THE EFFECT OF WOODPECKER PREDATION ON WOOD-BORING LARVAE OF FAMILIES SIRICIDAE (HYMENOPTERA) AND MELANDRYIDAE (COLEOPTERA)[1]

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Can. Ent. 99: 978–985 (1967)

Abstract

Woodpeckers consume wood-boring larvae of families Siricidae and Melandryidae leaving three distinct types of mark on the tree. The distribution of marks in relation to decreasing prey population indicates that tapping is the principal means of locating larvae. Forty per cent of siricids and two per cent of melandryids are consumed by woodpeckers on individual feeding trees; as siricid population increases the proportion of larvae taken decreases.

Introduction

The present study was undertaken in a small forest area near Fredericton, N.B. Red spruce, *Picea rubens* Sarg., and black spruce, *P. mariana* (Mill.) B.S.P., were the most common species, but there was much balsam fir, *Abies balsamea* (L.) Mill., and eastern white pine, *Pinus strobus* L. Hardwoods consisted mainly of white birch, *Betula papyrifera* Marsh., and trembling aspen, *Populus tremuloides* Michx. Much of the balsam fir was dead or dying.

The study attempted to measure the effect of woodpecker predation on larval populations of the woodwasp, *Sirex cyaneus* Fab. (Hymenoptera: Siricidae), and the beetle *Serropalpus substriatus* Hald. (Coleoptera: Melandryidae), in individual

[1]Contribution No. 5, Faculty of Forestry. Based on a thesis submitted in partial fulfilment of the requirements for the degree of Master of Science in Forestry, at the University of New Brunswick, May 1964. The study, of which this forms a part, was supported by a grant in aid of research from the National Research Council of Canada.

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trees. Siricids and melandryids have a 2- to 3-year larval and pupal developmental period in the sapwood, so woodpeckers can reach them only by excavating wood, thus leaving on trees a permanent record of the numbers of larval chambers exposed. These marks were analyzed on several trees to find predation percentage on larvae and to interpret how predators locate prey within the wood.

In extensive stomach analyses of North American woodpeckers, siricid larvae as part of the diet are either rarely mentioned (Beal 1911; Collinge 1915; Reisch 1928) or are considered unimportant items (Middlekauff 1960), but for European woodpeckers, siricid larvae are mentioned more frequently (Evans 1922; Scheidter 1923; Palmer 1958). No mention is made of melandryids in woodpecker diets.

Within the study area three species of woodpecker were observed, the arctic three-toed woodpecker, *Picoides arcticus* (Swainson), the northern downy woodpecker, *Dryobates pubescens medianus* Swainson, and the eastern hairy woodpecker, *D. villosus villosus* Linnaeus. There was no indication which species was responsible for feeding marks or if all three species were involved. The arctic three-toed woodpecker was the only species observed feeding on sample trees.

Woodpecker predation marks on sample trees were classed as follows:

(1) Class *a*, a single peck on the bark, usually leaving an imprint of the beak tip in the wood (Figs. 1 and 2),

(2) Class *b*, penetration of the wood, leading directly to a larval chamber (Figs. 3 and 4), thus indicating a successfully located prey,

(3) Class *c*, similar to class *b* in appearance but not leading to a chamber in the wood.

The origin of class *a* marks may have one or more of four explanations. They may result from birds drumming on trees bordering territories, from pecking at insects on the bark surface, from attempts to reach insects under the bark, or from birds testing the resonance of the wood in their search for wood-boring larvae. One aim of the study was to ascertain whether *a* marks are distributed at random or whether they follow the gallery system within the wood.

