

Observations on the Biology of *Dryocoetes betulae* (Coleoptera: Curculionidae) in Paper Birch in Northern Idaho

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ABSTRACT We describe the biology and life stages of the birch bark beetle, *Dryocoetes betulae* Hopkins, and report its second known occurrence in Idaho. One annual generation was observed with broods overwintering as larvae and sexually immature adults. The species is polygamous with a ratio of 1.8 females per male. Two females (rarely three) joined a male after he entered the bark, and each female created a 3- to 4-cm-long egg gallery with short lateral spurs. Eggs were laid in niches along each side of the main gallery. Larvae have three instars. No hymenopterous parasitoid was found; however, two apparent predators, *Rhizophagus dimidiatus* Mannerheim, and a clerid, *Thanasimus undatulus* (Say), were present in galleries. Two mites, *Histiostoma* sp. and *Proctolaelaps* n. sp., also occurred in galleries, and a nematode of the Order Rhabditida occurred in the midgut of larvae and adult *D. betulae*. An ambrosia beetle, *Trypodendron betulae* Swaine, also infested the basal stems apart from *D. betulae*. Stems of infested trees were infected with a root rot fungus, *Armillaria ostoyae* (Romagnesi) Herink. Several generations of beetles infested the basal portion of stems of either decadent or recently dead paper birch. This behavior preserves a scarce host resource and is enhanced by a relatively low fecundity and ability to establish new galleries without flight dispersal.

KEY WORDS Scolytinae, *Dryocoetes*, paper birch

The genus *Dryocoetes* Eichhoff is represented in North America by seven species, of which the birch bark beetle, *D. betulae* Hopkins, is the only one infesting broadleaved trees, primarily paper birch, *Betula papyrifera* Marshall (Bright 1963). The others infest conifers, particularly spruces (*Picea* spp.) and true firs (*Abies* spp.). All infest dying trees, except *D. confusus* Swaine, which kills subalpine fir, *Abies lasiocarpa* (Hooker) Nuttall, aided by a tree-pathogenic fungus (Molnar 1965). *D. betulae* and *D. confusus* form a rather sharply defined group characterized by the dense brush of hair on the female frons. *D. betulae* may be separated from *D. confusus* by having less dense frontal hair, presence of shallow punctures on the pronotal disk (asperate in *D. confusus*), flatter and less strongly impressed declivital interspaces, and by the host (Bright 1963).

The biology of *Dryocoetes* species has not been studied except for *D. confusus* in British Columbia, Canada, involving seasonal history (Mathers 1931) and response to pheromones (Stock 1981). Flight periodicity of *D. confusus* was studied in northern Utah (Hansen 1996) and in northern Idaho and western Montana (Gibson et al. 1997). Features of the head of larvae and the gastric caeca of larvae and adult *D. affaber* (Mannerheim) and *D. autographus*

(Ratzburg) (as *D. americanus* Hopkins) were described by Thomas (1957, 1967).

Dryocoetes betulae has been recorded rarely, especially in western North America. Three western records are from the United States: Washington (Metaline Falls), Idaho (Priest Lake), and Montana (unknown locality); two records are from southern British Columbia, Canada (Bright 1976, Furniss and Johnson 1987, 2002). The beetle also occurs in eastern North America, where it infests paper birch and (infrequently) American beech (*Fagus grandifolia* Ehrhardt), sweetgum (*Liquidambar styraciflua* L.), black cherry (*Prunus serotina* Ehrhardt), and pear (*Pyrus* sp.) (Baker 1972, Bright 1976).

The egg galleries and larval mines of *D. betulae* in yellow birch (*Betula alleghaniensis* Britton) were shown by Swaine (1918). Beal and Massey (1945) described the burrows (egg galleries) as being irregular with transverse, longitudinal, or diagonal branches. Bright (1976) did not address *D. betulae* specifically, but stated that, as far as is known, all species were polygamous, usually with three or four females being associated with one male. Each female constructs an egg gallery radiating from the nuptial chamber. Likewise, Wood (1982) presumed the biology of *D. betulae* to be essentially that described for the genus (i.e., “polygynous” with parental egg galleries radiating from a central nuptial chamber) and that it “evidently prefers limbs of its host” (but see Discussion) besides infesting stumps and boles of recently cut and unthrifty trees. We present here the

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Fig. 1. Distribution of paper birch (Little 1971) and location of study (black dot).

second record of occurrence of *D. betulae* in Idaho and describe its life stages, reproductive behavior, seasonal history at this location, associated organisms, and host tree characteristics.

