

8-1-1976

TB81: Investigations on the Life History and Habits of *Pityokteines sparsus* (Coleoptera: Scolytidae)

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INVESTIGATIONS ON THE LIFE HISTORY AND HABITS OF PITYOKTEINES SPARSUS (COLEOPTERA:SCOLYTIDAE)

G. P. Hosking and F. B. Knight

**LIFE SCIENCES AND AGRICULTURE EXPERIMENT STATION
UNIVERSITY OF MAINE AT ORONO**

TECHNICAL BULLETIN 81

AUGUST 1976

INVESTIGATIONS OF *PITYOKTEINES SPARSUS*

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AND HABITS OF *PITYOKTEINES SPARSUS*
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ACKNOWLEDGMENTS

The authors wish to thank Seven Islands Land Company for the provision of the study site, Louis O. House IV for generous field assistance, and Dr. Peter J. Alma for his review of this paper. The project was supported by a grant from the David Henry Scholarship Fund and was sponsored by the New Zealand Forest Service.

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SUMMARY

Pityokteines sparsus males initiated nests in dead and dying balsam fir primarily in the late summer in northern Maine. A nuptial chamber was constructed beneath the bark after which from 1 to 6 females were admitted to the nest. Each female cut a gallery of 37 cm mean length about the circumference of the host tree and deposited an average of 21 eggs in niches cut in the sides of the gallery. The larvae hatched after 10 to 12 days, mined at right angles to the parent gallery, and pupated after 4 to 5 weeks. The insect most commonly overwintered in the adult stage, emerging from the pupal chamber in the spring. Parent insects emerged from established nests and produced a second brood during the summer.

The developmental cycle of *P. sparsus* was influenced by variations in microclimate associated with changes in forest canopy cover. Spring emergence was two weeks earlier for broods in open areas, as opposed to those under full canopy, in 1974. During the same summer the rate of larval growth was twice as fast in the open compared with full canopy conditions.

The peak flight period for the insect occurred around the 11th of June in the Oxbow area, males flying 4 to 6 days before females. Flight had virtually ceased by early July. Temperature appeared to be the major factor influencing emergence and flight initiation. The insect's flight altitude within the stand varied, showing a slight concentration between 3 and 10 meters. Although males were less common than females in the population they were caught more often by window traps, suggesting a basic difference in flight behavior between the sexes.

The preferred feeding zone for the insect did not correspond with the zone of highest calorific value, but was correlated with the availability of nitrogen. The assimilation efficiency of the insect was determined to be 46%, strongly suggesting the utilization of cellulose. A food use efficiency of 6% was calculated for *Monochamus scutellatus*.

INTRODUCTION

The research reported in this paper was carried out over a 2½ year period from September 1972 to March 1975. The primary objectives of the study are summarized as: (1) to investigate the life history of *Pityokteines sparsus* (LeConte) in the Oxbow area of northern Maine; (2) to study the seasonal and daily flight behavior of the insect; (3) to investigate the food energy relations of the species.

Background

The spruce-fir forest of northern Maine contains predominantly red spruce, *Picea rubens* Sarg., and balsam fir, *Abies balsamea* (L.) Mill., with minor components of white spruce, *Picea glauca* (Moench) Voss; black spruce, *Picea mariana* (Mill.) B.S.P.; northern white-cedar, *Thuja occidentalis* L.; eastern white pine, *Pinus strobus* L.; tamarack, *Larix laricina* (Du Roi) K.Koch; eastern hemlock, *Tsuga canadensis* (L.) Carr.; red maple, *Acer rubrum* L.; sugar maple, *Acer saccharum* Marsh; paper birch, *Betula papyrifera* Marsh; yellow birch, *Betula alleghaniensis* Britton; balsam poplar, *Populus balsamifera* L.; bigtooth aspen, *Populus grandidentata* Michx.; quaking aspen, *Populus tremuloides* Michx.; white ash, *Fraxinus americana* L., and American beech, *Fagus grandifolia* Ehrh., (Hart 1964; Little 1953). Disproportionate reproduction of either spruce or fir following either logging or natural disturbance has led to almost pure stands in many areas.

Balsam fir grows well under conditions of low light intensity and abundant precipitation. It is able to withstand very low winter temperatures. However, the high incidence of butt rot in mature trees leads to increasing susceptibility to wind breakage with age (Bakuzis and Hansen 1965). Wind-broken trees provide a continuous supply of breeding material for both wood and bark-boring insects.

The economic value of balsam fir to the State of Maine is considerable, primarily as a softwood component of paper pulp. The ecology of this species is clearly suited to pulpwood utilization where harvest at an early age leads to reduced losses from wind damage and insect attack.

Spruce budworm, *Choristoneura fumiferana* (Clem.), has undoubtedly been the most destructive insect pest of balsam fir, though others may be important at times. Periodic and prolonged outbreaks of this insect in the coniferous forests of eastern North America have caused widespread mortality of both spruce and fir (Peirson 1950; Greenbank 1956; Turner 1952; Elliott 1960). Repeated heavy defoliation initially suppresses tree growth and may lead to mortality in less than five years (Belyea 1952a). Spray programs have been carried out repeatedly in

both Canada and the USA in an effort to forestall mortality until utilization is possible. The life history, habits and dynamics of spruce budworm have been discussed in some detail by Morris (1963).

Insects other than spruce budworm which may cause periodic mortality of balsam fir in eastern North America include eastern hemlock looper, *Lambdina fiscellaria* (Guen.); balsam woolly aphid, *Adelges piceae* (Ratz.); blackheaded budworm, *Acleris variana* (Fern.); balsam sawfly, *Neodiprion abietis* (Harris), and rusty tussock moth, *Orgyia antiqua* (L.). The insects affecting balsam fir have been reviewed by Clark and Pardy (1972) and Baker (1972).

Belyea (1952a) found *Pityokteines sparsus* the most common bark beetle in recently dead and dying balsam fir in northwestern Ontario. The insect's role, while feeding on dead and dying fir, is of some significance in the pathological deterioration of the tree. A better understanding of the relationship between *P. sparsus* and its host may contribute to our knowledge of the structure and function of the ecosystem in which spruce budworm operates.

Pityokteines sparsus has received little attention from entomologists apart from the occasional occurrence records during forest insect surveys. The species was first described by LeConte (1868) under the name *Xyleborus sparsus*. Original observations on the biology of this insect, made by Peirson (1923, 1927), suggested it was a primary enemy of balsam fir capable of causing rapid tree death. Felt and Rankin (1932) probably quoting Peirson, state that the insect prefers living, vigorous trees. Graham (1923) modified this view somewhat, suggesting the infestation of injured and weakened trees by *P. sparsus* might be an important factor in hastening mortality of balsam fir after spruce budworm attack. After looking at spruce budworm in Maine, however, Blackman (1919) suggested *P. sparsus* was essentially a secondary pest, attacking balsam fir already past recovery. Swaine (1924) briefly mentioned the beetle and stated, "It (*P. sparsus*) can in no sense be considered as primary"

In an investigation into the larval development of three bark beetle species, Prebble (1933) concluded three larval instars for *P. sparsus* on the basis of head capsule width measurements. The biology of the insect was investigated by Belyea (1951) as a section of his doctoral thesis in which he studied the death and deterioration of balsam fir following spruce budworm defoliation. His findings were published in two papers (1952a, 1952b); the first included the insect's relationship to tree death in which he found no involvement, and the second presented some notes on its basic biology. In the latter paper he included a discussion of his field observations with some statistical data on the size and development of nest systems. He did not record any information on

flight behavior, mortality factors, or climatic influences. Studies associated with European members of this genus are briefly reviewed by Belyea (1951).

All publications subsequent to Belyea's work use his papers as their main reference source (Bakuzis and Hansen 1965; Anderson 1960).

We were unable to substantiate either the claim by Craighead (1950) that *P.sparsus* is reported from larch or that of Doane *et al.* (1936) that its hosts include eastern pines, spruce, and larch. Doane *et al.* (1936) further claim *P.elegans* Sw. is commonly found in balsam fir. A misidentification may have occurred since this species, which is very similar morphologically to *P.sparsus* (Swaine 1916), has not been recorded by Belyea (1951) or ourselves. Much of the confusion concerning the hosts of *P.sparsus* probably stems from its close similarity to both *P.jasperi* Sw. and *P.elegans* (Swain 1916).

