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Do alpine Acridids have a shortened post-embryonic development?

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Zusammenfassung

Die Studie befaßt sich mit vier Acridienarten (*Bohemanella frigida*, *Podisma pedestris*, *Arcyptera fusca* und *Gomphocerus sibiricus*), die in ihrem natürlichen Gebirgsumfeld studiert wurden (2200 - 2750 m ü NN.). Die verfolgten Ziele bestanden in der Ermittlung des Entwicklungschemas (Anzahl Larvenstadien), so wie der Gesamtentwicklungsdauer dieser Arten und in der Untersuchung einer möglichen Verkürzung ihrer postembryonalen Entwicklung im Vergleich zu den Arten des Unterlandes. Im untersuchten Gebiet wurden vier Larvenstadien für *G. sibiricus* und fünf für *A. fusca*, *B. frigida* und *P. pedestris* festgestellt (für beide Geschlechter). Die mittlere Dauer eines Larvenstadiums beträgt ungefähr 10 Tage für jene Arten, die in großen Höhenlagen vorkommen (*B. frigida*, *P. pedestris*, *G. sibiricus*). Ihre gesamte Entwicklungsdauer beträgt somit 40 - 50 Tage, je nach Anzahl der Larvenstadien. Die Zahl der Stadien, die Gesamtdauer der postembryonalen Entwicklung und die Dauer eines Larvenstadiums sind im großen und ganzen vergleichbar mit den nahe verwandten Arten des Unterlandes. Eine verkürzte post-embryonale Entwicklung der vier untersuchten Arten wurde nicht eindeutig festgestellt. Ob die Larven vorzeitig ausschlüpfen, steht weiterhin zur Diskussion.

Summary

We studied the post-embryonic development of four acridids (*Bohemanella frigida*, *Podisma pedestris*, *Arcyptera fusca* and *Gomphocerus sibiricus*) in field conditions in high mountain (2200 - 2750 m). The aims were to establish the scheme of development (number of instars) and the duration of the larval development of these species, and to see if their post-embryonic development period is shortened in comparison with lowland species. The number of instars in the study area is 4 for *G. sibiricus* and 5 for *A. fusca*, *B. frigida* and *P. pedestris* (for both sexes). The mean duration of an instar is about 10 days for the three high-altitude species (*B. frigida*, *P. pedestris* and *G. sibiricus*). Thus their total development period is about 40 and 50 days, respectively, depending on the number of instars. The number of instars, the length of the total post-embryonic development period and the instar period are more or less comparable with those of closely related species inhabiting lowlands. Thus, we did not find any serious evidence of a shortened post-embryonic development in these four species. The precocity of hatchings is discussed.

Introduction

In high altitude environments, the short vegetation period restricts the growth period of insects and cold temperatures lower their growth rate (see for instance MANI 1962). In several species groups, high altitude species have a longer (biennial or triennial) cycle of development than lowland species.

Pluriennial cycles are known from a few North American high mountain Acridids. Unlike many species of other insect orders which have a short embryonic development period and a pluriennial larval period, these Acridids have a pluriennial egg period. Their post-embryonic development period is limited to one single season (UVAROV, 1977). In the case of European (boreo-)subalpine and (arcto-)alpine acridids, too, this period is restricted to one season; but there is no evidence of a pluriennial embryonic development yet (UVAROV 1977; NADIG 1986, INGRISCH 1995).

The larval development of alpine Acridids has to be achieved quite early in the season to allow enough time for adults to mature and reproduce. As the favourable time for hatching appears to be quite late, the post-embryonic development period must be very short.

It has been deduced from field observations that high altitude Acridids living in the Alps are characterized by a very fast larval development (DREUX, 1962; NADIG, 1986), but clear evidence and explanations of this phenomenon are still lacking. However, the recent work of INGRISCH (1995), who led his study in the same year as we in another valley of the Swiss Alps, brings some original phenological data for high altitude species, which are comparable with ours.

How do alpine acridids resolve this challenge? We try to examine the following hypotheses:

Hypothesis 1: the number of instars is reduced: The length of the development decreases with the number of instars.

Hypothesis 2: the mean duration of an instar (= the instar period) is shortened: The length of the development decreases with the duration of the instar period.

Methods

Field observations were made from late May to late September 1993. All our results are based on field data.

Study area

The Réchy Valley is a small, north-oriented valley of the swiss Alps, located on the left side of the Rhône Valley in Central Valais (Fig. 1). Observations were made in its higher part, called the "Haut-Val de Réchy" (2180 - 3148 m) (Fig. 2).

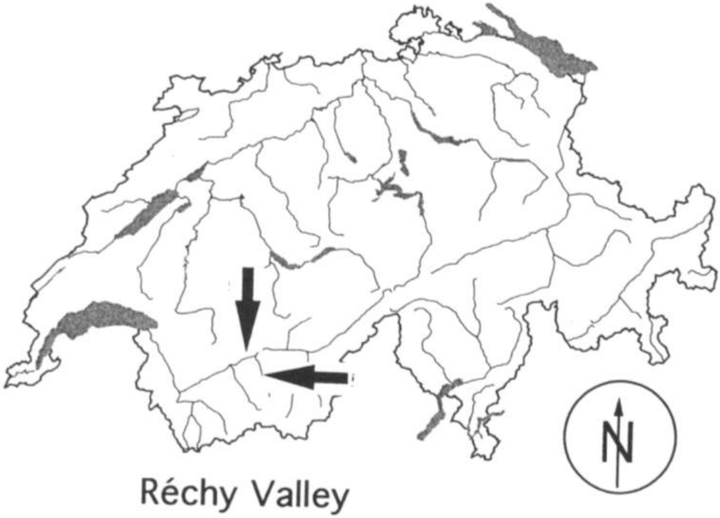

Fig. 1.: Location of the study area.

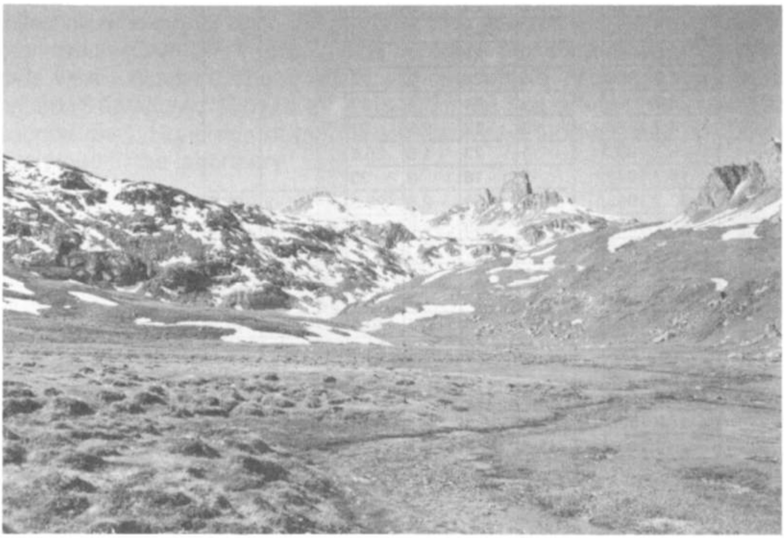

Fig. 2.: "Haut-Val de Réchy".

