BIENNIALISM IN *OENEIS MACOUNII* (SATYRIDAE)

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Biennialism in insects is that situation where the insects life-cycle takes two years to complete and imagos are produced but once every two years. It may be accompanied by biennial-flights, when in a given locality adults fly only in alternate years, or it may be accompanied by annual-flights. Unless biennial-flights are involved, biennialism is very difficult to perceive in nature without carefully working out the life-histories. Annual-flights may occur when the species is only partially biennial or when two allochronic populations are involved.

Many species of butterflies occurring in desert or near-desert regions are partially biennial. *Papilio rudkini* Comstock (Papilionidae), for example, is normally annual, but in especially dry seasons a portion of the population will remain in the pupal stage for an extra year before emerging. This is undoubtedly an advantage to the species as it reduces the risk of having an entire population wiped out in a particularly bad drought year.

Recognized cases of regular biennialism, however, are very rare in Lepidoptera and they are confined to species (almost exclusively Satyridae) that occur in arctic, alpine or at least boreal regions; suggesting that biennialism may be their means of coping with very short growing seasons. In the Palearctic Region, species with proven biennialism are restricted to *Oeneis jutta* (Hubner) and several species of *Erebia*, including *Erebia claudina* (Borkhausen) and *Erebia ligea* (Linnaeus); although a large number of *Erebia* and several other *Oeneis* are suspect. In the Nearctic Region, five species of the genus *Oeneis* (*jutta*, *macounii* (Edwards), *nevadensis* (Felder & Felder), *chryxus* (Doubleday) and *taygete* Geyer) are known to be biennial in at least part of their ranges; several other species, including *Erebia disa* (Thunberg) (Masters, 1969), *Erebia theano* (Tauscher) (Masters, 1971) and *Boloria polaris* (Boisduval) (Nymphalidae) (Masters, 1971), are highly suspect.

The best known example of polyennialism in insects is the "Periodical Cicada" or "Seventeen-Year Locust," *Magicicada septendecim* (Linnaeus) (Homoptera), which has a seventeen-year life-cycle that produces adult insects once every seventeen years. Quite a few "broods" of *M. septendecim* are recognized, however, with each brood occupying a restricted geographical area distinctly different from other broods, and

with each brood making its emergences as imagos on its own seventeen-year cycle.

Biennialism does not produce a picture nearly as complex as septendecennialism. However, in the genus *Oeneis* biennialism is usually accompanied by geographic brood territories. In most cases populations over extensive areas are on the same brood-cycle and alternation with another completely allopatric population on the alternate brood-cycle occurs only across a natural barrier such as a mountain range or desert. In *Oeneis* (e.g. *Oeneis jutta*) the areas of biennial alternation frequently correspond to areas inhabited by different subspecies; these subspecies are both allopatric and allochronic. When two biennial species of *Oeneis* inhabit the same region, although not necessarily the same habitat, they invariably alternate with each other and display very pronounced biennialism. In the genus *Erebia*, biennialism results in biennial flights in which nearby colonies randomly alternate with each other on the year of flight.

The types of *O. macounii* were collected at Nipigon, Ontario by Professor John Macoun in June 1884. The new species created quite a bit of interest and a number of persons journeyed to Nipigon to collect it, but with very mixed success. James Fletcher sought it in 1886, but got there in August and was too late for it, and again in 1887 which is the off year at Nipigon. Fletcher returned to Nipigon in 1888 with Samuel Scudder and was finally successful in getting it on July 5th. Fletcher wrote (1888) "I had been to Nepigon [sic! Nipigon] once before at exactly the right season and again a month later, but had not seen a specimen, and had begun to think that perhaps after all there might possibly be some mistake about the locality." *Oeneis macounii* was not taken for several more years at Nipigon, but Alberta specimens turned up and interest gradually diminished in the Nipigon colony.

As late as 1942, biennialism by *Oeneis macounii* was still not suspect. George Shirley Brooks had a summer cabin at Victoria Beach, Manitoba where he for years collected large numbers of *O. macounii* for exchange or sale. He wrote (1942) "*Oeneis macouni* [sic! *macounii*] Edw. has been taken only in a limited area at Victoria Beach where it flies at irregular periods among *Pinus banksiana*. One year it may be abundant, and then it may be abundant, and then it may not be seen for several years." Since all of Brooks specimens were taken in even-numbered years, it is surprising that he did not tumble onto the biennialism in this species—he collected it over a twenty year period at Victoria Beach.

