Life History of *Aeropedellus clavatus* (Orthoptera: Acrididae) in the Alpine Tundra of Colorado[1]

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ABSTRACT

Aeropedellus clavatus (Thomas), an alpine and boreal grasshopper, is resident at higher altitudes in the Colorado Rockies than any other acridian. A 5-season study of an alpine population sampled at 12,800 and 13,100 ft above sea level on Mount Evans, Colorado, involving 2838 specimens (including 1734 juveniles), revealed various adaptations to an alpine habitat: an abbreviated life cycle—only 4 juvenile instars; hatching while ice and snow are still present in the immediate surroundings, and sexual maturity reached in approximately 6 weeks thereafter; oviposition in basal portions of sedges and grasses; diapause apparently involving more than 1 season; feeding predominantly on sedges and grasses. The eggs and egg pods, and the various stages in development of both sexes, are described and illustrated.

The most abundant grasshopper in the alpine tundra of Colorado is *Aeropedellus clavatus* (Thomas). It occurs in alpine areas throughout the Front Range, the Sawatch Range, and the Sangre de Cristo Range of the Rocky Mountains, and it is, in our experience, the only species that has large populations above 12,500 ft (3800 m) in altitude. Its overall geographic range is from the Sacramento Mountains in New Mexico to Mount McKinley National Park in Alaska, but in the southern part of its range it does not occur below about 8600 ft. In northern Colorado it has populations at the lower edge of the foothills (at about 5700 ft above sea level) but does not invade the plains. Only in the northern Mountain and Plains States, and in Canada, is it widespread at lower elevations (occurring east to Minnesota and Manitoba). Thus, whether we consider latitude or altitude, it is boreal in distribution.

Its closest relatives are also boreal. The only other North American species in the genus, *Aeropedellus variegatus* (Fischer), ranges from the arctic slope of Alaska across Siberia and Europe to the Alps (Ramme 1951; Harz 1957). Dreux (1962) stated that *A. variegatus* occurs at the highest elevations of any Orthoptera in the French Alps and is there a rare relict. The American form was recognized as a subspecies, *A. v. arcticus* by Hebard (1935).

Another close relative of *Aeropedellus clavatus,* ecologically as well as morphologically, is the Old World *Aeropus sibiricus* (L.). This species has isolated populations in various mountains of Europe and central Asia and its range extends across northern Europe and Asia at lower elevations (Bei-Bienko 1928; Ramme 1951). It has large populations at high altitudes in the mountains of Europe (Guggisberg 1954; Harz 1957; Stevanović 1961).

Species with such boreal distribution not only must tolerate low temperatures but must have life cycles adapted to a short growing season. One adaptation to a short growing season appears to be a reduction in the number of juvenile instars from the 5 typical of most Acrididae (Uvarov 1928) to only 4 in these boreal forms. Bei-Bienko (1928) stated that this condition characterizes the majority of species of west-Siberian grasshoppers, including *Aeropus sibiricus.* He described the 4 stages in *A. sibiricus* and illustrated wing development with a series of drawings. Quite recently, Stevanović (1961), has published photographs of all developmental stages in this species.

Criddle (1926) stated that *Aeropedellus clavatus* has only 4 juvenile stages. He published a drawing of the first instar at that time but omitted most details of the life cycle. Our observations indicate that Criddle was correct in attributing only 4 juvenile instars to this species. We here illustrate these stages in both sexes, comment upon certain morphological

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details, and correlate the stages as far as possible with the progress of the season at high altitudes. (The 4 juvenile stages will be referred to as instars I, II, III, and IV.) We also consider various other adaptations of the species for its alpine habitat—in particular, its ovipositing in stubble, its feeding predominantly on grasses and sedges, and the possibility of an extended diapause.

POPULATIONS STUDIED

We have sampled populations of *A. clavatus* in several alpine areas of Colorado, but the alpine population studied most intensively has been that above 12,800 ft on Mount Evans, in Clear Creek County, Colorado, about 30 miles west of Denver. This population has been sampled frequently, particularly during the seasons 1958–1962, inclusive, in 2 areas a few miles apart. One of these areas is immediately northeast of Summit Lake, at 12,800 ft (3900 m) altitude. The other, at 13,100 ft (4000 m), is on the east side of a low saddle on the south slope of Mount Evans. Both areas are near the automobile road that goes to within a short distance of the summit, which is at 14,260 ft above sea level. Although *Aeropedellus* has been collected on Mount Evans up to altitudes of approximately 13,600 ft, and is resident there, only a few individuals have been taken above 13,100 ft.

