SOME ASPECTS OF THE BIOLOGY OF THE DEVELOPMENTAL STAGES OF *COLIAS ALEXANDRA* (PIERIDAE)

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ABSTRACT. Aspects of the larval ecology and behavior of *Colias alexandra* Edw., a pierid native to the Rocky Mountains, are described here. The study populations are univoltine (although bivoltine pockets exist) and monophagous, utilizing *Lathyrus leucanthus* Rydb. as a larval host plant. A high degree of specificity is exhibited by ovipositing females. Pre- and postdiapause feeding activity is described. Diapause occurs in the third instar; photoperiod and temperature are suspected as cues. Parasitoid and hyperparasite interactions are described, including a previously undescribed species of *Gelis* (Ichneumonidae). *Colias alexandra* occurs with several other species of *Colias*. Adult food sources are shared and, in one case, there is ecological overlap of the developmental stages.

In recent years agriculturally important members of the genus *Colias* have been among the most intensively studied and best known Lepidoptera. In comparison, relatively little is known about the biology of the developmental stages of other *Colias* species. This article summarizes observations made during four years of study on the larval ecology and behavior of *Colias alexandra* Edwards.

Colias alexandra, first described by Edwards in 1873, is native to the Rocky Mountains and occurs from New Mexico, northward to Alberta, westward to Nevada and British Columbia (Brown et al., 1957). Adults fly from late June to early August throughout montane meadows from approximately 1800 m to timberline. Univoltine and bivoltine populations exist, although univoltinism is predominant.

STUDY SITES AND METHODS

Observations on larval biology were made while monitoring a permanent demography plot (20 m × 20 m) from 1975 to 1978, along Brush Creek, 13 km SE of Crested Butte (Gunnison Co.), Colorado (2950 m). Relatively large populations of *C. alexandra* occur in this area (Watt, et al., 1977). They are univoltine and utilize *Lathyrus leucanthus* Rydb., a legume, as a larval foodplant. The vegetation within the plot is representative of this fescue grassland (see Langenheim, 1962) and was searched thoroughly (on hands and knees) for

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C. alexandra eggs and larvae. Plants with eggs or larvae were marked with flags. The behavior, developmental rates and mortality of the larvae were then recorded on a regular basis throughout the season. Additionally, ovipositing females were followed to observe host seeking and oviposition behavior (Stanton, 1975).

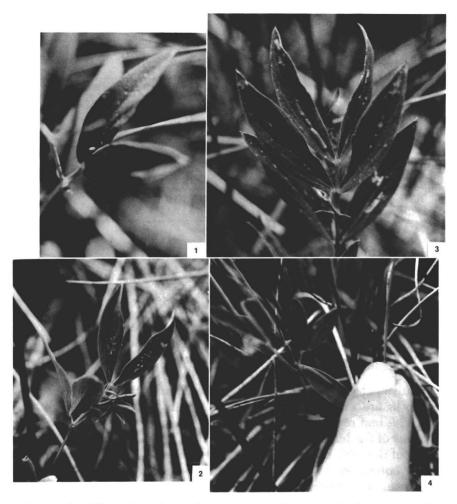## RESULTS AND DISCUSSION

Oviposition and Foodplant Choice

Females exhibit a high degree of specificity in oviposition. A single egg is deposited on the surface (usually abaxial) of the leaf of *L. leucanthus* (Fig. 1) with nearly 100 percent accuracy, although in the Brush Creek population, rare mistakes have been observed on *Agoseris glauca* (Pursh) Dietr. (Compositae). Other mistakes occur on two legume species, *Lupinus* sp. and *Vicia americana* Muhl, which are often found side by side with the host plant and which I find nearly indistinguishable from *L. leucanthus* when both are immature. Attempts to rear larvae on alternative native plants have proven successful in a few cases (*Lupinus* sp., *Trifolium longipes* and *Vicia americana*), but growth rates are slower (D. Henneberger, pers. comm., pers. obs.). Thus, while other host plants are known for *C. alexandra* (Ellis, 1973), members of a single population appear to be monophagous.

Multiple oviposition on a plant (i.e., more than one female ovipositing on a plant) is relatively rare (<10%, N = 1000), although females do not appear to scan the leaves visually as do *Heliconius* (Alexander, 1961; Gilbert, 1975), searching for eggs. On two occasions a single small plant (<10 cm in height, 12 leaves) was found with 5 *C. alexandra* eggs. The number of eggs per plant resembles a Poisson distribution, i.e., selection of a foodplant for oviposition appears to be a random process. No instance of multiple occupation of the same plant has resulted in multiple larval survival. Larvae of all instars react to disturbance by "rearing," a sudden upward movement of the head and first several segments, and are more easily dislodged during this activity. As a result, encounters with conspecifics may cause one or both to drop from the plant (pers. obs.). Also, cannibalistic habits of the larvae of this genus have been observed (J. Grula, pers. comm.) and have been found occasionally in lab colonies of *C. alexandra* (pers. obs.) when food is in short supply.

