ON THE ROLE OF THE TREE IN RELATION TO COLONIZATION BY IPS TYPOGRAPHUS L.

S. BOMBOSCH

Institut für Forstzoologie der Universität Göttingen
Büsgenweg 3
D-3400 Göttingen, Germany

INTRODUCTION

For roughly 200 years it was assumed that trap trees attracted the bark beetle *Ips typographus* by means of specific chemical compounds produced by the tree. After the aggregation pheromone was discovered, the importance of tree volatiles was at first more or less totally denied (Vité 1980).

Since Johann succeeded in proving that the combination of pheromone plus tree is, at times, considerably more attractive than the combination of Pheroprax plus plastic trap (Bombosch et al. 1982, Johann 1986a, 1986b), more attention has been paid to the tree even by pheromone supporters (Bakke 1985, Vité and Franke 1985). What follows is a brief synopsis of the findings thus far obtained on this question at our institute.

FLIGHT--A FUNCTION OF ENERGY RESERVES

After leaving their breeding tree or winter quarters, by no means all beetles react immediately to stimuli from trees or pheromones. A large proportion, on the contrary, fly directly from the forest surroundings into the bright sky. According to investigations by Botterweg (1982) and Gries (1985), the proportion of the total population made up of these migrating beetles and the length of the migratory phase of individual beetles depends on the individual beetles' energy reserves. These are determined earlier by the amount of nourishment at the larvae's disposal. The model calculations of De Jong and Saarenmaa (1985) were very successful in showing these shifts in the nutritional condition of individuals in a population.

These findings allow us to see that an *I. typographus* population contains at least two different groups of individuals: one which migrates and one which does not. The proportion of these two groups is not constant since the population density of the larvae, which is determinant here, depends upon the respective breeding trees available.

VERTICAL SILHOUETTES AND VOLATILES

Let us track the course of the migrating beetles. Their flight into the bright light brings about a great dispersion as a result of which, in addition to a high mortality rate, we can find *I. typographus* everywhere in the countryside (Bakke 1985, Sanders 1984, Gossenauer 1988). Their distribution is not

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uniform, however. The lowest densities are to be found in agricultural areas and in very dense young deciduous forest stands; conifer cultures are also less often visited than older deciduous stands. This indicates that both the vertical silhouette of the trees and the scents specific to spruce are important to the beetles after their migratory flight. This behavior leads to a more concentrated occurrence in spruce stands but also to the beetles' marked presence in deciduous stands. For this reason, according to our calculations, it is not possible to reduce population density with the help of traps (Table 1) (Bombosch in press). Gries et al. (1989) maintain that *I. typographus* would have no chance of survival if it were to find its breeding trees only by accident. As a lone insect, furthermore, it is not in a position to successfully colonize healthy spruce trees. This migratory portion of the beetle population, operating on its own, is dependent upon suitable fallen or standing stems. The silhouette and the odoriferous quality of the tree itself probably combine to help the beetles find such stems. All earlier attempts to increase the efficiency of trap trees, as recorded in the textbooks, point in this direction. To date, as far as I know, it has not been possible to analyze the chemical structure of the odoriferous substances produced by the tree. It is very unlikely that α-pinene alone is the attractive substance (Vité 1980) because if that were the case all conifers would be colonized. After the beetles have penetrated the bark, the attractiveness of the trees attacked is intensified by the secretion of pheromone. Genuine pioneer beetles initiate this process; every additional beetle that is attracted and produces pheromone in its turn increases the allure of the potential breeding place. In tests with the method developed by Dedek and Pape (1988a, 1988b) of applying methamidophos as an insecticide that takes effect only in the bark, it was noted that the beetle infestation on standing trees was concentrated at a few meters surrounding the pheromone dispenser, whereas beetles appear to colonize the entire length of fallen trees. After landing, then, these beetles seem to spread more intensively in a horizontal direction than vertically.

Numerous other species besides *I. typographus* colonize fallen spruce stems. According to Vité and Franke (1985), the range of species on these trees is determined by the types of change that occur in the bark. A dry change leads to colonization by *I. typographus*, *I. amitinus*, *P. chalcographus*. A wet change, whereby ethanol is released, is responsible for colonization by *Xylosandrus germanus* and *Trypodendron* sp. etc. Within these groups, diverging pheromones are suspected (Vité and Franke 1985) of causing the delimitation of the individual species' territories. In spring 1989 *I. typographus*, *I. amitinus*, *P. chalcographus*, and *P. polygraphus*, and also *T. lineatum* were found in very close proximity to each other on 3-m-long lower stem sections in the Solling hills.

TEMPERATURE EFFECTS ON FLIGHT

The demands, at least of the teetotallers, seem therefore to cover a very large range, and the importance of the deflecting pheromones is not exactly paramount. In my opinion, when trying to find out the causes for the different species' distribution on the stem, more attention should be directed to the temperature necessary for setting them into flight than has hitherto been paid. In 1987 we were able initially to observe a strong flight of *I. amitinus* in two low mountain ranges. When *I. typographus* flew 3 weeks later after a sudden onset of cold weather, it was able to colonize only those places that had been left open by its predecessor. It is thus quite conceivable that an exact spatial separation of the individual species occurs according to temperature thresholds when the temperatures rise slowly in spring, but that the commingling described above occurs when the temperature suddenly turns hot, using all species' thresholds.

