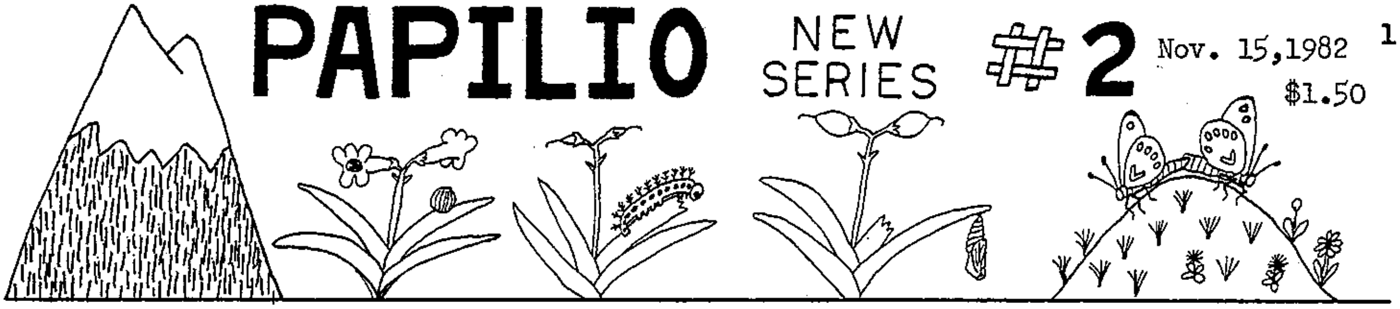


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# THE LIFE HISTORY AND ECOLOGY OF AN ALPINE RELICT, BOLORIA IMPROBA ACROCNEMA (LEPIDOPTERA: NYMPHALIDAE), ILLUSTRATING A NEW MATHEMATICAL POPULATION CENSUS METHOD

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Abstract. The egg, larva, and pupa of B. improba acrocnema are described and illustrated. The larval foodplant is Salix nivalis. There are five instars; overwintering occurs in the fourth instar, and perhaps also in the first instar. Adults fly slowly near the ground, and are very local. Males patrol to find females. Adults often visit flowers, and bask on dark soil by spreading the wings laterally. A binomial method is derived and used to determine daily population size. Daily population size may be as large as 655, and yearly population size may reach two thousand in a few hectares.

## Introduction

Boloria improba (Butl.) is a circumpolar butterfly, occurring from northern Scandinavia eastward to northern Siberia and arctic America. In North America it occurs from Alaska to Baffin I., south to central Alberta, and a relict subspecies acrocnema G. & S. occurs in the alpine San Juan Mts. of Colorado. The life history and ecology of improba were nearly unknown. This paper presents the complete life history and details of the life cycle, ecology, and behavior, studied from 1979 to 1981. In addition, a new method of computing the population size of one continuous mark-recapture sample is presented, which is useful for quick survey work on colonial animals like insects.

## Results

Hostplant. Eggs are laid singly on stems of Salix reticulata ssp. nivalis Hook. (ovipositions were observed at 10:35, 10:45, 11:01, 11:30, and 12:50, all times 24-hour standard time) and rarely on other plants adjacent to nivalis (one oviposition was seen at 11:15 under a leaf of Polygonum viviparum (L.) S. Gray). Lab larvae were fed mostly Salix arctica Pallas leaves, Salix babylonica L., and various other unidentified Colorado montane shrub Salix. Young larvae eat holes in the leaves; older larvae eat entire leaves from the side.

B. improba improba also feeds on Salix, including S. herbacea (L.) in Scandinavia (Bruun and von Schantz 1948), and "tiny dwarf very prostrate Salix with almost round, shining leaves" (this description fits S. reticulata L., of which S. reticulata nivalis is a subspecies according to Dorn 1977) in northwestern Mackenzie District, NWT (Wyatt 1957, pp. 143 & 146). B. improba is associated with willow in several other places.

Egg. Color tan. Rounded on the bottom, tapering to a flattened top, which is slightly more than half the diameter of the widest point (Fig. 4). There are about 22-28 vertical ribs, many of which join adjacent ribs near the top, and about 20 rectangular cells along the side between each pair of ribs. The top is covered with roughly oval cells which gradually become smaller toward the center (Fig. 5).

Number of instars. There are five instars based on head widths (first instar approx. .4 mm, second .6 mm, third 1.0 mm, fourth 1.4 mm, fifth 1.9 mm).

First Instar. The head (Figs. 12-13) is dark brown all over, with approx. 52 simple setae. The body (Figs. 1, 6-7) is cream-tan upon hatching, turning greenish-tan after feeding, then becoming tan with nine indistinct rows of brown. There are many simple setae, which are mostly on verrucae (a verruca is a chitin plate with several setae) or pinaculi (a pinaculum is a chitin plate with one seta), but there are no scoli (Fig. 1). A collar with about 10 setae is on the prothorax. The ventral pinaculi may be absent on abdomen segments 8-9. The number of setae varies somewhat on the verrucae (some figured with 4 may have 5 or vice-versa, some figured with 3 may have 4 or rarely 5). The setae on the suranal plate vary from 4-5 on each side also. From top to bottom (Fig. 1), the middorsal thin line (the heart) is brown, a narrow brown irregular band runs between the topmost row of verrucae, brown semicircular patches clasp the supraspiracular verrucae, a narrow brown line runs between the spiracles, and another narrow brown line runs below the subspiracular verrucae (Fig. 1).

Second Instar. The head (Fig. 14) is uniform reddish-black, with many simple setae. The body (Figs. 2, 8-9) is cream-tan with darker bands. There are many scoli (reddish-brown chitinous cones covered with setae) and a few verrucae and pinaculi (Fig. 2). The collar is now divided into three parts; the lower parts protrude almost enough to be called scoli. The suranal plate has many setae, and the tenth abdomen segment now has a subdorsal scolus. From top to bottom (Fig. 2), the middorsal heart-line is blackish, a cream line is next to it, a broad blackish band runs between and around the topmost row of scoli, a cream line is below the band, next is a blackish line, a faint grayish line is above the second row of scoli, a moderately broad blackish band connects the second row of scoli, a narrow faint gray line is below the band, a dark reddish-black narrow band runs through the spiracles, a broad tan band runs between and around the third row of scoli, a narrow faint brown line runs below these scoli, and the underside is creamy-tan. The overall appearance is light brown with a blackish head.