The fact that *Oeneis macounii* is biennial was well known by the 1960's,

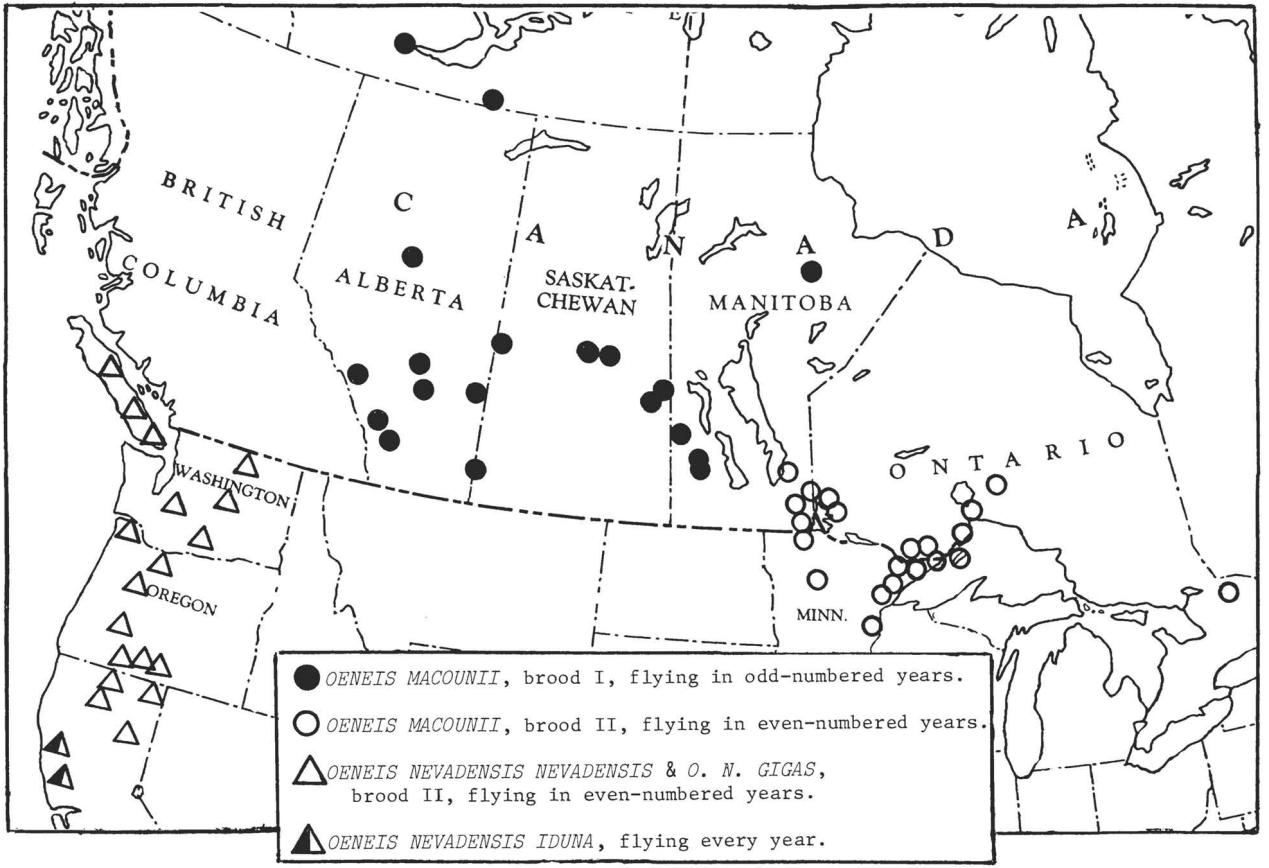

Fig. 1. Ranges of *Oeneis macounii* and *Oeneis nevadensis*, illustrating biennial flights and "brood territories."

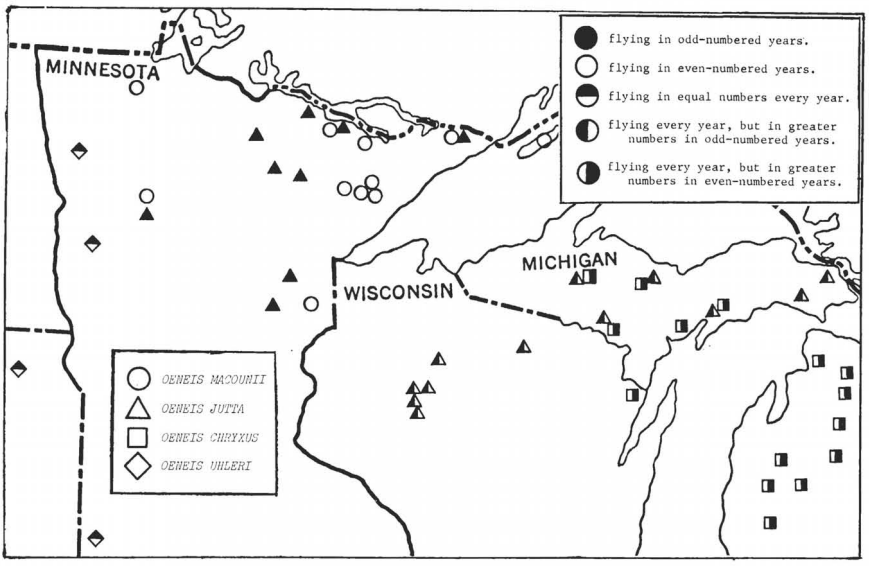

Fig. 2. Distribution of the genus *Oeneis* in Minnesota, Wisconsin and Michigan, illustrating alternation of annual flights.

but the first published record was by Masters, Sorenson & Conway (1967). C. S. Quelch first pointed out to me in 1966 that *O. macounii* colonies in Eastern Manitoba were on even-year cycles while those in Western Manitoba were on odd-year cycles. Since that time I have been gathering distributional and chronological data for all *Oeneis* species in order to demonstrate the point.