In the absence of detailed studies, the assumption that *P.sparsus* was a primary enemy of balsam fir, is quite understandable. The insect is commonly found in the fresh phloem of the bole of green trees. However, Baker (1972) is somewhat remiss in stating " *P.sparsus* is frequently injurious to balsam fir, killing large groups of trees. Pines, spruce and larch are also attacked . . ." The larval anatomy of *P.sparsus* is discussed in detail by Thomas (1957) who provides a key based on larval characteristics which separates this species from other eastern bark beetles.

Study area

The study area was located in Aroostook County, Maine, along State Highway 11, 22 kilometers south of Ashland on land managed by Seven Islands Land Company. The area of approximately 4 hectares was divided into two separate, and approximately equal portions (Fig. 1). Both were located within the 200 meter wide strips reserved from cuttings on either side of the highway. The site, situated on the broad crest of an east-west ridge, had a westerly aspect with a slope of about 10°

Spruce budworm defoliation, ranging from very light to very heavy on individual trees, occurred throughout the study area. Only a few trees had died, with strongly suppressed trees being most affected. Considerable wind breakage of balsam fir occurred throughout the site during the two-year study period.

The stand in Area I was composed of 30% balsam fir, 50% red and white spruce, with cedar, white pine, sugar maple, and yellow birch making up the remainder. Area II contained about 60% balsam fir, and

20% spruce. Paper birch was present in Area II, but cedar was absent, while other species were similar in density to Area I. Good regeneration of balsam fir was present throughout the site with some spruce and white pine occurring in Area I.

During May 1973, 26 balsam fir in Area I, and 22 in Area II were selected and numbered (Fig. 1). All numbered trees were 10 cm DBH or over, and showed some evidence of spruce budworm defoliation.

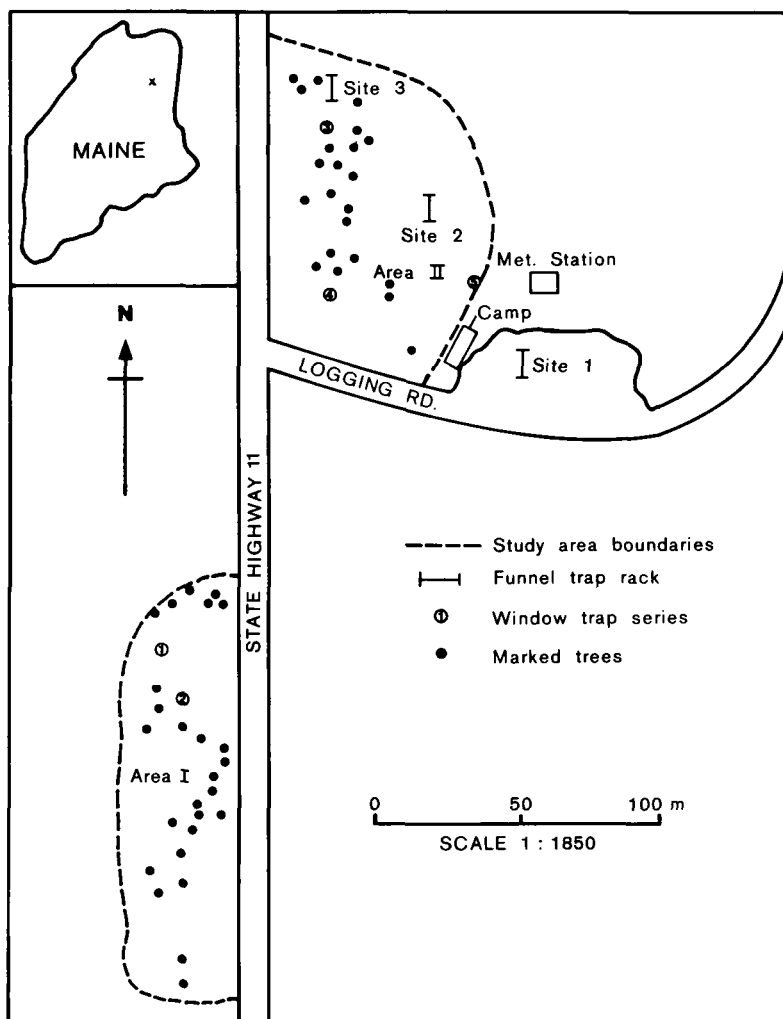


Figure 1. Sketch of study areas I and II.

Since very little mortality was occurring in the area a number of trees were preconditioned to provide breeding material for the bark beetle. The precondition treatment consisted of removing a two-centimeter band of bark and sapwood to a depth of a few millimeters from around the bole at a height of 30 cm above the ground surface. Fifteen trees were treated in Area I and ten in Area II. In each area the treated trees were selected randomly from among the numbered trees.

In a further effort to ensure adequate insect populations for the study, infected billets cut from trees on an area located approximately 4 km north of the site were placed around all numbered trees in Area I. Three billets, each one meter in length, were arranged at the base of each tree.

LIFE HISTORY AND FLIGHT BEHAVIOR

Introduction

The two workers who have made significant contributions to an understanding of the life history of *P. sparsus* are Prebble (1933) and Belyea (1951, 1952a, 1952b). Prebble determined the progression and number of larval instars; headcapsule widths conformed closely to predictions obtained by Dyar's Law (Chapman 1969).

Belyea (1951) gave a qualitative description of the insect's life history in northwestern Ontario, and included some statistics on nest dimensions and attack densities. The present study showed only minor variation from Belyea's outline, most of which may be attributable to differences in geographic location.

Materials and methods

Attack. An area of bark 15 cm wide was delineated, at a height of 1.5 m, on the bole of the 48 trees in Areas I and II. These were inspected at two-day intervals throughout the summer of 1973, and all borings in them were marked with color-coded pins. The five trees attacked over the summer were felled in early September, and the attack zones were excavated. Holes bored through the bark were determined to be entrances or emergences depending on their position in relation to the nest system.

Brood development. Two trees (DBH 12.2 and 12.6 cm) attacked early in the summer of 1973 were felled, and beginning at the butt end, 3 consecutive sections were cut from each bole, each 3.6 m long. The sections were marked into 12 consecutive 30 cm billets numbered from 1 to 12, and left in the felled position on the ground. A billet was selected at random from each section at weekly intervals, from these 3 nest systems from the surface in contact with the ground and 3 nest

systems from the upper surface were sampled. A total of 36 nests were sampled weekly. Data recorded for each were: bark thickness, area of nuptial chamber, length of parent gallery, number of egg niches, number and sex of adults, and length of larval galleries. The brood from each nest was collected and catalogued separately. Head-capsule widths were determined for all the larvae occupying each nest and were tallied by instar.

Logs which were placed around trees in Area I in the winter of 1972, and from which broods had emerged in the spring of 1973, were also used for nest statistics; 132 nests in 17 logs were examined. The following data were recorded: number of *P.sparsus* emergence holes, numbered of parasite or predator emergences, dead brood in larval galleries, dead adults in parent galleries, length of parent gallery, number of egg niches per parent gallery, and number of larval galleries per parent gallery. Total emergence over a 30 cm long cylinder was also noted. These data were used to calculate mortality up to the early larval stage and during the late larval-pupal stage.

Canopy influence on development. Three sites were selected within, or adjacent to, Area II for the erection of funnel trap racks. Site 1 was located in an old log yarding area and received full solar radiation throughout most of the day. Site 2 was located towards the eastern edge of Area II under a partial canopy estimated at 57% with a spherical densiometer (Lemmon 1956). Site 3 was situated under heavy canopy at the northern edge of Area II where canopy closure was estimated at 79%.

