Schlyter et al., 1987). In some of these 'aggressive' species, landing rates have been observed to be similar on host and non-host trees, suggesting that these beetles discriminate between hosts and non-hosts only after landing (Berryman and Ashraf, 1970; Hynum and Berryman, 1980; Moeck et al., 1981; Witanachi and Morgan, 1981). Thus, a second way bark beetles may find suitable host trees is by random landing and testing for both the proper host and the tree's resistance capability (Moeck et al., 1981; Wood, 1982). In this case, the population of beetles must cooperate so that any individuals that find a susceptible tree are able to release aggregation pheromone that directs other searching beetles to join the attack. This cooperation is to the advantage of the resident beetle as well as those joining since the tree, although weak, will attempt to resist with resin and might kill one attacking beetle eventually, but not the combined efforts of many beetles. Because beetles are difficult to observe flying through the forest, computer models have attempted to explore dispersal and host-finding behavior (Gries et al., 1989; Byers, 1993).

Gries et al. (1989) computer simulated host selection in *Ips typographus* L., a bark beetle using aggregation pheromone when killing Norway spruce, *Picea abies* (L.). They concluded this beetle was unlikely to use random flight and testing of intercepted trees as a mechanism for host-finding since the beetle would need to fly much farther (at least 60 km) than expected possible in order to find the widely spaced and rare susceptible host trees. However, their simulation model has deficiencies since trees were placed in a grid, and beetles took short flights limited to one of eight possible directions at random between adjacent trees. This flight pattern is unlikely for bark beetles seeking either host odors or pheromone that are widely distributed. Beetles would not want to often reverse direction in a purely random search thereby wasting time on visits to previously searched areas. Thus, beetles would fly generally forward to cover the most ground. Furthermore, I have observed bark beetles taking off from a tree to fly generally straight for tens of meters with some slight angular component (observations, Byers, 1991, 1995).

A more realistic simulation model would allow beetles to fly forward with steps where the heading could change gradually at each step in a random way so that the beetle could assume any position, as illustrated by Skellam (1973). Also, the trees would be placed at random (or spaced with a degree of randomness) and could be of any specified size (from trunk size to an effective attraction radius corresponding to a semiochemical). Thus, the objective here is to develop a more realistic model of bark beetle host-finding. The effects on host-finding of *Ips typographus* are explored in the model by varying such parameters as the beetle's effective flight speed and population density as well as the tree's effective radius and density of susceptible trees.

2. Methods

A computer simulation model for simulated movement of walking or flying insects in relation to mate-finding (Byers, 1991) as modified for catch by pheromone-baited traps (Byers, 1993) was used to simulate finding of susceptible host trees by bark beetles. In this model, each susceptible tree (formerly a trap) can catch any number of moving insects. The *X*- and *Y*-sides of the simulation area, number of insects, flight speed, number of trees, tree radius, and duration of the search period can be varied independently. Realistic flight of insects in two-dimensions is achieved by using polar coordinates in which the angle of directional movement is changed randomly at each step at most equal to the angle of maximum turn (usually $\leq 30°$), which can be either right or left (chosen at random) from the previous direction. The step length (usually about 0.5% of the area's side) and angle of maximum turn can be varied in the model but have little effect on mate-finding or catch results (Byers, 1991, 1993). When insects impact the area's boundaries, they rebound at a random angle. Initial angular directions and positions of individuals are chosen at random. The 'insects' move a step at a time up to the number of moves determined by the test duration and the speed of flight, or until caught by a trap. Insects are removed from the simulation if caught and the percentage of the initial population caught at the end of the test, or the time observed to catch all the insects, is recorded at the end.

Iterative equations (discussed subsequently) were derived that yield mean values identical, within statistical variation, to the results of simulations (Byers, 1993). The simulation model was used to validate selected results of the iterative equations. However, since the simulation model is time-consuming compared to the iterative equations (more than a million times slower with some parameters), only the iterative equations were used to generate results presented here. The simulation and iterative programs are available from the author (send IBM-compatible disk).