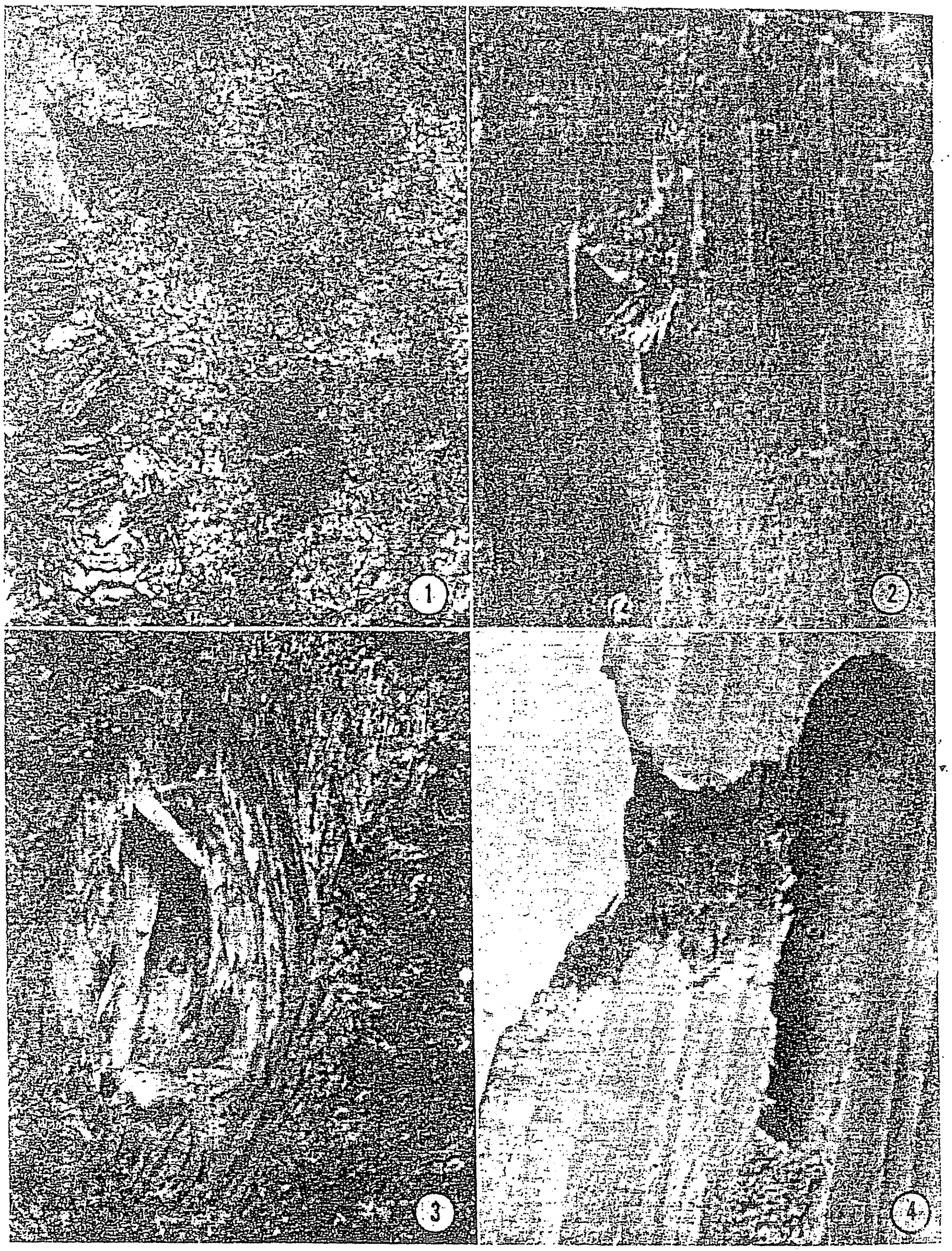
Blackford (1955) suggests that the irregular woodpecker drilling pattern on Douglas fir boles might represent accurate outlinings of larval dispersal beneath the thick bark and that it might indicate tunnelling habits of bark borers. In this study overlay diagrams were constructed to show the relative positions of woodpecker marks on the surface and borer galleries in the wood, and the actual numbers of marks and larval population were analyzed.

Methods and Results

The work was divided into two distinct phases. In phase I the relation between distribution of woodpecker marks on the wood surface and borer galleries within the wood was investigated. This phase involved intensive study of sections of two trees. In phase II nine dead trees were sampled to determine the approximate level of predation percentages on larvae.

Phase I: Two trees, A and B, which showed a high intensity of woodpecker attack, were studied. The woodpecker marks on nine 6-in. sections from three regions on the trees were plotted to scale. Each section was gradually cut from the surface so that all borer galleries were revealed and these were plotted to scale to superimpose the marks.

