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THE LIFE HISTORY OF *DASYPYGA ALTERNOSQUAMELLA* RAGONOT (PYRALIDAE) FEEDING ON THE SOUTHWESTERN DWARF MISTLETOE (*ARCEUTHOBIUM VAGINATUM*) IN COLORADO

KAILEN A. MOONEY

Department of EPO Biology, University of Colorado, Boulder, Boulder, Colorado 80309-0334, USA
kailen.mooney@colorado.edu

ABSTRACT. The immature stages, feeding and oviposition behaviors, patterns of larval abundance, and associated arthropod fauna of *Dasypyga alternosquamella* Ragonot (Pyralidae) on *Arceuthobium vaginatum* susp. *cryptopodum* (Hawks.), the Southwestern dwarf mistletoe, are described and illustrated. The study was conducted at the Manitou Experimental Forest, U.S.D.A. Rocky Mountain Research Station, Woodland Park, Colorado, where the Southwestern dwarf mistletoe parasitizes *Pinus ponderosa* (Laws.) *scopulorum*.

Additional key words: biological control, herbivory, Phycitinae, *Promylea lunigerella*, Blue Hairstreak.

Dwarf mistletoes have significant economic and ecological impacts on coniferous species throughout the West and have been called "the single most destructive pathogen of commercially valuable coniferous timber trees in several regions of Mexico, western Canada, western United States, and parts of Asia" (Hawksworth & Wiens 1996). Past work has catalogued the lepidopteran and other arthropod fauna associated with dwarf mistletoes (Stevens & Hawksworth 1970), but there is little or no natural- or life-history information is available for many of these species. *Dasypyga alternosquamella* Ragonot (Pyralidae, Phycitinae), a common herbivore of dwarf mistletoes can have significant effects on dwarf mistletoe standing biomass (e.g., Reich 1992), and could be an important agent of biological control for this important conifer parasite.

Dasypyga alternosquamella feed on multiple species of dwarf mistletoes (*Arceuthobium* spp. [Viscaceae]) throughout western North America (Heinrich 1920). This species was described by Ragonot (1887) from specimens collected in California. A description of larva and pupa were first given by Heinrich in 1920, and relevant information was again summarized by Heinrich in 1956. This is the first published work to provide basic natural- and life-history information on this species. In this paper I describe the immature stages of *D. alternosquamella*, larval feeding and oviposition behaviors, and a brief account of other dwarf mistletoe-associated arthropods at a field site on the eastern slope of the Colorado Rockies.

MATERIALS AND METHODS

This work was conducted at the Manitou Experimental Forest, an administrative unit of the U.S. Department of Agriculture Forest Service Rocky Mountain Experiment Station located in Woodland Park, Colorado. The field portion of the work was in a stand of pure 50 to 60 year old ponderosa pines (*Pinus ponderosa* var. *scopulorum* Laws.) growing at an elevation of 2414 m (39 06′40″N, 105 06″50′W). These trees are heavily parasitized by Southwestern dwarf mistletoe (*A. vaginatum* subsp. *cryptopodum* Hawks.).

All dwarf mistletoes (*Arceuthobium* spp.) are leafless, have highly reduced flowers, and are dioecious. Plants of *A. v. cryptopodum* (Fig. 1) reach a maximum height of approximately 20 cm and a single plant consists of multiple shoots emerging directly from the bark of host pine trunks and branches. Individual shoots range from 2–5 mm in diameter. Coloration is uniform within plants, but highly variable among plants including yellows, pale greens, and browns, often with reddish tints.

Southwestern Dwarf Mistletoe plants were collected from the field between 30 June and 1 August 1999 in individual plastic bags and brought into the lab on eight separate occasions. Individual plants ranged from 3 to 10 cm in height and in most cases only one or two plants were taken from any single host-pine. Both eggs and early instar larva were isolated from these plants using a dissecting microscope, as well as other arthropods associated with dwarf mistletoe.