Gries et al. (1989) used a density of 500 spruce trees/ha in their simulations of host-finding in *I. typographus*. However, the relationship between trunk diameter and density must be considered in the models presented here. Linear regression of data from Magnussen (1986) in his fig. 3, relating density of Norway spruce (300 to 900 trees/ha) and trunk diameter, shows that trees have an average diameter of about 0.29 m at 500 trees/ha. Thus, in all models (except where diameter was varied) the tree diameter was set at 0.3 m in a forest of density 500 trees/ha. *Ips typographus* beetles fly at about 1.9 m/s (Gries et al., 1989) or 2 m/s (Byers et al., 1989); the latter value was used in the models. Populations of flying *I. typographus* probably can vary up to some hundreds of thousands per km^2, but 9000/km^2 were estimated in one study (Byers et al., 1989) and used in the models except when density was varied.

3. Results

The first question that must be answered is how far would a beetle be expected to fly before being intercepted by the trunk of a tree in the above forest? If a beetle is released at random in the forest, then the average expected distance D that a beetle would fly before striking a tree is given by:

$$D = \frac{A}{2RK} = 66.67 \text{ m} \tag{1}$$

This distance of 66.7 m is also what a beetle would be expected to travel when flying away from one tree until intercepting another. This distance should be much larger than the expected average distance to the nearest tree (2.34 m) for a forest of Poisson distribution (Clark and Evans, 1954) since beetles can fly in any direction. The average flight distance beetles would fly before being intercepted by another tree can be calculated from Eq. (1) for different numbers of trees (K) per km^2 and different tree radii (Fig. 1).

If beetles fly forward with a random component until nearly striking a trunk, they might be able, at best, to instantly determine the susceptibility of a tree without the need to land. In this case, the flight speed would be the maximum of 2 m/s while searching for hosts. More likely, beetles must land on a tree for a period of time, possibly to bore through the outer bark, before they can determine the resistance of a potential host (Elkinton and Wood, 1980). This 'testing time' per tree is not known for

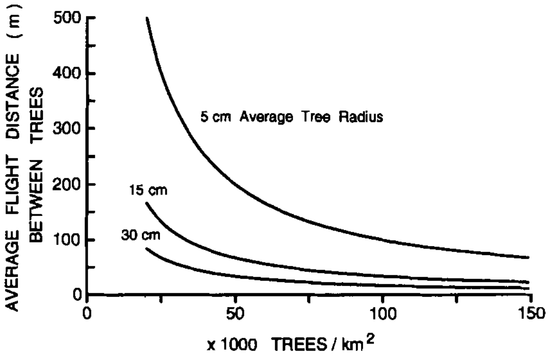

Fig. 1. Expected average flight distance a bark beetle would fly before striking a tree depending on the density of trees at three specific diameters.

any species of bark beetle, but can be hypothesized to range up to several hours. The effective speed (S) of a beetle would then be less than the flight speed (S_f) as found from the following equation:

$$S = \frac{D}{(D/S_f) + L} \qquad (2)$$

where L is the landing time on each tree.

The time required for the first beetle of a population to find a tree is next considered. Let R = radius of a tree trunk in m (e.g. 0.15), K = number of trees (e.g. 50 000), T = time, S = flight speed in m/s (e.g. 2), N = number of initial insects (e.g. 9000), and A = area in m^2 (e.g. 1 000 000), then the first beetle intercepts a tree in the forest after:

$$T = \frac{A}{2RSKN} = 0.0037\ \mathrm{s} \qquad (3)$$

This time is short indeed since it represents the time before the first of any beetles in the population contacts a tree.

