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**BIOLOGY AND ECOLOGY OF *MELANOPLUS BOREALIS*  
(ORTHOPTERA: ACRIDIDAE) IN FAIRBANKS, ALASKA  
WITH SPECIAL REFERENCE TO FEEDING HABITS<sup>1</sup>**

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**ABSTRACT**

Overwintered *Melanoplus borealis* (subspecies, *borealis* Fieber) eggs hatched within 10-15 days in mid-June. The nymphs molted 5 times and became adults in about 45 days in nature. In both sexes, sexual maturity was attained about 3 weeks after emergence and oviposition started 8-10 days after sexual maturity.

*M. borealis* is primarily a forb feeder as its mandibular morphology indicates but it also developed and reproduced exclusively on *Gramineae* in the laboratory.

In the Fairbanks area, Alaska, these grasshoppers were found in sunny open fields where vegetation was short and sparse enough to allow sunrays to penetrate to the ground surface. However, the size of the population in one habitat was never large. *M. borealis* hibernates as eggs from September to June of the following year.

**INTRODUCTION**

According to Gurney (1959), the subspecies, *Melanoplus borealis borealis* (Fieber) occurs throughout Alaska (including arctic tundra), Canada, British Columbia, and the northern parts of the United States. I had many disappointing experiences, however, looking for populations of this grasshopper in and around Fairbanks, Alaska (64° 54'N., 147° 50'W.) before I discovered one open field with a sufficient number of *M. borealis* to make this study possible. The difficulty was not due to the rareness of this species, but to the paucity of individuals in one habitat.

The biology and ecology of *M. borealis* has not been fully studied. As my previous experiences cover those *Acrididae* occurring in temperate regions of the world including the United States and Europe as well as tropical West Africa (Kaufmann 1965a, 1965b, 1968), I thought it would be worthwhile to study a species in the arctic for comparison. With this in mind I have paid special attention to the problems of adaptation of this grasshopper to the harsh and hostile environment of interior Alaska.

**OBSERVATION SITE**

The observation site used for this study was a sunny open field approximately 150 meters long and 100 meters wide surrounded by other physically similar fields and spruce woods. This site lay under snow from October to April; turned into a marsh land after snow melt until the end of May; and finally became free of standing water from June to September.

**METHODS**

In mid-June 1968, about 100 newly eclosed nymphs of *Melanoplus borealis* collected at the observation site in Fairbanks were reared in cages (30 x 30 x 30 cm with wire gauze covering the 4 sides and the top) in the laboratory. The cages were placed side by side facing an open window and received 8-12 hours of direct sunlight a day depending upon the month. A recording hygrothermograph was installed near the cages for registration of daily temperature and relative humidity.

Throughout the nymphal periods, each cage floor was covered by a metal water basin under a perforated plate with equally spaced holes through which food plants were made to

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stand in water (Kaufmann 1968). During the period of oviposition, an aluminum soil pan with sterilized soil replaced the water basin and the perforated plate.

To determine food preferences, 3 different species of plants were placed simultaneously in about equal quantity in each cage for 3 consecutive days. According to the results obtained at the end of this period, the food plants were categorized in 4 classes, namely: if all the plants were eaten, the plant was placed in Class 1; if one-half, in Class 2; if one-fourth, in Class 3; and if nibbled at, in Class 4.

The eggs laid in 1967 in the soil pan in the laboratory were put into a refrigerator with the initial temperature of 4°C, gradually lowered to -15°C from December to February, then gradually raised back to 4°C from March until mid-May, 1968.

#### GENERAL BIOLOGY

**EGGS:** The egg pods of *M. borealis* are straight or slightly curved, 8-18 mm long, and 3-5 mm thick, each containing from 2 to more than 30 eggs. The eggs are yellowish, cylindrical, 1 mm thick, and 3.5 mm long on an average. The incubation period was about 9 months including the diapause during winter. In nature, overwintered eggs hatched within 10-15 days in June and during two summers in the Fairbanks area no newly eclosed nymphs were found after June 23. The eggs did not hatch unless they were submerged in water in spring shortly before hatching (page 10). Thus, soil containing overwintered laboratory-laid eggs was sprinkled daily for 1.5 months with water after hibernation, but none of the eggs hatched.