On each site two series of logs, each comprised of four 1.5 m sections, were placed along a rack, and funnel traps erected on each (Fig. 2). Logs for series 1 were obtained from four trees each containing overwintering broods, and felled on 13th April 1974. A log cut from each tree was placed on each of the three study sites. Funnel traps were placed on all 12 logs. Series 2 was obtained from four trees attacked in the spring of 1974 and treated in the same way as series 1. Funnel traps on all 24 logs were cleared at four-day intervals during the month of June and eight-day intervals during July, August, and September. All insects were counted and sexed. The funnel trap area on each trap was excavated after emergence was complete to provide data on attack intensity, brood numbers, and brood emergence.

Brood development, parasitism, and predation were determined concurrently with the emergence from destructive sampling of logs attacked by *P.sparsus* in the spring of 1974. A 4 m log was placed on each of the three sites and sampled at eight-day intervals for brood development. Statistics on six nest systems in a 30 cm billet were recorded at each sampling.

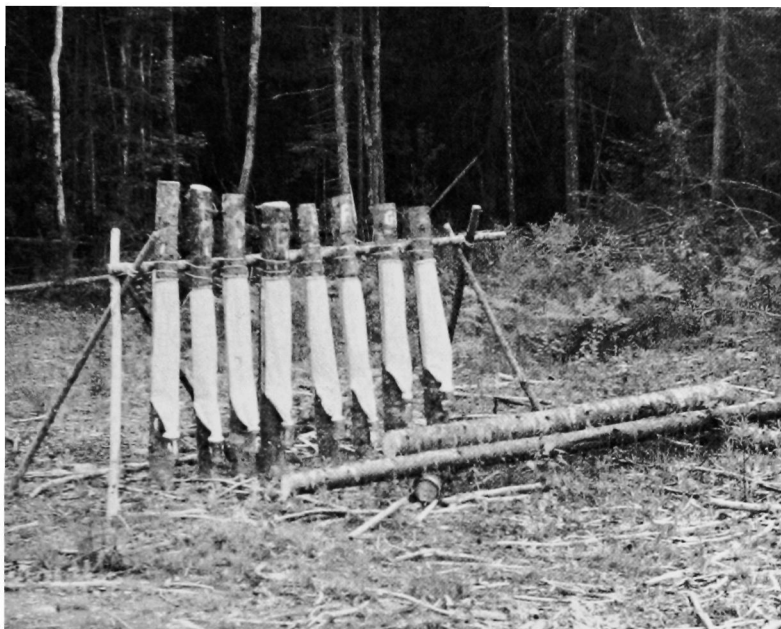


Figure 2. Logs and emergence traps in open area with brood sample log and parasite rearing log in the foreground.

Two additional 4 m logs were cut; one was placed in the open and another under full canopy. A 30 cm billet was cut from each at the time brood samples were taken and transferred to the laboratory where they were incubated in separate containers. All emerging parasitoides and predators were removed in late September.

Emergence. During the summer of 1973, ten funnel traps were placed on the boles of 9 trees (two on tree 27) one week after an attack was first observed. Emerging insects were collected in a glass jar containing 95% alcohol. The traps were inspected at two-day intervals and emerged adults counted and sexed. In early September 1973, all 9 trees were felled and the funnel trap sections removed. The remaining bole above the cut was tied upright to an adjacent tree and a new funnel trap attached in early May 1974. The cut sections were excavated in the laboratory and the following observations were recorded: area covered by trap, number of attacks, number of nests, number of parent galleries, number of emergences, area of phloem-cambium zone destroyed, area affected by *Monochamus scutellatus* (Say) galleries, estimate of mortality, developmental stage of insects. The funnel traps installed in early

May 1974 were inspected at 4-day intervals until activity ceased, after which the logs were excavated as for the 1973 sections.

Flight. Collections were made using window flight traps (Fig. 3) based on the design of Chapman and Kinghorn (1955). The trap was modified by replacing the liquid-filled collecting tray with a removable glass slide spread with the sticky material Tack Trap^R. This modifica-



Figure 3. Window trap string 5 in Oxbow study area.

tion gave a larger collecting surface and allowed easier servicing. The window area of each trap measured 0.25 m² and the collecting surface 0.066 m², projecting evenly either side of the glass window (Fig. 4).

Fifteen traps were arranged in five series of three. All traps were surrounded by a spruce-fir mixture. Each series of traps was supported by a braced spar pole projecting approximately 3.5 meters from the supporting tree at a height of about 10 meters (Fig. 3). The three traps

^R Registered trade mark, Animal Repellents Inc., Griffin, Ga.

were linked by three meter lengths of nylon cord and the whole series raised to give sampling heights of 1.5, 4.5, 7.5 meters, at the window midpoint. The lowermost trap was stabilized by loose lateral cords (Fig. 4). Each series was supported by pulleys attached to the spar pole and could be raised and lowered for removal and replacement of collecting slides.

The possibility of moving reflections in the glass of suspended traps affecting catch efficiency was recognized. During the summer of 1973, a control trap was erected in a ridged frame adjacent to the lowest trap in series 5. The glass windows were cleaned as required to remove dust and splash marks.

Collections were made daily throughout the summer of 1973, beginning in early June and continuing until mid August, then weekly until mid September. Slides were changed between 8 am. and 10 am. *P. sparsus* specimens were sexed and discarded. Collections were made every four days from late May until early June in 1974, and then every eight days terminating in early September. All procedures and equipment were the same as in 1973 with the exception that the single control trap was eliminated.



Figure 4. Window flight trap used in *Pityokteines sparsus* study.

Climatic data. A weather station was tended daily during the summer of 1973. Instrumentation consisted of a hygrothermograph, standard rain gauge, maximum-minimum thermometer and pyroheliograph. Records were discontinued in 1974 after a significant correlation was found between the Oxbow readings and those at Squa Pan Dam, a station contributing to national climatic data and located about 15 km north of the study area. This station, located in the Aroostook Valley along with the study area, showed a significant difference only in rainfall recordings, most of which resulted from intense local thunder storms occurring throughout the summer period.

Data processing. A computer program was developed in FORTRAN IV programming language for the analysis of brood development.

All other analyses were made using the Statistical Package for the Social Sciences (S.P.S.S.) (Nie, Bent, and Hull 1970) computer program. This package, although designed specifically for use with social science surveys, is ideally suited to discrete population analysis in many fields. The package has the capability of multiple-regression analysis as well as a wide range of statistics.

Results and discussion

Attack. Nest initiation by male beetles was first observed in 1973 on June 4, and in 1974 on June 2. A large number of freshly attacked trees were examined throughout the Oxbow area. In all cases bud elongation had failed to occur during the current spring, although the phloem-cambium zone was usually still fresh and white and contained no evidence of staining. Of the 48 trees marked in the winter of 1972-73, only five were attacked in the spring of 1973, even though many more showed moderate to high spruce budworm defoliation. An additional 9 marked trees had been attacked by mid June 1974. All but one of these 14 trees were included in the 25 which were ring-barked at the time of marking, the exception being a strongly suppressed individual. Clearly, *P.sparsus* initiates attack on balsam fir only after an irreversible physiological decline in the vigor of individual trees. It is unlikely this insect plays a role in the death of balsam fir severely defoliated by spruce budworm, since it only attacks those trees beyond the recovery stage. These observations support Belyea's (1952a) findings.

Male beetles emerged 2 to 3 days before females and attacked suitable host material. Most attacks on the five trees monitored in 1973 occurred in June, although one was not attacked until late July, and three sustained some attack until mid August. All trees intensively exploited by the insect showed a similar infestation pattern. Initial attack was heavy, always accounting for more than 50% of the total number of nests for the season. This period, confined to 2 or 3 days, was followed

by a rapid decline in attack intensity. The attack pattern strongly suggests the presence of pheromones, probably in the male frass produced during the initiation of the nest, as is common in other species of bark beetles (Borden and Stokkink, 1971).

Attack was confined to the main stem of the tree in all cases, although the top was utilized down to 4 cm diameter. Attack spacing varied considerably with entrance holes as close as 2 cm in heavily infested trees. Heavy infestations (Fig. 5) always tended to over-exploit the phloem-cambium zone with late stage larvae forced to feed in the sapwood or outer bark. Eight broods per 100 sq cm was not uncommon in heavily attacked trees. Competition for food appeared to be a major cause of mortality at high infestation levels. No statistical differences were found between attack intensity at different heights on the main stem.