The iterative equations that follow were derived by summing the times required for each individual of the population to intercept a tree trunk. K can also represent the number of susceptible trees rather than all trees, and would then be a small percentage of the number of trees in the forest. How many susceptible trees is a matter of conjecture and depends on forest conditions, but was varied in the models from 1 to 1000 trees/km^2. Also, the time a beetle can search is ill-defined but could only occur when the temperature was over 19°C and while the beetle was able to fly (Annila, 1969; Byers and Löfqvist, 1989). In most models, 8 h was used since it is known that *I. typographus* can fly this long on flight mills, and longer if allowed to feed on spruce and take intermittent flights (Forsse and Solbreck, 1985; Forsse, 1991). Thus, the time (T) for a certain proportion (P) of the initial population (N) to find the rare susceptible trees (K) can be found with the following iterative equation:

$$T = \sum_{C=0}^{NP-1} \frac{A}{2RSK(N-C)} \qquad (4)$$

where C is the catch or encounters with susceptible trees. The relationship between hours searching by 9000 beetles at an effective maximum speed of 2 m/s (no landing per tree) in a 1 km^2 area for several densities of susceptible trees (1 to 1000/km^2) where all 50 000 trees have a radius of 0.15 m is shown in Fig. 2 (from Eq. (4)). All beetles find the susceptible trees (at 1000/km^2) within a few hours, while 15.9% of the population find susceptible hosts in 8 h if there are only 10 of these trees per km^2 (0.02% of all trees).

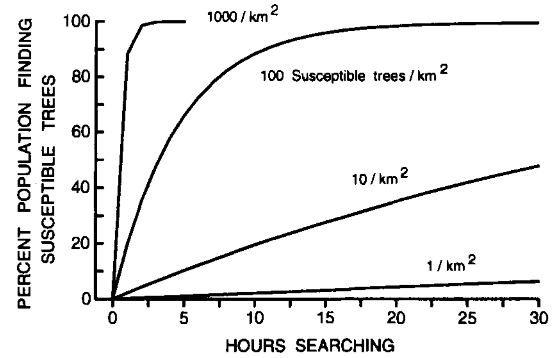

Fig. 2. Effect of time (hours searching) on the percent of the simulated bark beetle population finding susceptible trees (1 to 1000/km^2) in a forest of 50000 trees/km^2. All trees have a radius of 0.15 m and beetles are assumed to fly at 2 m/s (0 s landing per intercepted tree).

The length of time a beetle tested a tree they landed upon would affect the effective speed (S) during an 8 h search and consequently the proportion

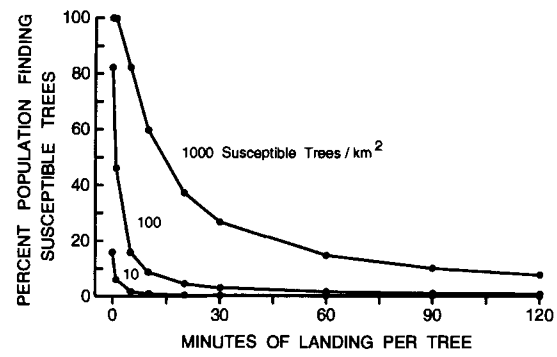

Fig. 3. Effect of varying the time a beetle lands on an intercepted tree to test its susceptibility on the percent of the population of 9000 searching beetles that find 10 to 1000 susceptible trees in a forest of 50000 trees each of 0.15 m radius during an 8 h period in a 1 km^2 area (beetles fly at 2 m/s between landings).

of the population finding susceptible hosts (Fig. 3, using Eq. (2) and Eq. (4)). The number of beetles from the population of 9000 searching in the forest that find susceptible hosts in 8 h depends on the density of these hosts (e.g., 1 or $10/\text{km}^2$) and the time spent testing trees landed upon (Fig. 4). For example, if beetles on average test trees they land upon for 20 min and there are 10 trees/km^2 available for colonization, then 42 beetles find these trees, or an average of 4 beetles per tree (Fig. 4). These beetles, by definition, are able to attack the susceptible hosts and produce aggregation pheromone. The pheromone attracts beetles from several meters and would, in effect, increase the radius of the tree, causing more beetles to find these trees.