Each of the 2 areas is characterized by grass-sedge vegetation. The higher area, here called the saddle area, is very rocky and has little continuous ground cover (Fig. 1). The area near Summit Lake (Fig. 2) does have a continuous cover of vegetation, which includes a considerable number of forbs as well as grasslike plants. The plants present in the saddle area indicate a rather light snow cover or nearly snow-free condition in winter (Marr 1961); and both areas are free from winter snow well before the end of June, this fact also indicating that they are not areas of significant snow accumulation.

FIG. 1.—The saddle area on Mount Evans (13,100 ft). Mid-July.

Fourteen trips for collections and observations were made to the Summit Lake area and 13 to the saddle area during the seasons 1958–1962, inclusive. On one occasion the ground at the higher station was covered with hail, and on another, with sleet, and no specimens could be found at either time. On all other trips collections were made at both areas.

FIG. 2.—The Summit Lake area on Mount Evans (12,800 ft), June 27, 1962. The collecting station is in the immediate foreground. Note that the lake is still almost covered with ice but snow has disappeared from the collecting area.

We determined and recorded the developmental stage of every specimen; sexes of adults, and in some cases of juveniles, were also recorded. At Summit Lake, on the 14 collecting trips, 1527 specimens of *A. clavatus* were taken and 927 of these were juveniles. At the saddle area, on the 13 collecting trips (11 of them "successful"), the total collection comprised 1311 specimens and 807 of these were juveniles.

The collections were not strictly quantitative but do justify comparisons between stations and dates. Years of collecting, and observations of other collectors, have convinced us that counting sweeps has no real quantitative validity unless the sweeps are all made by the same individual, and even then is of no value in comparing different species. (Dreux (1962) makes the observation on the basis of his experience in the French Alps that such technique gives "very deceptive" results.) Each collection made in the present study involved 30 to 40 minutes of continuous observation and collecting, all specimens that could be collected by net or by hand being taken. On most trips either 3 or 4 experienced collectors took part.

Numbers of specimens taken varied considerably from collection to collection, the smallest including 19 specimens of *A. clavatus,* the largest, 284. These variations were largely a reflection of weather conditions at the time of collecting, grasshoppers being much more active during sunshine than under a cloudy sky. (Differences in air temperature between sun and shade are striking at the altitudes here involved.) Weather was an even more important factor in determining size of collections than age distribution in the population, though one usually does make larger collections when a larger proportion of the population is in early stages—the total population being larger, of course, at such times.

Not all specimens were killed and preserved. A good many were brought back to the laboratory alive to be used for securing eggs or for running tests of food selection. Such specimens were included in all counts.

HATCHING AND POST-EMBRYONIC DEVELOPMENT

The eggs of *A. clavatus* begin to hatch at elevations above 12,000 ft on Mount Evans during the last half of June. At that time snow is still abundant in all accumulation areas, and some ice is still present on Summit Lake (Fig. 2). The earliest date on which we have actually made a collection was June 27, 1962, at Summit Lake, at which time all juvenile stages were present but instar I was almost as abundant as all other stages combined. On that same date, a sleet storm occurred at the saddle area and, although collecting was attempted, no specimens could be found. Good collections were made at both stations on July 2, 1960, at which time all stages were present at Summit Lake and the first 3 juvenile instars were present in the saddle area.

At no time were we early enough to find only first-instar juveniles, but on 2 occasions at 13,100 ft (July 2, 1960, and July 11, 1962), instar I was abundant and constituted more than 80% of each collection. On the former date, 225 instar I specimens were collected in a total of 284; on the latter date, 84 in a total of 93. We doubt if we would find an extended period in which only instar I is present, corresponding with that reported by Stevanović (1961) for *Aeropus sibiricus* in the mountains of Yugoslavia.

On the basis of our collections we believe that most hatching occurs at about the end of June at 13,100 ft and 10–14 days earlier at 12,800 ft, but that a few individuals hatch before the bulk of the new population. A few specimens are already in the third instar when most eggs are hatching. Hatching occurs over a considerable period of time. We have collected instar I as late as the first week in August, but only a few eggs hatch after the middle of July, and these late individuals certainly never reach maturity. There is evidently some variation in hatching time from year to year, and from one location to another, in response to weather conditions, and we have evidence that the season at 13,100 ft is definitely later than that at 12,800 ft—later by a larger factor than would be expected if the small difference in altitude were the only thing involved. (The higher station is more exposed to wind, and the lower station has a somewhat more southern exposure, both features exaggerating the difference dependent upon altitude alone.)

