

FIELD OBSERVATIONS ON FOREST *OENEIS* (SATYRIDAE)

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Based on their ecological preferences,¹ the *Oeneis* of the Nearctic Region can be placed in three groups: forest species, including *Oeneis macounii* (Edwards), *Oeneis nevadensis* (Felder & Felder), and *Oeneis jutta* (Hübner); prairie and steppe species including *Oeneis uhleri* (Reakirt), *Oeneis chryxus* (Doubleday), *Oeneis alberta* Elwes, and the closely related *Neominois ridingsii* (Edwards); and the arctic taiga-tundra/alpine summit species including *Oeneis taygete* Geyer, *Oeneis bore* (Schneider), *Oeneis melissa* (Fabricius) and *Oeneis polixenes* (Fabricius). Excepting *O. chryxus*, which frequently ventures into both forest and mountain top environments, these butterflies occupy restricted biotopes. The *Oeneis* have remarkably complex adult behavior patterns which, in the forest species, are very similar and apparently based on three primary instincts: (1) sexual reconnaissance and rendezvous including territory occupation, (2) thermoregulation, and (3) feeding.

OENEIS MACOUNII (Edwards)

Like some of the other species in the genus, *O. macounii* has a two year life cycle and flies only in alternate years. From Riding Mountain, Manitoba and westward it flies in odd numbered years while to the east it flies in even numbered years. It is local and restricted in habitat to open jack pine forests (Masters, Sorensen & Conway, 1967). The life cycle and local nature of colonies contribute to a paucity of records, but *macounii* has a wide range from the east slope of the Rockies in Alberta (Elwes, 1893) east to Algonquin Park, Ontario (Durden, *in litt.*) and south to Pine County, Minnesota (Rysgaard, 1939).

We have made detailed observations on *O. macounii* in Minnesota and Manitoba (Masters *et al.*, 1967; Masters & Sorensen, 1968a). Both sexes could be distinguished readily on the wing due to differences in flight behavior. Females fly slowly and aimlessly through the pine forest. Males are more active, repeatedly perching on favorite leaves that serve

¹ Generalizations on ecological preferences are based on our personal observations, together with information from about 30 references in the literature to habitats of North American *Oeneis*.

as observation points over small clearings. From such a vantage points they drive away other males that come into view and wait for a female. When a male is captured, he will often be replaced by a new male in an hour or two, occupying the same glade, frequently using the same perch.

Territoriality in *O. macounii* appears to be a mechanism developed for the purpose of acquiring a mate (Masters *et al.*, 1967). A territory usually consists of a small glade which a male can observe and patrol from a strategic perch. Usually the perch will be among the green leaves on a tree branch or at the top of a low bush, but frequently it will be on a bare twig. The nature of the chosen perch does not seem to be as important as its location. If an observer remains stationary nearby, the male butterfly becomes unaware and can be observed at close range. Observing (JHM) that a particular butterfly would return again and again to the same perch, it had seemed a simple matter to move a camera and tripod into the glade, focus on the perch and wait; but the presence of observer and camera seemed to alter the topography of the clearing from the butterfly's point of view and another perch was selected, usually closer to the camera. One such butterfly under observation was captured and allowed to be replaced by another male; the habits of the replacement and his selection of perches were almost identical to those of his predecessor.

Behavioral thermoregulation of *O. macounii* is best demonstrated by our observations at Riding Mountain, Manitoba during 1967. On June 23, a cold cloudy day with the temperature never exceeding 55° F., no *macounii* were observed flying and the only individuals located were hanging on the undersides of leaves near the ground. On June 24th the sky was clear and the temperature reached 68° F., *macounii* were active and always landed with their wings open into the sun. June 25th was a hot day for Riding Mountain at 80° F. The butterflies were still active, but after alighting they quickly folded their wings and sometimes leaned slightly away from the sun. These behavioral differences are related to thermoregulation and involve control of the amount of wing surface exposed to the sun. Clench (1966) cites the importance of thermoregulation to butterfly behavior and concludes that the opening and closing of the wings is one of several devices that permit control of the amount of solar heat received, the wings being the butterflies' primary area for heat exchange. With a slight modification to lower thresholds, our observations correlate rather well with the six heat zones that Clench cites for butterfly activity. For other *Oeneis*, such as *O. alberta* (Brown, 1952), these thresholds are significantly lower.

Feeding seemingly played a minor role in *macounii*'s daily behavior.

Regularly used glades usually contained a few flowers which were visited for brief periods throughout the day, and the butterfly returned to his overlooking perch.