The entire population of beetles flying at maximum effective speed (2 m/s) would find ten widely scattered susceptible hosts in 8 h if aggregation pheromone from beetles in these trees attracted beetles within an effective radius of 15 m (Fig. 5). If the effective speed of beetles was only 0.0092 m/s due to landing for 2 h on each tree tested, then 7.66% or 689 beetles (69/tree) locate susceptible hosts in 8 h (Fig. 5). This indicates that when the few susceptible trees are located by a small proportion of the population and they produce pheromone, a much larger proportion of the population can then find these effectively larger trees. However, the process is gradual since each beetle that finds the tree and produces pheromone only increases the tree's effective radius a small amount. This increase in radius increases the rate at which beetles arrive on the tree which in turn increases the radius and so on.

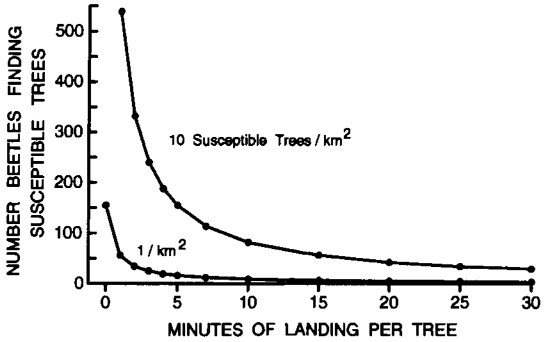

Fig. 4. Effect of varying the time a beetle lands on an intercepted tree to test its susceptibility on the number of beetles in a population of 9000 beetles that find 1 or 10 susceptible trees in a forest of 50 000 trees each of 0.15 m radius during an 8 h period in a 1 km^2 area (beetles fly at 2 m/s between landings).

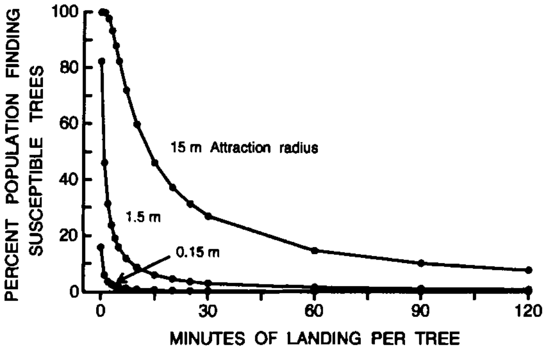

Fig. 5. Effect of varying the time a beetle lands on an intercepted tree to test its susceptibility on the percent of the population of 9000 searching beetles that find 10 susceptible trees in forests of 50 000 trees of three different diameters during an 8 h period in a 1 km^2 area (beetles fly at 2 m/s between landings).

The effective attraction radius (EAR) is a method for comparing the relative strengths of semiochemical attractants regardless of the population density of flying insects (Byers et al., 1989). The EAR represents a spherical radius (in the simulations a circular radius) that would be needed by a passive trap (without baits) to catch the same number of insects as a baited trap (or attractive tree). A synthetic pheromone bait for *I. typographus* releasing 50 mg/day methyl butenol and 1 mg/day *cis*-verbenol approximates that released by at least 150 males (Birgersson et al., 1984), and this bait had an EAR of about 2 m (Byers et al., 1989). Thus, assuming a linear increase in radius (Y) with the number of beetles attracted (1:1 sex ratio), then $Y = X/150 + 0.15$ gives a radius of 2 at 300 beetles (Fig. 6). Perhaps a more realistic relationship yielding the same radius of 2 at 300 beetles is $Y = 2\ln(X + 1)/\ln 300$ (Fig. 6) since attraction rates of insects commonly are related logarithmically to pheromone release rates (Byers and Wood, 1981; Tilden and Bedard, 1985; Byers et al., 1988).