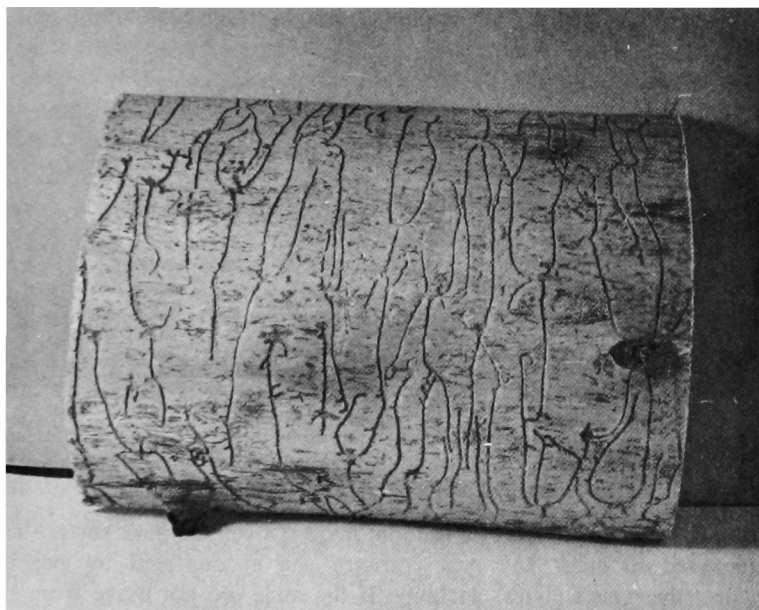


Figure 5. Nest systems of *Pityokteines sparsus* at high population levels (0.4X actual size).

The entrance tunnel was bored by the male and contrary to Belyea (1951, 1952b), was not always slanted upwards from the bark surface. The angle of the tunnel appeared to be strongly influenced by bark topography; the beetle's preference for the edge of bark flakes often led to an upward angle. However, a significant number of entrance tun-

nels were found on smooth bark where, without excavation, they could not be distinguished from a horizontal emergence tunnel. The male beetle constructed an irregular nuptial chamber (Fig. 6) half in the phloem-cambium zone and half in the sapwood. The chamber averaged 6 sq mm in area and was completed in 2 to 4 days. At this time, up to 6 females were admitted to the nest.

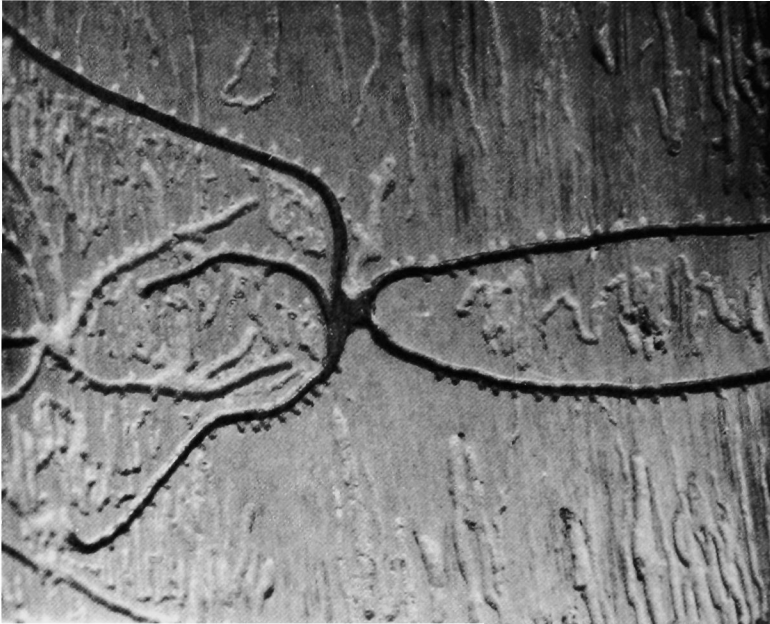


Figure 6. A typical nest of *Pityokteines sparsus* with the 5 parent galleries artificially darkened (1.5X actual size).

The female moved in a random manner over the bark surface and attempted to enter any nest entrance she encountered by pushing against the male's elytral declivity. If the male did not move from the entrance tunnel to the nuptial chamber and permit entry, the female resumed random wandering.

Parent gallery. Copulation presumably occurred in the nuptial chamber. Each female then initiated a separate gallery following the circumference of the tree and cut equally into the phloem and sapwood. A number of abortive tunnels were observed. These usually extended less than 5 mm from the nuptial chamber. The female, while periodically rotating about her longitudinal axis, excavated the tunnel with a clip-

ping action of her mandibles. The frass was cleared backward about 1.5 body lengths until the female had difficulty crawling over the accumulation to resume tunnelling. At this juncture, the frass was pushed to the nuptial chamber from which it was ejected by the male who was in the entrance tunnel with his declivity toward the opening.

The cross-sectional area of the parent tunnel was such that the body hairs of the female, which probably act as a sensing device, just touched the sides. The body hairs were also observed to prevent the adhesion of balsam fir resin to the insect's cuticle. The abundant long hairs may be of major importance in allowing the insect to attack and breed in the resinous bark of balsam fir immediately after tree death.

Oviposition. Egg niches (Fig. 6) were cut at intervals along the sides of the parent tunnel during construction. An egg was deposited in each, always positioned in the outer section of the niche against the phloem tissue, with its long axis parallel to the parent tunnel. This orientation was maintained by a packing of fine sapwood frass which was also used to seal the niche. Where two parent tunnels ran parallel and close together (1 or 2 cm part), almost all egg niches were cut on the two most distant walls of the gallery pair, reducing future larval competition in the limited area between the two tunnels (Fig. 6). The distribution of niches along the parent gallery varied from an even spacing to some degree of clumping. However, greatest density of egg niches was commonly in the proximal part of the parent gallery.

Larval development and pupation. The eggs hatched after approximately 10 to 12 days, and the young larvae entered the phloem tissue at right angles to the parent tunnel. The larvae ingested all the host tissue removed in the tunnelling process, producing a tightly packed resinous deposit of faecal material posteriorly. Not until the second instar did the larvae begin to engrave the sapwood, although maximum use of the phloem-cambium zone still occurred during subsequent growth. The larval gallery proceeded in a straight line at right angles to the parent tunnel until pupation occurred, unless crowding interfered. In heavily attacked trees the gallery was often highly convoluted, utilizing every part of the phloem-cambium zone. Food competition was intense under these conditions and high larval mortality occurred. Larvae fed in either the sapwood or outer bark when the phloem-cambium zone was exhausted, a phenomenon which was never observed in lightly attacked material. Mortality was apparent in both excessively dry and wet material, especially where fungal invasion had occurred beneath the bark.

Three larval instars were determined for the insect from head capsule measurements (Fig. 7), confirming the finding of Prebble (1933).

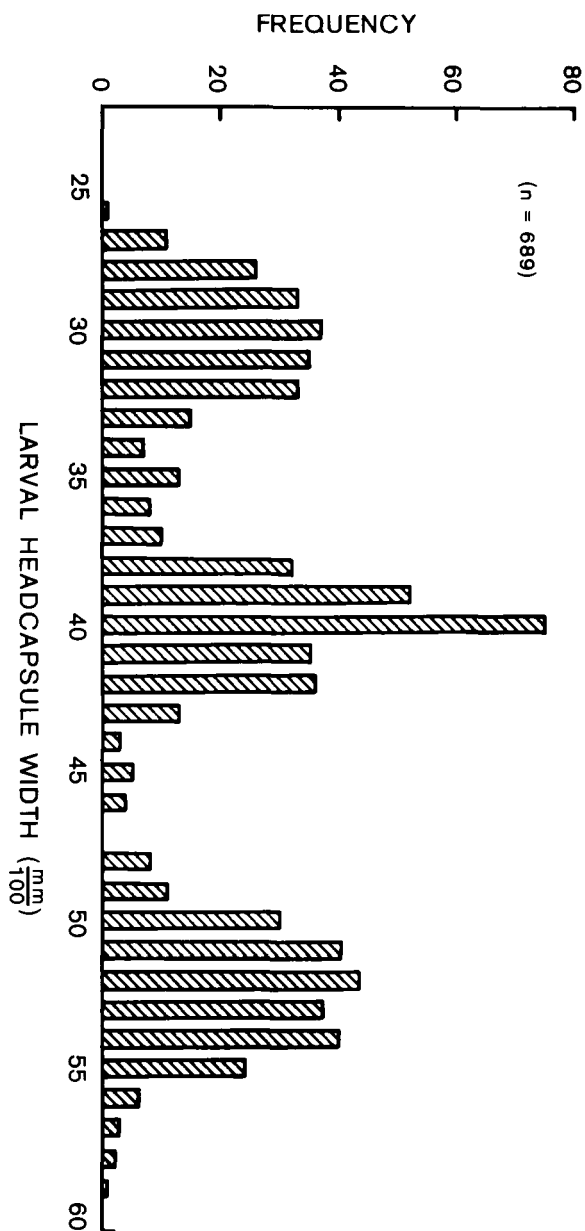


Figure 7. Distribution of larval headcapsule widths of *Pityokteines sparsus*.