OENEIS NEVADENSIS (Felder & Felder)

Oeneis nevadensis occurs in the Cascade and Sierra Nevada ranges from southwest British Columbia to Sonoma County, California. Comstock (1927) adequately and briefly described the habitat of *O. nevadensis*: "It is a forest dweller, delighting in little open glades where spots of sunlight filter through the leafy canopy, in which it sports with a nervous jerky flight." Guppy (1962) observed *Oeneis nevadensis gigas* Butler on Vancouver Island and indicated that males are usually collected in clearings along the tops of ridges and that these clearings probably serve as a rendezvous for mating. A male would establish his territory on a hilltop and would drive off other males coming into view. Females were presumed to fly to the hilltops to mate and then to disperse to other areas for egg laying. Guppy's "hilltopping" theory explains the territorial habits of the males and accounts for the relative scarcity of females.

Oeneis nevadensis appears to be as similar to *O. macounii* in habits as it is morphologically. Indeed, the two occupy a very similar biotope and functional niche on opposite sides of the Rockies and are probably subspecies of each other. In the past they have been rather arbitrarily separated into two species because of misconceptions about the *macounii* habitat and the lack of male androconial patches or male *macounii*. In his revision of the genus, Elwes (1893) was unable to separate female *macounii* from *nevadensis*. Brown (1964) affirms that male *macounii* do have androconia, though they are more inconspicuously restricted to the area of the veins. We have discovered that the androconia are more in evidence on *macounii* from westward populations.

OENEIS JUTTA (Hübner)

Oeneis jutta is one of the most widespread species in the genus and is found in the Palearctic as well as Nearctic. In the Nearctic it is found across the arctic from Alaska to Newfoundland, south to Maine and Minnesota and, in the Rockies, to Colorado and Utah. Masters and Sorensen (1968b) review subspeciation in *O. jutta*.

Oeneis jutta occurs in black spruce/sphagnum bogs which at first glance appear to be quite different from the habitat of either *O. macounii* or *O. nevadensis*. However the best "jutta bogs" are those where black spruce and tamarack are of medium density and the sunlight filtering through them creates small glades similar to those in the jack pine forests inhabited by *O. macounii*. Labrador tea and other ground cover in

the bog present an uneven floor with many perches suitable for males.

Oeneis jutta ascerta Masters & Sorensen, flying in Minnesota bogs, has habits similar to those we observed for *O. macounii*. Males establish territories consisting of small sunlit clearings and fly out at all intruders. They return again and again to a favorite perch which might consist of a tuft of cottongrass, as observed by Nielsen (1964), the top of a clump of labrador tea or laurel, a tree trunk or dead limb of a fallen spruce, or a low growing tamarack or spruce. Females differ in flight and habits from the males and wander without apparent direction through the bog; sometimes flying to the top of a tamarack tree, a habit never observed in males. Females are more frequently encountered along the edges of bogs and this accounts for their preponderance in some collections. Apparently territory occupation serves to acquire a mate for *jutta* just as it does for *macounii* and *nevadensis*. In one instance we (JHM) observed two males hovering about the end of a spruce branch: on closer investigation, it was discovered that a freshly emerged female with her wings still wet was under the branch. This indicates that a female scent as well as vision serves to attract males to females.

O. jutta generally perch with wings closed during most types of weather, and they quickly disappear if cloud cover obscures the sun. In the evening, several hours before sunset, the males come out into larger clearings to cavort in the last rays of sunlight; at these times they fly in closer contact with each other and with less belligerent appearing behavior. Possibly they obtain enough solar energy from the sun to extend the length of their day, but perhaps it is only an exhibition of phototropism. We (JTS) observed a group of about 15 *jutta* engaging in this type of activity near noon on a cloudy day in Koochiching County, Minnesota.

Oeneis jutta ridingiana Chermock & Chermock appears to be the subspecies endemic to Riding Mountain and the nearby uplifts of western Manitoba; it is a small and relatively brightly adorned *jutta*. Acid spruce/sphagnum bogs are edaphic climax forest situations (maintained by wet acid soil conditions rather than climate). The gradual seral succession of bogs is obvious to one who visits them in Minnesota and then on Riding Mountain, for Riding Mountain bogs are old with dense growths of black spruce and relatively dry turf. The density of these forests seems to be a detriment to *jutta* because the open sunlit patches are not found in them. *O. jutta* seemed to be scarce or rare here and preferred the edges of the bogs where the most sunlight penetrated. Cottongrass (*Eriophorum spissum* Fern.), the *jutta* foodplant, was also scarce in these bogs and restricted to their more open edges.