We were unable to hatch *A. clavatus* eggs from the high-altitude populations but did hatch and rear specimens from a low-altitude population. We also reared juveniles collected at high altitudes to the adult stage. In both cases we found only 4 juvenile instars. And, as a matter of fact, distribution of size groups in the population clearly demonstrates the existence of only 4 juvenile instars.

Our best clues to the time intervals occupied by these 4 stages in the field, and to the entire period between hatching and mature adults, are in the series of collections made in 1959. These collections did not begin early enough that year to give us hatching time for the bulk of the population, the first collection being July 6, but by comparison with collections in other years, and by considering age distribution in the

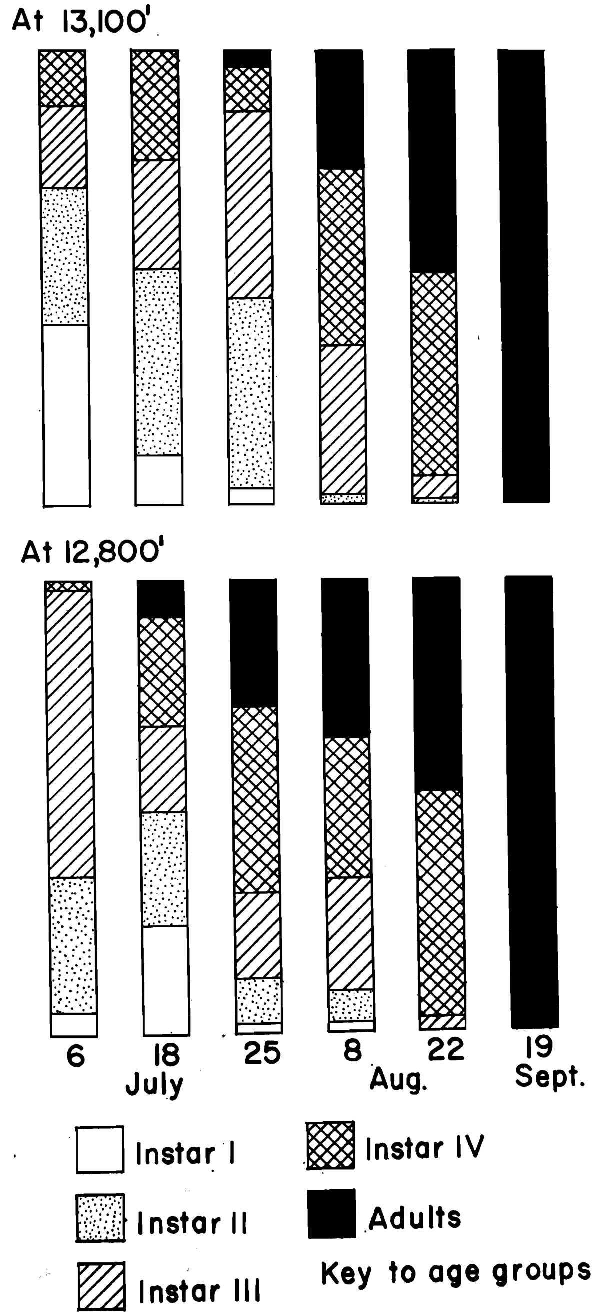

FIG. 3.—Age distribution in 1959 collections of *Aeropedellus clavatus* on Mount Evans. Each column represents a single collection, those in the upper tier from the saddle area, those in the lower tier from the Summit Lake area. The proportionate heights occupied by different symbols in a column correspond, in percent of total specimens, to the relative numbers in different age groups in that particular collection.

collections we made (Fig. 3), we can make a fair estimate of the times involved.

The total period from hatching to adult appears to be approximately 6 weeks on the tundra. The average period in instar I is probably no more than a week, and the last 2 juvenile instars occupy longer time intervals than do the first 2. These intervals are suggested by Fig. 3, which shows the seasonal shift in proportions of age groups. On July 6, instar I was the most numerous age group at 13,100 ft, but at 12,800 ft instar III was the most numerous. By July 25, instars II and III were the most numerous at