The first larval instar had the shortest developmental time (1 to 2 weeks), while the second and third were about equal (2 to 3 weeks).

Prior to pupation many larvae excavated individual emergence tunnels. Each tunnel led directly from the pupal chamber to a point just beneath the bark surface. Some mortality occurred at this stage in most broods. The cause of this mortality was not determined.

Pupation occurred in a cell which was invariably constructed in the phloem-cambium zone unless crowding prevented. In heavily infested material the cell was found in either the sapwood or outer bark. In the summer of 1973 pupation first occurred on the 27th July, and the first teneral adult was recorded on August 3. The pupation period of 8 to 10 days was somewhat shorter than that reported by Belyea (1952b). The minimum period of development from egg to adult was 58 days under partial shade in the Oxbow area. Table 1 summarizes nest dimensions and brood production for the summer of 1973.

Table 1

Mean dimensions and brood production of *Pityokteines sparsus* nests (n = 132)

	Mean	S.E.
Area of nuptial chamber (sq mm)	6.01	0.25
Number of parent galleries	3.06	0.09
Total length of parent galleries (mm)	111.20	0.72
Total number of egg niches	65.15	0.44
Total number of larval galleries	33.48	0.29
Emergences	3.85	0.14

The influence of canopy density on the development and emergence of *P. sparsus* was found to be highly significant. The differential development of broods under three canopy conditions was followed throughout the summer by brood sampling. Figure 8 shows regression lines relating larval gallery length to time, for all three canopy conditions. No significant difference in the slope of the lines exists between the 57% and 79% canopy cover, but a highly significant difference exists between these two and the open condition.

Head capsule measurements of the broods sampled show a similar pattern to the larval gallery dimensions. Broods in the open passed more rapidly through the larval instars and reached maturity about 2.5 weeks earlier than those under full canopy. Broods under partial and full canopy conditions showed less advanced development at the time of entering winter diapause than those in the open. At that time broods under the canopy consisted of larvae, pupae, and adults, while those in the open had all reached the adult stage.

Variation in development rate with changes in canopy density was attributed to the influence of solar radiation on the temperature regime within the forest.

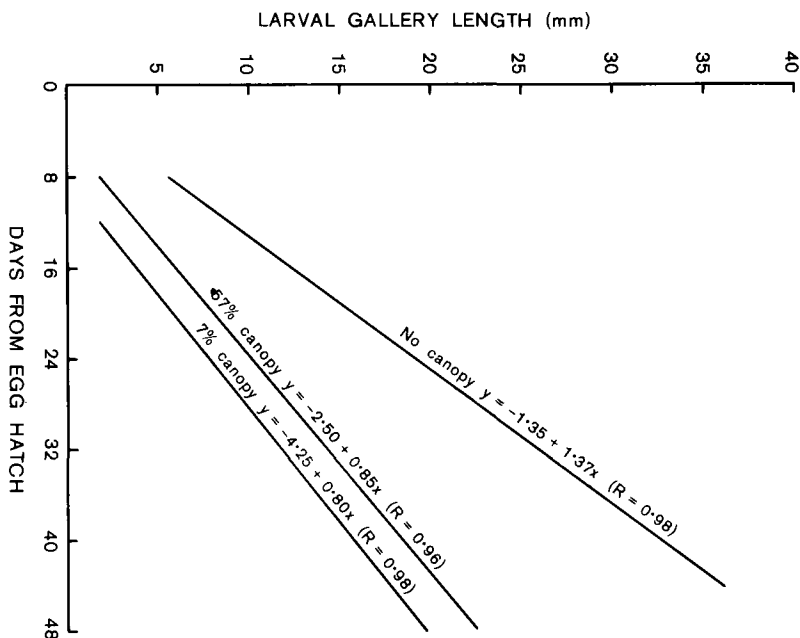


Figure 8. The relationship between canopy cover and larval development of *Pityokteines sparsus*.

Emergence. *Pityokteines sparsus* overwinters in either the adult or larval stages. Diapause is facultative and is easily broken by elevated temperatures. Two periods of emergence were observed in the field during 1973, one in late spring and the other in early fall. Fall emergence was only observed in material exposed to direct solar radiation where larval development was accelerated. The most common condition involved a single annual emergence. However, canopy density has a strong influence on the timing of the spring emergence. Distribution in time of emergence from open, partial canopy, and full canopy conditions is shown, (Figure 9). The delay in emergence is most marked between the open and partial canopy areas, but is still distinct in a comparison of partial and full canopy. All logs sampled contained late instar larvae when placed on the three sites in mid April. The differences in emergence time of the insect under the three conditions studied was a result of more rapid development in the late larval-pupal stage, and earlier occurrence of threshold emergence temperatures, with decreasing canopy density. Development and emergence of many scolytid species have been shown to be influenced strongly by temperature (Beckwith

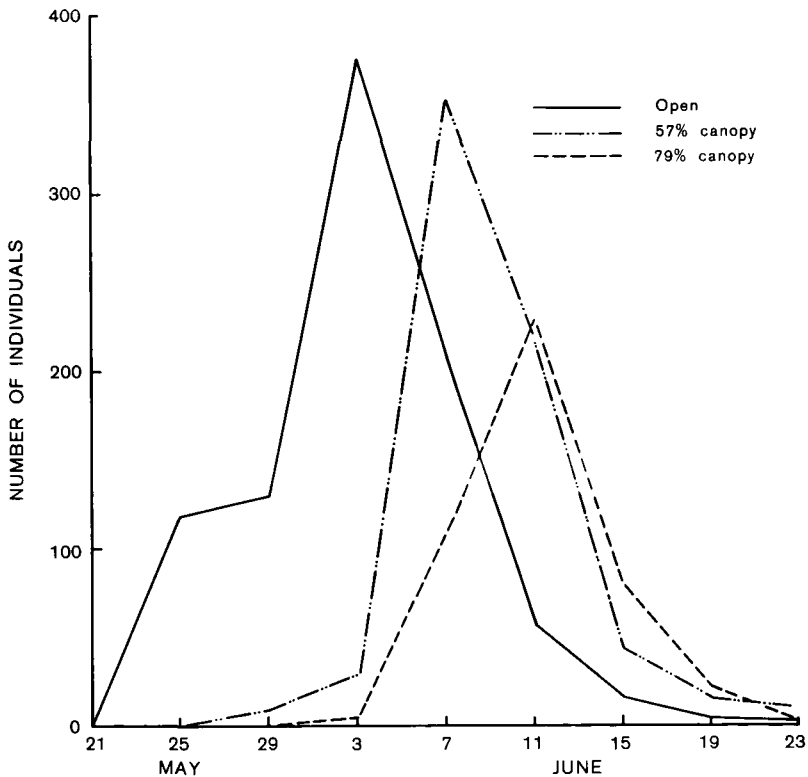


Figure 9. Total emergences from Series 1 logs in the open, 57%, and 79% canopy densities.

1972; Hosking 1972; McMullen and Atkins 1962; Rasmussen 1974).