Interestingly, the habitats of other *Oeneis* species seem to be related to

edaphic situations. The jack pine forest habitat of *O. macounii* is an edaphic condition which in this case is maintained by well drained sandy soil. Virgin prairie (the habitat of *O. uhleri varuna*) is usually thought of as a climax community, but Sauer (1950) regards it as a nearly stable subclimax community maintained by fire—somewhat the same level as an edaphic climax community. Steppe, or short grass prairie, is possibly similarly maintained by fire. If one distinguishes between tundra and taiga (Polunin 1959, regards taiga as the sparsely timbered country near the northern limit of arborescent growth), most of our arctic *Oeneis* are found on taiga rather than tundra. Mackay (1966) considers taiga as an edaphic climax community that is maintained by discontinuous permafrost that inhibits subsurface drainage and gives the soil a grainy character. The taiga will not yield entirely to trees in a warming trend but much of it might actually yield to tundra “through the establishment of a sphagnum-moss ground cover, a resulting shallowing of the active layer, and an eventual favoring of the tundra succession.”

Oeneis jutta reducta McDunnough is found in an atypic situation in Colorado. There are no spruce or tamarac bogs in Colorado, but there are many beaver-dam/willow bogs. Wherever lodgepole pine forests border these bogs, one is apt to find *O. jutta*. *Oeneis jutta reducta* has apparently found an unique biotope to meet its needs which include the bog for breeding and larval food, and the pine forest for adult social patterns which are probably not unlike those of eastern *jutta ascerta*. Willow/beaver bogs certainly don't constitute a climax situation, but in the tension zone between them and the climax lodgepole pine forest is a long enduring subclimax community if the beaver populations are not disturbed. Don Eff (in Brown, 1954) very adequately describes the Colorado habitat: “It is found in the dry areas among the lodgepole pines, especially where the growth is not too thick and the trees are large in size, and where the green ground is dappled with sunshine and shadows. . . They love the rotten logs and the sides of trees and in spite of the multitude of flowers nearby never visited any.”

OENEIS CHRYSUS (Doubleday)

Oeneis chryxus is primarily a prairie and steppe species, but in some areas it has a tendency to move into other habitats. We observed at Stagecoach Meadows, Gunnison County, Colorado that *O. chryxus chryxus* was found in the open “meadow,” but more commonly at the edge of the woods surrounding it. In this tension zone between forest and steppe, there were many fallen trees and open areas. *O. chryxus* in this area seemed to favor perches on fallen trees and the attitudes of males for each

other was reminiscent of what we had observed for *Oeneis macounii* and *jutta*. We were unable to observe a consistent behavior for *chryxus* on the Colorado steppe.

OENEIS UHLERI (Reakirt)

Our observations on *Oeneis uhleri uhleri* at Hall Valley, Park County, Colorado, indicate that the prairie and steppe species may also have complicated social patterns. The habitat here was a rather dry slope with grasses the predominate growth. The slope rose from a roadbed at a 30° incline for about 50 feet and then to a 20° incline before extending another 30 feet to the edges of a pine forest. The favored spot for *O. uhleri* was at the "break" on this incline. Males alighted in the short grass along this crest and seemed to space out five to eight yards apart, but periodically flew straight up to flutter in fixed positions several feet off above the ground for 30 to 60 seconds. The butterflies, while in hovering flight, were difficult to approach from below. They spotted the investigator about five yards away and then allowed the wind to carry them rapidly up hill and out of sight. On the other hand, a butterfly in hovering flight could be easily approached and netted from above. We believe that these butterflies were surveying the downhill terrain while in hovering flight and that this is a primary method of sexual reconnaissance. Aerial encounters between males along the crest were also much in evidence. Quite likely they are able to maintain "territories" even on the uniform terrain of the steppe.

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A NEW SUBSPECIES IN THE *CERCYONIS MEADI* GROUP (SATYRIDAE)

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Cercyonis meadi (Edwards) is a rare species in collections, due partly to the scattered and isolated geographic distribution of its populations in the Rocky Mountain states and the inter-mountain West. The senior author has accumulated extensive series of this species from all areas, and a full report of the species' biology, variation, and distribution will be published shortly in a comprehensive treatment of the genus *Cercyonis*.

A unique new subspecies of this red-patched *Cercyonis* was discovered by the authors in the San Luis Valley of southern Colorado, in late summer of 1964. This ecologically strange basin is situated at above 7,500 feet elevation, yet is extremely arid and unforested, with saltbush (*Atriplex*) the dominant vegetation. This habitat is quite different from the usual coniferous forest associations of typical *Cercyonis meadi meadi* (Edwards) and *C. meadi mexicana* (Chermock), and the San Luis Valley butterfly is equally distinct. In order to make the name available for inclusion in a forthcoming popular book, this subspecies is described here.

***Cercyonis meadi alamosa* Emmel & Emmel, new subspecies**

Holotype, male. Expanse, 39.3 mm. Forewing length, 21.2 mm. *Forewings, superior surface:* Dull brown, with a russet red patch around the two forewing ocelli. Both ocelli pupilled with white scales. *Hindwings, superior surface:* Dull brown, with well-marked, pupilled black ocellus at anal margin. *Forewings, inferior surface:*