The "Haut-Val de Réchy" is relatively cold and dry, with a late snow melt. Habitually, June, July and August are the only months with positive mean air temperature. The air temperature usually falls below 0°C in every months of the year. The mean annual total precipitation is 1200 mm / year; snowfall accounts for half. The weather during the field season (1993) was quite cold (Fig. 3), with snowfall in June and July. Atmospheric temperature was measured eight times a day at 2800 m with a probe situated 1 m above the soil; mean values are mean arithmetic values of the eight numbers. Some gaps are visible on the figure and are caused by technical deficiencies. Climate near the ground was also measured, 6-7 cm above the ground, in the shade of wooden board (Tab. 1).
Five study sites were defined in supra-subalpine grasslands (Nardetum) and alpine meadows (Caricetum curvulae) from 2200 to 2750 m (Fig. 4). Description of the sites are given in Tab. 2.

Tab. 1: Air temperature measured 6-7 cm above the ground.

date	site 1 (2200m)		site 2 (2335m)		site 5 (2570m)	
	min	**max**	min	**max**	min	**max**
31.5.1993						
4.6.1993	-2	**20.5**				
7.6.1993	2	**21.5**	2	**22**		
10.6.1993	3.5	**23**	3	**24**		
13.6.1993	-2	**20.5**	-2	**20.5**		
18.6.1993	0	**21**	-1	**21.5**		
22.6.1993	3.5	**24**	2	**25**		
28.6.1993	-1	**24**	-1.5	**21**		
4.7.1993	3	**23**	-2.5	**27**		
8.7.1993	-1	**23**	-1.5	**25.5**		
15.7.1993	-2	**18**	-3	**23**		
23.7.1993	-2	**24**	-2.5	**23.5**	-2	**22.5**
28.7.1993	-1	**24.5**	-0.5	**25**	-0.5	**18**
3.8.1993					-1	**20**
11.8.1993	-0.5	**26**	-1	**28**	1	**18**
18.8.1993					2	**19.5**
29.8.1993	-2.5	**27.5**	-4	**30.5**	-3	**21.5**
2.9.1993	-2	**19**	-3	**24.5**		
3.9.1993					-3	**13.5**
12.9.1993			-4	**23**	-4	**14**
17.9.1993	-4	**19.5**				
9.10.1993	-5.5	**21.5**	-7	**26**		

Species
Four of the seven species of Acrididae present in the Haut-Val de Réchy were studied:

three high-altitude species:
1) *Bohemanella frigida* (BOHEMAN, 1846): arcto-alpine
2) *Podisma pedestris* (LINNAEUS, 1758): boreo-subalpine
3) *Gomphocerus sibiricus* (LINNAEUS, 1767): boreo-subalpine

and one middle-altitude-species
4) *Arcyptera fusca* (PALLAS, 1773): eurosiberian

Capture method
Grasshoppers were collected by hand along the length of a path from the lower to the higher part of the site. Individuals encountered were caught; the ones which jumped sideways were followed and rapidly captured. This simple and efficient method was inspired by VOISIN's ILA (Indice linéaire d'abondance) method (VOISIN, 1985). Most of the sampled individuals were anaesthetized by CO_2 and released. Observations were made as often as possible, generally at 4 - 8 days intervals (Tab. 3).

Scheme of development (number of instars)
Each instar of the four species was separated on the basis of morphological (especially the differenciation of the terminal abdominal segments and of the external genitalia) and biometrical (postfemur and pronotum sizes) criteria. The detailed morphology of each instar of the four species will be described in another publication (CARRON, in prep.). The numbers of instars of *A. fusca* and of *B. frigida* were unknown. Those of *G. sibiricus* and *P. pedestris* were already described (STEVANOVIC 1961, IL'ENKO 1930 for the first species; PICHLER 1957 for the second one). Hundreds of individuals were caught in the whole study area and examined in the laboratory.

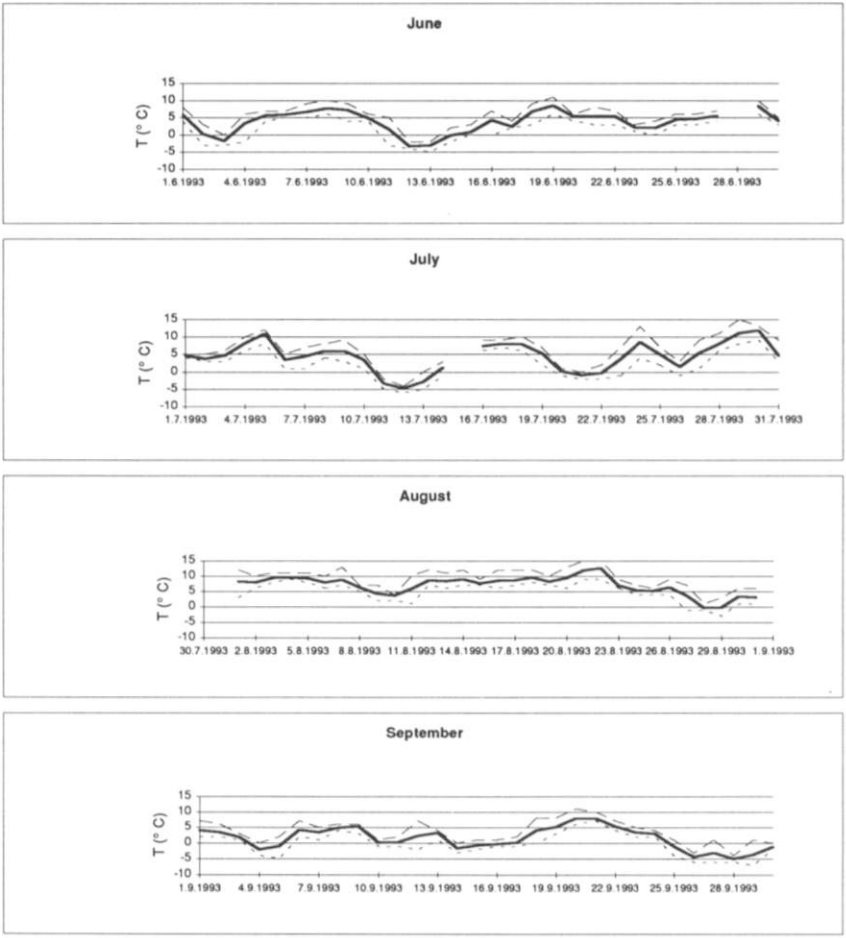

Fig. 3.: Minimum, mean (thick line) and maximum air temperature during summer 1993. See text for details on measuring method.