Third Instar. The head is uniform dark brown with many setae. The body is tan with brown or blackish bands, in overall appearance brown with a subdorsal cream line. The reddish-brown scoli and verrucae are like those of the fourth instar (Fig. 3), although a few extra small verrucae and pinaculi occur in some individuals at least (see fourth instar). The details of body color pattern are like those of the fourth instar (Fig. 3).

Fourth Instar. The head is blackish-brown, except for a paler (brown) subdorsal bar extending forward on top of the head for about 1 mm (approx. halfway between the median line and the side), a brownish-black patch lateral to this bar beside the neck, and a paler (brown) small patch just above the ocelli. The head has very many setae. The reddish-brown scoli and other body structures (Fig. 3) are mostly positioned like those of the second instar, although the scoli are longer. The lower part of the first instar collar has now become a scolus. Some of the smaller verrucae and pinaculi are present or absent in different individuals: the pinaculum on the mesothorax (below & behind the second scolus) is present only in one fourth instar and a third instar, and the same pinaculum on metathorax is present only in a third instar. The ventral pinaculum on abdomen segment 7 is present only in one third instar, and the verruca above it is only in one fourth and a third instar. The ventral verruca on abdomen segment 8 is only in a third instar, and the verruca above it is absent in some fourth instars. The ventral two verrucae on abdomen segment 9 are present only in a third instar. From top to bottom (Fig. 3, on A2-3) the heartline is brown, a tan line is beside it, a broad blackish band is between and around the first row of scoli, a bright conspicuous narrow cream band runs below these scoli, a fairly broad blackish band is next, and the remaining pattern is faintly developed: a tan line runs along the top of the second row of scoli, a brown band connects these scoli, another tan line runs along the bottom of the second row of scoli, a broad brown band containing the spiracles occupies most of the space between the second and third rows of scoli, a grayish-tan broad band is between and around the third row of scoli, a fairly broad brown band is beneath these scoli above the row of verrucae, a faint brown band is around the verrucae, and the underside is grayish-tan. At and below the second row of scoli, these pattern details are rather faint, and the overall color is tan.

Fifth Instar. The head is like the fourth instar head, and has about 150 setae (Fig. 15); the color pattern is like that of the fourth instar. The body is brown with various darker or lighter lines and bands; the overall appearance is dark brown with a conspicuous cream subdorsal line. The reddish-brown scoli and other structures are like those of the fourth instar (Fig. 3). The body pattern (Fig. 3, on A5-6) is very similar to that of the fourth instar. From top to bottom, the heartline is faintly brown, a broad light brown band is beside it, a broad band connects the bases of the scoli in the first row of scoli (this band is blackish in front of the scolus and brown behind the scolus on each segment), a conspicuous cream line runs below the first row of scoli, a broad blackish band is below this line, a brown line runs along the top of the second row of scoli, a fairly broad dark brown band connects the scoli of the second row, a brown line runs along the bottom of the second row of scoli on the abdomen, a broad slightly darker brown band contains the spiracles on the abdomen, a broad tan band surrounds the third row of scoli on the abdomen (this band and the band around the spiracles are both light brown on the thorax), a slightly darker brown band is below the third row of scoli, and the underside is light brown.

Pupa. The shape (Figs. 16, 17, 19) is roughly like that of Speyeria nokomis (Edwards) (Scott 1982) except that there is a dorsal bulge instead of a saddle behind the thorax. The proboscis extends slightly beyond the wingtips, and the antennae extend almost to the wing tips. The base of the wings form conspicuous shoulders, and a lateral notch occurs just posterior to the wing base (Figs. 16-17). On the ventral side of the cremaster (Fig. 18) two horseshoe-shaped arms extend forward; a small heart-shaped indentation lying between the tips of the arms just behind abdomen segment 8 represents the male sex-mark (in butterfly females this mark is a long straight groove; Scott 1975). The dorsal side of the cremaster has a hemispherical rough rim around a central duckbill-shaped spatula. About 50 reddish-brown crochets are on the end of the cremaster. A dark smooth crescentic band on the side of the head (Fig. 17) anterior to the eye evidently represents the orbit of the eye. The rest of the pupa is rough (rugose) with numerous darker irregular striations, although the intersegmental membranes behind abdomen segments 4-6 are fairly smooth. There are subdorsal bumps (Fig. 16) on the prothorax, metathorax, and the first three abdomen segments (corresponding to the first row of scoli in the larva), and a slight suggestion of these bumps occurs on the fourth abdomen segment and even on the base of the antenna. Middorsal bumps (Fig. 16) occur on the anterior edge of abdomen segments 2-8; these bumps are slight on segments 2-4 and 8, but are prominent on segments 5-7, where they are about as high as wide, and act as pivots for the side-to-side movement of the abdomen (only the joints between 4-5, 5-6, and 6-7 can move, and the movement is side-to-side only, no up-and-down movement is possible). Spiracles occur only on the side of abdomen segments 2-7 (Fig. 19).

The color pattern of the pupa changes somewhat during development. A few hours after pupation, most of the larval pattern is still visible. The wings, head, and legs are brown, and the thorax is mostly brown. From top to bottom on the abdomen, there is a broad gray middorsal band, then a band of dark brown patches (on the front of each segment) alternating with grayish patches (on the rest of each segment)(this band corresponds to the band through the first row of larval scoli), next is a cream line (this line represents the conspicuous subdorsal cream line of the larva; it is even evident somewhat on the three thorax segments), a brown band is next, then a narrow ochre line, then a line of dark brown dashes at the joints between segments (corresponding to the band through the second row of scoli of the larva), another ochre line, a broad brown band, and finally the underside is mottled darker brown (with grayer subventral dashes posteriorly on each segment and lighter brown mid-ventral patches posteriorly on each segment).