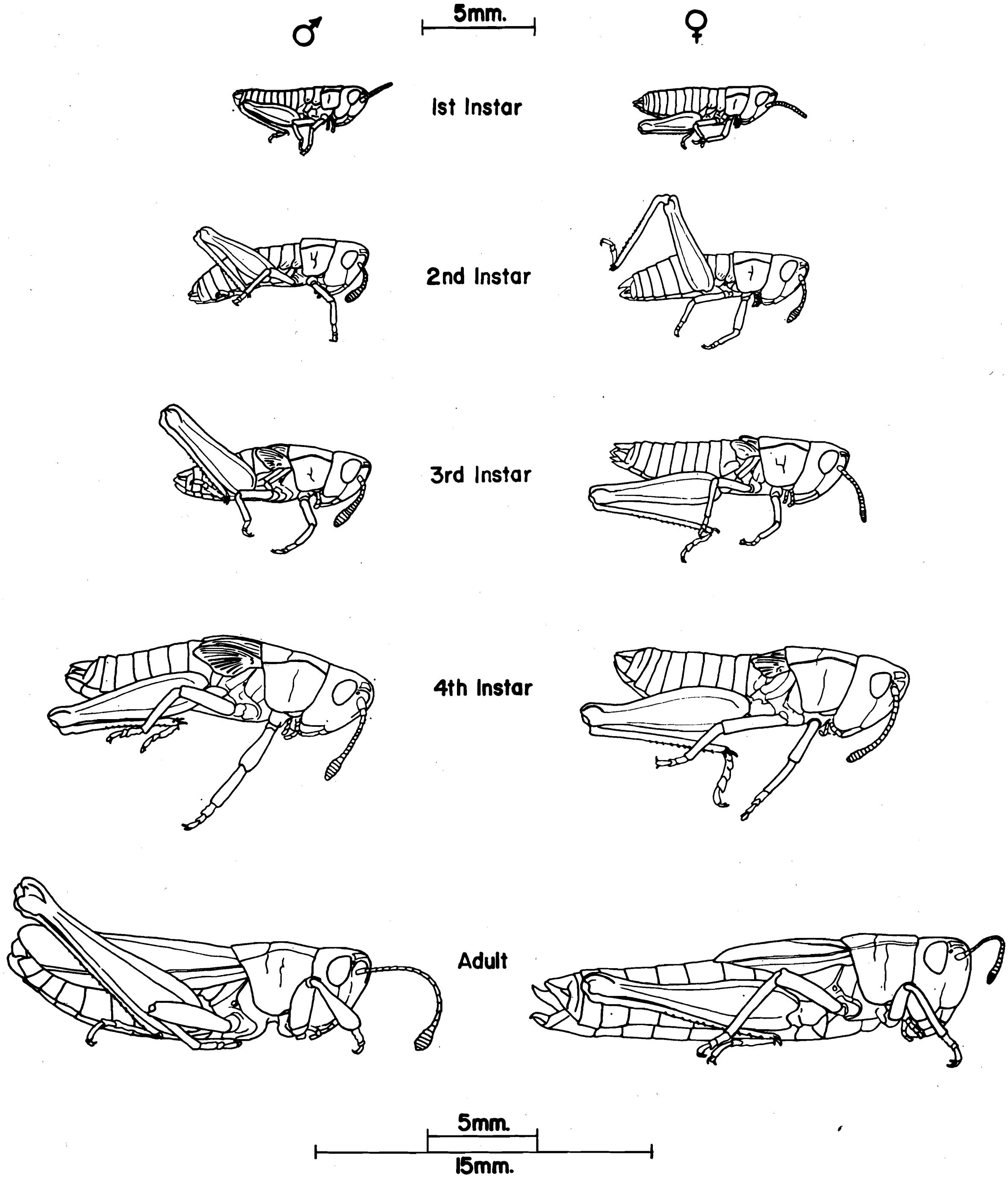

FIG. 4.—Postembryonic stages in the development of *Aeropedellus clavatus* in alpine tundra. Males are represented in the left column, females at the right. All specimens drawn were collected at the Summit Lake area, at an altitude of 12,800 ft on Mount Evans.

13,100 ft, and in approximately equal numbers; on the same date at 12,800 ft instar IV was the most numerous but more than ¼ of the population was already adult. By August 22, practically the whole population was adult or in instar IV at both stations; and on September 19 all individuals collected in both populations were adult. Collections in other years indicate that juveniles, even in the last instar, are rare at either station after the first of September.