Tab. 2.: Description of the study sites.

	site 1	**site 2**	**site 3**	**site 4**
Altitude (m)	2200	2335	2380	2520
Exposition	SE	SE-E	SE-E	E
slope (°)	30	27	20	12
snow melting	very precocious (before mid-May)	precocious (mid-May to early June)	precocious (late May to early June)	precocious to late (early June to early July)
Vegetation	subalpine grassland with Ericaceae and small bushes	subalpine grassland with a few small bushes	subalpine grassland	alpine meadow
Phytosociology	*Potentillo-Nardetum, Junipero-Arctostaphyletum*	*Potentillo-Nardetum*	*Potentillo-Nardetum* with Plantago alpina	*Nardetum and Caricetum curvulae* (mosaic)
Total veg. cover (%)	90 à 100	90 à 100	90 à 100	80 à 90
Small bushes cover (%)	45	5	0	0
species	*Vaccinium myrtillus* *Vacc. gaultherioides* *Rhododendron ferr.* *Juniperus nana*	*Juniperus nana*	-	-
Mean height of vegetation (cm)	5 (3-20)	5 (2-8)	3 (1-5)	4 (3-5)
Species ...**studied**	*P. pedestris* *B. frigida* *A. sibiricus* ***A. fusca*** *S. lineatus*	*P. pedestris* ***A. sibiricus*** *S. lineatus*	***P. pedestris*** ***B. frigida*** ***A. sibiricus***	*P. pedestris* ***B. frigida*** ***A. sibiricus*** *S. lineatus*

Tab. 3.: Dates of sampling.

date	site 1	site 2	site 3	site 4	site 5
	(12 samples)	(11 samples)	(13 samples)	(13 samples)	(11 samples)
31.5.1993	S 1	1/2 snow			
4.6.1993	S 2	S 1	snow		
7.6.1993			S 1		
10.6.1993	S 3	S 2	S 2		
18.6.1993	S 4	S 3	S 3	snow	
22.6.1993			S 4	S 1	
28.6.1993	S 5	S 4	S 5	S 2	snow
4.7.1993	S 6	S 5	S 6	S 3	S 1
8.7.1993	S 7	S 6	S 7	S 4	S 2
15.7.1993	S 8	S 7	S 8	S 5	S 3
23.7.1993	S 9	S 8	S 9	S 6	S 4
28.7.1993	S 10	S 9	S 10	S 7	S 5
3.8.1993				S 8	S 6
11.8.1993	S 11	S 10	S 11	S 9	S 7
18.8.1993			S 12	S 10	S 8
29.8.1993	S 12	S 11	S 13	S 11	S 9
3.9.1993				S 12	S 10
12.9.1993				S 13	S 11

Tab. 4.: Duration (in days) of each instar of the four studied species, in each site. For *B. frigida*, site 3, we observed an important movement of adults out of the site: the value of the duration of the 5th instar was strongly lenghtened (visible on Fig. 10), and we had to give a "corrected more probable value" of *10 days*.

species	site	2nd instar	3rd instar	4th instar	5th instar	1st instar (= mean instar period)	total
A. fusca	1	14.4	15.9	12.9	8.4	12.9	**64**
P pedestris	3	6.7	12.5	8.4	14.1	10.4	**52**
B. frigida *(corrected values)*	3	7.3	7.2	12.0	*10.0*	*9.2*	***46***
B. frigida	4	13.3	10.9	13.1	5.1	10.6	**53**
B. frigida	5	10.2	4.9	9.1	12.1	9.1	**45**
G. sibiricus	3	12.4	11.9	7.2		10.5	**42**
G. sibiricus	4	13.1	6.9	11.6		10.5	**42**
G. sibiricus	5	6.1	8.3	12.4		9.0	**36**

Duration of the post-embyonic development

We have drawn percentage development curves for each instar (except the first): y (x inst.) = number of ind. of the xth inst. / numb. of the xth inst.+ numb. of ind. of previous instars.

Values extend from 0 to 1. Theoretical logistic growth curves were fitted to the field data. The x-axis is the number of days (0 = beginning of the observations). The duration of the xth instar was measured as the distance between its curve and the following curve at the 0.5 level. For the 1st instar, percentage of occurence was reported, and its duration was calculated as the mean of the values of the other instars. This method was inspired by BEGON (1983) and GAGE & MUKERJI (1976). Emigration of the imagos out of the study site was observed in one case and the value for the last instar had to be corrected. Reliable values were obtained from four of the five sites and from three populations of *B. frigida*, three of *G. sibiricus*, one of *A. fusca* and one of *P. pedestris*.

Results

Scheme of development (number of instars)

For both sexes, 4 instars were observed for *G. sibiricus* (N=296) and 5 for *A. fusca* (N=156), *B. frigida* (N=668) and *P. pedestris* (N=328). The "vermiform larva" (UVAROV, 1966) instar is not counted. No additional intermediate instar was observed.

Duration of the post-embyonic development

Fig. 5-8 show the evolution of the instar composition of the populations. Phenological differences in the larval period between the four sites reflect altitudinal and harshness gradient. Comparisons between species in a site show differences in the hatching time: larvae of *B. frigida* are the first to hatch, and those of *G. sibiricus* are the last (about 10 to 15 days after *B. frigida*). Larvae of *P. pedestris* hatch only a few days after those of *B. frigida*. This succession *B. frigida-P. pedestris-G. sibiricus* in the hatching time could be seen in the four sites, even if it is not completely reported on the figures.

Development percentage curves are visible on Fig. 9-12. The durations of the instars periods are reported on Tab. 4. The mean duration of an instar is about 10 days for the three high-altitude species (*B. frigida, P. pedestris* and *G. sibiricus*). Thus their total development period is about 40 (*G. sibiricus*) and 50 days (*B. frigida*, *P pedestris*), respectively, depending on the number of instars. The mean instar period of *A. fusca* is a little longer (12.9 days) and its total development period reaches 64 days.

Note that adult emergence of the different species on the same site occurs quite simultaneously, as the late *G. sibiricus* has a shorter post-embryonic development.