Phase II: Nine trees, numbered one to nine, ranging in size from 3 to 6 in. in diameter and 25 to 36 ft in height, were selected to show a wide range of intensity of woodpecker attack. The lower 12 ft of the trees were cut into twelve 1-ft



FIGS. 1–4. 1, two *a* marks on the surface of bark. 2, an *a* mark showing an imprint of the beak tip in the wood. 3, surface view of a *b* mark showing access into a siricid larval chamber. 4, a radial longitudinal view of a *b* mark leading to a siricid larval chamber.

TABLE I

Coefficients of correlation between numbers of *a* marks and total length of galleries within quarter sections at three heights on trees A and B

Tree	Height (ft)	d.f.	Coeff. of correl.	Prob.
A	0 – 1.5	10	0.83	99%
	16.0–17.5	10	0.20	—
	31.5–33.0	10	0.48	—
B	0 – 1.5	10	0.70	95%
	16.0–17.5	10	0.29	—
	31.5–33.0	10	0.16	—

sections and the three classes of woodpecker marks and adult insect emergence holes were counted. Each 1-ft section was halved and the lower half used as a sample to estimate larval population; thin slices were split tangentially from the surface and the larvae encountered were enumerated by species. Thus, for every 1-ft section the following data were available:

(a) total population of two larval species in the wood,
(b) numbers of each species taken by woodpeckers,
(c) numbers of class *a* and class *c* marks.

For trees A and B, coefficients of correlation were calculated for the relationship between numbers of class *a* marks in each quarter section and corresponding total gallery lengths, in three groups according to height above ground (d.f. = 10); these are shown in Table I.

A summary of basic data from trees 1 to 9 is shown in Table II. The coefficient of correlation was calculated for the relationship between the sums of the numbers of class *a* marks and siricid population in 1-ft sections of six trees (d.f. = 10) and a significant straight-line relationship could be drawn (Fig. 6). Also from trees 1 to 9 numbers of siricid larvae taken by the predators were plotted against larval population in 4-ft sections. The best-fitting line was calculated by computer and found to be a second-order curve (Fig. 7). Values lying on this curve were converted into predation percentages, plotted against the same base line of larval populations, and a mean curve drawn (Fig. 8).

Siricid galleries are usually vertical on the trees and never branched, while melandryid galleries are usually horizontal and often branched; these characteristics enable identification of the larval species taken by woodpeckers at *b* marks.

TABLE II

Number of woodpecker marks, population of two species of larvae, predation per cent, and ratios $b/(b+c)$ and a/b on three height regions on trees 1 to 9

Height (ft)	No. of marks			Siricid		Melandryid			
	a	*b*	*c*	Pop.	% pred.	Pop.	% pred.	$b/(b+c)$%	a/b
0– 4	794	97	71	228	41.7	73	2.7	58	8.2
4– 8	489	44	28	98	43.9	82	1.2	60	11.1
8–12	221	10	12	53	17.0	42	1.4	45	22.1
Total	1504	151	111	379		197			
Mean					38.8		2.0	57	

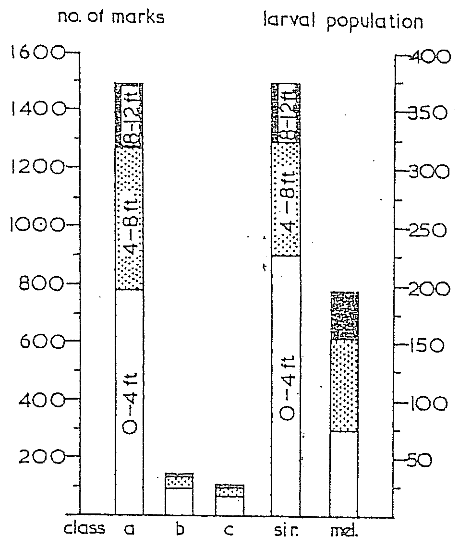


Fig. 5. Histogram showing the intensity of woodpecker attack at three heights on trees 1 to 9, and its relation to the distribution of siricid and melandryid larvae.

Figures 1 to 4 show the appearance of *a* and *b* marks. Class *c* marks are similar in size and shape to *b* marks which are generally oval and orientated vertically on the tree. The average mark from trees A and B measured 0.26 by 0.45 in., and in class *b* the average depth at which larvae were taken by woodpeckers was 0.34 in.