The last 2 juvenile instars have erect wing pads, in this respect corresponding with the fourth and fifth instars of most Acrididae. The first 2 instars lack erect wing pads and therefore correspond with the first 3 instars of most Acrididae. One might expect to find a significantly larger gap in size between 2 of the early stages than between later stages, since it appears as if 1 of the 3 early stages has been "dropped out," but the developmental stages are "evenly spaced." The 4 stages are so well adapted to the shorter cycle that size increase is essentially regular in all molts. Fig. 4, which illustrates all stages in both sexes, suggests this fact.

Morphological changes of particular interest are the development of the knobs on the antennae (in both sexes) and the inflation of the anterior tibiae (of the male). These are both features of the Mount Evans population, though enlargement of the anterior tibiae is not typical of all alpine populations in Colorado (Alexander 1961). Since the clubbing of the antennae is a species character, while inflation of the anterior tibiae of the male is only a population trait, it is interesting to note that clavate antennae are evident as early as instar II, involving in this and all subsequent stages the 7 terminal segments, while the inflated tibiae do not appear until the last molt. Both traits characterize the Old World relative, *Aeropus sibiricus,* throughout its range, but according to the photographs reproduced by Stevanović (1961) the onset of development of these characters is at the same stages as in *Aeropedellus clavatus,* the inflated tibiae of the male, a general species trait, still not appearing until the last molt.

Males mature earlier than females. The male/female ratio was above 1.0, except in 1 small collection, in all collections of adults before the first week in August at 12,800 ft and before the second week of August at 13,100 ft. There was then a shift in favor of females, and by September, at both stations, females outnumbered males by about 50% or more.

Ovipositing occurs mainly during the last part of August and into September—until winter weather destroys the adults, usually about the end of September. Our latest collection, made at Summit Lake on September 25, 1958, comprised 24 adults; of these, 6 were males and 18 were females.

EGG PODS AND EGGS

The egg pods are dark brown capsules 11.0 to 12.5 mm long by 5.5 to 6.0 mm in diameter. They are deposited in the basal portions and among the roots of sedges and grasses (Fig. 5). The hummocks selected are used repeatedly, viable egg pods often being fused to older, empty pods, or even deposited within them.

FIG. 5.—Clump of *Carex ruprestris* collected at the saddle area on Mount Evans, July 2, 1960. This contained about 36 egg pods of *Aeropedellus clavatus,* one-third of these containing viable eggs. A few pods can be seen here, the most conspicuous one being to the left and below the center of the photograph.

A copious, spongy secretion surrounds the eggs and binds them into a firm, compact mass (Fig. 6A). The pod has no neck; the foamy secretion forms an apical pad that covers the eggs to a thickness of about 1.6 mm. The frothy, spongy secretion is small celled throughout, being slightly smaller celled in the apical pad. In the wall of the pad are incorporated plant material and sand grains. The frothy secretion is dark coffee-brown; the eggs are light tan. The egg pods usually contain 5 to 7 eggs arranged in 2 rows, and the eggs are inclined at an angle of about 30° from the vertical.

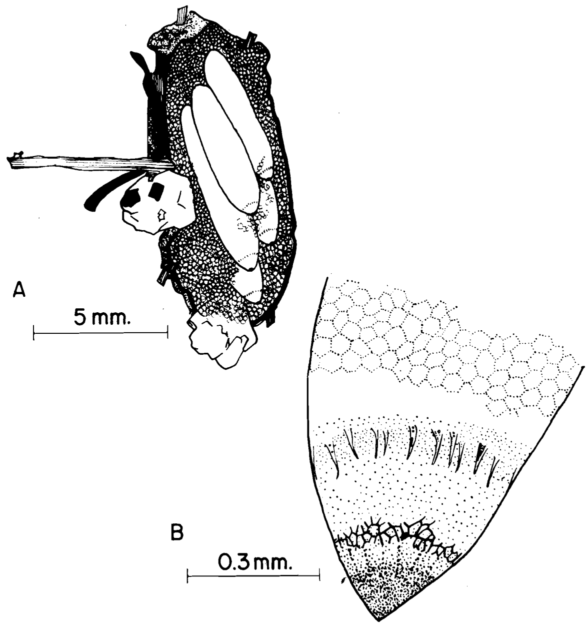

FIG. 6.—A. Dissected egg pod, exposing the spongy secretion and 5 eggs in position; plant material and sand grains are incorporated in the wall. B. Sculpturing on micropylar end of an egg.

a time, and their differential feeding was observed and recorded. Caged specimens were kept 5 to 23 days for observation, and as many as 16 different species of plants were offered individuals from a single population. Plant specimens were collected in the field when the grasshoppers were collected, placed in plastic bags, and taken back to Boulder.