The overall sex ratio of spring emergence from 595 broods was 1 male to 1.5 females, a highly significant difference from the ratio of 1 male to 3.06 females found in parents of developed nests. This change in the ratio of males to females during the period between emergence and nest initiation can only be accounted for by a differential mortality between the sexes over this period.

Many parents established broods in the late spring, then re-emerged during the early to mid-summer period and established a second brood. The proportion of parents exhibiting such behavior averaged 57 percent for all trees in 1973. Both males and females were involved. The female parent often emerged by cutting a new exit hole at the terminal end of the parent gallery. Those parents which failed to re-emerge died in the nest system. Most re-emergence was completed by late July.

Second broods established by re-emerging parents generally reached the late larval stage before winter diapause occurred. However, mature insects which had overwintered as either adults or larvae emerged at the same time in late spring. Feeding by overwintering larvae resumed in early spring, allowing them to catch up in development with the overwintering adults awaiting the higher temperatures necessary to stimulate emergence.

Mortality factors. Mortality attributable to predators and parasites was extremely low in the population under study. Insects associated with *P.sparsus* were collected from emergence traps and brood samples throughout 1973 and 1974. These data were supplemented by laboratory rearings in 1974.

One predator and two parasitoids were definitely associated with developing broods of *P.sparsus*. The predator has been identified as *Medetera* sp. (Dolichopadidae), a dipteran genus which has been reported attacking a number of bark beetle species including *Dendroctonus brevicomis* LeConte (Stark and Dahlsten 1970), *D.ponderosae* Hopkins (De Leon 1935) and *Scolytus scolytus* (Fabricius) (Beaver 1966). Although occasional heavy infestations of the predator occurred, most trees supported very low populations. Larvae of *Medetera* sp. were observed feeding in the larval galleries of *P.sparsus*. Adults were collected from emergence traps in early June 1974 after overwintering in the larval stage.

A chalcid parasitoid of the family Pteromalidae was collected on a number of occasions from the pupal cell of *P.sparsus* and was also reared from billets in the laboratory. The insect is in the genus *Cecidostiba* which has been reported from *Dendroctonus brevicomis* (Stark and Dahlsten 1970), *D.adjunctus* Blandford (Chansler 1967) and *Ips* spp. (Bushing 1965) along with several other species of scolytids. Although some individual broods were heavily parasitized by this species, it was uncommon in the population as a whole.

Three individuals of a braconid parasitoid were reared from billets in the laboratory. The species was never collected in the field. All three specimens emerged from the log originally placed in the open area.

Attack by *Medetera* sp. occurred during early to mid June, with larvae well established by early July. Laboratory rearings indicated that both the chalcid and braconid attack in late June or early July.

The primary mortality factor in most broods was competition for food. Even at low infestation levels, food competition occurred where parallel parent galleries were closer than about 1.5 cm. The geometry of the galleries relative to one another was most important in determining the available food for individual larva. Since feeding larva would not impinge upon another mine, many obtained insufficient food even

though all phloem-cambium material in a given area was not utilized. The very high mortality between larval instar II and emergence (Table II) was almost entirely attributable to competition for food.

Table 2
Partial life table for *Pityokteines sparsus* (mean values per parent gallery, n = 403) for 1973

x	Nx	Mx	100M/N	Sx
Age interval	No. alive at beginning of x	No. dying during x	Mx as percentage Nx	Survival rate within x
Eggs and instar I	21.29	10.35	48.62	0.52
Instar II to emergence	10.94	9.80	89.58	0.10
*Emerged adults	1.14	0.31	26.86	0.73
Parent adults	0.83			
GENERATION			96.08	0.04

* Due to expected male loss after emergence

Brood destruction by *Monochamus scutellatus* larvae was generally less than 10% over the whole life cycle of *P. sparsus*, although occasional logs showed up to 50% of the broods destroyed by the sawyer. Mean mortality in the fall was found to be 0.2% while by early June of the following year it had risen to almost 6%. Clearly, heaviest mortality occurred in the spring prior to emergence. The ecological requirements of *M. scutellatus* and *P. sparsus* are almost identical. However, populations of the sawyer in the study were too low to be of significance in the mortality of the bark beetle.

In the limited life table presented in Table II the first mortality class was determined from a comparison of egg niches with larval gallery occurrence. Instar I is included in this class as the small larvae generally leave no trace of their mine in the sapwood surface. The mortality in this class probably resulted from failure of eggs to hatch and failure of young larvae to establish themselves in the feeding zone. No evidence of parasitism was found, but predation by *Medetera* sp. remains a possibility.

The second class, including all stages from instar II to emerging adults, was determined from the number of larval galleries and their associated emergence holes. High mortality in this class was primarily caused by competition for food, with parasitism and predation being of importance in some broods.

The third class accounts only for the loss of males determined from the change in sex ratio between emergence and nest establishment.

The total generation mortality of 96.08% is probably a conservative estimate, but is in keeping with that found for *Dendroctonus brevicomis* (Stark and Dahlsten 1970), and very similar to static populations

of *Scolytus scolytus* (Berryman 1973) and *Dendroctonus ponderosae* (Knight 1959).

Flight. The flight peaks shown in Figure 10 conform closely to emergence peaks determined by funnel traps (Fig. 9). The preconditioning of trees and a limited amount of windthrow in the study area resulted in a sharp increase in the population of *P. sparsus* from 1973 to 1974.

Window trap collections showed males were in flight 2 to 3 days before females. This observation is consistent with the earlier emergence of males into funnel traps, noted earlier in this section.

Temperature appeared to be a major factor in the initiation of emergence and flight. A temperature increase from 22.7°C to 27.8°C between June 8 and 9, 1973 stimulated a sharp increase in emergence which was reflected in window trap catches (Fig. 10). Peak flight activity in 1973 and 1974 occurred during the second week in June and was

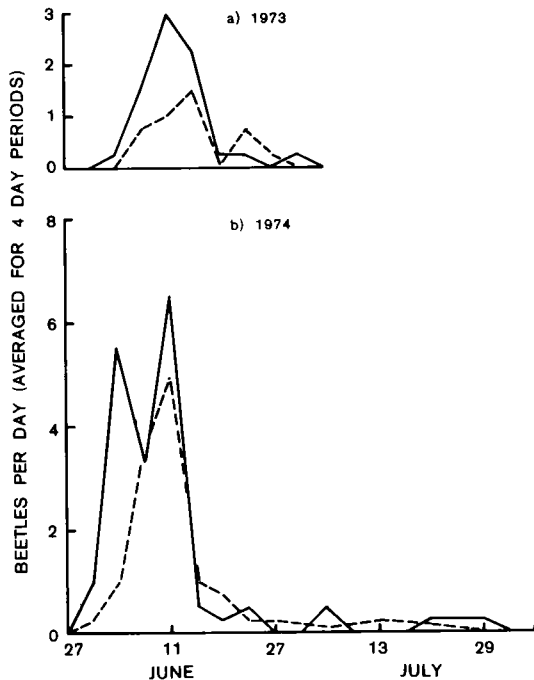


Figure 10. Window trap catches of *Pityokteines sparsus* males (—) and females (---) for (a) 1973 and (b) 1974.

followed by a sharp decline. Few insects were collected after the third week in June, and most were probably re-emerging parents flying for the second time that season.

A distinct shift in catches from one trap series to another occurred from 1973 to 1974. Trap series 3 accounted for only 9% of the catch in 1973 but 51% in 1974, while series 5 decreased from 63% to 20% over the same period. This change in flight density over short distances was probably a result of two biological factors, discontinuity of host material and flight behavior of the adult beetle. Individual trees suitable for infestation were unevenly distributed throughout the area. If the adult flight distance was short this discontinuity of host material was likely to be reflected in the catches of different trap series.

Clearly, variations in catch of individual window traps over a number of seasons are unlikely to reflect population changes of the insect over extensive forest areas. Consideration of trap series 5 alone would suggest a decline in the population of *P. sparsus* from 1973 to 1974 in the Oxbow area. This is contrary to general observations and the data from 15 window traps. A large number of traps suitably randomized in their location would be necessary to accurately determine overall population trends. This consideration is likely to apply to many species of Coleoptera at endemic population levels. Studies of the type carried out by Beckwith (1972), using only one or two traps in each area, may be subject to considerable error when used to compare the relative abundance of different scolytid species. A single highly infested tree close to a trap could disproportionately influence calculations.

