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PREDATION BY AMPHIBIANS AND SMALL MAMMALS ON THE SPRUCE BUDWORM (LEPIDOPTERA: TORTRICIDAE)

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ABSTRACT

Stomach-content analyses of pitfall-trapped amphibians and small mammals showed that the eastern American toad, *Bufo americanus americanus*, and the wood frog, *Rana sylvatica*, preyed on late instars and moths of the spruce budworm, *Choristoneura fumiferana*. The spotted salamander, *Ambystoma maculatum*, and the masked shrew, *Sorex cinereus*, also preyed on late instars of the spruce budworm.

Known predators of the spruce budworm, *Choristoneura fumiferana* (Clem.), include both invertebrates and vertebrates (Jennings and Crawford 1985). Of the vertebrate predators, birds are the best known and most extensively studied (Dowden et al. 1953, Morris 1963, Crawford et al. 1983, Crawford and Jennings 1989). Although small mammals have long been implicated as potential predators of the spruce budworm (Morris et al. 1958, Morris 1963, Otvos 1981, Kelly and Régnière 1985), definitive evidence of such predation generally has been lacking, except for the red squirrel, *Tamiasciurus hudsonicus* (Bangs), (Dowden et al. 1953, Jennings and Crawford 1989). Because of their dependence on fresh water, amphibians generally are considered unimportant predators of forest insects (Buckner 1966). Nevertheless, budworm larvae and pupae are susceptible to predation by terrestrial vertebrates, such as amphibians and small, insectivorous mammals, when the large larvae drop from host-tree crowns to the forest floor (Morris and Mott 1963, Kelly and Régnière 1985). Amphibian populations were monitored during budworm-suppression projects in Maine (Banasiak 1974, Peterson 1976, Sassaman 1978), but predation on the spruce budworm was not determined.

Here we describe for the first time predation by amphibians (both anurans and caudates) on late instars and moths of the spruce budworm. We also provide definitive evidence of predation by small mammals (insectivores) on late instars of *C. fumiferana*.

MATERIALS AND METHODS

Study Sites. We pitfall-trapped amphibians and small mammals for two years (1977, 1978) in a spruce-fir (*Picea-Abies*) forest that was heavily infested with the spruce budworm. Individual study sites were 48–61 km northwest of Millinocket,

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Piscataquis County, Maine (45°45′–46°10′ N, 68°55′–69°20′ W). Portions of the forest had been strip clearcut, resulting in alternating clearcut and uncut residual strips. We investigated 5 strip-clearcut stands and 5 nearby dense (uncut) stands in 1977; 7 strip-clearcut stands and 3 dense stands were investigated in 1978. For details of study-site vegetation, sampling design, and associated invertebrates, see Jennings et al. (1984, 1986a, 1986b, 1988).

Pitfall Traps. For both study years, we used 40 large-capacity pitfall traps (Houseweart et al. 1979) to capture terrestrial amphibians and small mammals. Each trap bottle (1 liter) contained ca. 300 ml of a 1:1 mixture of ethylene glycol (antifreeze) and 70% ethanol as a killing-preservative agent. Four traps were placed in each strip-clearcut stand (5 replications, 1977; 7 replications, 1978); one trap each in two clearcut strips and in two adjacent uncut residual strips (see Fig. 1, Jennings et al. 1984). Correspondingly, four traps were placed in each nearby dense (uncut) stand investigated (5 replications, 1977, 3 replications, 1978). Traps were open continuously and their contents collected weekly for 10 weeks (26 May–4 August) in 1977, and for 11 weeks (18 May–3 August) in 1978. Total sampling effort was 5580 trap nights.

Identifications. Pitfall-trap contents were transferred to small jars and transported to the laboratory where collections were sorted and identified. Amphibian identifications follow Conant (1975); small mammal identifications follow Burt and Grossenheider (1976) and Godin (1977). All vertebrate identifications were verified by comparison with museum specimens retained in the Department of Wildlife, and Department of Zoology, University of Maine, Orono. Voucher specimens of collected amphibians and small mammals have been deposited in the collections of the Department of Wildlife, College of Forest Resources, University of Maine, Orono.

Stomach-Content Analyses. Digestive tracts of captured amphibians (n = 134; 5 desiccated specimens not dissected) and of small mammals (Insectivora only; n = 41) were removed and their contents examined with a stereomicroscope. Larval mandibles, pupal cremasters, and moth genitalia were compared with a reference collection of the spruce budworm and associated insects. The chitinized mandibles, cremasters, and genitalic parts are the most reliable diagnostic structures for identifying remains of *C. fumiferana* in predator stomachs (Crawford and Jennings 1982). For amphibian stomach contents, larval instars of the spruce budworm were determined by head-capsule size (McGugan 1954). Because larval head capsules are seldom found intact in small mammal stomachs, we estimated instars based on relative mandible size, i.e., ocular estimates of mandible size compared with reference material.

RESULTS

Amphibian Numbers and Species. One hundred thirty-nine amphibians representing two orders, five families, five genera, and six species were pitfall-trapped in spruce-fir forests of northern Maine. The species and total numbers trapped were: eastern American toad, *Bufo americanus americanus* Holbrook, (n = 64); wood frog, *Rana sylvatica* LeConte, (n = 62); redback salamander, *Plethodon cinereus* (Green), (n = 9); red-spotted newt, *Notopthalmus viridescens viridescens* (Rafinesque), (n = 1); spotted salamander, *Ambystoma maculatum* (Shaw), (n = 1); and blue-spotted salamander, *Ambystoma laterale* Hallowell, (n = 2). Anura (toads, frogs) were found in all three forest conditions studied; Caudata (salamanders, newts) were found mostly in uncut residual strips and in dense (uncut) stands.