We noticed along the edges of melting snow patches that the hatching of the four species begins early in the season, 10 to 14 days after snow melting for *B. frigida*. In well-exposed slopes, like the site 1, larvae of *B. frigida*, *P. pedestris* and *A. fusca* could be found already in late May (first access to the study site and first observations: 31.5.95).

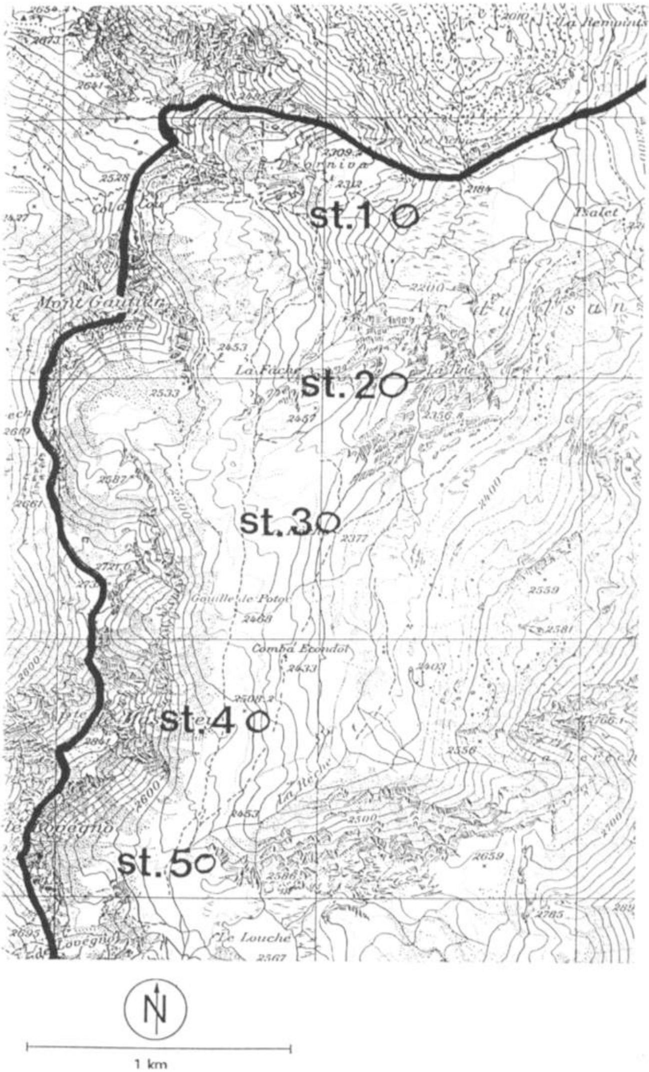

Fig. 4.: Study sites (= "stations" = st.) in the "Haut-Val de Réchy".

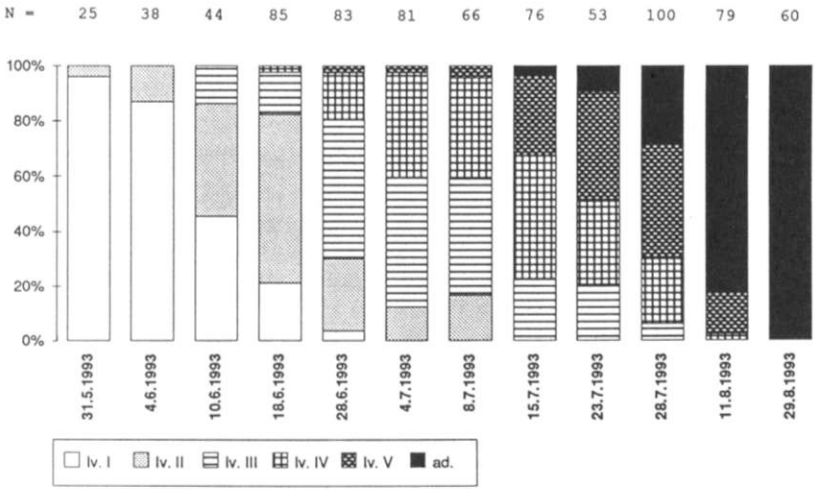

Fig. 5.: Evolution of the demographic structure in the population of *A. fusca*, in site "st1".

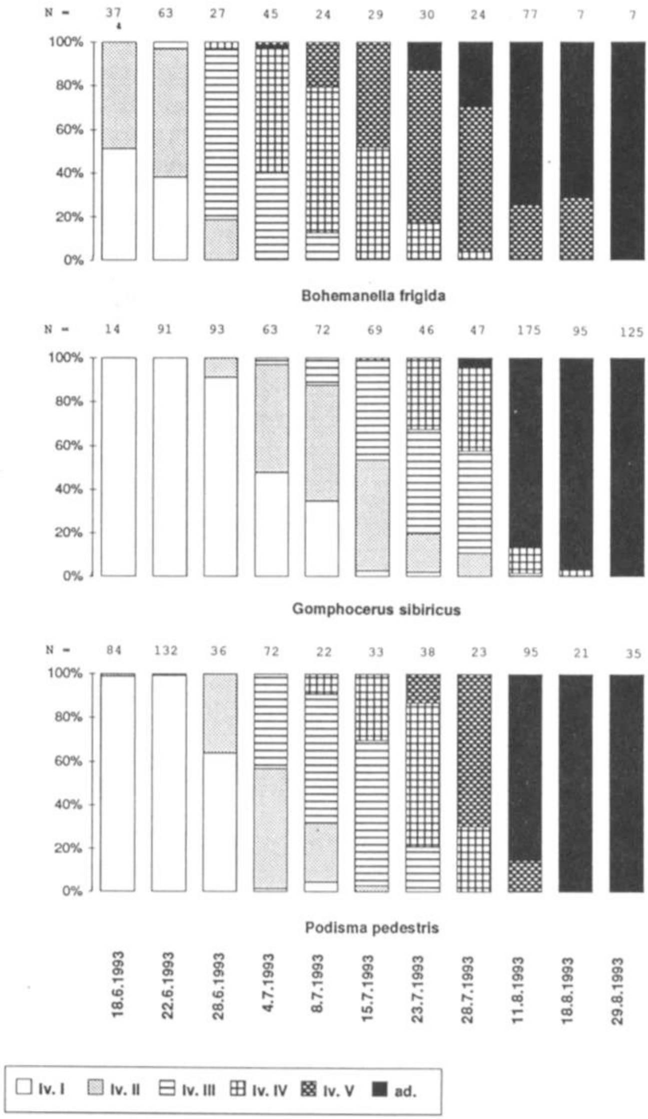

Fig. 6.: Evolution of the demographic structure in the population of *B. frigida*, *G. sibiricus* and *P. pedestris* in site "st3".