Materials and Methods

The study was located at 756 m above sea level in Beaver Creek drainage at the northwest end of Priest Lake, Bonner County, ID (Fig. 1). The area was originally granted to the Northern Pacific Rail Road and then sold to a lumber company. It passed into private ownership in 1921 and has remained undisturbed since then. The forest consists mainly of western red cedar, *Thuja plicata* Donn, western hemlock, *Tsuga heterophylla* (Raphinesque-Schmalz) Sargent, and paper birch. The shade-tolerant conifers (cedar and hemlock) have become dominant, forming a closed canopy and causing the shade-intolerant birch to become decadent and susceptible to the birch bark beetle. We visited the area in 1994 during 12 May, 25 May, 15 July, and 30 July; in 1995 during 17 April; in 1996 during 7–8 February, 3 June, and 11 August; and in 2005 during 2–4 May. At those times, we recorded the size and condition of infested trees, determined in-

festation characteristics and seasonal history of the insect, and obtained infested stem sections for rearing and study at Moscow, ID.

Because of the scarcity of susceptible, shaded-out, paper birch, we found only 16 infested trees during the course of this study. They ranged from 23 to 61 cm in diameter and 15 to 24 m in height. We examined seven of these trees at three successive time intervals. Five trees were felled to determine height of infestation and to obtain stem sections for rearing and detailed examination in the laboratory.

At Moscow, stem sections were kept at room temperature to rear progeny of *D. betulae* and associated organisms. Galleries were excavated periodically to determine details of reproductive behavior and to describe egg galleries. We determined the number of instars by observing egg hatch and molting and by measuring larval headwidths microscopically with a micrometer disc. Immature stages were preserved and described. Associated insects, mites, and nematodes were collected for identification by specialists. The midguts (mesenteron) of mature larvae and adults were dissected in water to count the globular and elongate gastric caeca for comparison with those reported by Thomas (1967) for *D. affaber* and *D. au-*

tographus. Voucher specimens consisting of all stages of *D. betulae* are deposited in the W. F. Barr Entomological Museum, University of Idaho, Moscow, ID.

Results

Life Stages

Egg. The pristine egg is satiny white, oblong in shape, and 0.90 mm average length (range, 0.82–1.00 mm) by 0.51 mm average width (range, 0.48–0.54 mm) ($n = 25$).

Larva. Mature larvae are whitish with honey-color heads and black mandibles that have three distinct denticles. The body is C-shaped; the dorsal and ventral surfaces are covered with microampullae. A narrow, lightly sclerotized, band is located on each side of the dorsal surface of the prothorax, and a somewhat diamond-shaped, lightly sclerotized, area is located on the middle of the ventral surface of the prothorax. In lateral aspect, the body segments are well defined with three folds, the middle one of which protrudes more. Average and range of head widths of the three instars ($n = 25$ each) were LI = 0.40 mm (0.39–0.42 mm), LII = 0.56 mm (0.49–0.63 mm), and LIII = 0.83 mm (0.68–1.09 mm). Body length of LIII varied from 3.5 to 4.5 mm.

The gastric caeca are “globular” and “elongate” in shape (Thomas 1967). The caeca are aligned in a row on each side of the mid-gut; the elongate caeca are located dorsad of the globular caeca. The number of globular caeca varied in number from 11 to 17 per side (mean = 13.6, $n = 38$); the elongate caeca varied in number from 2 to 4 per side (mean = 2.3, $n = 38$). Globular caeca were 0.2 mm in diameter; elongate caeca were 3 times longer and 0.5 times narrower than the globular caeca. Larvae of *D. affaber* and *D. autographus* have 7–13 globular and 1–3 elongate caeca per side (Thomas 1967).

Pupa. The pupa is of the general Scolytinae type, varying in length from 3.8 to 4.6 mm (mean = 4.3, $n = 9$). The pronotum is widest at its base, evenly curved forward to a rounded anterior edge, and has four evenly spaced setae protruding from each side. Mature pupae have conspicuous, darkened mandibles with adult dentation. The wings extend free of the body at a shallow angle. The ninth abdominal segment is prominent and contains a narrow, pointed, caudal spine extending outward at 45° from each side; other abdominal segments lack features such as spines or lobes.

Adult. The adult stage is reddish brown and varies in length from 2.8 to 4.5 mm (Bright 1963). Adults have an evenly convex pronotum, obliquely truncated antennal club, flattened spinose distal portion of the tibiae, and a flat declivity (convex in *D. autographus*) with the sutural and third interspace slightly elevated. The frons of females is more densely clothed with yellow hairs than that of males (Bright 1963).

