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OVIPOSITION BEHAVIOR AND LARVAL BIOLOGY OF THE ENDANGERED UNCOMPAHGRE FRITILLARY *BOLORIA ACROCNEMA* (NYMPHALIDAE)

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ABSTRACT. *Boloria acrocnema* is an endangered relict arctic nymphalid restricted to fewer than five mountain peaks in Colorado, USA. Females lay eggs singly on snow willow, *Salix reticulata nivalis* (Salicaceae), and eggs hatch 23 to 32 days later. The larvae are most likely biennial and pass though one to possibly two instars before overwintering. However, evidence of an annual life cycle is also presented. Later instar larvae break diapause in mid to late June and feed on snow willow leaves. Pupation occurs in the host plant litter and adults emerge 21 to 32 days later.

Additional key words: annual life cycle, biennial, immatures, Salicaceae.

The Uncompahgre fritillary, *Boloria acrocnema* Gall and Sperling (Nymphalidae) was discovered in 1978 on Mt. Uncompahgre in the San Juan Mountains, Hinsdale County, Colorado, and subsequently described by Gall and Sperling (1980) as a new species. Three active colonies of the species were known during the course of this study: a colony at Mt. Uncompahgre, the type locality (UP1); a colony approximately 4 km southwest of the type locality (UP6); and a colony on Redcloud Peak approximately 20 km SSE of the type locality (RC1). Both sites are on or are adjacent to public lands; RC1 is located within Bureau of Land Management (BLM) lands, and UP6 exists just outside the Big Blue Wilderness Area of the Uncompahgre National Forest. Extensive searching during 1988 led to the discovery of two additional locations, but butterfly numbers were low and they were not considered breeding colonies (Brussard & Britten 1989). During the 1995 flight season, however, Colorado Natural Heritage Program biologists confirmed the presence of butterflies at these locations and at another location in the La Garita Mountains (Aaron Ellingson, pers. comm.). Additionally, a private collector has reported the location of another colony (Paul Opler, pers. comm.). Total colony number is now seven.

Boloria acrocnema, in similarity with some other alpine butterflies, is considered but not confirmed to have a biennial life cycle, wherein each brood overwinters twice and development occurs over three summers, thus creating odd- and even-year populations (Scott 1982, 1986, Brussard & Britten 1989). The larvae of *B. acrocnema* feed on a single

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host plant, snow willow, *Salix reticulata* L. spp. *nivalis* (Hooker) Love (Salicaceae), a species common in mesic alpine environments (Weber 1987).

The species' larval life history has been studied in the laboratory by Scott (1982). Here, I report on the larval life history of *B. acrocnema* as described from 3 years of field observation. I suggest that some *B. acrocnema* individuals complete their life cycle in a single year i.e., during two summers, and discuss how a "staggered" dynamic may affect the results of demographic studies for this endangered butterfly.

STUDY SITES AND METHODS

Research was conducted from 1991–1993 at two of the three known *B. acrocnema* colony sites, RC1 (37°57'N, 107°25'W) and UP6 (38°04'N, 107°25'W). Both sites exist on slopes with a northeast exposure and range in elevation from 3800–3970 m, with UP6 lower than RC1. Each site has abundant patches of *S. reticulata nivalis*, the larval host plant, and both have a variable array of nectar sources including *Erigeron vagus* Payson (Asteraceae), *E. simplex* Greene (Asteraceae) and *Silene acaulis* L. ssp. *acaulescens* (Williams) Hitchcock and Maquire (Caryophyllaceae), the most commonly used nectar sources by *B. acrocnema* (Seidl 1995). The sites differ in area: RC1 is approximately 10 ha, and UP6 is approximately 1.2 ha.

Female *B. acrocnema* were followed during 1991–1993 at RC1 and UP6 to locate oviposition sites. Females were followed by an observer at a distance of approximately 3 m. If an oviposition was observed, the location was marked with a survey flag and then searched for eggs. Leaves on which an egg was deposited were classified as to stage and development. Records were kept of how well the egg was adhered to its substrate, each egg's development and changes in color and ridge shape. Finally, a record was kept of whether the egg hatched or if it became desiccated or otherwise appeared infertile. Egg locations were marked with an aluminum tag and a metal stake and were returned to the following summer to search for developing larvae.