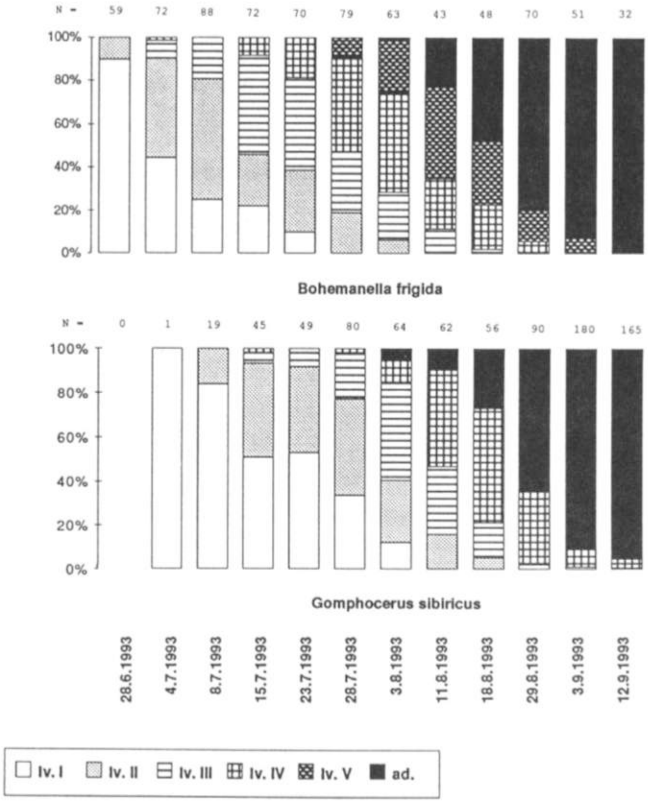

Fig. 7.: Evolution of the demographic structure in the population of *B. frigida* and *G. sibiricus* in site "st4".

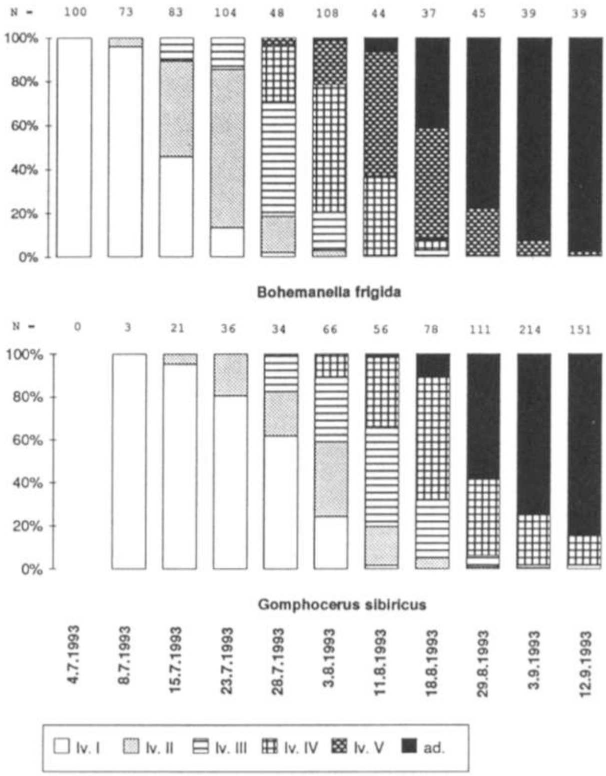

Fig. 8.: Evolution of the demographic structure in the population of *B. frigida* and *G. sibiricus* in site "st5".

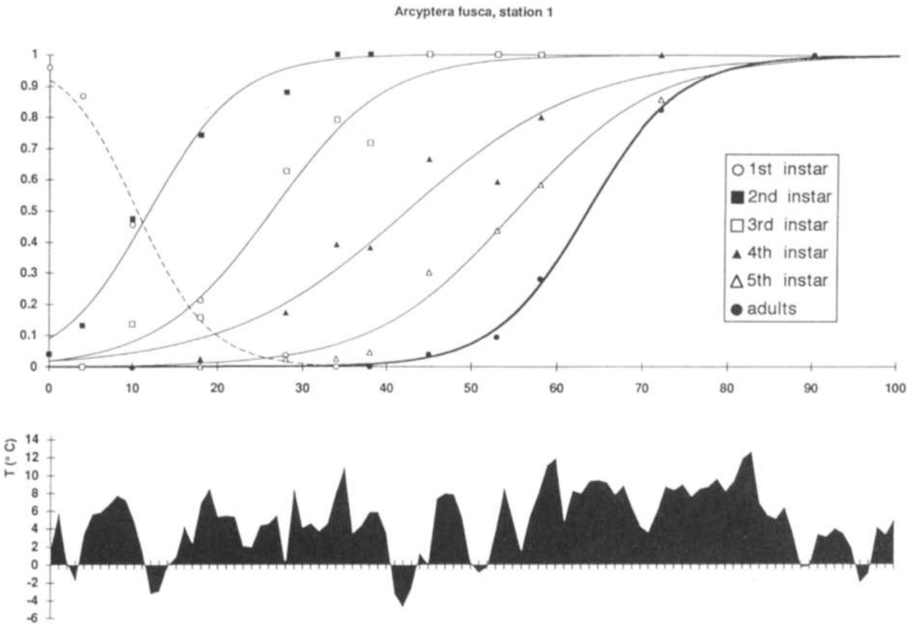

Fig.9.: Percentage development of each instar (details in text). "station 1" = site 1. X-axis: number of days. Lowest figure: mean air temperature.