The dynamic process of host-finding and increase of effective attraction radius of attacked trees can now be modeled. Eq. (4) is used with a modification for R with $P = 1$. As each beetle (C) finds a tree, the average effective radius of susceptible trees with an initial radius $R = 0.15$ m increases linearly as in Eq. (5)

$$T=\sum_{C=0}^{NP-1}\frac{A}{2\left(R+\dfrac{C/K}{150}\right)SK(N-C)} \tag{5}$$

or logarithmically as in Eq. (6).

$$T=\sum_{C=0}^{NP-1}\frac{A}{2\left[R+\dfrac{2\ln((C/K)+1)}{\ln 300}\right]SK(N-C)} \tag{6}$$

These equations were used to generate the curves shown in Fig. 7A and B, respectively. Initially as each beetle C finds a susceptible tree, the effective radius increases and rapidly allows more beetles to find these trees, but then the population density declines gradually reducing the rate of recruitment in spite of the large effective radius (Fig. 7A,B). The rates at which the effective radii are increased depend on the population density, at higher densities the radii are increased rapidly and catch proportionately more of the population (Fig. 7A,B). When the beetles can not produce pheromone and thus do not change the effective radius of a host tree, then the percent of the population finding trees is not affected by the population density (dashed line in Fig. 7B).

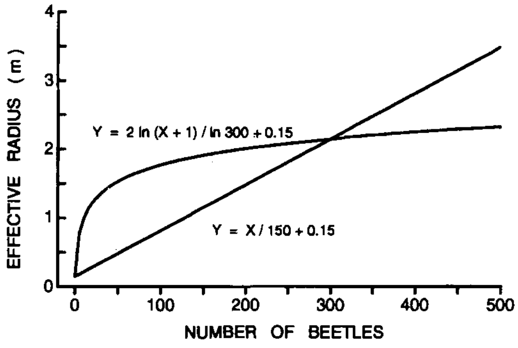

Fig. 6. Theoretical effective radius of susceptible trees under attack by bark beetles in which aggregation pheromone effectively increases the tree's radius depending on the number of beetles finding the these trees and producing pheromone. The logarithmic and linear relationships intersect at an effective radius of 2 m and 300 beetles (see text for more details).

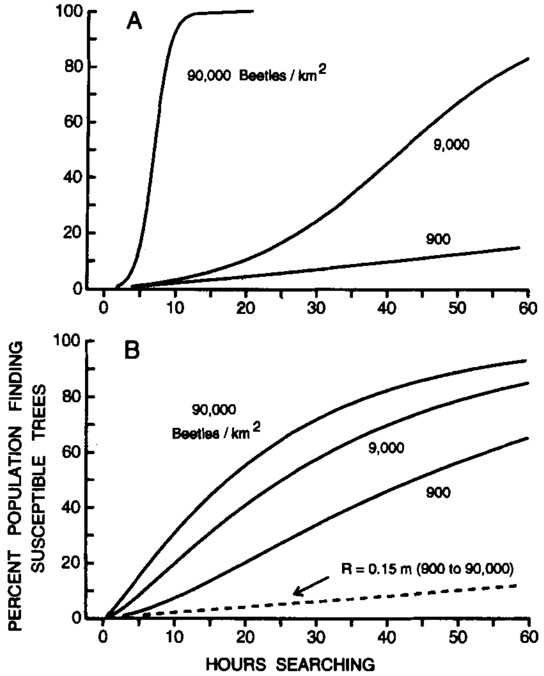

Fig. 7. A. Effect of time (hours searching) on the percent of simulated bark beetle populations (900 to 90000) finding 10 susceptible trees in a forest of 50000 trees/km^2 in which the effective radius of susceptible (attacked) trees increase linearly (from Fig. 6) as beetles find the susceptible trees and produce pheromone (from Eq. (5)). B. Effect of time (hours searching) on the percent of simulated bark beetle populations (900 to 90000) finding 10 susceptible trees in a forest of 50000 trees/km^2 in which the effective radius of susceptible (attacked) trees increases logarithmically (from Fig. 6) as beetles find the susceptible trees and produce pheromone (from Eq. (6)). Beetles are assumed to fly at 2 m/s but land for 5 min on intercepted trees to test their susceptibility.