Several days after pupation, the larval pattern is still somewhat evident on the abdomen. The overall color is mottled brown. Between the still-present subdorsal cream lines, the metathorax and first two abdomen segments are brown, segment 3 is slightly brownish-gray, segments 4-8 are grayish-tan. Just lateral to the middorsal line on the abdomen are blackish patches, placed anteriorly on each segment. These blackish patches are roughly oval on segments 1-4, and grow progressively larger posteriorly, from very small on segment 1 to large on segment 4; the patches are roughly triangular on segments 5-7 (the acute angles of the triangles are medially and posteriorly on each segment), and the triangles become larger posteriorly. Below the subdorsal cream line is a dark brown band, then a narrow tan line, a row of faint brown dashes at the front of each segment (corresponding to the second row of scoli of the larva), another narrow tan line, a broad band of brown irregular patches anteriorly on each segment that blend into the tan background, then a broad light tan band centered on the spiracles, then a broad brown band, a broad area of light tan (with brown posteriorly on each segment), then brown mid-ventrally. The wings are now brown with the veins clearly indicated by dark brown. The antennae are tan and checkered, the legs and proboscis are mottled brown. The orbit is blackish. On the transverse anterior rim of the head is a white transverse band, which has a black band just dorsal to it. The top of the thorax is mottled brown. The wing joint and the forewing flange (dorsal to the basal half of the anal wing vein) are dark brown. The small strip of the hindwing that appears above the forewing is dark brown. A middorsal blackish line on top of the thorax splits into a dark brown V on the posterior half of the mesothorax (Fig. 16). In dorsal view, the mesothorax is dark brown laterally.

On the day prior to adult emergence, the larval pattern has disappeared completely. The overall appearance is blackish-brown, with an array of gray peaks between black patches on top of the abdomen (Fig. 16). The head and thorax are blackish-brown. The wings are blackish-brown with black veins. The abdomen (Fig. 16) is blackish-brown on segments 1-3, segment 4 is grayish-black dorsally, segments 5-7 are grayish-black laterally but are gray in volcano-like middorsal peaks (the peak top being the anterior bump-like pivots mentioned above) and are black in roughly hemispherical patches adjoining the peaks (the patches blend laterally to grayish-black), and segments 8-9 are grayish-black. The middorsal bumps are cream on abdomen segments 4-8. The posterior rim of abdomen segments 4-6 is dark reddish (very narrowly reddish dorsally, but slightly wider reddish laterally), then there is a yellow subdorsal longitudinal dash (shown on Fig. 16 by two short parallel dashes) in the translucent yellowish rim behind these segments (these represent the last vestige of the larval subdorsal cream line), and the intersegmental membrane itself is red mottled with cream on these segments (seen when the abdomen wiggles side-to-side when the pupa is touched). The cremaster is brown. The ventral side of the pupa (Fig. 17) is dark mottled brown. The basal half of the proboscis and the antenna shaft are reddish-brown. The legs are mottled reddish-brown. A cream transverse band is just ventral to the anterior transverse rim on the blackish head.

Comparison with other *Boloria*. The immatures of a few other *Boloria* species are known. Older larvae of *B. selene* lack the subdorsal pale band of *improba* and have very long subdorsal prothorax scoli (Turnbull, 1979). Pupae of *selene* have more prominent subdorsal conical bumps, and eggs have fewer vertical ribs (Scudder 1889). The colors of larvae and pupae of *B. bellona* are more similar to those of *improba*, and *bellona* (and *improba*) lacks the long prothorax scoli of *selene* (Scudder 1889). However, the *bellona* pupa has longer subdorsal abdomen bumps than those of *improba*

(Scudder 1889). The first instar larva of improba has more setae than do the other Boloria I have raised. For instance, the dorsal-most row of setae in improba (Fig. 1) has four setae on most segments, whereas in B. eunomia and freija there are mostly two setae, and in titania only one. The B. titania first instar has only 3 setae above the spiracles of each abdomen segment, as in most butterfly larvae. All four species have many setae below the spiracles. All the other Nymphalidae I have studied (except Speyeria and Morpho) have only three setae above each abdomen spiracle on each side, and two just beneath, so the progressive increase of number of setae in Boloria is a derived trait, and improba (which has the most setae) is the most derived species known.

Life Cycle. In the lab at about 20°C, the egg stage lasts about 10-15 days, and the first three instars take about 26 days until they moult to the fourth instar, which diapauses and refuses to feed even when fresh leaves and 24-hour light are provided. In spring, the fourth instar takes about 4 days at about 22°C before moulting to the fifth instar, which takes about 3 days to pupation at about 22°C. The pupa then lasts about 9½ days at 20°C. Overwintering was accomplished in a refrigerator with wood blocks about 3x3x4 cm with 1 cm diameter holes drilled in them; the wood blocks are soaked occasionally and cheesecloth prevents the larva from escaping (techniques of Mattoon et al. 1971). After several months (5 months; perhaps only 2-3 months are necessary) the potted Salix arctica plants were brought indoors to leaf out and the larvae were placed with fresh leaves on moist paper towels under an inverted jar and a light placed near them about 14 hr./day. The first three instars eat very little, but the 4th and 5th instars eat perhaps 7-10 whole S. arctica leaves per larva.

These data are translated to nature as follows. Eggs are laid mostly in late July, the eggs take several weeks to hatch, and the first three instars feed on Salix nivalis leaves until they reach the 4th instar mostly in Sept. They diapause, the leaves drop off the willows, and late fall and winter snows cover most of the habitat until sometime in June. Then the snow melts, the plants leaf out, and the 4th-5th instar larvae feed voraciously for a week or two, then pupate. The pupa takes about two weeks and adults emerge in mid to late July. Young larvae possibly also overwinter (my larvae were given 24-hour light and about 20°C) as part of a biennial life cycle. The egg and first three instars take up to 40 days to grow in these warm lab conditions, so in the cold alpine zone they may take much longer, and in some years the first winter snow comes in early Sept.; the S. nivalis leaves apparently drop off by mid Sept. Edward Pike (pers. comm.) found that Alberta B. improba are biennial on even-numbered years, but the Colo. improba flew every year from 1978 to 1981, although numbers seem to have been greater in 1978 and 1980 than in 1979 and 1981. The poor winter snowfall in 1981 may have contributed to low numbers then. At least three other alpine butterflies are biennial in the San Juan Mts.: Oeneis chryxus (Dbldy) on even years, Erebia theano (Taus.) on even years, Pyrgus centaureae (Ramb.) on odd years.