Table 1. Calculation of the reduction of the population of *Ips typographus* by different success of trapping

Parameter	Spruce clearcuts 10 ha	Spruce stands 90 ha	Total population	Reduction rate %
Distribution (Johann, Gossenauer)	20%	80%		
Assumed population/ha	200	800		
Total	2,000	72,000	74,000	
Reduction on clearcuts				
Johann, Beuke (-17%)	-340	72,000	73,680	0.4
Weslien (-30%)	-600	72,000	73,400	0.8
Hypothetical (-50%)	-1,000	72,000	73,000	1.3
Assumed population (Bakke)	6,000	68,000	74,000	
Reduction on clearcuts				
Johann, Bueke (-17%)	-1,020	68,000	72,980	1.4
Weslien (-30%)	-1,800	68,000	72,200	2.4
Hypothetical (-50%)	-3,000	68,000	71,000	4.0
Hypothetical (-100%)	-6,000	68,000	68,000	8.1

TEMPERATURE AND LIGHT EFFECTS ON PIONEERS

In contrast to fallen trees, healthy, standing stems cannot be colonized by single beetles since for that a simultaneous attack by many individuals is necessary. Aggregation is supposed to materialize as single, pioneer beetles land on the tree and then attract more and more beetles by the production of contact pheromone, until finally the number of insects necessary for a successful attack is present (Vité 1980). This hypothesis assumes that beetles, having once landed, do not fly away again, and leaves open the question by which criteria the first beetles choose their landing place and what it is that triggers the mass attack.

Our observations suggest that pioneer beetles do not play a part in the colonization of standing trees. On standing spruce trees we have never as yet found increasing congregations before the beetles' penetration. On the contrary, in the spring of 1989 we found, apart from numerous stem sections on the ground that had been attacked, single standing trees exhibiting "Spechtspiegel" on the lower part of their stems. Spechtspiegel are small pale patches appearing on the bark where the squamae have been removed by woodpeckers or other birds in search of xylophages. We also found one tree with ten, and three trees each with one, unsuccessful boring attempt. This indicates that the bulk of the insects in the *I. typographus* population we observed was searching for wood lying on the ground, but that a few individual insects reacted to standing trees and attempted to attack them (e.g. the Spechtspiegel). An attack on standing trees does not, therefore, require presence of many beetles reacting in the same way. It was also evident that Spechtspiegel and boring attempts did not occur at random around the stems, but always faced south to southwest. This observation accords with the long known fact that when standing trees are attacked, mass propagation in a beetle "nest" is usually to be found where the sun shines in the afternoon. As the triggering stimulus for beetles in search of suitable standing wood, differences in the trees' warmth may be of more decisive importance than their scents. The number of beetles attacking, however would not depend on the strength of the allurement, but on the number of beetles reacting to particular degrees of warmth of the trees. These may represent the nonmigratory portion of the population mentioned earlier. The fact that an attack on a standing tree always occurs in the immediate vicinity of an earlier attack in a beetle nest speaks in favor of this hypothesis. It can also be observed that the infestation of wood lying on the ground subsides in the course of a gradation (Bombosch 1954). This may be the result of a deterioration in the larvae's nutrition due to increasing population density together with a simultaneous reduction of breeding possibilities causing a continuous reduction in the number of migrating individuals. Since the relationship between the number of beetles and suitable breeding places is not constant, the question why each blowdown that is colonized by *I. typographus* does not endanger neighboring stems can still be answered. But the question to what extent this part of the beetle population reacts to pheromone traps still remains completely open. The investigations begun by Sahota and Peet (1988), whose objective is to characterize the quality of bark beetle populations, should contribute to considerable progress in the elucidation of this complex of questions.

SUMMARY

When assessing *I. typographus* populations, one should differentiate between the proportion of migratory and nonmigratory individuals. The reason for this difference may be found in changes in the larvae's nutrition. Individuals in the migratory proportion set off alone and are dependent on finding suitable stems. They search for them purposefully, probably because of the silhouette and primary attractive substances of these trees. The first to colonize intensify the tree's allurement by pheromone secretion. They are genuine pioneer beetles.

With respect to breeding suitability of the tree, the beetles' requirements do not seem to be as restrictive as has hitherto been assumed, since *I. typographus* and *T. lineatum* can be found next to each other on the same stem. As for spatial distribution of the individual species on the stem, not only deflecting pheromones but also the temperature conditions and differences in the beginning of the flying period of the individual species should be considered. In beetle nests, the attack of standing trees may be caused by the nonmigratory portion of the beetle population. Temperature differences between the trees may function as directing stimuli. A mass attack would not be determined by intensity of the allurement, but by the number of nonmigratory beetles in the given population.

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