All populations fed predominantly on grasses and sedges, but the alpine populations showed a greater disposition to feed on forbs than did those from lower elevations. They regularly ate the arachnoid pubescence and succulent leaves of *Cirsium hookerianum* Nutt., an alpine thistle, but did not eat any other forbs supplied from their normal habitat.

All parts of the following alpine grasses and sedges were eaten by caged specimens of *A. clavatus* from the tundra collecting stations on Mount Evans (nomenclature from Weber 1953, and Harrington 1954): *Festuca ovina* L., *Poa rupicola* Nash, *Agropyron subsecundum andinum* (Scribn. and Smith), *Trisetum spicatum* (L.) Richt., *Deschampsia caespitosa* (L.) Beauv., *Kobresia bellardi* (All.) Degland, *Carex arapahoensis* Clokey, *Carex chalciolepis* Holm., and *Carex ruprestris* All. (= *Carex drummondiana* Dewey). The following grasses from lower elevations also were greedily eaten: *Poa pratensis* L., *Eragrostis cilianensis* (All.) Link., and *Agrostis alba* L. To a lesser extent there was feeding upon the leaves of the following grass and sedge from low elevations: *Bouteloua gracilis* (H.B.K.) Lag., and *Carex nebraskensis* Dewey.

Three alpine forbs offered these specimens were refused, *Sedum rhodanthum* A. Gray, *Geum rossi* (R. Br.) Ser., and *Phacelia sericea* (Graham) A. Gray. Two forbs not from the alpine habitat, in addition to the alpine *Cirsium* previously mentioned, were eaten, *Sonchus oleraceus* L., and *Taraxacum officinale* Wiggars.

Crop Examinations.—Specimens for this study were collected July 18, 1959, at the 2 high altitude stations on Mount Evans. The adults were from the saddle area, and the juveniles were from the Summit Lake population. The crops of the adults were preserved immediately after collection by removing the heads from the rest of the body, the head, with attached crop, being placed in 10% formalin. The immature stages were killed in a cyanide jar and, after the collection had been enumerated, were placed entire in 10% formalin.

For examination, each crop was detached, placed on a microscope slide, and torn apart with dissecting needles under a binocular dissecting microscope. The contents of the crop were spread, a drop of Williams' modified gum syrup adhesive was added (Williams 1959), and a cover glass was applied. The preparation was examined unstained, using a microscope with light polarizing filters. The plant fragments were examined to determine whether they were from forbs or from grasses or sedges—on the basis of shape of guard cells, shape and arrangement of epidermal cells, and arrangement of vascular elements. Fifty-four specimens of all stages of development were examined. The results are summarized in Table 1.

This sample indicates that immature stages show more variability in feeding than do adults, but that all stages show a preference for grasses and sedges. In addition, these observations prove that all stages in the alpine *A. clavatus* will feed upon some forbs in their natural habitat. Although the fragments were not determined to species, it was apparent that several species of grasses and sedges were eaten. From characteristics of cells and trichomes, it was apparent also that at least 2 species of forbs were eaten. Most of the forbs fragments were bits of petals. In addition to the plant fragments in most crops, 1 instar II specimen had its crop filled entirely with insect remains—the membranous wings of a dipterous or hymenopterous insect.

Mandible Pattern.—The mandibles of 24 adult specimens and 10 instar IV juveniles of *A. clavatus* from the Summit Lake and saddle area collecting stations were examined critically. Considerable variation in the mandible pattern was seen, only part of which was due to wear with age. The pattern varies from the typical graminivorous type, with low, unbroken molar ridges and even, truncate incisor dents, to the mixed feeding pattern in which the molar areas are broken into 2 rows of grooved dents, and in which the incisor dents are acutely pointed. Mandible pattern thus correlated with other observations, suggesting that *A. clavatus* is adapted primarily for grass feeding but that it shows some tendency toward being a mixed feeder, eating a few forbs as well as grasses and sedges.

Table 1.—Food of *Aeropedellus clavatus* as determined from examination of crop contents.

	Juvenile instars				
	I	II	III	IV	Adults
Number of crops examined	10	10	10	10	14
With grasses and sedges only	8	4	6	7	13
With forbs only	0	3	1	1	0
With grasses and forbs; grasses predominant	0	0	2	0	1
With grasses and forbs; forbs predominant	1	2	1	1	0
With grasses and forbs about equal	1	0	0	1	0
With chitin only	0	1	0	0	0

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