The larvae have a quiescent period of up to a day before moulting, and the prepupa wanders some and rests for a day before pupating.

Older larvae eat young leaves, whereas young larvae (if there is an annual cycle) must contend with old tough leaves. If the life cycle is biennial, however, the very young larva probably overwinters (as in arctic Boloria, see Scott 1981), and the very young through third instar larva eats fresh leaves the year after the egg was laid.

Flight Habits. Adults have a rather slow fluttering flight about 10-20 cm above ground, frequently landing. Females spend perhaps only 1/5 of their time flying, males perhaps 1/4 or 1/3. Mark-recapture studies show that walking across a piece of habitat causes only a small part of the population to fly and be observed at one time. When disturbed, adults can fly rather fast. Adults seem to be rather local, although I found one male about 50 m from a colony.

Mating. Males patrol to find females for mating. Males patrol and chase other adults all day, as late as 15:40. A patrolling male was observed pursuing a Speyeria mormonia (Bdv.) also. At 9:05 an unsuccessful courtship was observed in which both sexes fluttered their wings somewhat while the male crawled after the female through the grass.

Adult Foods. Adults often feed on flowers, including pink Silene acaulis L., blue Erigeron sp., Hymenoxys grandiflora, and Phlox multiflora. A female was also observed probing the earth with her proboscis at 10:00; the volcanic soil there lacks concentrations of salts, so she was probably seeking moisture or organic nutrients.

Predation. No actual predation was seen, although two wings were found under a rock during a search for larvae; some arthropod probably dragged a live or dead adult under the rock.

Basking. Adults bask with wings spread laterally on dark soil to raise the body temperature.

Habitat. Colonies of B. improba acrocnema are in dense concentrations of Salix nivalis. Colonies are only one to several hectares in size. S. nivalis is always more widespread and each colony is restricted to only part of the area of foodplant. The foodplant depends on accumulation of winter snow for moisture, so it would seem that the presence of improba in the San Juan Mts. is due to the greater precipitation there than in the rest of Colorado. B. improba may occur in other ranges also. Alpine species are notoriously disjunct, and the habitat requirements of improba are so specialized and poor for other butterflies (except for B. titania (Esper)) that improba could occur elsewhere in Colo., Utah, Wyo., and Mont., despite past collecting there. The habitat of arctic improba is very similar to that of improba in Colo.

The yearly time of emergence seems to depend on when the snow melts at each site; the earlier the snowmelt, the earlier the flight. This phenomenon occurs even between subsites at the type locality. Adults were abundant on steep slopes there on July 18, 1980, in addition to the flatter parts of the colony, whereas late in the flight period in 1979 (Aug. 3) adults occurred only on the flatter parts where snow lingers longer.

Adult Population Size. Adults were abundant on July 18, 1980 at the type locality. 99 were marked, and only 13 were recaptured. 68 adults were marked in morning and early afternoon, and in late afternoon only 3 of 41 adults handled were recaptures. This gives a population estimate of 68/(3/41)=929, although this estimate is inferior to the one now calculated.

A New Method of Mark-recapture Analysis. In attempting to analyze my data of July 18, 1980, for B. improba, I realized that none of the current methods were constructed for the data gathered. My sampling program was to net one or more adults at each spot, mark some or all of them and release them (without unique marks on each adult), perhaps collect (remove) some, then move to another spot and repeat the process (recording recaptures), repeating it continuously during the day until an adequate idea of the population was obtained. This type of sampling program is desirable for B. improba because it occupies a small area so enough data can be gathered in one day, and a longer study was impossible. Previous methods require discrete intervals between marking and recapturing (the Jolly-Seber method and Lincoln Index, etc.), or require unique marks on each adult (the Jolly-Seber and Craig methods, etc.).

At each (i) of s sampling occasions, $y_i$ adults are marked and released, $d_i$ adults are collected and not released, and $m_i$ adults are recaptured ($m_1=0$). The procedure is continuous until sampling ceases. At each sampling occasion, the number of recaptures expected is the number of adults sampled ($y_i+d_i+m_i$) times the probability that each adult was previously marked. This probability is the cumulative number of adults marked prior to the current sample ($\sum_{j=1}^{i-1} y_j$) divided by the population size N (N is treated as a constant if few are collected compared to N):

1) expected $m_i = (y_i + d_i + m_i) \left(\sum_{j=1}^{i-1} y_j\right) / N$

It is easily proven that the expected number of recaptures (equation 1) is the same as that derived from the binomial distribution:

$(p + q)^{(y_i + d_i + m_i)}$, where $q = \left(\sum_{j=1}^{i-1} y_j\right)/N$ and where $p = 1 - q$. The binomial distribution specifies the probabilities of obtaining the integers 0, 1, 2, 3, . . . of marked (recaptured) adults out of a sample of $(y_i + d_i + m_i)$ adults. The total number of recaptures expected in each sample is the number of recaptured adults found in the sample, times its probability from the binomial distribution, summed over all possible number of recaptures possible at each sample, which equals equation 1. When the sampling ceases, the total number of recaptures expected throughout the program (R) is the sum of the number expected at each occasion, or:

$$2) \qquad R = \sum_{i=2}^{s} m_i = \frac{\sum_{i=2}^{s} \left[ (y_i + d_i + m_i) \sum_{j=1}^{i-1} y_j \right]}{N}$$

N is easily obtained from equation 2:

$$3) \qquad N = \frac{\sum_{i=2}^{s} \left[ (y_i + d_i + m_i) \sum_{j=1}^{i-1} y_j \right]}{\sum_{i=2}^{s} m_i}$$

If collecting occurs roughly uniformly along with marking, the N estimated will be approximately the average of the two N's obtained if collecting were done after sampling or before sampling, so $\frac{1}{2} \sum_{i=1}^{s} d_i$ can be added to equation 3 to approximate the N estimate without collecting.

