OBSERVATIONS ON PHENOLOGY, DEVELOPMENT, AND MORTALITY OF LARVAE OF THE HAZELNUT WEEVIL (CURCULIO OBTSUS (BLANCHARD): CURCULIONIDAE) IN NUTS OF BEAKED HAZELNUT (CORYLUS CORNUTA MARSHALL: BETULACEAE) IN THICKETS IN MAINE\textsuperscript{1}

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Abstract.—Little is known about the biology of the hazelnut weevil Curculio obtusus (Blanchard), though closely-related species are widespread and well studied. The objective of this study was to document details of development of larvae in nuts, including mortality factors, assessment of the infrequent phenomenon of multiple infestation of nuts, and confirmation of 4 larval instars. Samples of beaked hazelnuts taken every 4 days over the course of the summer, 1995, revealed the development of larvae through 4 instars, beginning with eggs in early June and progressing through 4th-stage grubs exiting nuts in late August. At the peak of infestation, in early August, 71% of the sampled nuts were infested with weevil larvae. Decay and non-formation of nut kernels accounted for an estimated 10% mortality among the larvae. Multiple infestation accounted for an additional 8% mortality due to interference competition. Nut predation also caused mortality of an estimated 10% of larvae.

The genus Curculio (Curculionidae; Curculioninae) is comprised of 27 species of nut- and acorn-infesting weevils in North America (Gibson, 1969). Most (23 species) inhabit oak trees (Quercus spp.); only C. obtusus, the hazelnut weevil, is known to specialize in hazelnuts (Corylus spp.) in the eastern half of the United States (Hamilton, 1890; Brooks, 1910; Gibson, 1969, 1985a, 1985b). This weevil exploits the nuts of wild (Corylus americana Walter) and beaked (C. cornuta Marshall) hazelnut not only for food at all stages but also for oviposition sites (Gibson, 1969).

Adult Curculio species emerge from the soil in early summer and fly to the nearest host tree or shrub where they feed on immature nuts or acorns and mate (Gibson, 1969; Raney and Eikenbary, 1968). The species are dimorphic; the females’ rostra are somewhat to much longer than those of males, depending on species, and are used to excavate egg chambers in the nuts as well as to feed (Brooks, 1910; Gibson, 1969).

The vermiform Curculio grubs are reported to pass through 4 instars feeding inside their host nuts, destroying the nut kernel in the process. At maturity in the fall, they chew an exit hole in the nutshell and drop to the ground where they immediately burrow almost straight down, to depths from 9 to 28 cm among pecan weevils (C.

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caryae [Horn]) (Gibson, 1969; Harris, 1975; Harp and Van Cleave, 1976; Harrison et al., 1993), and enter a state of diapause. *Curculio* species pass the majority of their lives as subterranean diapausing larvae. The length of diapause varies within species; Menu and Debouzie (1993) found, for example, that up to 4 years could be spent underground by a small proportion of chestnut weevil (*C. elephas* Gyllenhall) grubs in France; 32–56% emerged after 2 to 3 years.

The few references to the hazelnut weevil *C. obtusus* consist mainly of early naturalist descriptions (e.g., Hamilton, 1890; Brooks, 1910; Hutchings, 1927). Few details have been reported about its biology, though its host species range from Quebec to Georgia and westward into the midwestern U.S. (Fernald, 1950; Gibson, 1969). Furthermore, its host species have at times been considered to have commercial potential, particularly in Canada (e.g., Hutchings, 1927; St. Pierre, 1992).

*Curculio obtusus* larvae develop singly in a nut, unlike many of their congeners. Vrbl et al. (1979, p. 363) assert, of the European hazelnut weevil *C. nucum* L., that ≤4 eggs can be found in the shell of cultivated hazelnuts (*Corylus avellana* L.) in Slovenia, “but into the fruit itself there creeps only 1 larva.” Multiple infestation, which occurs at a low level among *C. obtusus* (Gibson, 1969), is maladaptive; as with *C. nucum*, only 1 larva will succeed in nuts containing >1 larva (pers. obs.).

Interior galls and other deformities in the nutshell are caused by this species in wild and beaked hazelnuts and also by the European hazelnut weevil in cultivated hazelnuts (Rabaud, 1913; Gibson, 1969; Meyer, 1987). *Curculio obtusus*, unlike the other *Curculio* species, has been reported to pass 2 instars feeding in the soft shell and shell lining before passing into the kernel (Gibson, 1969).