The caeca are aligned on the midgut as in larvae except that some elongate caeca occur ventrally as well as laterally. The “globular” caeca were more peg-

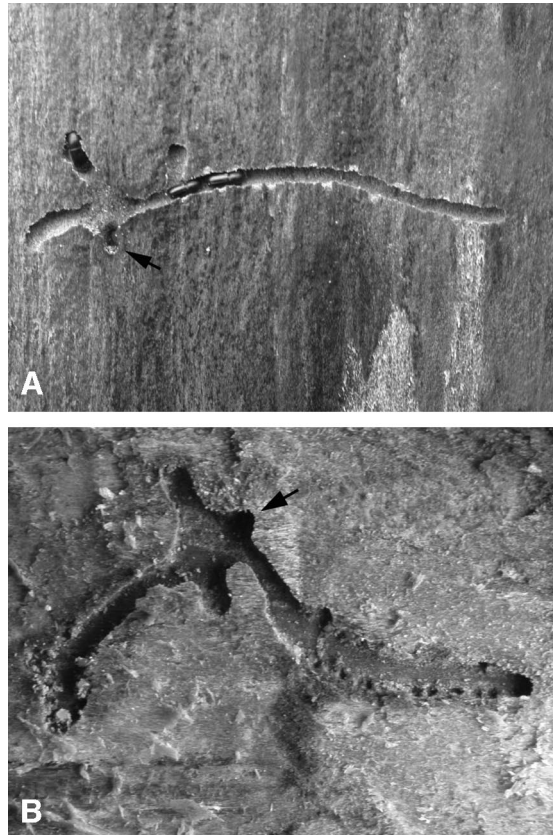


Fig. 2. *Dryocoetes betulae* egg galleries under construction as seen on inner phloem surface of paper birch. Arrows indicate location of entrance holes. (A) Branch at right contains a female followed by a male; a second female has begun another branch at left. (B) A typical two-branched egg gallery. See text for details.

like in shape than in the larval stage and varied in number from 10 to 17 per side (mean = 12.6, $n = 46$). The total number of elongate caeca per individual varied from 4 to 11 (mean = 7.1, $n = 23$). Adults of *D. affaber* and *D. autographus* have 7–12 globular and 2–6 elongate caeca per side (Thomas 1967, sample size not given). During this study, 144 parent and brood adults taken randomly from intermingled gallery systems were accumulated and sexed, and the aggregate sex ratio was 1.8 females per male.

Gallery System

Entrance holes were located at lenticels, perhaps because their rough surface provided traction; elsewhere the bark is smooth. We observed that egg galleries consisted typically of two branches 3–4 cm long with short “turn around” spurs in which no eggs were deposited (Fig. 2A and B). Rarely, egg galleries had three branches. The branches curved across grain and were exposed on the phloem surface but did not score the xylem. Their outline, however, was stained black on the wood surface, perhaps because of an associated

fungus. The egg galleries were kept free of frass, which was granular and reddish brown in color when expelled onto the bark surface.

Fecundity was difficult to determine because most galleries were under construction, and egg laying was incomplete or were older and their larval mines so intermingled that they could not be related to their gallery of origin. However, no egg occurred in the first centimeter of a female's gallery, and we counted four to nine eggs per centimeter in a sample of 10 galleries, totaling 15 cm of "productive" gallery. Thus, a 4-cm-long gallery (3 cm of productive length) might have 12–27 eggs, and this conforms well with our impressions gained from general observations of galleries throughout the study. In any case, the greatest confirmed number of brood occurred in a gallery in mid-August 1996 that had 17 eggs, 6 LI, 8 LII, and 1 LIII (total, 32). Because the range of developmental stages in this gallery indicates that oviposition may have ceased and based on our observations of many other galleries, we propose that 32 brood could be near the upper limit of fecundity.

Eggs were deposited along opposite sides of the gallery in niches. Their long axis was at right angle and not parallel to the length of the gallery. After hatching, larvae mined irregularly outward from the egg gallery for up to 7 cm depending on available space. Mature larvae prepared shallow pupal cells by pressing their body repeatedly against the wall of their cell, matting it firmly.

Seasonal History

Our observations in the field and laboratory throughout this study indicated one annual generation at this location, as reported for *D. confusus* in British Columbia (Mathers 1931, Stock 1981). Eggs were observed from mid-May to mid-August, resulting in a small portion of broods attaining the adult stage before winter; most, however, overwintered as larvae. For example, a sample of 478 brood on 3 May 2004 was composed of 2 LI, 68 LII, 335 LIII, and 73 adults; thus, 85% were larvae, conforming to our general observations.