For practical calculations, six columns are used on a data worksheet: 1) $d_i$; 2) $y_i$; 3) $m_i$ (the sum of the entries in this column is the total number of recaptures R); 4) $(d_i + y_i + m_i)$; 5) sum of the previous y's up to the current sampling occasion (the bottom line of this column is the total number marked); 6) the product of columns 4 and 5 (the sum of this column divided by the total number recaptured is the population size).

The method assumes only that the marked adults mix into the population upon release, and that mortality and dispersal between the start and end of the program can be ignored, so it seems ideal for insects which fly upon release and live long enough to have little mortality within one day. The method does not require a unique mark on each adult, and does not require discrete sampling occasions. The binomial distribution applies to small samples, so there is no bias for small sample sizes. The method is quite useful, because it reproduces exactly the number and sequence of everything done in the program (marking, collecting, recapturing) that can affect the outcome. The method is essentially the same as exact computer simulation of the sampling program. The only difference between the predicted number of recaptures from equation 2 and that actually found, given the correctness of the assumptions, are due to chance. Furthermore, the method is useful for studying subdivided populations, even when data is poor in some of the subdivisions, as noted below. The method is easy to calculate, and should prove very useful for quick survey work, when not enough time is available for full mark-recapture study using the Jolly method (which requires 3 or more days per study), and for fragile or endangered species which cannot withstand the harassment of a full-scale study. The B. improba hostplant grows in mats which are impossible to avoid stepping on, so the hostplant trampling in a Jolly-type study should be avoided. Another advantage of the method is that the short period of sampling required by the method makes mortality relatively unimportant, improving the population estimates.

For the B. improba data, the numerator of equation 2 is 7587, and 13 total recaptures were found of 99 total marked, so using equation 3, and adding the correction for collecting, $N = (7587/13) + 31 = 615$. Adults may not have mixed completely throughout the colony during the short time it was sampled. Dividing the population into the two areas of abundance, and calculating each separately, $N = (4374/12) + 20 = 384$ in the southern part, plus $N = (502/1) + 11 = 513$ in the northern part, or 897 total. The 513 is unreliable to use, because one more or one less recapture there would have changed it greatly. However, assuming that the proportion of the total population in the larger and smaller areas are the proportions marked or collected in each (.635 and .365), and using the additivity of number of recaptures, then:

$$4) \quad R = R_1 + R_2 = \frac{4374}{.635N} + \frac{502}{.365N} = \frac{8264}{N}$$

Because $R = 13$, $N = 634$, and adding the correction for collecting, $N = 665$. This estimate is the best I think, although it is very similar to the previous estimate. Equation 4 shows that if the population size had been only 300, 27 recaptures would have been expected, far greater than the number observed, and $N = 400$ would have produced 21, still too high. A population of 1100 would produce only 7 recaptures, etc.

Equation 3 is completely accurate only when all $d_i$'s are zero. I submitted the method to Dr. George M. Jolly, the author of "Jolly's stochastic method", who (pers. comm.) stated that the method is valid. He also stated that my inquiry brought to light the need for a modification of the method allowing for adults removed from the population, and he responded by deriving maximum likelihood estimates (not yet published, but derived using the methods of Jolly 1979) for the population size and variance for this method that take into account adults removed from the population. Jolly's method is iterative, requiring an initial estimate of N, which equation 3 will provide. Jolly advised that Bailey's correction is not needed. The population estimate using Jolly's method is 654.78 (standard deviation 158.5).

Simulations of the marking program of July 18 with rice grains were also made. Replacing a natural grain with a blackened one represents marking, removal represents collection, drawing a blackened grain represents recapture, two bowls of grains represent two subpopulations. Grains are collected and marked in the sequence followed in the field, stirring the cup after each sample, and the recaptures are recorded. The 16 simulations done followed the recapture predictions above roughly, although a greater number of recaptures generally occurred (10 of 15) than predicted by equation 3, such that a population of 700 was mostly likely to produce 13 recaptures. The only simulation that produced exactly 13 recaptures had a population of 800. The rice simulations support the higher estimate of Jolly's modification of the method and equation 4.

Yearly Brood Size. An estimate of the total number of adults during 1980 emerging at the type locality can be made (Fig. 20). On July 18, the total population was about 655, but 600 can be used as a safe estimate, with a nearly equal sex ratio. The data for July 24-30 show an extreme decline for males and a gradual decline for females at the end of the flight, with female survival slightly greater than that of males (Gall & Sperling 1980). The brood curves of Fig. 20 are modeled from: 1) curve-fitting by eye through the population data points; 2) the known shape of butterfly brood curves which are roughly normally distributed (bell-shaped), symmetrical about the mean, with the start somewhat truncated; 3) the well-known and mathematically demonstrated (Scott 1977) 1-2 day lag in emergence of females after males; 4) the necessity for making the total brood size equal for males and females (butterflies have equal sex-ratios). The estimates for July 24 and 30 are not good because they are based on less robust methods than the rest. The population curve of females is slightly higher than that of males because they have slightly greater survival. The survival rates are based on the studies reviewed by Scott (1974a, b; females average slightly higher survival than do males). The survival rate for males is assumed to be .75 per day at the start, .7 in the middle of the brood, and .65 at the end; the rate for females is assumed to be .8, .75, and .7 for start, middle, and end. Survival rates decrease slightly during the brood due to the aging population. Gall & Sperling (1980) gave estimates of survival rate (male .57, female .70); these estimates are rather low, undoubtedly because they are based on the dying adults at the end of the yearly flight. The number of each sex dying each day is found by multiplying the daily population size (from the curves of Fig. 20) by the daily mortality rate (one minus the survival rate). The total number of adults emerging for the entire brood equals the total number dying, which is, for Fig. 20, 1012 males and 1007 females, or 2019 total for the 1980 brood. If the low survival rates of Gall & Sperling are more correct than the rates assumed, the 1980 brood size is much larger (2644, or 1452 males and 1192 females, using their survival rates and the population curve of Fig. 20). Because the peak population size was probably closer to 655 (Jolly's estimate) rather than 600, and the start of the flight was unsampled and therefore inaccurate, and survival rates are not precise, one can conclude only that the 1980 yearly total was about two thousand.