**NYPHS:** *M. borealis* nymphs molt 5 times; individuals of various instars were found from mid-June to the end of July, but after July 25, the grasshopper population in the field consisted exclusively of adults (Table 1). In captivity, mortality was highest in the first 2 instars and this is also probably the case in nature. The total nymphal period was about 45 days in the field (Table 1).

Table 1. Percentages of nymphs and adults of *M. borealis* in the Observation Site in June and July, 1967 and 1968 in Fairbanks.

Date	1st	2nd	3rd	4th	5th	Adults
6/10	100	0	0	0	0	0
6/15	60	40	0	0	0	0
6/20	40	50	10	0	0	0
6/25	8	40	40	12	0	0
6/30	0	10	45	35	10	0
7/5	0	0	20	52	28	0
7/10	0	0	8	35	40	17
7/15	0	0	0	9	28	63
7/20	0	0	0	0	15	85
7/25	0	0	0	0	0	100

**ADULTS:** Adults appeared from the middle to the end of July within a period of 15-20 days in nature. In the laboratory, emergence took place between July 10 and August 3, and although the first mating was observed on July 28, it did not become very common until August 7. In both sexes, sexual maturity was attained about 3 weeks after emergence. Mating normally occurred during the warmest part of the day and the pairs remained *in copula* for 10-15 minutes only. Oviposition began 8-10 days after mating and lasted from mid-August to mid-September in nature, until October 1 in the laboratory. The female pushed approximately one-half of her abdomen straight into the soil for several minutes and

the resulting egg holes were often covered up with loose soil particles by the back-and-forth movement of her jumping legs. During her entire oviposition period, an average female produced 4-6 egg pods, each containing an average of 15 eggs (Table 2). From the end of

Table 2. Developmental Periods, nymphal mortality, body weights, lengths of body and hind femur, adult longevity and fecundity of *M. borealis* reared on different diets (see text for food plants provided in each cage).

	Cage 1	Cage 2	Cage 3
	Developmental periods, days		
First stadium	10.3 (8-11)	11.0 (8-12)	10.5 (8-11)
Second stadium	9.3 (7-15)	8.8 (6-15)	9.6 (8-14)
Third stadium	12.9 (7-19)	13.2 (8-22)	13.4 (8-22)
Fourth stadium	9.8 (9-11)	9.6 (8-12)	9.9 (9-13)
Fifth stadium	9.5 (8-11)	10.4 (8-15)	10.7 (9-14)
Total	51.8	53.0	54.1
	Nymphal mortality		
No. nymphs at start	30	35	30
No. death during:			
First stadium	4	4	5
Second stadium	3	4	4
Third stadium	2	1	2
Fourth stadium	0	0	2
Fifth stadium	1	0	4
Total nymphal deaths	10	9	17
Percent mortality	33.3	25.7	56.7
No. adults reared	20	26	13
	Body weight, mg.*		
Adult (male)	254.2 (211-304)	263.3 (209-303)	209.8 (193-223)
Adult (female)	376.8 (255-555)	298.3 (262-352)	270.5 (175-400)
	Length of body, mm		
Adult (male)	21.2 (19-22.5)	21.7 (21-23)	19.4 (18-20)
Adult (female)	22.7 (21-25)	24.1 (19-28.5)	22.8 (19-28)
	Length of hind femur, mm		
Adult (male)	11.1 (9.5-12)	11.4 (11-12)	9.7 (9.10)
Adult (female)	12.1 (11.5-13)	11.2 (10-14)	11.3 (10-12)
	Adult longevity and fecundity		
Longevity, days			
Male	69.4 (48-90)	67.4 (45-88)	74.6 (51-92)
Female	76.0 (53-110)	66.2 (40-85)	75.2 (55-102)
Minimum period of emergence to oviposition, days	28.0	30.0	30.0
Duration of oviposition, days	30.0	30.0	30.0
Mean no. pods/female	6.3	4.1	5.8
No. eggs/pod	14.5 (11-30)	17.2 (5-35)	13.9 (3-26)
Mean no. eggs/female	91.4	70.5	70.6

\*measured 1-2 days after emergence.