Prediapause Larval Behavior

Eggs are white when oviposited and turn pink (characteristic of the genus) within 48 hours if fertile. The mean egg development time in

FIGS. 1–4. *Colias alexandra* prediapause stages. **1,** egg on *Lathyrus leucanthus* leaf; **2,** second instar larva feeding on *L. leucanthus* in characteristic manner leaving vascular tissue intact; **3,** just-molted third instar; **4,** diapausing third instar larva.

the field, oviposition to hatching, is 11 days (Table 1). At hatching, the egg shell is at least partially consumed by the larva. Feeding on a leaf begins with the chewing of a small hole on the surface. This behavior results in characteristic "pinholes" and has been observed for other species of *Colias*, e.g., *eurytheme* (Sherman & Watt, 1973), *philodice* and *meadii* (pers. obs.). Occasionally more than one pinhole is initiated. Once feeding has begun the larvae assumes a cryptic green coloration characteristic of the genus (Gerould, 1922; Sherman

Table 1. A timetable for *Colias alexandra* developing in the field (13 km SE of Crested Butte, Colorado, elev. 2950 m). This table summarizes data gathered in 1977 and 1978.

Stage	1977			1978		
	Mean	S.D.	N	Mean	S.D.	N
Egg (oviposition–hatching)	11.02	0.72	97	11.34	0.77	73
1st instar (hatching–1st molt)	9.22	0.86	90	8.89	0.76	82
2nd instar (1st–2nd molt)	12.24	1.6	50	9.99	0.97	54
3rd instar (2nd–diapause)	6.51	0.91	29	8.11	1.10	31
Diapause						
3rd instar (diapause–3rd molt)	2.41	0.73	7	3.09	0.81	6
4th instar (3rd–4th molt)	6.01	0.95	7	5.77	1.21	6
5th instar (4th–5th molt)	4.86	1.19	4	5.37	0.93	5
Pupa (pupation–eclosion)	12.73	1.62	3	14.12	1.56	3

& Watt, 1973). The head remains black until the first molt. Mean development time in the field from hatching to first molt is 9 days (Table 1).

As it develops, the larva begins to enlarge one of its original pin-holes. Most feeding is done from a position on the midrib of the leaf. A fine "network" of vascular tissue from the ventral side of the leaf is left behind as feeding continues (Fig. 2). From late first through third instars larval feeding produces these networks. On a mature leaf, networks are maintained between the midrib and the border of the leaf. The leaf remains turgid as the larva avoids the tougher vascular portions of the leaf. Feeding, in general, is restricted to the distal two-thirds of the leaf, although immature leaves as well as tendrils may be totally consumed by second and third instar larvae.

Movement of early instars is minimal, involving moving along the midrib between feeding and resting—a distance of half to the entire length of the leaf (1–2 cm). Movement to a new leaf or branch occurs in conjunction with molting (Fig. 3); however, even after moving, larvae often return to previously occupied sites to feed. First instar larvae rarely leave the site of their first network. By late third instar, a larva may have left a dozen or more networked leaves, having travelled to two or three branches, but having never left the plant on which the egg was placed by the female. Exceptions occur when the tops of two or more foodplants are in contact, in which case the larva may wander to another plant.

After a feeding period, the larvae move down the midrib toward the stem to begin a resting phase. The position of the resting larva relative to the leaf is a highly specific character. First through third instar

larvae assume a position on the midrib, head "stemward," on the distal third of the leaf. Each successive instar positions itself in closer proximity to the stem. This resting position is frequently not visible from above due to the overlapping position of the leaves on each branch. This behavior has been observed in other legume feeding *Colias*, e.g., *eurytheme* (Sherman & Watt, 1973; Hayes, 1975) and *philodice eriphyle* (pers. obs.). It is possible that this position is simply a good location to avoid incidental disturbance which may result in dislodgement from the plant. Should a larva become dislodged, the result is probably fatal. On the ground, the larvae are susceptible to predation by a variety of ground inhabitants, especially spiders and ants (pers. obs.), and desiccation (Strauss, 1978). The resting position may also be a microclimate adaptation (Waterhouse, 1960), as the overlapping leaves and branches produce a shading effect which is maximally effective closest to the stem. This behavior may serve as an avoidance mechanism from visual predators (e.g., Gerould, 1922) or parasitoids. Two hymenopterous parasitoids have been reared from fifth instar larvae (Figs. 5 and 6): *Apanteles flavicornis* (Ichneumonidae) which also was obtained from *C. philodice eriphyle* larvae and *Nepiera* sp. (Brachonidae). Additionally, a new species of *Gelis*, a hyperparasite (Ichneumonidae), has been reared from *A. flavicornis* which emerged from *C. alexandra*.