The numbers of *a*, *b*, and *c* marks and larval population both decreased with height on the trees (Fig. 5). The overlay diagrams showed that attack does follow gallery distribution, but there is little support for the suggestion that woodpeckers locate larvae by following the course of single galleries.

Trees A and B were used for feeding by arctic three-toed woodpeckers at the time of sampling, so all larvae are assumed to have been currently available to the predators; also, since there were few insect emergence holes, total larval gallery length in the wood provided a suitable measure of current larval infestation. If indeed woodpeckers do tap tree surfaces to test the wood for larvae, the *a* marks would be related to the amount and distribution of gallery system. Table I, showing coefficients of correlation between numbers of *a* marks and gallery lengths, indicates that linear relationships do exist for the lower sections of trees A and B, but not for the middle and top sections. In six trees a significant linear relationship between numbers of *a* marks and siricid population in 1-ft sections up to a height of 12 ft (Fig. 6) further suggests that numbers of pecks might reflect the intensity of search for prey and actual food content in the wood.

Efficiency of excavation for prey is indicated by ratios of number of successful strikes (*b* marks) to total number of attempts ($b + c$) and calculated in Table II for three height regions on trees 1 to 9. In the region up to 8 ft, efficiency is approximately 60% while at 8 to 12 ft it decreases to 45%.

Predation per cent, calculated as 100 $\times$ number of larvae consumed by woodpeckers/total population, is approximately 2% of melandryids and 40% of siricids. For siricid larvae, predation percentages are plotted against total populations in

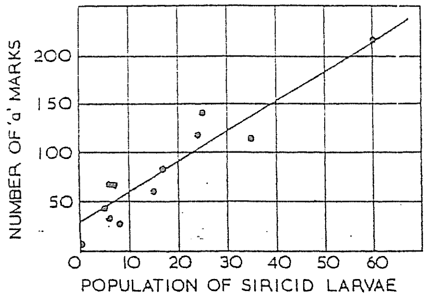


FIG. 6. Relationship between the total numbers of *a* marks and populations of siricid larvae at 1-ft intervals on trees 4 to 9.

4-ft sections of trees 1 to 9 (Fig. 8). For the region up to 8 ft above ground level the points describe a downward concave curve, showing that percentage of prey consumed is highest when prey population is least and that this percentage decreases at a decreasing rate as prey population rises. Points obtained between 8 and 12 ft on the trees are distributed randomly. Table II shows that in the higher region predation percentage is only 17 while in the lower 8 ft it is 42. The scattered larval populations above 8 ft on the trees are less frequently located by woodpeckers, indicated by the difference in distribution of points between the two regions in Fig. 8.

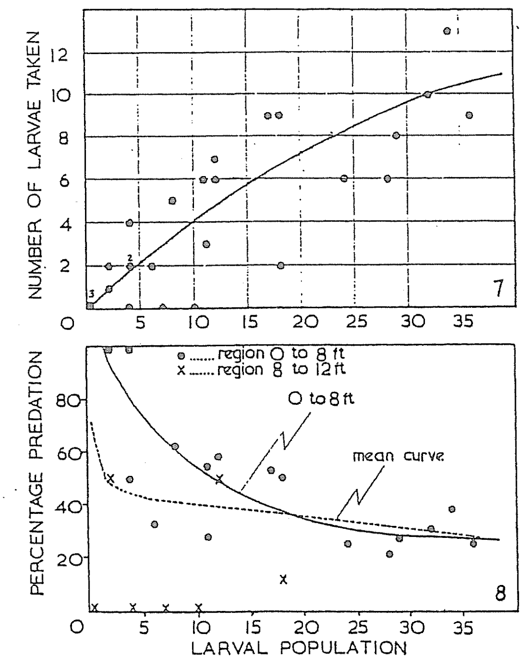


FIG. 7. Relationship between numbers of siricid larvae taken by woodpeckers and total larval population in 4-ft sections of trees 1 to 9.
FIG. 8. Relationship between proportion of siricid larvae taken by woodpeckers and total larval population in 4-ft sections of trees 1 to 9, showing the difference between two regions on the trees.