The population size in 1981, which had very low snowfall (1980 had very large snowfall), seemed to be much lower. The other colonies (based only on 1-2 visits to each) were much less populous than was the type locality colony in 1980, although no mark-recapture studies were done on them. Of course, adults of this local Colo. species should not be collected when abundance is low.

Taxonomic Status. B. improba acrocnema was named as a distinct species, but is clearly a subspecies of improba. Jon H. Shepard, who is currently revising Boloria, and L. Paul Grey, who published a genitalic survey of Boloria and its relatives (dos Passos & Grey, 1945) both assign it as a subspecies of improba (pers. comm.). The wing pattern is clearly like that of improba, including the rounded wing shape, the very large diffuse brown postmedian forewing spots, the soft gray outer half of ventral hindwing, the overall appearance, and most details of wing pattern. The ventral hindwing median band is variable even in arctic improba; it is paler southward in both B. improba improba vs. improba acrocnema, and in B. astarte distincta (Gibs.) vs. astarte astarte (Dbldy), suggesting that the convergence in this character may have some basis in natural selection. The genitalia are very similar in improba improba and improba acrocnema.

B. improba acrocnema was named as a distinct species because of a numerical taxonomy study comparing selected characters among B. improba improba, improba acrocnema, B. frigga (Thunb.), B. bellona (Fab.), and B. epithore (Edw.); the closest relative of acrocnema was found to be improba, and the difference between improba and acrocnema was comparable to the difference between frigga and bellona. However, some important characters were missed in this study, such as the large size and diffuse edges of the forewing postmedian spots of improba improba and improba acrocnema, the soft gray outer half of ventral hindwing of these taxa, the details of wing shape (improba acrocnema and some improba improba have quite rounded forewings, B. epithore has fairly rounded forewings, B. frigga and B. bellona both have a highly angled forewing tornus, but the apex of frigga is pointed and the apex of bellona is truncated--the numerical taxonomy study represented this variation by only three states of only one character), the alpine vs. forest or lowland habitat, the weak vs. fast flight, Salix vs. Viola hostplants. B. improba improba and improba acrocnema are allopatric; B. frigga, bellona, and epithore are sympatric with each other and with improboa improba or nearly so, but are allopatric with improba acrocnema (frigga and bellona range within about 100 km of improba acrocnema). The numerical taxonomy study also included numerous characters of little or no value, and many characters which are merely different expressions of the same character (forewing shape, for instance) and are therefore redundant. A major flaw in this numerical methodology is that morphological difference often has little to do with speciation; "sibling species" are valid species which differ very little morphologically, and some forms within one species may be very distinct (such as Limenitis arthemis arthemis (Drury) vs. arthemis astyanax (Fab.), the female forms of Papilio dardanus Brown, the yellow vs. black forms of Papilio glaucus L.).

Ecologically, B. improba improba and improba acrocnema are virtually identical. They have the same prostrate round-leaved Salix larval foods. They occur in the same moist tundra habitat. They are both local, and they share the same weak fluttering flight. B. improba acrocnema is a relict population of improba that has been stranded since the last glaciation 10000 years ago, and has since developed some differences. These differences may have partly developed from inbreeding when the populations were at low levels (lab-rearing does not change the appearance of adults significantly, so there seems to be little environmental influence on the wing pattern), although the brighter coloration and the paler ventral hindwing median band of Colo. populations are probably due to natural selection, as noted above. The rounded forewings of Colo. adults may have resulted from the very small area of the colonies; the adults which had more pointed wings, which in butterflies generally fly more strongly than do adults with rounded wings, may have dispersed more than the more rounded-wing adults, leaving the latter to produce the next generation in the colony. Although the colonies are local, the persistence of improba in Colo. for 10000 years (and the high density attained) proves that Colo. improba is successful.

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Literature Cited

Bruun, H., & M. von Schantz 1948. Till kannedomen om Brenthis improba Btl. ssp. improbula Bryk (Lepidoptera). Not. Ent. 29:82-89.

dos Passos, C.F., & L.P. Grey 1945. A genitalic survey of Argynninae (Lepidoptera, Nymphalidae). Amer. Mus. Novitates No. 1296, pp. 1-29.

Gall, L.F., & F.A. Sperling 1980. Population study of Boloria acrocnema. Xerces Society Conservation Report, Aug. 1980.

Jolly, G.M. 1979. A unified approach to mark-recapture stochastic models, exemplified by a constant survival rate model. In: R. Cormack, G. Patil, D. Robson, eds., Sampling Biological Populations. Int. Coop. Publ. House, Fairland, Md. Statistical Ecology Series 5:277-282.

Mattoon, S.D., R.D. Davis, & O.D. Spencer 1971. Rearing techniques for species of Speyeria (Nymphalidae). J. Lepid. Soc. 25:247-256.

Scott, J.A. 1974a. Lifespan of butterflies. J. Res. Lepid. 12:225-230.

Scott, J.A. 1974b. Adult behavior and population biology of Poladryas minuta (Lepidoptera, Nymphalidae) and the relationship of the Texas and Colorado populations. Pan-Pacific Entomologist 50:9-22.

Scott, J.A. 1975. Early stages of seven Colorado Hesperia (Hesperiidae). J. Lepid. Soc. 29:163-167.

Scott, J.A. 1977. Competitive exclusion due to mate searching behavior, male-female emergence lags, & fluctuation in number of progeny in model invertebrate populations. J. Anim. Ecol. 46:909-924.