Because dwarf mistletoes are not free-living and only grow on conifers, *D. alternosquamella* were not reared on living host plants, but instead they were

FIG. 1. The Southwestern dwarf mistletoe parasitizing ponderosa pine. Scale bar 10 cm.

FIG. 2. *Dasypyga alternosquamella* adult. Scale bar 1 cm.

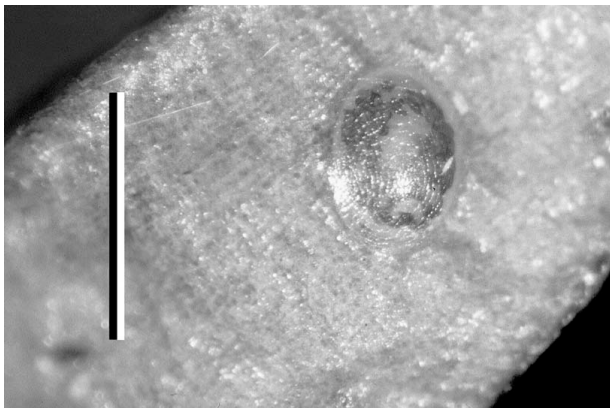

FIG. 3. *Dasypyga alternosquamella* egg on Southwestern dwarf mistletoe. Scale bar 1 mm.

reared individually in clear plastic petri dishes lined with filter paper in a laboratory facility. The larvae were fed small (2–5 cm) shoots of dwarf mistletoe collected from the same general location as the larvae themselves, and they were replenished with fresh plant material approximately every third day. The filter paper linings of each petri dish were wetted on a daily basis. The lab building was neither heated nor cooled, and petri dishes were stored in the open near a window where they received indirect but not direct sunlight. Although every precaution was taken to maintain a "natural" rearing environment within the laboratory facility the quality of harvested food plants, as well as other environmental variables, likely differ to some extent from that of a living plant.

Larval head capsule widths and resting body lengths were measured using a stereomicroscope with an ocular micrometer. Head capsule widths were taken daily while resting body lengths were taken only at the time of molting. Five larvae were reared from eggs through pupation, three larvae were collected at second instar and reared through pupation, and one additional larva was collected at the third instar and reared through pupation. All pupae were measured and weighed approximately two months after pupation. Voucher specimens of adults reared for this work are housed at the University of Colorado Museum in Boulder, Colorado.

To determine egg hatch-time 25 field-collected eggs were reared at least through first instar. To document pupation behavior several late-instar larvae were reared on dwarf mistletoe plants still attached to clipped pine branches in a terrarium with several centimeters of soil and needles in the bottom. The pine branch, dwarf mistletoe, and soil were subsequently searched for pupae. Larval feeding behaviors both in the laboratory and in the field were recorded.

RESULTS

Oviposition. Eggs and first instar larvae appeared in the field beginning 30 June 1999 and the last eggs were found on 3 August 1999. As the egg stage lasts approximately seven days (see below), adult emergence likely began sometime in the middle of June. In two years of fieldwork at this site, I have seen an adult (Fig. 2) only once in the field during the day and have not observed oviposition and other adult behaviors. These behaviors may be occurring nocturnally. Eggs were laid singly, although the frequent presence of multiple larvae of different instars on a single plant suggests that ovipositing females may not make any effort to avoid plants on which previous oviposition has occurred.

Eggs. Eggs are circular, approximately 0.5 mm in diameter, and slightly domed in shape (Fig. 3). They are light red in color with slight white mottling, especially along the margins, and adhere tightly to the surface of the dwarf mistletoe shoots, thus becoming readily visible in the field. Eggs were never found on the pine foliage or branches. The dates of oviposition of the 25 eggs collected from the field are not known, but all hatched within eight days. Specifically, one hatched eight days after collection, six hatched seven days after collection, and the other 18 hatched in less than seven days, suggesting a maximum egg stage of seven to eight days. Without knowing the actual dates of egg laying minimum egg stage duration can not be estimated.