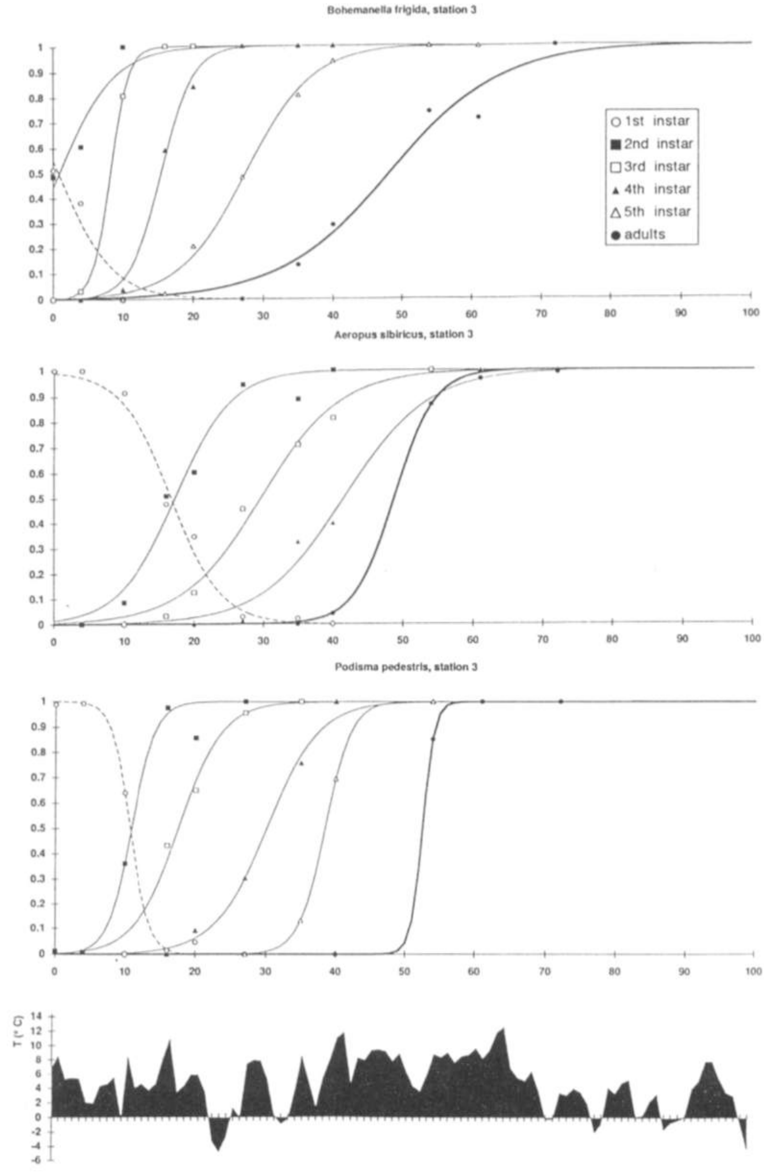

Fig.10.: Percentage development of each instar (details in text). "station 3" = site 3. X-axis: number of days. Lowest figure: mean air temperature. *Aeropus sibiricus* = *Gomphocerus sibiricus*.

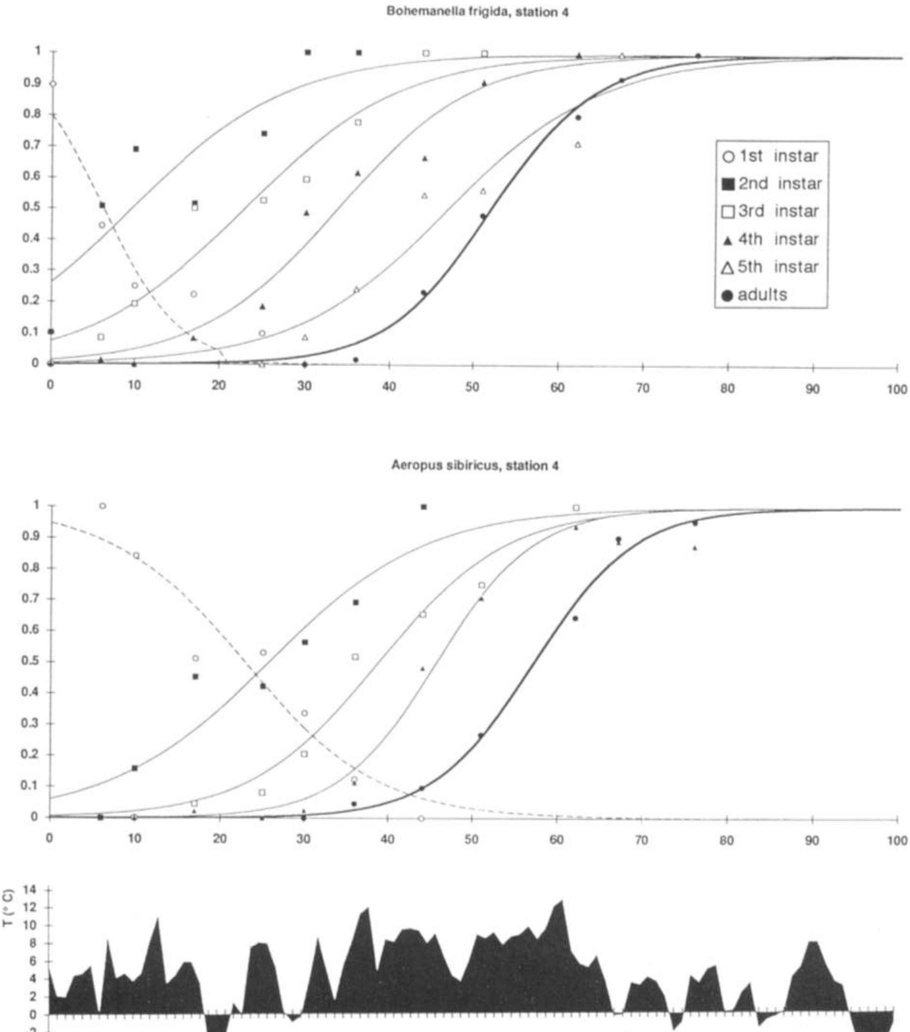

Fig.11.: Percentage development of each instar (details in text). "station 4" = site 4. X-axis: number of days. Lowest figure: mean air temperature.
Aeropus sibiricus = Gomphocerus sibiricus.