July to the end of August, a few females were seen occasionally sprinkling eggs to the ground from wherever they happened to be at the time. These egg masses were amorphous, seldom well wrapped in egg pods, and quickly dried. At least one of these females was unmated. I have observed a similar phenomenon in many species of Acrididae in central Europe and tropical Africa. After the beginning of September, mating became infrequent in cages, as all the females were concentrating on oviposition. At this time, males sometimes mounted females either in early morning or late at night when female resistance was at minimum; these males were usually kicked off later when the ambient temperature rose to 23°C and above. In such cases, copulation lasted 12 hours or more, instead of the normal 10-15 minutes as stated above. Since such a mating did not occur earlier in the season when females were fully receptive, it is to be regarded as abnormal. Nevertheless, this phenomenon is not rare in caged grasshoppers as it was very commonly observed in other Acrididae including *Melanoplus differentialis* in this country and *Zonocerus elegans* in East Africa (Kaufmann, MS).

In a sample size of 200, the male-female ratio of *M. borealis* was 43:57. The adults died toward mid-September in nature. In the laboratory, 50% died by the end of September, and 90% by mid-October. The adult longevity of *M. borealis* was about equal in both sexes except in Cage 1 in which a few females survived until the end of November (Table 2).

#### FEEDING HABITS

**FOOD PREFERENCE:** *M. borealis* is primarily a forb feeder as its mandibles with pointed dents indicate (Fig. 3), although it can also develop and reproduce on species of *Gramineae*. A wide variety of forbs serve as food but like most other acridians, *M. borealis* prefers certain plants to others.

Results of the food preference tests performed on both nymphs and adults of this grasshopper in the laboratory were as follows. Of the 14 species of plants used for the tests, *Taraxacum officinale* and *Parnassia palustris* were in Class 1; *Plantago rugellii*, *Petasites frigidus*, *Solidago multiradiata*, *Trifolium pratense*, *Geum macrophyllum* (flowers only) and *Achillea sibirica* (flowers only) were in Class 2; *Hordeum jubatum*, *Calamagrostis canadensis*, and *Arctagrostis latifolia* were in Class 3; *Epilobium angustifolium*, *Salix padophylla*, *Equisetum arvense*, *Achillea sibirica* (leaves only), and *Geum macrophyllum* (leaves only) were in Class 4.

In nature, the grasshoppers were seen feeding on *Petasites frigidus*, *Trifolium pratense*, *Taraxacum officinale*, and *Parnassia palustris*.

**Effects of Differential Feeding.**—Newly eclosed nymphs of *M. borealis* were divided into 3 similar cages, each containing 30-35 individuals and were fed with the species of plants found at and in the vicinity of the observation site. The food plant provided in each cage were:

Cage 1 (grasses and forbs)

Grasses: *Calamagrostis canadensis*, *Arctagrostis latifolia*, and *Hordeum jubatum*.

Forbs: *Taraxacum officinale*, *Parnassia palustris*, *Plantago rugellii*, *Solidago multiradiata*, *Trifolium pratense*, *Geum macrophyllum*, *Petasites frigidus*, and *Achillea sibirica*.

Cage 2 (forbs only)

*Taraxacum officinale*, *Parnassia palustris*, *Plantago rugellii*, *Solidago multiradiata*, *Trifolium pratense*, *Geum macrophyllum*, *Petasites frigidus*, and *Achillea sibirica*.