Larvae. *Dasypyga alternosquamella* has six instars. Heinrich (1920) provides a formal description and illustration of larval characters. The size (head capsule width and larval length) and instar duration of each stage are shown in Table 1. The average duration from egg hatch to pupation was 47 days (N = 7, SE = 0.76) over which time larvae grew from a mean length of 1.19 mm (N = 5, SE = 0.048) at hatching to 16.56 mm (N = 9, SE = 1.034) at pupation (Table 1).

First instar larvae feed on the plant surfaces including terminal shoots and flowers, presumably because they are unable to penetrate the harder exterior surface of the dwarf mistletoe shoots. Later instars (Fig. 4) frequently mine shoots, often entering the shoot at the base and moving distally. Large aggregations of frass can accumulate at the

TABLE 1. Mean values for head capsule width, pre- and post-molt body lengths of resting larvae, and instar duration for *Dasypyga alternosquamella*. Sample sizes (N) given in column two, standard errors (SE) follow each measurement. Post-molt body length for instar one is size at time of hatching.

Instar	N	x̄ head capsule width mm (SE)	x̄ post-molt body length mm (SE)	x̄ pre-molt body length mm (SE)	x̄ instar duration days (SE)
1	5	0.15 (0.005)	1.19 (0.048)	1.61 (0.093)	7.33 (0.558)
2	8	0.20 (0.004)	1.62 (0.093)	2.30 (0.088)	6.5 (0.563)
3	9	0.29 (0.010)	2.31 (0.088)	3.25 (0.124)	6.38 (0.263)
4	9	0.43 (0.012)	3.26 (0.124)	5.36 (0.288)	6.33 (0.471)
5	9	0.64 (0.011)	5.37 (0.288)	8.25 (0.310)	7.11 (0.351)
6	9	0.96 (0.111)	8.26 (0.310)	16.56 (1.034)	14.78 (0.760)

entry holes to the shoots, and is not typically found within shoots. Because *D. alternosquamella* begins feeding at shoot bases, even small amounts of feeding result in the death of the entire shoot.

Whether or not the larvae move among separate dwarf mistletoe plants is unclear. However, when disturbed, larvae of all instars will either drop from the plant on a line of silk or depart and travel across pine branches. There are typically many dwarf mistletoe plants on a single tree at this study site, making larval movement among plants feasible in at least some instances. Frequently a larva which has dropped will then ascend the same line of silk to return to its original location.

Heinrich (1920:84) notes that "the color of the individual larvae varies in harmony with the color of the individual batches of mistletoe on which they feed." The coloration of larvae is variable, and generally this range of variation is similar to some host plant colors, but no close association between larval color and host plant color was observed. Furthermore, larval coloration did not change as a function of color of the dwarf mistletoe plants on which they were fed in the laboratory.

Pupae. *Dasypyga alternosquamella* has a single generation per year and over-winter as pupae. Sixth instar larvae drop to the ground and in the litter and soil they construct a small chamber of frass, soil and silk where they pupate. This chamber is approximately 10 mm in length and 4 mm in width and just encloses the pupae with little excess room. Pupae (Fig. 5) average 9.1 mm in length (N = 8, SE = 0.34) and 2.8 mm in width (N = 8, SE = 0.11). Two months after pupation average pupal weight was 35.4 mg (N = 7, SE = 1.94).

Larval abundance. During the course of this study 284 larvae were collected on 112 plants for an overall average of 2.5 larvae per plant. Most of these larvae were used in an unrelated field experiment. Larval abundance was quite variable in both space and time. For instance, on 12 July only five of the 10 *A. vaginatum* (collected from approximately as many host pines) had larvae, and the mean was 0.5 larvae per plant. On 3 August all of 16 *A. vaginatum* (collected from approximately as many host pines) had larvae, and larval abundance ranges from 1 to 10 per plant with a mean of 3.25 per plant. On this same date (3 August), an additional 146 larvae were collected from 18 dwarf mistletoe plants all growing on a single tree for a mean of 8.0 larvae per plant. In general, larval abundance appeared to increase over the course of the summer, peaking in mid-August, but larvae were still common into the middle of September.