Associated Organisms

Most trees were also infested in their bases by an ambrosia beetle, *Trypodendron betulae* Swaine (Coleoptera: Curculionidae), which bored into sapwood in areas not occupied by *D. betulae*, beginning in late April. The bronze birch borer, *Agilus anxius* Gory (Coleoptera: Buprestidae), which commonly infests ornamental paper birch in urban areas in northern Idaho, was not prevalent here. Larval mines, presumed to be those of *A. anxius*, were observed only in the upper stem of one felled tree. No hymenopterous parasitoid was encountered during the study, and none is listed for *D. betulae* by Krombein (1979). However, *Rhizophagus dimidiatus* Mannerheim (Coleoptera: Monotomidae [=Rhizophagidae]), and a clerid, *Thanasimus undatulus* (Say) (Coleoptera:

Cleridae), were observed in brood chambers, apparently preying on *D. betulae* larvae. *R. dimidiatus* is reported to be a predator of *Ips perturbatus* (Eichhoff) (Coleoptera: Curculionidae) in Alaska (Graves et al. 2004), and the species *R. grandis* Gyll. is effective in controlling *Dendroctonus micans* (Kugelann) (Coleoptera: Curculionidae) in Europe (Evans and King 1987). *T. undatulus* is a well-known predator of bark beetles in western North America but had been recorded previously only in association with coniferous bark beetles (W. F. Barr, personal communication).

Galleries and brood chambers contained two species of mites: *Histiostoma* sp. (Acari: Histiostomatidae) and *Proctolaelaps* n. sp. (Acari: Ascidae). The *Proctolaelaps* species resembles *P. fiseri* Samsinak, which is associated with *Dryocoetes* spp. and other genera of bark beetles in Europe and with *Ips* spp. in the southeastern United States (E. E. Lindquist, personal communication). A nematode of the Order Rhabditida occurred in the lumen of midguts of larvae and adult *D. betulae*. Massey (1974) lists *Ektaphelenchus prolobos* Massey (Aphelenchida: Ektaphelenchidae) from *D. confusus* in New Mexico but none from *D. betulae*. White mycelia fans of a root-rot fungus, *Armillaria ostoyae* (Romagnesi) Herink (Agaricales: Tricholomataceae), (Williams et al. 1986) were common under the bark in the bases of infested trees and its black, threadlike, rhizomorphs infiltrated the egg galleries and larval mines of *D. betulae*, most conspicuously after broods were no longer present.

Host Tree Characteristics

All infested birch were suppressed by shade-tolerant conifers and were dead or nearly so. Some possessed a few leaves on remnant live branches but most had no live crown, and some had even shed their smaller branches that had died earlier. Trees with an extensive live crown were not infested. *D. betulae* typically infested the lower bole, which had a visibly evident high moisture content when bark was removed. All infested trees had evidence of root-rot fungus in their bases (Williams et al. 1986), and the phloem had a sour odor.

Discussion

We determined and clarified several details of the biology and anatomy of *D. betulae*. This insect was restricted to the main stem, particularly in the base, and did not infest limbs, contrary to Wood (1982). The species is polygamous, but its galleries are distinct from those of *D. confusus* in having lateral spurs for turning around (in the absence of an enlarged central nuptial chamber) and fewer branches because of a lower ratio of females to males. The posterior gastric caeca of adult *D. betulae* are somewhat peglike in shape rather than globular as indicated for *D. affaber* and *D. autographus* (Thomas 1967), and caeca of adults and larvae are more abundant than in the latter two species.

During our study, we observed only one beetle to have flown from stem sections during rearing. Commonly, however, new galleries extended from existing gallery systems or were created separately in adjacent uninfested phloem by new adults without their having flown. That, in combination with a relatively low rate of fecundity, serves to conserve a very limited susceptible host resource. Such behavior is also displayed by the willow bark beetle, *Trypophloeus striatulus* (Mannerheim), in Alaska (Furniss 2004).

Considering that paper birch occurs transcontinentally (Fig. 1), it seems unusual that *D. betulae* has been recorded at so few localities, particularly in its western distribution, and that these western localities lie along the southern fringe of birch distribution. Our observations indicate that populations of this beetle in our study area (Fig. 1) require or benefit from very moist, uninfested, phloem in bases of mature paper birch that are recently dead or dying from suppression by cedar and hemlock. According to Mahoney (1998), "paper birch is shade intolerant and in Idaho it usually self-thins by age 20 or 30 and then shade-tolerant fir, cedar, and hemlock, reproduce underneath and gradually replace the birch. With nearly 100 yr of fire suppression and more recent commercial discrimination (ridding of birch in preference for conifers) and losses to pathogens, the composition of birch has been drastically reduced. . . ." Thus, the undisturbed environment in which birch reaches maturity and dies from shading has diminished in occurrence, largely because of human settlement and forest use. It is noted that the only Washington record of *D. betulae* was 77 yr ago (1929), and the Montana record is believed to have occurred also in that time period when forest conditions favored the occurrence of this bark beetle.

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