A preferred elevation of flight within the forest stand was not clear from the data collected during the study. However, Table III shows the lowest traps, at 1.5 m, caught fewest insects in all categories, while the middle traps, at 4.5 m, caught most in all but one category. It would appear that most insects were flying in the 3 to 10 m zone of this forest, although a significant number were present at lower levels. In keeping with Hosking and Knight's (1975) observations concerning flight elevations of other scolytids in the region, *Pityokteines sparsus* might be expected to show a diffuse flight pattern. Its attack is not confined to a definite height on its host tree. Although attack is found from ground-level to a 4 cm diameter top, the thick lower bark is often rejected. This behavior may be related to reduced catches at 1.5 m. No information was collected on flight above 7.5 m.

A most interesting observation arising from Table III is the ratio of females to males. The ratio from flight traps was 1 to 1.6 for 1973, and 1 to 1.4 for 1974. The ratio in the emerging brood was 1 to 0.66, and in nest parents 1 to 0.33. This sharp reversal suggests a fundamen-

tal difference in the flight behavior of males and females. Although one-third less males than females emerged from broods, flight trap data suggest they were 1.5 times more common in flight.

Several possibilities exist to explain this disparity in sex ratios. Females may fly at a different height and would not be sampled by the window traps. Table III shows almost identical distributions for both males and females by trap height, suggesting this hypothesis is not valid. The window trap may be more efficient in the capture of males than females; an unlikely situation in view of the very similar size of both sexes. The more likely explanation lies in the difference in the biological role of the two sexes. The male actively seeks suitable host material for nest initiation, while the female is probably aided in nest location by a male pheromone. Hence the period of flight is likely to be of much

Table 3
Window trap catches of *Pityokteines sparsus* by sex for 1973 and 1974

Trap height (m)	Males			Females			Grand total
	1973	1974	Total	1973	1974	Total	
7.5	14	29	43	11	17	28	71
4.5	16	30	46	10	25	35	81
1.5	11	16	27	5	10	15	42
Totals	41	75	116	26	52	78	184

shorter duration for females compared with males. The probability of trapping males is increased as a result of the greater length of time spent in flight. This hypothesis is compatible with the higher male mortality between emergence and attack already discussed.

FOOD energetics

Introduction

The concept of ecological efficiencies is reviewed in some detail by Kozlovsky (1968) who includes a tabular clarification of past terminology. All definitions used in the present study are those of Odum (1971).

Ecological efficiencies have been determined for a wide variety of individual animal and plant species as well as complete ecosystems. These determinations may be important indicators of the ecological position of the system being measured, as well as a key to the basic metabolic processes of individual species. The degree of error in any efficiency determination is largely a function of the life style of the organisms being monitored, and hence of the accessibility of the required information. Insects developing subcortically in woody plants are particularly suited to accurate determinations of assimilation efficiency. Assimilation efficiency is defined by Odum (1971) as:

$$\frac{A}{I} = \frac{t}{t}$$

where A = assimilation;
 I = energy intake;
 and t = trophic level

The energy base of subcortical insects can be easily characterized both chemically and physically, and is generally of a homogeneous nature. The excretory energy is most often confined within a tunnel or chamber; thus its volume can be related to the volume of ingested material. For most species, volumes of both ingested and excreted material are sufficient for calorific determination. Clearly, the life style of these insects is ideally suited to the input-output technique of study.

The subcortical zone is also amenable to comparisons of efficiency between insects of different taxonomic groups, and varying developmental cycles, feeding in virtually the same niche. The large number of individuals infesting a single host, a common characteristic in many species, removes much of the variability encountered between hosts.

The total lack of studies investigating the assimilation efficiencies of subcortical insects prompted the authors to examine this factor in *Pityokteines sparsus*. The paucity of data concerning the chemical, calorific, and physical nature of the feeding zone in balsam fir suggested an analysis of the total calorific values of the feeding zone components might yield some valuable information.

The present study was designed to determine the assimilation efficiency of *P. sparsus* and compare it to some limited data obtained from the sawyer *Monochamus scutellatus*. The total calorific content of each of the three feeding zone components (sapwood, phloem-cambium, bark) was also determined.

Materials and methods

Calorific determinations. Samples were taken from a dying tree on the University of Maine Forest. The bark, phloem-cambium, and sapwood of the tree as well as the composite feeding zone of the mature larva were sampled (Fig. 11).

All samples were dried to constant weight at 45°C and ground in a Wiley mill. The ground samples were stored in a desiccator and pellets made immediately prior to bombing. Calorific determinations were made in a Parr adiabatic oxygen bomb calorimeter.

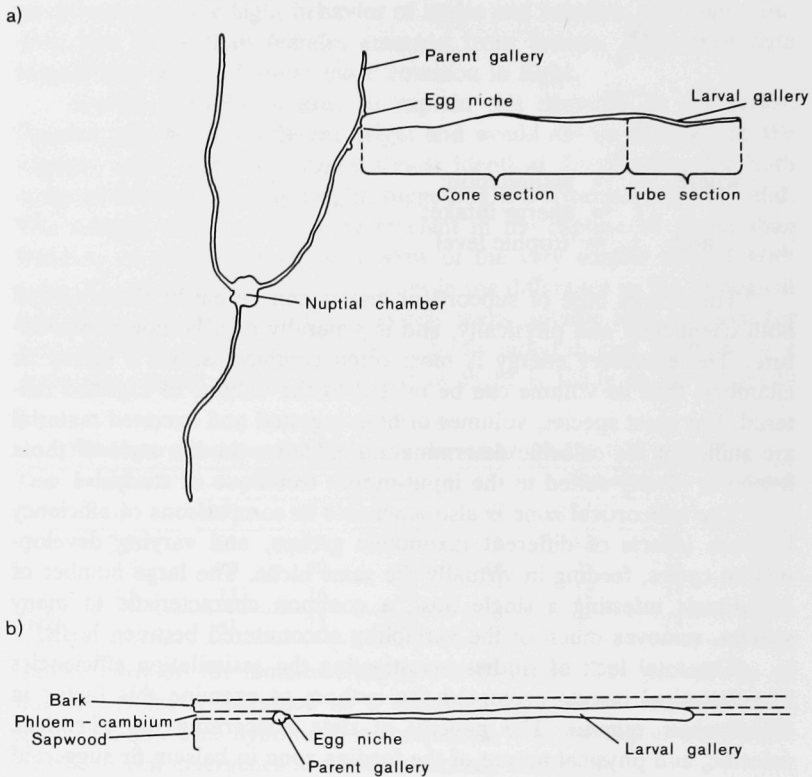


Figure 11. (a) Gallery system of *Polyokteines sparsus* showing volume divisions of the larval gallery (actual size). (b) Diagrammatic representation of a larval gallery showing its spatial distribution in the phloem-cambium and sapwood zones.

Assimilation efficiency determination. The larvae of *P. sparsus* fed by boring a continuous tunnel from egg hatch to pupation (Fig. 12). All the excavated material was ingested and the feces packed into the tunnel posteriorly. Thus, by calculating the volume of the tunnel, weight of total fecal material (frass) produced, and density of the feeding zone material, an input-output model could be derived based on calorific determinations.

The tubular feeding galleries were assumed to approximate a cone until the latter part of final instar feeding. From this point until pupation, volume was determined on the basis of a cylinder (Fig. 11). Ten well developed galleries were divided into these two components and their volumes calculated.