The objective of the current study was to investigate and document details of larval development of the hazelnut weevil, including an assessment of the phenomenon of multiple infestation, determination of mortality factors, and confirmation of the number of larval stages. These observations were part of a larger study that included documentation of adult behavior and intershrub movements detailed by Treadwell (1996).

**MATERIALS AND METHODS**

**Study site and host plant descriptions:** The study was conducted in a secondary succession of woodland in T32 MD, Hancock County, Maine (44°58′N, 68°27′W), at an elevation of ca. 82 m, on land owned by Champion International Corporation and minimally maintained for primitive camping. The plant community consisted of a grey birch (*Betula populifolia* Marshall)-beaked hazelnut-blueberry (*Vaccinium angustifolium* Aiton) sere on sandy soil. The site was chosen because of a profusion of “brush-stage” (Hsiung, 1951) hazelnut thickets and observations of a high degree of hazelnut weevil activity in the area the previous summer.

Beaked hazelnut, so-called for the projecting involucre of united bracts which enclose its nut, is a monoecious shrub distributed throughout woodlands and forests of central North America. It is one of only 3 species of *Corylus* native to North America and is grouped by some in the hazel family, Corylaceae, along with *Ostrya* Scopoli and *Carpinus* L. (ironwood), *Betula* L. (birch), and *Alnus* B. Ehrhart (alder) (Fernald, 1950). Others place *Corylus* in the family Betulaceae (Hsiung, 1951). It sprouts vigorously from underground modified stems and, in New England and the
Adirondacks, is one of the 6 most common shrub-stratum species in successional progressions from overgrown pastures to climax forests of hemlock (Tsuga canadensis [L.] Carrière.), beech (Fagus grandifolia Ehrhart), and sugar maple (Acer saccharum Marshall) (Hsiung, 1951). In situations of high light intensity, found by Hsiung (1951) to be the critical factor in density of Corylus cornuta, the shrub attains maximum vegetative reproduction and can appear as dense thickets.

Larval development of the hazelnut weevil: Samples of 75–>100 nuts (x = 103 ± 18 nuts, N = 22 samples) were collected haphazardly from thickets every 4 days from 12 June to 4 September 1995 for dissection, to monitor larval development as well as progression of nut damage. Nuts were transported on ice and immediately stored in a freezer until dissection under a microscope within 3 days. Dissected nuts were categorized as (a) intact (no damage to nut meat), (b) no kernel (shell fully formed but containing only a cottony lining), (c) decayed, (d) weevil-infested (containing eggs, larvae, or exit hole), and (e) damaged but not infested (i.e., outwardly punctured and/or deformed). Weevil eggs and larvae at each of 4 stages found in dissected nuts were counted and preserved in 70% ethanol. Twenty-four individuals of each of the 4 assumed larval stages were selected randomly and the width of their head capsules measured with an ocular micrometer in a dissecting microscope.

RESULTS

A total 2,269 nuts were collected and dissected between 12 June and 4 September 1995 at 4-day intervals. Of these, 873, or 38.5%, were infested with weevil eggs or larvae, with a peak 70.6% infestation occurring on 7 August (Fig. 1a). Decayed nuts peaked at 30.4% on 18 July (Fig. 1b).

Eggs were first found in the layers of nutshells on 20 June (Fig. 2), 17 days after the first adults were observed and 2 days after adults were first observed mating (Treadwell, 1996). First instars were found feeding in nut shell layers or interior galls beginning on 6 July, about 2 weeks after the onset of oviposition. Fourth instars were found beginning on 7 August, when percentage of total nuts infested with this stage suddenly increased from 0 to >17%. Exit holes were first observed in the 11 August sample. Complete larval development, from egg to exit, thus takes about 36 days.

Weevils had emerged from 71.4% of the infested nuts in the 4 September sample. Sampling was discontinued at this date because predation on nuts, presumably by the many red squirrels (Tamiasciurus hudsonicus gymnicus [Bangs]) and chipmunks (Tamias striatus L.) in the area, had become noticeably heavy on 27 August. Empty shells were more and more frequently found strewn under the shrubs and thickets, and natural nut drop had also begun by this date; thus nuts for sampling were difficult to find. Additionally, the proportion of nuts with no kernel increased from ca. 20% on 27 August to almost 40% on 4 September (Fig. 1b).