In my map (Fig. 1) the known localities for *Oeneis macounii* and the closely related *Oeneis nevadensis* (Felder & Felder) are shown. It is readily apparent that three distinct "brood territories" exist. The break between *Oeneis nevadensis* and *O. macounii* is the Rocky Mountains. The break between the eastern, even-year brood and the western odd-year brood of *O. macounii* is Lake Winnipeg and the Red River Valley, which is the former location of Glacial Lake Agassiz. The southernmost localities for *Oeneis nevadensis* are for subspecies *iduna* (Edwards) which apparently flies annually. The allochronic eastern and western populations of *Oeneis macounii* have been isolated from each other at least 18,000 years, since before Lake Agassiz was formed in the late Pleistocene, however they exhibit no phenotypic distinctions that would warrant the designation of subspecies.

Oeneis jutta occurs through most of the range occupied by *Oeneis macounii* and is also a biennial species. The most remarkable circumstance about this is the fact that *O. jutta* has the most pronounced biennialism where it comes into the same range as *O. macounii* and it alternates years with *Oeneis macounii.* This can be seen in the map (Fig. 2) showing a portion of the area where the two species are sympatric. The same dividing line (Lake Winnipeg—Red River Valley) that divides the eastern and western populations of *Oeneis macounii*, separates an eastern odd-year cycled population (subspecies *ascerta* Masters & Sorensen) from a western even-year cycled population (subspecies *ridingiana* Chermock & Chermock). In Minnesota where both species occur together, *O. jutta* is religiously biennial and can be taken only in odd-numbered years. In Wisconsin, east of the range of *O. macounii*, *O. jutta* may be taken in any year but exhibits a very strong population "pulse" occurring in vastly greater numbers in odd-numbered years. The further east you go, which is more distant from the range of *O. macounii*, the weaker this pulse becomes.

It would be attractive to theorize that interspecific competition has created the alternation in the annual flights of these two species, but this does not seem likely. For one thing, the two species have completely different habitats; *O. jutta* occupies sphagnum-moss/black spruce bogs while *O. macounii* inhabits sandy ridges where jack pine grows. Both species are territorial and have very similar adult behavior, however. A thorough discussion of the bionomics of these two species is given by Masters & Sorenson (1969).

Other species of *Oeneis* that occur in the Lake Superior region include *Oeneis uhleri varuna* (Edwards) and *Oeneis chryxus strigulosa* McDunnough (Fig. 2). *O. uhleri* is a prairie inhabitant which apparently occurs every year in fairly equal numbers. *O. chryxus strigulosa* occurs southeast of the range of *O. macounii*, apparently having a habitat association with sedimentary rocks. *O. chryxus* flies every year in Michigan, but exhibits a strong "pulse" with much more pronounced flights in even-numbered years—thus alternating with *O. jutta.*

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PHYCIODES TEXANA (NYMPHALIDAE) IN CALIFORNIA

A collecting trip to the Providence Mountains of eastern San Bernardino County, California, on 18 May 1973, resulted in a surprise capture—a new state record. While hiking down the south fork of Bonanza King Mine Canyon, I spotted two little dark butterflies flying close to the streambed. Both were captured at 1530. Confirming my initial suspicions, they were two males of *Phyciodes texana* (Edwards). One was in fairly good condition, the other rather worn. The two captured specimens were the only *texana* sighted that afternoon. This appears to be the first recorded capture of this species in California. It was not figured in any of the older books on California butterflies. And it was not mentioned in the recently published book, *The Butterflies of Southern California* by Thomas C. Emmel and John F. Emmel (Los Angeles County Museum of Natural History and the Ward Ritchie Press).

Captures of Arizonan butterflies are not unusual in the mountains of eastern San Bernardino County. Although part of the Mojave Desert, the Providence Mountains, the Ivanpah Mountains, the New York Mountains and the Sacramento Mountains tend to resemble in fauna and flora the Sonoran Desert of southern Arizona. These ranges adjacent to the Colorado River Valley receive more rainfall than the lower portions of the Mojave Desert. And they have a rainfall distribution similar to the Sonoran Desert, with winter rains being supplemented by thunderstorms in the summer. It is not surprising, therefore, that we get occasional reports of *Phoebis sennae* (Linnaeus), *Phoebis agarithe* (Boisduval), *Colias caesonia* (Stoll), *Eurema mexicana* (Boisduval), *Limenitis bredowii eulalia* (Doubleday) and *Strymon columella* (Fabricius) from this region. Lepidopterists should be on the lookout for other Arizona butterflies straying into this area. This unique region may very well produce other new state records.

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