Amphibian Predation on Spruce Budworm. For both study years, amphibians fed on larvae and moths of the spruce budworm (Table 1). However, the percentage of pitfall-trapped amphibians that had eaten budworm prey was low (< 7.5%, n = 134). Numbers of spruce budworm prey per stomach ranged from 1 to 6; most

(70%) were late instars (L_5, L_6), the key age interval that influences generation survival of the spruce budworm (Morris 1963).

Small Mammal Numbers and Species. Forty-six small mammals representing two families, four genera, and five species were pitfall-trapped in strip-clearcut and dense (uncut) spruce-fir stands of northern Maine. The species and total numbers trapped were: masked shrew, *Sorex cinereus* Kerr, (n = 33); smoky shrew, *Sorex fumeus* Miller, (n = 1); pygmy shrew, *Microsorex hoyi* (Baird), (n = 7); red-backed vole, *Clethrionomys gapperi* (Vigors), (n = 2); and southern bog lemming, *Synaptomys cooperi* Baird, (n = 3). Most (90.2%) of the Insectivora were trapped in strip-clearcut stands, both in residual (uncut) strips and in strip clearcuts. Although few Rodentia were caught, they were trapped in all three forest conditions studied.

Small Mammal Predation on Spruce Budworm. Digestive tracts of 16 (48%, n = 33) masked shrews and 3 (44%, n = 7) pygmy shrews contained insect larval mandibles (range 1–8). One tract of a masked shrew had an insect pupal cremaster. However, only two of these insect parts could be positively identified as remains of *C. fumiferana*. One distinctive spruce budworm mandible was found in each digestive tract of 2 masked shrews, both captured on 30 June 1977 in residual strips. A possible mandible of the spruce budworm also was found in the digestive tract of 1 pygmy shrew, but positive identification was impossible because distinctive features (mandibular teeth and condyle) were missing.

DISCUSSION

Our stomach-content analyses of amphibian foods provides the first evidence that *Ambystoma maculatum* preys on larvae of the spruce budworm. The results of this study also indicate that both spruce budworm larvae and moths are included in the diets of *Bufo a. americanus* and *Rana sylvatica*. All three species of amphibians should be added to the list of known predators of the spruce budworm (Jennings and Crawford 1985).

We suspect that amphibian predation on the spruce budworm is opportunistic, and is influenced by prey availability and prey activity. Only the more active life stages (i.e., larvae and moths) of the spruce budworm were eaten by amphibians. Although pre-pupae and pupae of the spruce budworm also may drop from host-tree crowns to the forest floor (Morris and Mott 1963, Kelly and Régnière 1985), none were eaten by the pitfall-trapped amphibians (Table 1). Hence, these less active, generally immobile life stages may escape detection by amphibians.

Because some amphibians frequently eat ants (Hamilton 1954, LeClair and Vallières 1981), and most budworm life stages are susceptible to predation by ants (Finnegan 1978, McNeil et al. 1978), secondary predation may occur when ants transport budworm prey back to the nest. At least four of the eastern American toads examined during this study contained both budworm and ant prey in their stomachs.

Our stomach-content analyses of small mammals confirms previously suspected but unsubstantiated predation by *S. cinereus* on large larvae of the spruce budworm. Otvos (1981) included the masked shrew among three small mammals suspected to feed on the spruce budworm in Newfoundland; however, stomach-content analyses were not made. Our study indicates that the masked shrew, and possibly the pygmy shrew, should be added to the list of vertebrate predators of the spruce budworm (Jennings and Crawford 1985).

The extent and relative importance of predation by amphibians and small mammals on the spruce budworm generally are unknown. Kelly and Régnière (1985) concluded that predation on spruce budworm pupae on the forest floor was high (72.5% per day), and was largely attributable to vertebrate predators. No doubt the susceptibilities to predation by terrestrial vertebrates varies among the different

Table 1. Predation by amphibians on the spruce budworm based on stomach-content analyses (N = 134) of pitfall-trap collections, Piscataquis County, Maine.

Date	Predator species	Habitat*	Spruce budworm number and life stage**
1977			
30 June	*Bufo a. americanus*	D	3 - L_6
30 June	*Rana sylvatica*	R	1 - L_5
30 June	*Rana sylvatica*	R	1 - L_6
21 July	*Bufo a. americanus*	C	1 - $L_?$
4 Aug.	*Rana sylvatica*	D	1 - ♀ moth
1978			
1 June	*Bufo a. americanus*	D	1 - L_5
15 June	*Bufo a. americanus*	D	1 - L_3, 3 - L_4, 1 - L_5, 1 - L_6
15 June	*Ambystoma maculatum*	D	1 - L_4, 1 - L_5, 1 - L_6
22 June	*Bufo a. americanus*	D	1 - L_5, 1 - L_6
20 July	*Bufo a. americanus*	R	1 - ♂ moth

*D = dense (uncut) stand; R = uncut residual strip; C = clearcut strip.
**$L_3 \ldots L_6$ = instar.

budworm life stages (eggs, larvae, pre-pupae, pupae, moths). Such predation also may be influenced by budworm behavior (e.g., larval-pupal droppage from host-tree crowns; increased mobility of starved larvae; moth-flight activity) and population density (i.e., potential-prey abundance). Predator abundance and feeding behavior (generalist vs. specialist) also are factors.

The large-capacity pitfall trap used in this study was primarily designed to capture terrestrial invertebrates such as ants, carabid beetles, phalangids, and spiders (Howseweart et al. 1979). Because this trap has a plastic funnel (15 cm) that tapers to a 2.54-cm diameter spout, it no doubt was selectively biased toward capture of small-sized amphibians and insectivores. For future studies, larger-diameter traps with drift fences may yield substantially greater catches.

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