4. Discussion

Gries et al. (1989) modeled the host-finding of *I. typographus* in a simulated spruce forest of 1 km^2 of 50000 'trees' with 3000 to 16500 susceptible hosts and from 20000 to 100000 flying beetles (values standardized for comparison here). Four sub-models were tested in which 'beetles' had flight paths that were either random or upwind, and with or without the effective size of 'trees' enlarged to simulate primary attraction. They concluded that for random search to be effective in locating susceptible trees and maintaining population levels, a longer flight dispersal is required than is possible (assuming a maximum 3 km flight dispersal). They gave the impression that an 'upwind' flight strategy is what beetles in nature should employ since simulated beetles located most host trees in the upwind model. However, this result must depend on the wind speed since a wind speed matching the flight capacity would not allow upwind search to proceed. Previous models indicate that a straight path would yield the maximum interception rate of susceptible hosts per distance travelled, but that the rate of directional changes (randomness) has surprisingly little effect on the rate of encounters with hosts (Byers, 1991). In fact, beetles could cover more area with less energy expense by flying downwind, especially at higher wind speeds, until perceiving pheromone, whereupon they would fly upwind using anemotactic mechanisms (Byers, 1995). Bark beetles, including *I. typographus*, generally fly away from release sources in all directions unless winds are strong when they appear to passively drift with the wind (Meyer and Norris, 1973; Helland et al., 1984; Byers et al., 1989; Salom and Mclean, 1991; Zolubas and Byers, 1995).

The results here suggest that bark beetles can find hosts at much lower population densities of beetles (9000) and also at lower densities of susceptible trees (1 to 1000) than those tested by Gries et al. (1989) above. The reason beetles find the few susceptible trees in my models even at endemic levels of beetles, as they must do in nature, is that the few pioneer beetles that intercept susceptible trees through 'random' flight recruit other beetles that would not otherwise find these trees, thereby enlarging the effective radius of the attacked tree by means of aggregation pheromone.

Both the model here and that of Gries et al. (1989) consider the distance beetles might disperse. Gries et al. (1989) measured the weight loss of beetles until they choose to feed on a fresh spruce log and compared this weight loss to that of flying beetles in order to estimate a maximum flight capacity of 3 km (before choosing to feed). However, this distance of 3 km reflects the distance a beetle might disperse until feeling 'hungry' rather than a maximum dispersal ability. For example, Jactel and Gaillard (1991) flew *I. sexdentatus* on rotary flight mills connected electronically to a computer. They found that 50% of these beetles could fly more than 20 km and 10% more than 45 km based on about 50 interrupted flights. In another study where *I. typographus* were placed on a flight mills, the longest continuous flight was 6 h and 20 min (Forsse and Solbreck, 1985). This would mean that a few *I. typographus* could fly up to 45.6 km at a speed of 2 m/s without resting (Byers et al., 1989). In the models here, flights were a maximum of 8 h (Figs. 2–5) depending on landing time, or ranged up to 60 h (Fig. 7) with 300 s landing per tree. It might be possible for beetles to replenish their energy and fat reserves for further flight by feeding on host phloem, and they can live for up to 2–3 weeks during the spring dispersal period while attempting flights in a cage on the forest floor (Byers and Löfqvist, 1989).

One major uncertainty of the present models is whether, and for how long, beetles land on a tree to determine its susceptibility. This landing time per intercepted tree was varied from 0 to 2 h (Fig. 3 and Fig. 5). Elkinton and Wood (1980) found that *I. paraconfusus* apparently could not discriminate the host, ponderosa pine, from a non-host, white fir, until after penetrating the outer bark and contacting the phloem, whereupon the beetles left the boring sites in white fir. The time to penetrate white fir bark was not measured precisely but appeared to take several hours. In contrast, this beetle appears to reject another native non-host, incense cedar, much more rapidly since bark was rarely penetrated. If beetles take as long as a day to determine the suitability of a host tree, this would significantly alter the finding-rates suggested here. However, beetles that had to leave relatively resistant trees might be able to feed long enough to renew their flight dispersal ability. Using the same parameters as in Fig. 2, but landing times of 24 h, 9 beetles can find 9 of 100 susceptible trees in 12 h, and then begin to produce pheromone. With the model of logarithmically increasing radii (Fig. 7B), 10% of 90000 beetles that landed 24 h per tree would find 1000 susceptible trees in 31.3 h.