Discussion and Conclusions

It is commonly assumed that woodpeckers use tapping as an important means of locating larvae, but other senses such as smell and hearing may also play a part. Roberts (1932) suggests that wood-boring larvae make sounds which could be heard by a bird with a keen sense of hearing. However, this probably applies to larvae of sawyer beetles (Coleoptera: Cerambycidae), which constitute one of the most important items in the diet of downy, hairy, and arctic three-toed woodpeckers (Beal 1911) and which can be heard even by the human ear from some distance. Roberts also suggests that larvae may have an odour sufficiently strong to be detected by woodpeckers. Forbush (1927) records that, after a woodpecker strikes its bill into wood, it holds the point of one mandible in the dent so that vibrations of the insect are conveyed through the beak and skull of the bird to the brain. This again may apply to the location of cerambycid larvae which have stronger mouthparts than siricids and which are more active in the wood. Since woodpecker *a* marks follow distribution of siricids and melandryids up the tree (Fig. 5), they are taken to indicate the extent of search and to be related to larval location. This assumption is supported by evidence in Fig. 6 of a significant relationship between numbers of *a* marks and total population of larvae available.

Feeding birds were not observed on trees 1 to 9 near the time of sampling, so many melandryids may have infested trees only since the last visit by woodpeckers, thus explaining a low percentage predation on this species. Many larvae, however, were in late stages of development during sampling so that this supply of food was probably available to birds for several months, yet it was almost entirely ignored. Food preferences among alternative prey in the area and difficulty of larval location owing to irregular boring habits of melandryids compared with siricids are two factors which may contribute towards the low predation intensity.

As prey population becomes more scattered with height up the trees, a larger surface area of wood is required to be tested per larva and the ease with which larvae are located by means of tapping is reduced. To illustrate this, the number of *a* marks for each larva consumed (*b* mark) in the lower 4 ft of the tree averages 8.2, while between 4 and 8 ft the average is 11.1 and between 8 and 12 ft it is 22.1 (Table II). Thus, more tapping is required per larva consumed as density decreases up the tree.

The shape of curve shown in Fig. 7 of number of prey consumed against prey density corresponds to that found by Holling (1959) for a basic type of functional response, showing that number of prey consumed increases at a progressively decreasing rate as density of prey rises. Holling states that this functional response is similar to those of insect parasites and predators. Figure 8, showing predation percentage against prey density, indicates that no relationship exists for the region 8 to 12 ft on the trees; prey from scattered larval populations are less frequently located by the predators and when one or two are consumed a large proportion is represented. The curve in Fig. 8 representing the lower 8 ft on the trees shows that percentage of prey consumed decreases as prey density increases. The downward concave predation curve obtained in this study has appeared in previous works (Tothill 1922; Tinbergen 1960). Tinbergen found that in Dutch pine woods, tits destroyed a smaller proportion of their prey, pine beauty moth caterpillars, as they became more abundant and he explains this on the probability of encounter hypothesis. Similarly, in his study on fall webworm in New Brunswick, Tothill counted webs pulled out by birds and found that the proportion of webs destroyed was much higher when caterpillars were scarce than when they were abundant.

An important predator characteristic is preference for a prey. Different woodpecker species probably display different functional response towards particular prey species. Three species of woodpecker were seen on the study area, the arctic three-toed, hairy, and downy woodpeckers, so the total effect on siricid populations may have been somewhat different had only one species been present. Besides food preference, ability to detect, capture, and kill prey are important characteristics. Alternative food supply is important in its 'buffering' effect (Holling 1959). Alternative sources of food on the study area included bark beetles, other wood-boring coleopterous larvae, and ants. The combination of these factors has probably reduced considerably the effects of the functional response.

This study makes no reference to predation effect on insect populations over a large area, but only on localized populations in individual feeding trees. Many dying or dead trees in the area contain siricid and melandryid larval populations untouched by woodpeckers so the overall predation effect is considerably smaller than that measured in this study.

Acknowledgments

I wish to thank Professor N. R. Brown and Dr. L. J. Mook of the Forest Research Laboratory at Fredericton for their guidance and advice throughout the course of the study and for their criticism of the manuscript.

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(Received 28 February 1967)