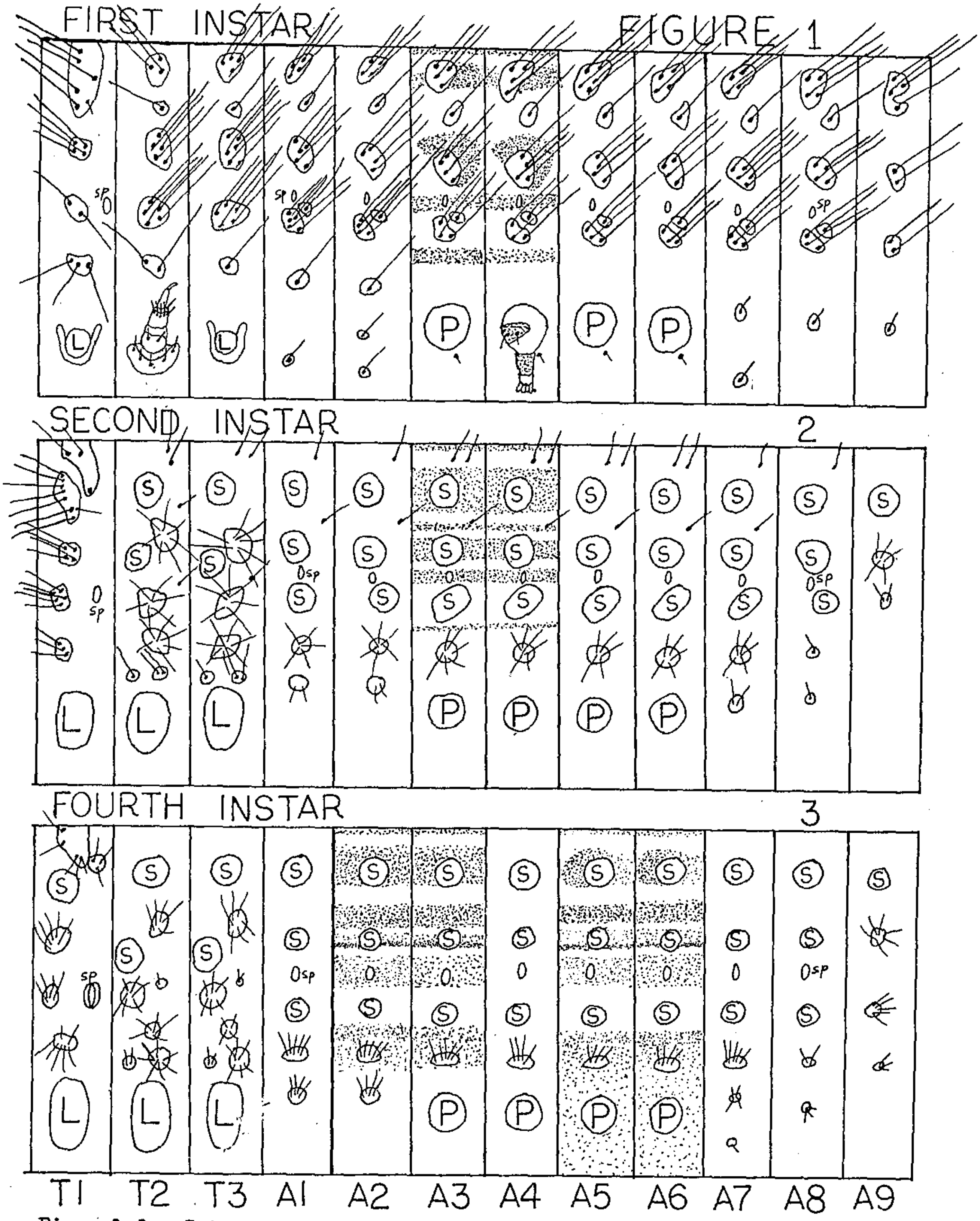
Scott, J.A. 1981. Hibernal diapause of North American Papilionoidea and Hesperioidea. J. Res. Lepid. 18:171-200.

Scott, J.A. 1982. Early stages of Speyeria nokomis. J. Res. Lepid. 20:12-15.

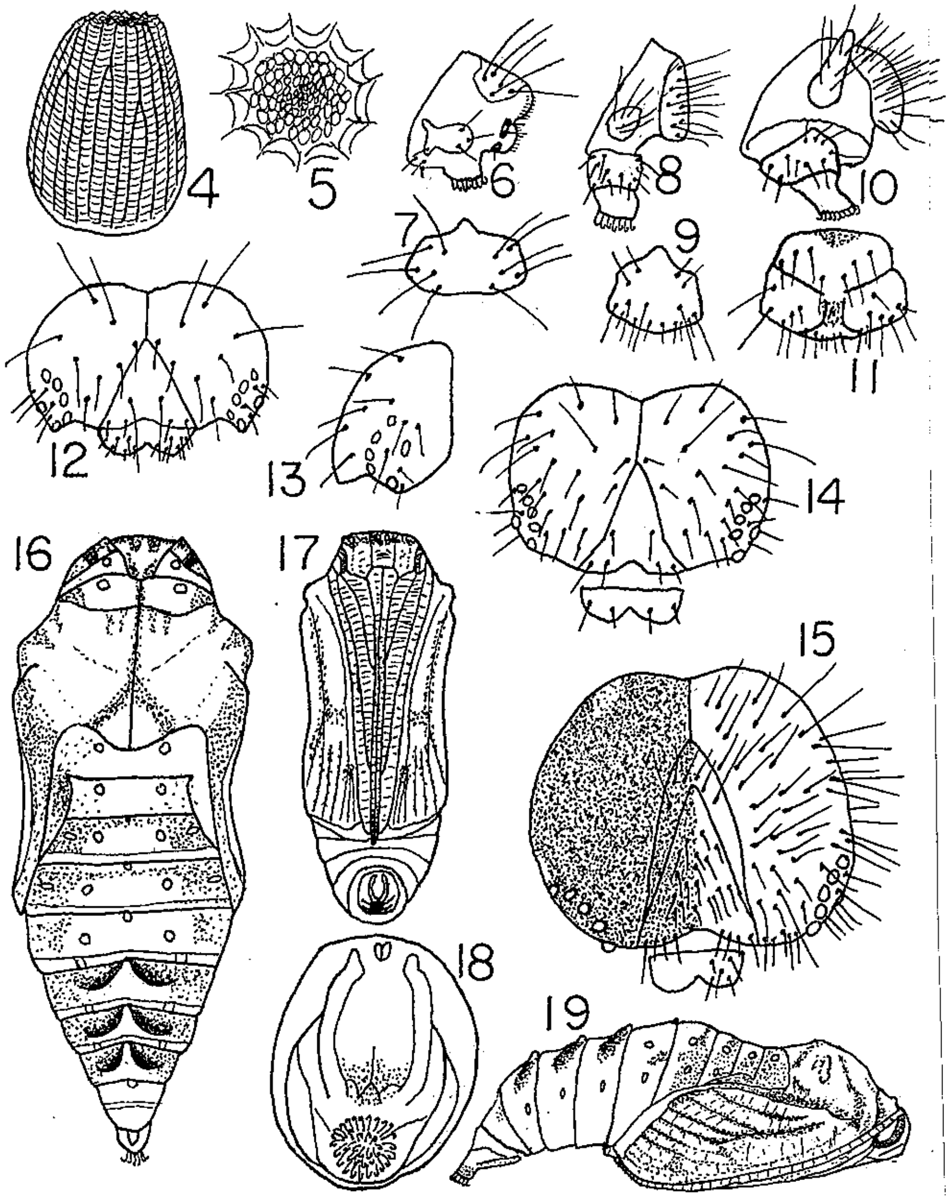
Scudder, S.H. 1889. The butterflies of the eastern United States and Canada, with special reference to New England. Cambridge, Mass.