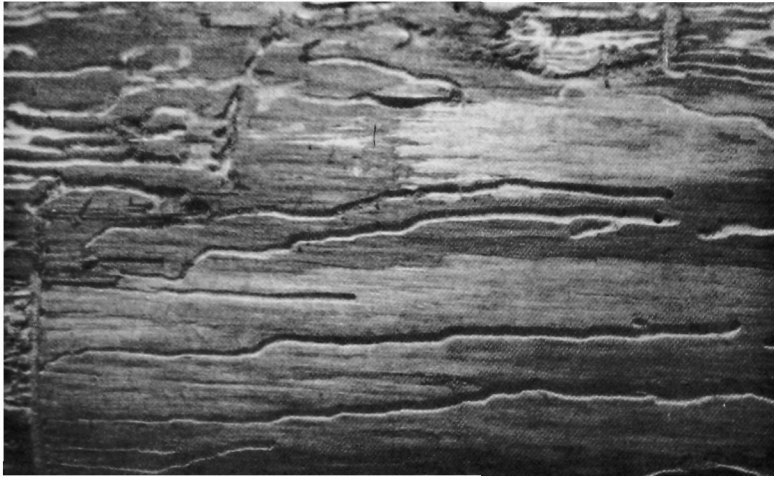


Figure 12. Sapwood portion of larval galleries of *Pityokteines sparsus* at low nest density (1.3X actual size).

The frass from each gallery was collected, oven dried and weighed. The density of the feeding zone material was determined from the oven-dry weight of a given volume of material. Volume was measured by liquid displacement. A quantity of frass was collected and ground after oven drying. Its calorific value was determined for comparison with that of the feeding zone.

The data for *Monochamus scutellatus* were based on the measurement of a single gallery and its frass content. The irregular nature of the insect's galleries made volume determinations difficult, and introduced the possibility of considerable error in the derived values. Further, this insect did not ingest all the excavated tunnel material, wood shavings being a common frass component.

Results and discussion

Calorific values and feeding zones. The calorific value of food materials is often a poor indicator of its nutritive value in the metabolism of individual animal species. Information concerning the chemical composition of the food and digestibility of the major components by the animal is essential in the estimation of overall food value. Digestion in all animals is selective to some degree and often highly so (Bissell and Weir 1957; Silver and Colovos 1957). Materials of high calorific value may have a large portion of their energy locked in compounds which cannot be utilized by the consumer. This factor is particularly important

in a consideration of wood and bark feeding insects. Much of the energy in wood is bound in lignin and cellulose, the former rarely utilized by insects and the latter only by those supporting certain enzymes or microorganisms. Preferred feeding zones, or food types, are more likely to correlate with the availability of certain easily utilized chemical components, such as simple sugars or nitrogen, than total calorific value.

The preferred feeding zone of *P.sparsus* in balsam fir clearly does not coincide with the zone of highest calorific value (Table IV). The analysis of feeding locations showed the order of zones from highest to lowest preference to be phloem-cambium, sapwood, bark.

Two of the most critical metabolic requirements of living organisms are nitrogen and carbohydrates. Nitrogen, as an important constituent of extracellular and intracellular enzymes, nucleic acids, lipoprotein membranes, and chitin, is of particular importance during periods of rapid growth. Cowling and Merrill (1966) showed a 10 to 40-fold greater nitrogen content in the conifer cambium zone when compared with mature xylem. This high level of nitrogen declined with maturation of the xylem tissue. A similar pattern has been shown during the maturation of the phloem tissue (Browning 1963).

Table 4
Calorific values of *Pityokteines sparsus* frass, *Monochamus scutellatus* frass, and balsam fir components

Material	*Mean calories	**% variance
Bark	4891	0.80
Phloem-cambium	4580	0.06
Sapwood	4681	0.42
Feeding zone	4625	0.30
<i>Pityokteines</i> frass	4524	0.10
<i>Monochamus</i> frass	4593	0.60

* Mean of two determinations

** Percent variance between two determinations

Côté *et al.* (1968) demonstrated a proportional increase in cellulose, in relation to other polysaccharides, with xylem maturation.

It is probable the choice of feeding zones by *P.sparsus* is strongly influenced by nitrogen and sugar concentrations along with the negative effect of uronic anhydride and tannins concentrated in the bark.

The utilization of different feeding zones is clearly a function of larval age. The newly hatched larvae invariably fed in the cells of the phloem-cambium zone, only venturing into the sapwood when their size could no longer be accommodated in this narrow region.

Assimilation efficiency. The determination of assimilation efficiency for *P.sparsus* was made according to Odum's (1971) definition. Care was taken to reduce the measurement errors at all stages, especially

gallery volumes and frass weights which involved very small values (Table V). Variances between replications of bomb runs were less than 0.5% for feeding zone and frass determinations (Table IV). The assimilation efficiency of 46.35% for this insect (Table VI) is well within the limits derived for other animals (Odum 1971). Few data are available specifically for insects, although Gere (1956) reports assimilation of 29% of the calorific value of ingested food for a lepidopterous larva, and Smalley (1960) 27% for a grasshopper. In a recent paper Van Hook and Dodson (1974) report a 50% assimilation efficiency for the yellow-poplar weevil *Odontopus calceatus* Say.

According to Chapman (1969), scolytids possess neither microorganisms nor cellulose, although the occurrence of a hemi-cellulose has been demonstrated. The absence of microorganisms is disputed by LeFay and Thuillier (1969) in the scolytid *Ips sexdentatus* Boerner. Irrespective of the mechanism involved it is difficult to believe *P. sparsus*,

Table 5
Volume and frass weights of ten *Pityokteines sparsus* larval galleries

Sample No.	Gallery volume (mm ³)	Dry weight frass (g)	Dry weight frass per cc (g)
1	20.73166	0.00562	0.2711
2	13.22989	0.00319	0.2411
3	19.02252	0.00324	0.1703
4	16.58928	0.00368	0.2218
5	10.35666	0.00309	0.2983
6	40.01836	0.00600	0.1499
7	12.87810	0.00318	0.2469
8	46.68905	0.00741	0.1587
9	42.58539	0.00782	0.1836
10	31.40900	0.00766	0.2439
Mean			0.2186
S.D.			0.0447

with an assimilation efficiency of 46%, does not utilize the cellulose of its ingested food. The lack of cellulose utilization would eliminate 45 to 50% of ingested food (Timell 1957). Lignin accounts for a further 29%, and uronic anhydride for 3.8% (Clermont and Schwartz (1951). Thus a total of more than 75% of ingested food is eliminated from assimilation. Clearly, some use must be made of this large fraction of food intake.

The efficiency determination for *Monochamus scutellatus* (Table VI) is not an assimilation efficiency but a feeding zone use efficiency; that is, the total calories extracted for a given volume of tunnel excavated. This includes both ingested and non-ingested material. No information is available on the mode of selectivity of ingested and non-in-

Table 6
Feeding efficiencies of *Pityokteines sparsus* and *Monochamus scutellatus*

	<i>P. sparsus</i>	<i>M. scutellatus</i>
Input (cal/g feeding zone)	4625	4625
Output (cal/g frass)	4524	4593
Mean frass per tunnel (g)	0.0050	
Mean volume per tunnel (mm ³)	25.3509	
Frass density (g/cc)	0.2186	0.3770
Feeding zone density (g/cc)	0.3985	0.3985
Calories/cc input	1843	
Calories/cc output	989	
Calories/cc assimilated	854	
*Assimilation efficiency (%)	46.35	
*Feeding zone use efficiency (%)		6.10%
* Efficiency =		
(Fresh density) (Input cals)—(Frass density) (Output cals)		100
		X —
(Fresh density) (Input cals)		1

gested material. The efficiency value is of interest as a comparison with *P. sparsus* of the calories extracted from a given volume of feeding zone material by a cerambycid larva feeding in the same ecological niche. Clearly, better utilization of a given volume of food material has advantages in both food gathering energy expenditure and during conditions of limited food supply. The difference in efficiency between these two insects may have far reaching implications in their biology, ecological position, and population dynamics.

Populations of *P. sparsus* are able to build rapidly in transient food supplies such as extensive areas of blowdown or trees killed by pests and diseases. Population levels fluctuate widely, and show a rapid response to favorable conditions. The advantage of a high assimilation efficiency and short developmental period are obvious in the exploitation of this ecological situation. *Monochamus scutellatus*, by contrast, has a much longer developmental period (2 to 3 years), and is unable to respond to transient food supplies lasting only one or two years. Its population levels remain more constant and fluctuate on a much longer time scale. Under these conditions, selection for high efficiency in food use has not been, nor need not be, as strong as for the bark beetle.

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