Cage 3 (grasses only)

*Calamagrostis canadensis*, *Arctagrostis latifolia*, and *Hordeum jubatum*.

Three different species of fresh plants were supplied *ad libitum* simultaneously in about equal quantity at each feeding. Temperature and relative humidity averages for the duration of the experiments are given in Table 3, and the results of the test are presented in Table 2. The diet of *Gramineae* alone (Cage 3) produced small, light-weight individuals and the nymphal mortality was high. However, in other respects, these grass-reared acridians did

Table 3. Mean monthly temperatures and relative humidities during the *Melanoplus borealis* feeding experiments in 1968 in the laboratory.

Month	Mean Temp. (C)	Mean RH (%)
June	23.4	1.0
July	26.0	57.1
August	24.8	60.9
September	22.9	53.3
October	20.2	50.7

not differ greatly from the other 2 groups especially in regard to developmental days and fecundity. This is rather remarkable and is to be regarded as adaptation to the arctic environment where summer is short and available species of food plants are greatly limited. It should be mentioned in this connection that in central Europe, typically forbivorous forms such as *Psophus stridulus* and *Oedipoda coeruleascens* never survived on grasses more than a few days. Likewise, typically graminivorous grasshoppers such as *Euthystira brachyptera* and *Chorthippus parallelus* did not eat forbs at all (Kaufmann 1965).

**FEEDING BEHAVIOR IN RELATION TO VARIOUS FACTORS:** In captivity feeding began at 16°C in nymphs and 13°C in adults; the upper limit was 38°C for both. The optimum temperatures for feeding, however, were 23-35°C. The acridians fed throughout the day.

*Melanoplus borealis* is a geophilous species with small arolia and is normally found on or near the ground where it is warmest during the sunny hours of the day (22-15 hours/day from June to August). Accordingly, feeding takes place on the plant within several centimeters from the ground. In cages, however, the grasshoppers frequently shifted their positions following the movement of the sun (see Behavior page 10). Consequently, in early morning the acridians aggregating on the cage floor ate the lower parts of the food plants as in nature, later they fed on the leaves closest to the vertical cage-wall, and finally, at midday, fed on the tips of plants close to the ceiling where the grasshoppers rested. Thus, the food plants eaten depend on where the grasshoppers are situated at the time of feeding, and since they rest on the warmest spots available, the food which happens to be near them is taken, regardless of food preferences. This is the very reason why in the laboratory, the food plants nearest the sunny side of the cage were eaten first: those at the shady side, on the other hand, were left alone if the ambient temperature was below 20°C, but entirely eaten at 23°C and above at which temperature the insects frequently jumped and flew and thus became dispersed all over the cage.

On sunny days at 23-32°C, several rows of *Calamagrostis canadensis* (Class 3) were placed along the sunny side of the cage facing the windows and those of *Taraxacum officinale* leaves (Class 1) of equal height on the shady side opposite. The adults of *M. borealis* first fed on the front row of *Calamagrostis* leaving the rest untouched and later consumed all the *Taraxacum* leaves (Fig. 1A). When the position of *Taraxacum* in the cage was reversed, the acridians ate all the *Taraxacum* first and later some of the *Calamagrostis* blades from each row (Fig. 1B). The young nymphs, on the other hand, fed on only the first few rows of *Calamagrostis* if these were on the sunny side (Fig. 2A), but ate all the *Taraxacum* when the position of this food plant was reversed (Fig. 2B). Thus, not only the quantity of preferred food eaten was greater than that of a less preferred plant, but also the feeding pattern of adults and young nymphs differed from one another under similar environmental conditions. These results were essentially the same as those for *M. differentialis* studied in Maryland but no "stair case" pattern was observed in *M. borealis* (Kaufmann 1968).