Turnbull, C.L. 1979. Adaptive changes in morphology and behavior of Clossiana selene larva (Lepidoptera: Nymphalidae). Ent. News. 90:125-130.

-Dorn, R. 1977. Willows of the Rocky Mountain States. Rhodora 79:390-429.
Wyatt, C.W. 1957. Observations on Boloria distincta. J. Lepid. Soc. 11: 143 & 146.


Figs. 1-3. Setal patterns of larvae. S=scolus, P=proleg, L=leg, sp=spiracle (spiracles on abdomen segments 2-7 are shown without sp). Round or oblong structures having several setae are verrucae; round structures having one seta are pinaculi. The body pattern is drawn onto some of the abdomen segments; on Fig. 3, the fourth instar pattern is on A2-3, and the fifth instar pattern is on A5-6. The first instar leg is drawn on T2 of Fig. 1, and the proleg on A4.



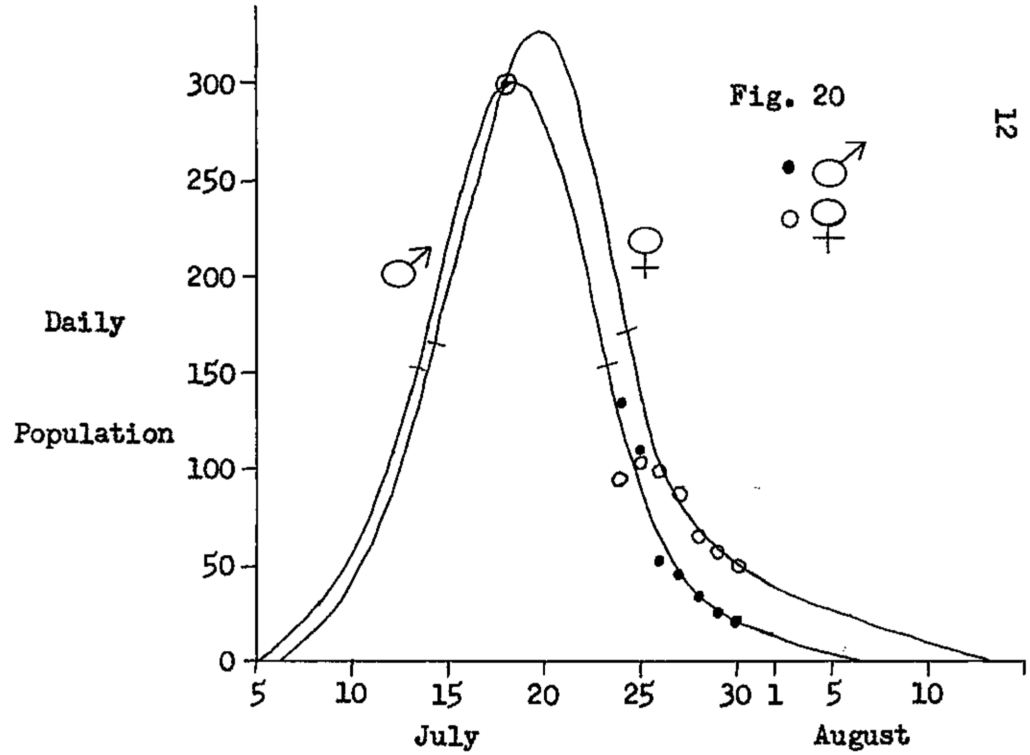




Fig. 4. Egg, side view. Fig. 5. Egg, top view. Fig. 6. First instar abdomen segments 10-11, left lateral view. Fig. 7. First instar suranal plate. Fig. 8. Second instar abdomen segments 10-11, left lateral view. Fig. 9. Second instar suranal plate. Fig. 10. Fourth instar abdomen segments 10-11, left lateral view. Fig. 11. Fourth instar suranal plate. Fig. 12. First instar head, front view. Fig. 13. First instar head, left lateral view. Fig. 14. Second instar head, front view. Fig. 15. Fifth instar head, front view. Setae drawn on left side, pattern drawn on right side. Fig. 16. Pupa, dorsal view, showing pattern of the older pupa. Fig. 17. Pupa, ventral view. Fig. 18. Pupa segments 9-11 including cremaster, ventral view (heart-shaped male sex-mark is at top). Fig. 19. Pupa, right side (lateral) view. Fig. 20. Population size daily during 1980 (for explanation see text).

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