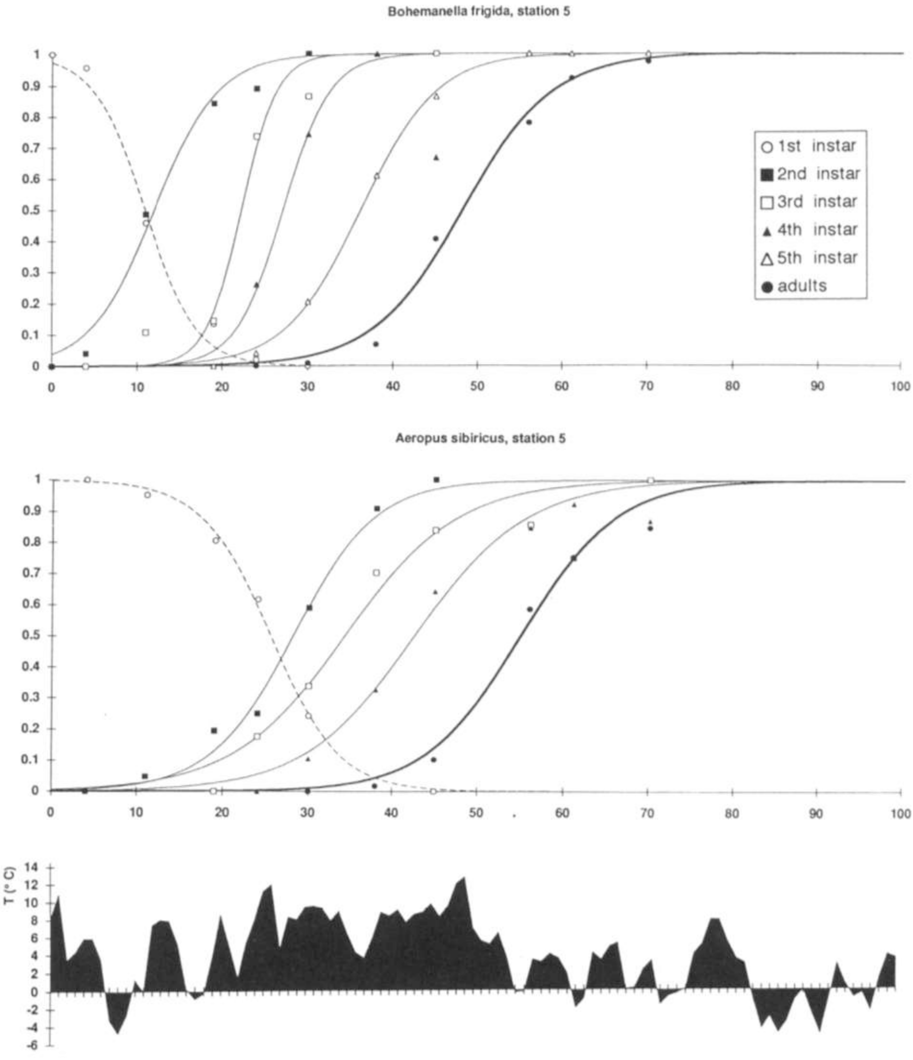

Fig.12.: Percentage development of each instar (details in text). "station 5" = site 5. X-axis: number of days. Lowest figure: mean air temperature. *Aeropus sibiricus* = *Gomphocerus sibiricus*.

Discussion

Results were obtained from one single season (1993) and comparisons with lowland species values are difficult because of the lack of precise field data; nevertheless, we can see that:

- the number of instars is not reduced (Hypothesis 1 rejected)

The number of instars of the three high altitude species is low but not inferior to that of closely related species (5 for *B. frigida* and *P. pedestris*: Catantopinae, 4 for *A. sibiricus*: Gomphocerinae) (Tab. 5).

Tab. 5.: Number of instars: comparison between our results and the literature data.

	min	max
Podisma pedestris (our result)	5	5
Miramella alpina	5	5
Odontopodisma decipiens	5	5
Bohemanella frigida (our result)	5	5
Melanoplus sanguinipes (New York)	5	6
Pezotettix giornai	6	6
Calliptamus italicus (Italy)	5	6
Euthystira brachyptera	4	4
Euchorthippus pulvinatus	5	5
Gomphocerus rufus	4	4
Aeropus sibiricus (W. Siberia)	4	4
A. sibiricus (our result)	4	4
Aeropedellus clavatus (Colorado)	4	4
A. variegatus (swiss Alps)	4	4
Chorthippus scalaris	4	4
C. albomarginatus (Yakutia)	4	4
C. biguttulus (swiss Jura)	4	4
C. mollis (swiss Jura)	5	5
C. brunneus (England)	4	4
C. vagans	4	4
C. parallelus (England)	4	4
Omocestus ventralis	4	4
O. viridulus (England)	4	4
Arcyptera fusca (our result)	5	5
A. microptera (Kazakhstan)	4	5
A. flavicosta	4	4
Stenobothrus nigromaculatus	4	4
S. lineatus (England)	4	4
Myrmeleotettix maculatus (England)	4	4

- the mean duration of an instar does not seem shortened (Hypothesis 2 possibly rejected).

The instar period does not seem lower than that of lowland species (literature data are generally not statistically comparable estimates; see Fig. 13).

Thus, the duration (in days) of the total post-embryonic development period of the three high altitude species seems to be more or less comparable with closely-related lowland species' values (Fig. 14). It appears to be correlated more with the number of instars than with the ecology of the species. There is a need of further field investigations.

So, we may doubt a distinctively accelerated or shortened post-embryonic development in any high altitude species, and INGRISCH's (1995) results are comparable with ours. It is interesting to see that *B. frigida*, the species which reaches the highest altitude (in the Haut-Val de Réchy and more generally in the Alps) does not have the shortest post-embryonic development period. Checking the phenology of other species, like *Epipodisma pedemontana*, for instance, would be of great interest.

Furthermore, we think that a very short post-embryonic development is not the only possible adaptative character of life for acridids in an alpine environment. The precocity of eclosions, particularly visible in our species with 5-instars development schemes (*B. frigida* and *P. pedestris*) appears to be of importance. ANDER (1950) also observed the precocious hatching of *B. frigida*, starting "practically immediately when warm weather sets in".

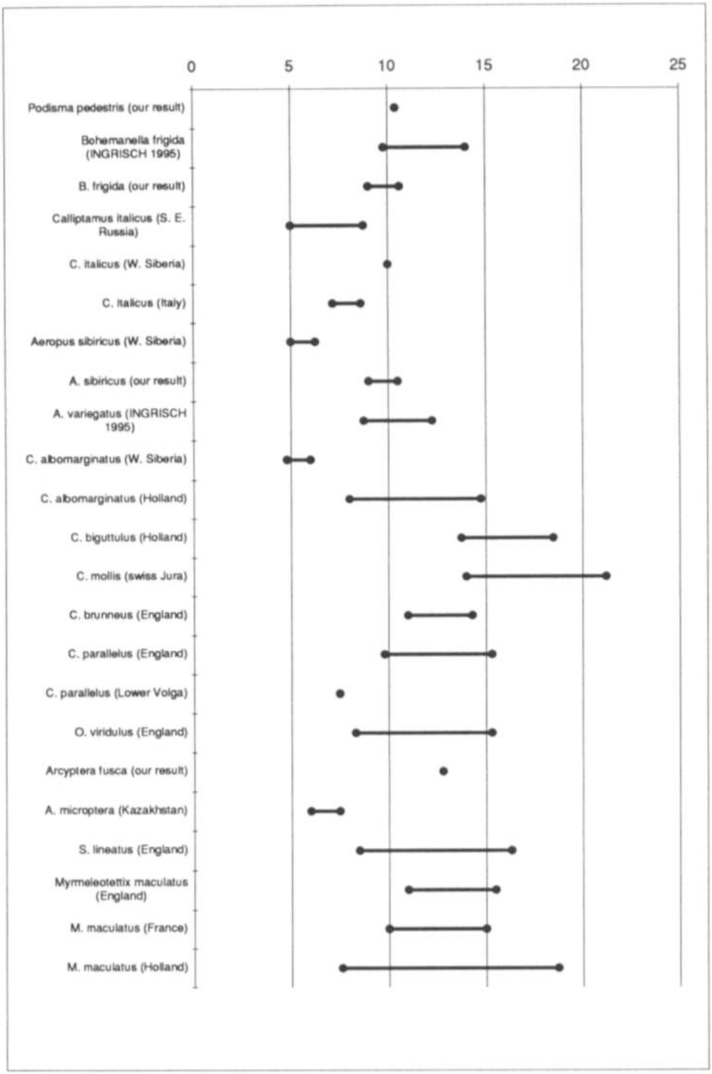

Fig.13.: Mean duration (in days) of an instar: comparison between our results and the literature data.