Multiple infestation occurred in 70 nuts, or 8% of the total 873 infested, and peaked on 30 July, when 22.6% of infested nuts contained >1 larva (Fig. 1a). The majority of multiple inhabited nuts contained 2 larvae, though 10.4% contained 3 larvae and a single nut contained 4 larvae (Fig. 3). In only 2 cases was a 4th-stage larva found in association with another larva. In one of these, surprisingly, the 4th instar was found partially consumed by a much smaller 2nd instar.
Fig. 1. Hazelnut weevil larval infestation, beaked hazel nut conditions, and climatic conditions at T32 MD, Hancock County, Maine, 28 May–4 Sept. 1995. (a) Percent of nuts infested, and percent of infested nuts containing >1 larva, in samples collected at 4-day intervals; (b) percent punctured/damaged, decayed, and no-kernel nuts in samples collected at 4-day intervals; (c) daily rainfall, solar radiation, and average air temperatures.
Eggs appeared most often in the top \( \frac{1}{2} \) or \( \frac{1}{4} \) of the shell. First instars were observed to feed first within the shell layers, sometimes within the exaggerated thickness of a gall, until breaking through to the shell lining. They then fed in the lining in a fairly straight line down to the bottom of the nut. Entry into the kernel was made at a distinctive round hole chewed through the thin skin, and ecdysis to the 2nd stage occurred soon after this. There was no evidence for feeding in the shell lining by 2nd instars.

In the early stages, multiple larvae could easily be found by looking for multiple entry holes into the kernel. Sometimes, however, one larva could be tracked between holes connected by longitudinal ruts in the lining; some would apparently sample the nut kernel before settling down to feeding.

Mean head capsule widths among the 4 stages appeared to vary only slightly from the predictions of Dyar's Law (Dyar, 1890); i.e., a constant ratio (in this case ca. 0.60) between the head capsule widths of each successive stage (Fig. 4).
Anomalous trends in the data: A peak and then decline in proportions of infested nuts seems counter-intuitive: the proportion of nuts infested by weevils should level off at some point, since the nuts do not renew themselves and infestation is a permanent state. Pucci (1992: 9) reported a similar trend in data for European hazelnut weevils *C. nucum* infesting commercial hazelnuts in Italy, and attributed it to "the fruit drop effect": hazelnuts with larval exit holes tended to drop earlier than uninfested nuts. A similar phenomenon among beaked hazelnuts infested by *C. obtusus* would mean that the chances of picking an uninfested nut improve after a peak of infestation in early August, though the chances of its being decayed or unfilled are also greater (Fig. 1a). Probably these latter are lighter, lack abscissive mechanisms (why waste resources on an unfruitful shell?), and are instinctively passed over by nut predators; thus they will appear in greater proportions at the end of the season.

Two reasons might be given for the large proportion of 1st instars found in the sequential samples of nuts (Fig. 2). First, because eggs were deposited in shell layers it is likely that an unknown number were overlooked in dissection. An effort was made to examine all punctures and wounds in the shell, but eggs were observed to rupture and spill extremely easily, so some "disappeared" in the dissection process; numbers of eggs are most likely under-reported. For these reasons, occurrence of >1 egg is no doubt also under-reported.

Secondly, some first instars lingered into the final sample, a full 8 weeks after this stage had first appeared. An extended first larval stage would cause an exaggeration of their abundance proportionate to the other stages; members of the same cohort would be counted >1 time. Lowered quality or availability of nutrients has been shown to inhibit ecdysis in many insect species. Sehnal (1985) found, for example, that caterpillars of the greater wax moth *Galleria mellonella* (L.) molted after 15 hours on a normal diet but required 40 hours when the diet was mixed equally with sawdust. Release of prothoracicotropic neurohormone, which stimulates release of molt-inducing ecdysone, has been shown to be dependent on attainment of a certain "critical" body size increment (Sehnal, 1985).
First instars in the last few samples were all found in decaying nuts or nuts with no kernel. Apparently the cottony parenchyma of no-kernel nuts can sustain the life of a weevil larva but does not provide sufficient nutrients or appropriate cues for ecdysis. Besides obviously decaying and unfilled nuts, many “normal-appearing” kernels might have been affected by some factor, such as the long period of no rain as nuts were forming (Fig. 1c), which lowered their quality enough to inhibit ecdysis. **Factors in mortality of larvae:** Conditions of unfilled nuts and decay appear to be major mortality factors among young weevil larvae. Females unwittingly deposit eggs into shells in which kernels do not form and/or into which fungi and mycetophilous flies enter, in many cases, ironically, through the weevil oviposition puncture (Winston, 1956), and initiate a decay process. Larvae hatch into an environment unsuitable for growth and development but many subsist for weeks before dying of desiccation or starvation.