In 1992 and 1993 a total of five late third and fourth instar larvae were found, described and placed in enclosures. Although these larvae were found near marked oviposition sites, none were seen at the exact location of the previous summer's oviposition sites. In 1992, each larva was enclosed within snow willow habitat in a 1 m × 1 m × 15 cm lidded wood-screen enclosure. In 1993, each larva was enclosed in an unlidded Lexan (similar to Plexiglas) enclosure of the same dimensions. The glass-like surface of the Lexan prevented caterpillars from escaping. The Lexan design proved to be more similar to natural conditions i.e., air temperature and exposure to precipitation. Activity, development and

morphology of larvae, especially as they developed into pupae and then into adults, were noted.

RESULTS

Oviposition behavior. In 1991 follows were conducted from July 17 to August 9 and ovipositions were seen July 17 to August 2. In 1992 follows were begun July 8 to August 4 and ovipositions were seen July 14 to August 4. Finally, in 1993 follows were begun June 30 to August 6 and ovipositions were seen during that same period. Sixty-four oviposition sites were found during the 1991–1993 field seasons. Fourteen eggs were laid on the underside of *Salix reticulata nivalis* leaves, 14 eggs were laid at the base of a leaf or on the petiole, 13 eggs were laid on the top side of the leaf, 11 were laid on *Salix reticulata nivalis* leaf litter, 2 were laid at the base of a *Salix reticulata nivalis* plant, 1 was laid on the stem of a catkin and the remaining 9 were laid within *Salix reticulata nivalis* habitat but on different plants, including grass, moss, *Erigeron* spp., *Silene acaulis*, and *Salix arctica* Pallas (Salicaceae). Female *B. acrocnema* preferred opened *Salix reticulata nivalis* leaves to unopened: of the 55 ovipositions on *Salix reticulata nivalis* only one was recorded on an unopened leaf.

Female *B. acrocnema* often walked among *Salix reticulata nivalis* patches testing leaves (abdomen extended toward leaf but no egg deposited) before actually ovipositing. For the follows conducted during 1991 and 1992, I recorded testing behavior as well as oviposition behavior. In 1991, 4 of the 18 ovipositions recorded were directly preceded by testing. In 1992, 8 of the 15 ovipositions recorded were preceded by testing.

The eggs, when first laid, are cream colored and become pink to tan or grey after 3–5 days. All eggs were closely observed and their development was followed until they either fell to the ground or into the litter and were lost, hatched into first instar, or appeared dead or desiccated. Many of the eggs were not well cemented to *Salix reticulata nivalis* plant material. Of the 64 ovipositions recorded, 41 fell preventing further observations. An additional 6 eggs became desiccated and 13 showed development but no hatching by the end of the study. No first instar larvae were seen in 1991, and early winter snowfall in 1992 prevented further observations. In 1993, however, there was evidence of 4 eggs having hatched: 2 first instar larvae were actually seen emerging from their eggs (Fig. 1) and 2 other egg casings showed signs of recent hatching. The period between oviposition and hatching ranged from 23 to 32 days (July 25 to August 16 and July 20 to August 20, respectively).

Larval Life History. Five third and fourth instar larvae (Fig. 1) were identified using criteria from Scott (1982) and followed in the enclosures to adult emergence during 1992 and 1993. Of those 5, three lar-

FIG. 1. Immature stages of *Boloria acrocnema*. Clockwise from top left: first instar and egg casing, third instar, pupa, fourth instar.

vae successfully produced adults, while 2 died of unknown causes. In 1992, larvae were found on June 29 and July 2, and in 1993 a single later instar larva was found July 7. All later instar larvae were found at RC1 near oviposition sites, determined the previous summers. Caterpillars were observed feeding and basking for 2–3 days before nesting (larvae make a leaf shelter) and pupation. During the hours prior to nesting, larvae were observed to move rapidly around the enclosures and appeared to test areas for possible pupation sites. This behavior included crawling under litter, beginning to make a nest and then arresting movement. Finally, each caterpillar chose a site with densely packed litter and nested. In one case the larva burrowed under a large dead leaf and attached itself horizontally to the underside of the leaf, silking together debris (dead leaves, lichens, and bits of grass) to form a nest. No movement occurred after nesting and pupation began. In 1992, adults eclosed on August 2 and on August 7. Both of these larvae had pupated on July 7 (Fig. 1). In 1993, pupation was observed on July 9 and the butterfly eclosed on July 29. Therefore, in 1992 and 1993 the duration of pupation was 21 to 32 days.