Associated fauna. In addition to *D. alternosquamella*, at least three other species of lepidopteran herbivores were also found feeding on *A. vaginatum*. The most abundant of these three, *Promylea lunigerella glendella* Dyar (Pyralidae, Phycitinae), was only slightly less abundant than *D. alternosquamella*. These two phycitines can be distinguished by the fact that the head capsule widths of sixth instar *P. l. glendella* is a mean of 0.75 mm (N = 6, SE = 0.0097; Mooney in prep.), approximately 20% smaller than the mean of 0.96 mm (N = 9, SE = 0.111) for *D. alternosquamella*. Although Heinrich (1920) describes and

FIG. 4. Sixth instar *D. alternosquamella* and Southwestern dwarf mistletoe. Scale bar 2 cm.

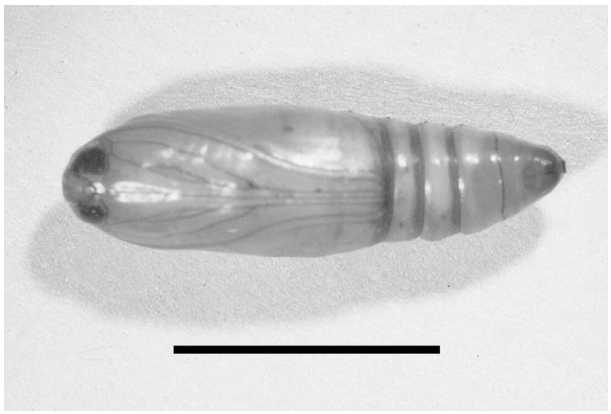

FIG. 5. Pupae of *D. alternosquamella*. Scale bar 5 mm.

illustrates larval *D. alternosquamella*, the only description of *P. l. glendella* is that of the adult (Dyar 1906, Heinrich 1956). Far less common, but also feeding on *A. vaginatum* was *Callophorys* (*Mitoura*) *spinetorum* Hewitson (Lycaenidae), the Blue Hairstreak. On three occasions cryptically colored geometrid larvae were also found feeding on the dwarf mistletoe. Most attempts at rearing *C. spinetorum* (nine of 10) and all attempts at rearing the geometrids were unsuccessfully due to parasitoids. In addition to lepidopterans, *Neoborella tumida* (Hemiptera: Miridae) and unidentified mites (Acari) were common and, especially the latter, present on most plants. The relatively high abundance of both *N. tumida* and the mites, along with the fact that no predation events were observed, suggests they are herbivores.

DISCUSSION

The feeding behavior of *D. alternosquamella* is consistent with the general patterns previously described for related taxa: Almost all pyralids are concealed feeders, and the Phycitinae in particular are known to feed within host plants (Neunzig 1987). What may be somewhat unique is that *D. alternosquamella* apparently changes feeding modes during their development; they are terminal shoot feeders early in their ontogony and later progress to mining modes. Because dwarf mistletoes are leafless, it is the shoots that are mined, and this feeding might more properly be compared to stem boring.

This mining has significant consequences for dwarf mistletoes. *Dasypyga alternosquamella* can be abundant, and because it feeds on shoots even low levels of herbivory results in death of all plant tissue distal to the site of herbivory. Other, unrelated work has documented the nearly complete destruction of all dwarf mistletoe shoots by *D. alternosquamella* in a several-hectare area of heavily parasitized ponderosa pines near Boulder, Colorado during the summer of 1998 (unpubl. data). At the Boulder site, *D. alternosquamella* was the only abundant herbivore. At the Manitou Experimental Forest the lepidopteran assemblages appeared to be more diverse; *P. l. glendella* was nearly equal in abundance to *D. alternosquamella*. The nature and consequences of interactions between *D. alternosquamella* and other dwarf mistletoe associated fauna are unknown, but diversity between sites can vary.

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