Ten percent of the nuts in sequential samples over the season showed evidence of rot or decay, with or without ubiquitous, unidentified microscopic maggots—from 1 to 15 in any one nut. Winston (1956) reported *Fusarium* sp. and *Penicillium* sp. responsible for initiating decay in acorns of red oak (*Quercus rubra* L.) in Illinois. He also found maggots, identified as *Mycodiplosis* sp. and *Rubsoamenia* sp. (Cecidomyiidae), to be spreading spores of the fungi. As in the case of maggots observed in hazelnuts, they created areas of decay around themselves; weevil larvae in maggot-infested nuts are certain not to survive.

An unconscious sampling bias might have been introduced against decayed nuts in the field because of their often obvious appearance. A more accurate estimate of their effect on larval populations can be gained by analyzing an absolute sample of nuts (N = 1,246) collected from 33 discrete beaked hazelnut shrubs on 3 August 1995 (Treadwell, 1996). Here 15.3% of the total were in a state of decay that rendered the nut kernel unfit for weevil sustenance. An accurate count of larvae in decaying nuts could not be kept because the cadavers were also broken down by invading hyphae and maggots. Decay and no-kernel conditions together claim ca. 25% of a hazelnut crop. If 40% of those nuts are weevil-infested (Treadwell, 1996), an estimated 10% of total larvae do not survive because of pathological nut conditions.

Since it appears that ca. 30 days are required to complete larval development after ecdysis into the 2nd instar, grubs that were still at 1st instar on 15 August, 9–10% of the larval population, most likely did not survive. Quality of mature nuts can be assumed to be quite different from that of young developing kernels with which early instars normally coincide. Additionally, the fate of the hazelnut itself became more and more tenuous as the summer came to an end.

As mentioned, red squirrels and chipmunks were observed at this site and were noted by Hsiung (1951) to consume or bury “the great proportion of the [beaked] hazelnut crop” at a Minnesota study site. It is not known whether these two rodents have any preference for uninfested nuts. Grey squirrels (*Sciurus carolinensis* Gmelin), however, have been observed to detach and sniff or taste European hazelnuts infested with *C. nucum* before discarding them (Lloyd, 1968). White-footed mice (*Peromyscus leucopus* Thomas) prey on detached acorns of white oak (*Q. alba* L.) with no preference for those infested or uninfested by larvae of the weevils *Curculio pardalis* (Chittenden) and *Conotrachelus naso* LeConte (Semel and Andersen, 1988).
Additionally, detached nuts were observed in the laboratory either to desiccate or to start decaying within a few days.

Multiply-infested nuts account for another 8% of larval mortality. These represent larvae that were selected out by a critical interference competition between nuthatches. Since multiple larvae reached levels of >20% of infested nuts in the sequential random samples, a competitive "edge" inside the nutshell might seem a measure of fitness.

In the similar case of the cowpea weevil Callosobruchus maculatus (Fabricius), small beans can sustain only 1 larva to maturity. Among the larva of this species, in any bean regardless of size one larva will out-compete any others in survival. Mitchell (1983) speculates that interference competition, "activity which directly or indirectly limits a competitor's access to a resource" (Prokopy et al., 1984, p. 307), might have evolved to ensure the success of at least one larva, rather than a situation of exploitation competition in which both would die if consuming a small bean equally until it was depleted. For the hazelnut weevil there can be no doubt as to the optimum competition strategy; 1 larva can and usually does consume an entire kernel.

In summary, then, these observations suggest almost 30% mortality among nut-infesting hazelnut weevil larvae due to decay, interference competition, and nut predation. Conclusion: The inside of a hazelnut seems a relatively secure, insulated habitat for growth and development. At the scale of a weevil, however, this environment presents a variety of hazards to which the insect has adapted and evolved. Evidence of parasitization of nut-inhabiting larvae was not detected, but rearing of larvae extracted from nuts, in a controlled environment, would reveal whether parasitization has taken place. Additionally, a longer-term study would shed some light on questions regarding synchronicity of life cycle with host plant phenology.

ACKNOWLEDGMENTS

The field assistance of Bancroft Whitely is gratefully acknowledged. This study was supported, in part, by the Maine Agricultural and Forestry Experiment Station and The Graduate School of the University of Maine. This article is published as Maine Agricultural and Forestry Experiment Station Publication MAFES No. 2114.

LITERATURE CITED


Received 15 October 1996; accepted 3 September 1997.