The model here assumes beetles fly equally in all areas. However, many bark beetle species in the spring fly along forest edges (next to a clearcut) when temperatures are just above the threshold for flight (Forsse and Solbreck, 1985; unpublished data). This behavior may be due mostly to temperature conditions, but also could be due to the fact that more susceptible trees are found along the clearings due to solar and wind stress. Later in the flight period, when temperatures are optimal, beetles appear to fly within the forest as well (Forsse and Solbreck, 1985; unpublished data). The boundary in the model should not affect conclusions concerning nature, assuming adjacent forest areas have similar numbers of susceptible trees and beetles – so that immigration and emigration are equal.

The model suggests that long-range primary attraction to host tree volatiles is not necessary for host finding and selection in many species of bark beetle, especially species that have a potent aggregation pheromone. For example, the attraction of the important pest species, *D. brevicomis*, *I. paraconfusus* and *I. typographus* to host volatiles is very weak or non-existent (Moeck et al., 1981; Schlyter et al., 1987), while they are attracted over several meters to aggregation pheromone (Byers, 1983; Byers et al., 1989). Other bark beetles such as *D. ponderosae* and *Scolytus multistriatus* are attracted to either aggregation pheromone or host volatiles (Gore et al., 1977; Gara et al., 1984).

Some bark beetles such as *Pseudohylesinus nebulosus*, *T. piniperda* and probably *Hylurgops palliatus* do not appear to use an aggregation pheromone (Ryker and Oester, 1982; Byers et al., 1985; Klimetzek et al., 1986; Byers, 1992). In these species there may be little selection pressure to evolve aggregation pheromones since they respond over several meters to plant volatiles from wounds and decay that reveal the location of a susceptible host. Evolution of an olfactory response to host volatiles is more probable in species with normally low population densities and widely dispersed host plants.

The host-plant finding model here can be regarded as a predator–prey encounter model where the predator remains stationary; for example, ant lions in their conical pits feeding on ants. Speakman (1986) derived equations for the optimal search speed of a predator when searching for stationary prey of a specified density. His equation for the time spent searching is of interest here and was equal to the reciprocal of the encounter rate. This rate was equal to the search speed multiplied by D, where D was the density of prey along the search path. DeVita et al. (1982) express an encounter rate between individuals of a population moving at random with a specified speed as:

$$Z = \sqrt{2}\, n^2 \sigma \bar{v} \qquad (7)$$

where n is animal density, σ the size, and $\bar{v}$ the mean speed. These encounter rate equations assume a constant density of animal which is not the case in the present model since beetles stay when finding a suitable host tree.

Another related model is the functional response equation of Holling (1959). This well-known equation defines the encounter rate between predator and prey as the amount of area covered in a unit of time multiplied by the prey density and total search time. His equation does not account for depletion of the prey during the period. Royama (1971) and Rogers (1972) modified the Holling equation to account for exponential decay of prey densities over time in the 'random predator equation':

$$N_a = N(1 - \exp[-aPT]) \qquad (8)$$

where N_a is the number of prey eaten during total time T at an attack coefficient a and predator density P and initial prey density of N (with no handling time). This equation uses the attack coefficient (area of search per unit time) to address the effective radius and speed of prey or predators. Their assumption of exponential decay of prey densities agrees with my equations, for example, plotting the decline in population level with time for the parameters with 100 susceptible trees (Fig. 2) yields data fitting perfectly an exponential equation ($Y = 101.3e^{-0.218X}$). In fact, Eq. (8) can be used to answer the same questions addressed here when the attack coefficient is made equal to $2RS$.

The iterative equations with appropriate modifications can be used to describe many kinds of encounters and functional responses in mating and predator–prey systems and thus could be useful as submodels in population dynamic models of greater complexity.

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