Diapause

Late third instar larvae cease feeding activities and move to an untouched leaf or to a neighboring plant (Fig. 4). These larvae are sluggish, appear somewhat swollen and lighter green in color with a darkened head capsule which is small relative to the body. *C. alexandra* overwinter as a diapausing third instar larvae. The cues for the initiation of diapause in *C. alexandra* have not been determined although photoperiod and temperature are jointly suspected (Ae, 1958; Hayes, unpubl. data). Diapausing individuals either remain on the plant and eventually are buried in the leaf litter when the plant falls or they crawl down the stem to the base and enter the litter to overwinter. The litter and snow cover very likely buffer the larvae from the extremes of winter.

The factor(s) responsible for diapause termination are as yet unknown, but increased daylength and ground temperature are believed to play roles in the resumption of activity. Synchrony of emergence of the larvae with the new growth of the larval foodplant is critical. The larval host plant, *L. leucanthus*, emerges in the spring at different times throughout the population range, thus a flexible diapause terminating cue would be advantageous. In fact, larval diapause may be

FIGS. 5–8.   *Colias alexandra* postdiapause stages. **5,** parasitized fifth instar larva; **6,** pupae of *Apanteles flavicornis* reared from fifth instar larva; **7,** fifth instar larva; **8,** pupa.

an adaptation to avoid mature and less nutritious growth late in the growing season.

Postdiapause Larval Behavior

After emerging from diapause the postdiapause larvae begin to feed at once and the third molt occurs soon after activity resumes. The

fourth and fifth instar larvae are more mobile than young larvae, larvae of each instar foraging over approximately a one square meter area. Larvae may initiate feeding with the characteristic networking, but rapidly progress to consuming all the leaf material. Often whole leaves are consumed and tender new plants may be reduced to a piece of stem before a larva moves on. Larvae feed from a position on the leaf or stem. The mean field development time of the later instars, third to fourth molt is 6 days and fourth to fifth molt is 5 days (Table 1).

During resting phases these larger larvae retreat to the stem. The later instars have distinct lateral stripes which mimic highlights on the plant stem (Fig. 7), as do other *Colias* (Sherman & Watt, 1973). Again the resting position may serve as a predator or parasitoid avoidance mechanism, represent a microclimate selection adaptation or provide a secure footing for the immobile larvae. At the cessation of feeding the fifth instar larvae position themselves among the leaves of a host plant or sage or within a dense clump of grass as the pupation process begins. Characteristic of the genus, the new pupa is a solid green which changes within a few hours to display lighter lines that mimic leaf highlights as it dries and hardens (Fig. 8). The mean field development time of the pupa, pupation to emergence, is 14 days.

Interactions with Congeners

C. alexandra is the "middle" of three species of *Colias* whose often overlapping habitats lie along an elevational gradient in this area of the Rocky Mountains. *C. philodice eriphyle* is found from the high plains to 2700 m and *C. meadii* occupies the alpine zone above timberline. Also present in this area is the non-legume (*Salix*, Salicaceae) feeding *C. scudderi* and the frequent migrant from lower elevations, *C. eurytheme*.

C. alexandra interactions with *C. meadii* are minimal since their breeding areas are often separated by forest. There are occasionally years when *C. eurytheme* migrates in large numbers into this area from New Mexico, but its interactions with resident species are unknown. It does successfully utilize *L. leucanthus* as a larval foodplant (Hayes, unpubl. data). *C. scudderi* and *alexandra* do not share the same family of larval host plant, but often share adult nectar sources with *C. eurytheme* and *p. eriphyle* during the overlapping flight periods (Watt et al., 1974). Generally, nectar resources do not appear to be limiting in this region. The preferred larval foodplants of *C. p. eriphyle* are *Vicia americana* and *Trifolium* spp. (Stanton, unpubl. data). Under some conditions, such as low soil moisture conditions in 1977, *C. p. eriphyle* will utilize *L. leucanthus* for oviposition in sig-

nificant numbers during one or both broods (Hayes, unpubl. data). Additionally, the parasitoid, *A. flavicornis* has been reared from *C. p. eriphyle* and may utilize *alexandra* and *p. eriphyle* as alternative hosts, although the exact relationship is unknown.

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