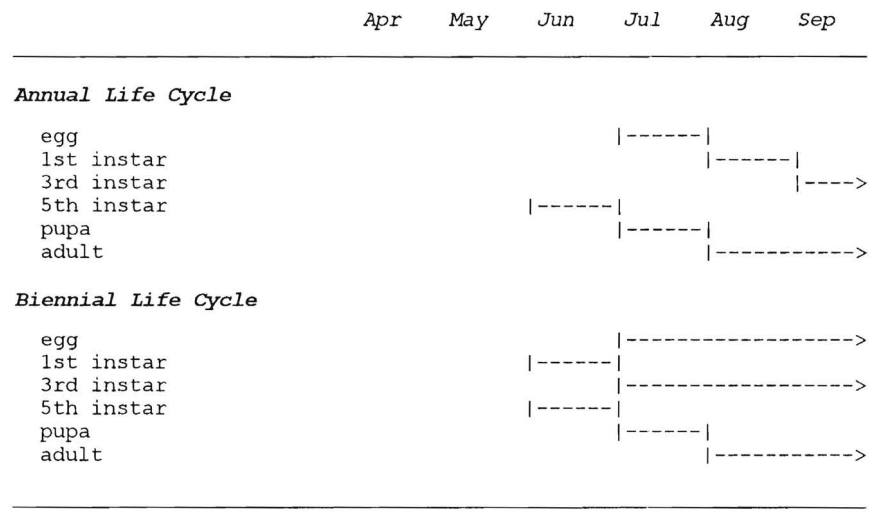

FIG. 2. Hypothetical timeline of annual and biennial development for *Boloria acrocnema* if egg is oviposited during late June during any given year.

Salix reticulata nivalis was the only observed larval host plant, and *B. acrocnema* may be restricted to this species. Pre-pupating caterpillars consumed the top or apex of each unopened leaf. As the leaves developed and opened, the missing apex of each of the three leaves was evident.

Boloria acrocnema larvae typically ate large sections taken from the top of the leaf and often from the tops of all unopened leaves, as described above. Feeding damage on either side of a leaf and single bites in the center of the leaf were also observed. There was one brief instance of a caterpillar eating a *Salix reticulata nivalis* root just prior to nesting.

DISCUSSION

Singly-laid eggs and solitary larvae are characteristic in many *Boloria* species; haphazard egg laying is also characteristic of nymphalid butterflies (Scott 1986), most notably *Speyeria*. The choice of oviposition sites, nearly always on *Salix reticulata nivalis* and almost never on the closely related and equally abundant *Salix arctica*, is intriguing. *Salix* species are known to contain the phenolic compounds salicin and salicortin as feeding deterrents against herbivores (Palo 1984). Future physiological and chemical studies of *Salix arctica* and *Salix reticulata nivalis* and their corresponding levels of phenols may clarify why *B. acrocnema*'s association to *Salix reticulata nivalis* is so specific.

A previous study of larval development of *B. acrocnema* determined the duration of the egg stage to be 10–15 days, with an estimate for first

instar to adult being approximately 42 days (Scott 1982). The data provided here suggest that although a biennial life cycle is probably the typical timespan, an alternative annual cycle is also possible. For instance, in 1993 ovipositions were observed on June 29 at RC1 (Fig. 2). The time from egg stage until hatching was determined to range from 23 to 32 days in the field. An egg laid in late June or early July could have the time to develop into a first instar larva by July 30 and into a third instar that same summer, usually having more than a month to develop before *Salix reticulata nivalis* leaves become senescent and the first snows arrive. The following year (Fig. 2) third instars develop through fifth instar, pupation and eclosion.

Brussard (1991) reasoned that *B. acrocnema* individuals may be staggered such that some butterflies develop in 2 years and others in 3 or more years, depending on the varying ecological conditions (rainfall, air temperature, quality of host plant). Brussard and Britten (1989) used the term "leakage" to describe how even-year brood individuals may, by completing their life cycle in 3 years, become members of the odd-year brood, or vice versa. It is suggested here that some individuals may develop in a single year creating a scenario similar to what Brussard (1991) described.

Variable developmental time spans may result in inaccurate demographic data if a biennial life span is assumed. Because *B. acrocnema* is an endangered species and is the subject of a recovery plan, population fluctuation and demographics play a central role in assessing the species' status. The accuracy of indexes of abundance or population estimates is essential. Currently, *B. acrocnema* demographic studies describe population estimates for odd- and even-year broods (Brussard & Britten 1989, Britten et al. 1994, Seidl 1995). Laboratory studies which would manipulate natural conditions and time phase relationships between *B. acrocnema* and *Salix reticulata nivalis* are needed to assess the proportion of individuals likely to complete their life cycle in a single year. An equation which calculated this proportion would give us a more precise index of abundance or population estimate by which to judge the status of this endangered butterfly.

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