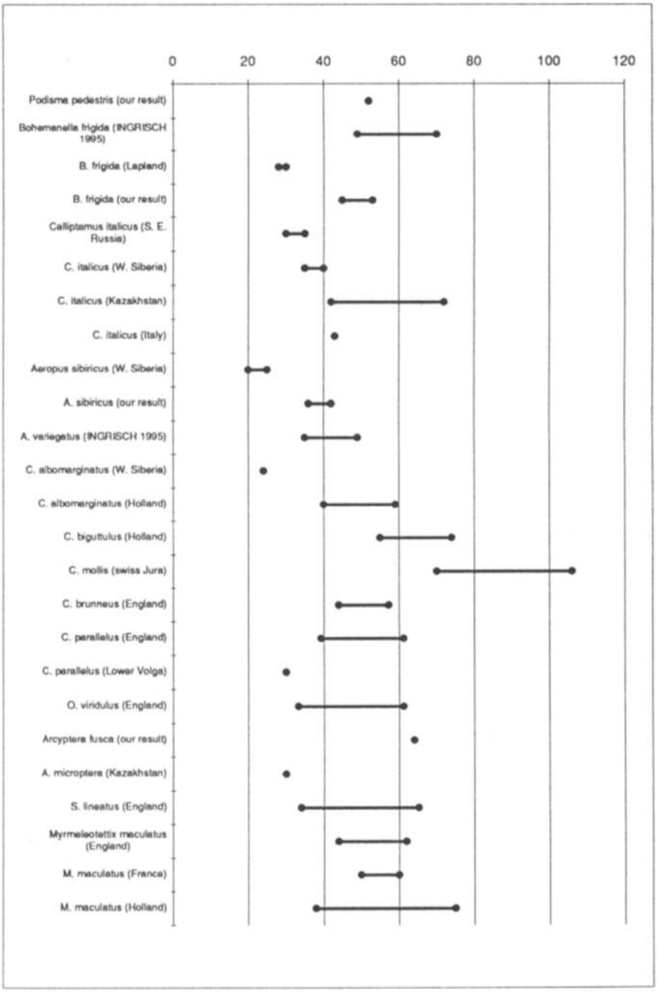

Fig. 14. Total duration (in days) of the post-embryonic development: comparison between our results and the literature data.

On the other hand, as the development rate increases with air temperature (UVAROV, 1977), the development of high-altitude species should be longer than that of lowland species. Microclimatic conditions on the ground in an alpine environment are very different than those 1 m above the ground. Our measures a few cm above the ground show this contrast (Tab. 1). High temperature near ground level and strong insolation probably make the environment of Acridids very favourable. This may explain why the development of the alpine species is not much longer than that of lowland species.

In late May a lot of young larvae of the different species were already found in well-exposed slopes (around site 1). The amount of accumulated snow during winter and spring vary from one year to another, but hatching after snow melting happens quite early. Snow-free periods for the four studied species begin later than in lowlands because of altitudinal gradient, but their hatching is more precocious.

This was probably overlooked, as access to high altitude meadows can be difficult because of the variable amount of remaining snow. It may be an explanation for why the developement of high altitude species is often supposed to be very short. However, if snow melting is very late (north-exposed slopes, very high sites), many larvae may not reach the imago stage and die (see *G. sibiricus* in site 5, Fig. 8).

Early snow melting in the mosaic of well-exposed sites and precocity of eclosions after snow melting probably make the developement period of the high mountain Acridids longer than it was thought to be. Fig 15 shows a schematic representation of the development of alpine acridids in high altitude.
This brings us to a new question: how can eclosions happen so early after snow melting ? Two hypotheses could explain this phenomenon:
- The embryonic development is far advanced at the beginning of the first winter (ANDER, 1950), because the microclimatically most favourable sites are selected for oviposition. We observed that at the highest (±2770 m.) sites, B. frigida was almost only present on south-facing slopes, where soil thermic inertia may play a decisive role (CARRON, 1994).
- The development cycle is biennial for the populations living in the least favourable areas (CARRON, 1994, INGRISCH, 1995).

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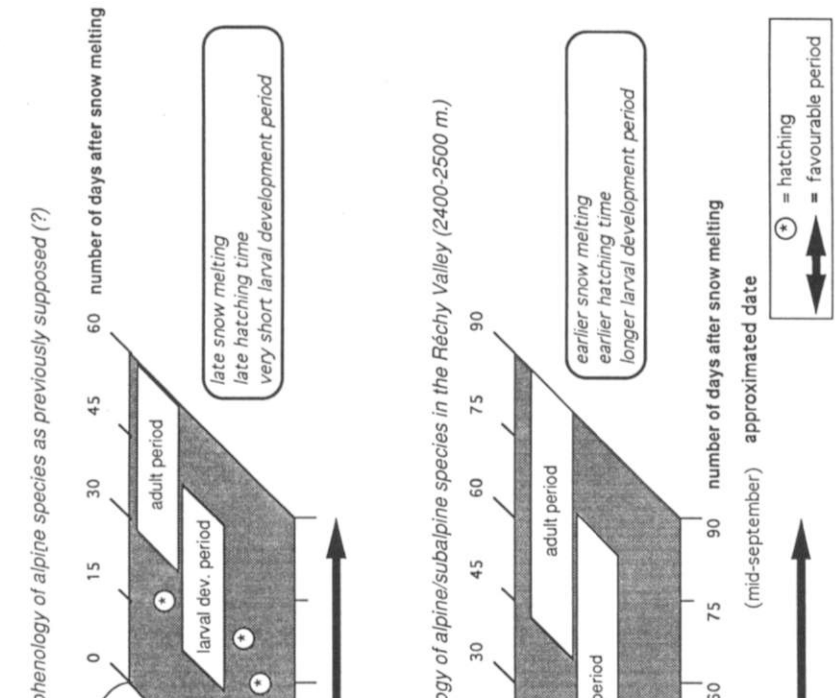

Fig. 15. Schema of the phenology of the high altitude acridids.

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