In captivity, beside the normal food plants mentioned above, both nymphs and adults sometimes fed on egg pods and dead grasshoppers of their own species as well as on dried

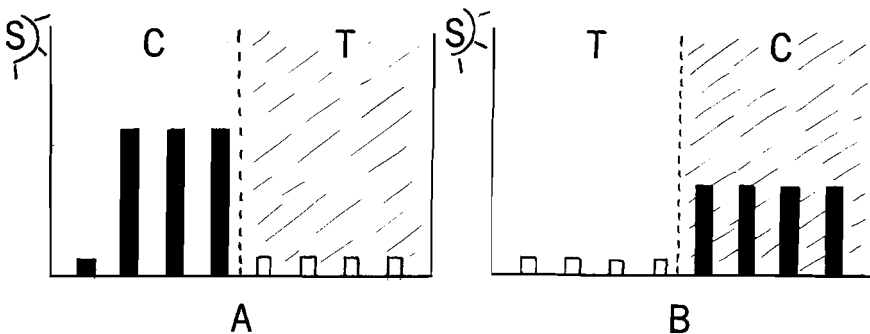


Fig. 1.—Influence of light and food preference on the feeding of adult *Melanoplus borealis*. A, side view of the cage with rows of *Calamagrostis* (black) and those of *Taraxacum* (white); B, the same cage with the position of *Taraxacum* reversed. C, *Calamagrostis canadensis*; T, *Taraxacum officinale*; S, the sun; cross hatched, shady area. Height of columns is that of stumps left after feeding; the tallest column denotes original height of plants.

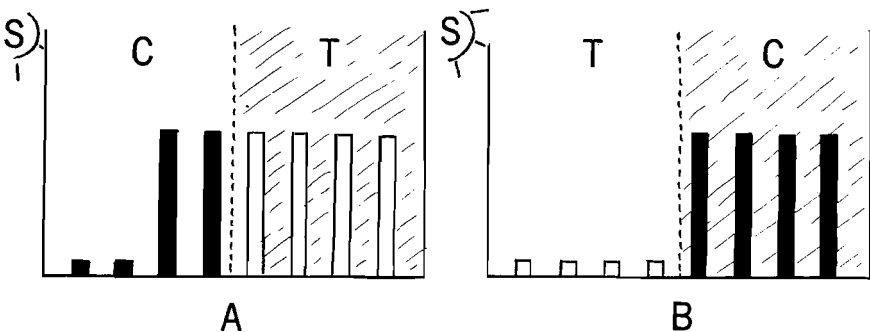


Fig. 2.—Influence of light and food preference on the feeding of young nymphs of *Melanoplus borealis*. Other explanations as in Fig. 1.

leaves or grass blades on the ground. Water was sucked eagerly on warm days. On exceptionally warm days with the ground temperature reaching 45°C, feeding was limited to early mornings and late afternoons and the grasshoppers remained sluggish during the hottest hours of the day. This, however, was rather exceptional in the arctic environment.

**SOME MORPHOLOGICAL FEATURES RELEVANT TO FEEDING HABITS:** The incisors of both right and left mandibles of *M. borealis* are extremely sharp. The molars of the right mandible are likewise sharp but smaller than the incisors while those of the left mandible consist of one sharp and 2 blunt teeth (Fig. 3). In general, these mandibular teeth are sharper than found in any of the other forbivorous species such as *Psophus stridulus*, *Oedipoda coerulescens*, or *Melanoplus differentialis* studied by the author (Kaufmann 1965a, 1968). Accordingly, *M. borealis* is definitely a forb feeder although in reality this acridid could also develop on grass blades. Mandibles of nymphs did not differ from those of adults except in size and the proportions of light and dark areas. Tooth abrasion in old adults at the time of death was considerable as both molars and incisors were reduced to mere stumps (Fig. 4).

The morphology of the maxillae closely resemble that of *M. differentialis* with slender laciniae and sharp terminal teeth. The abrasion of the maxillary teeth in old adults were less pronounced than the mandibular teeth.

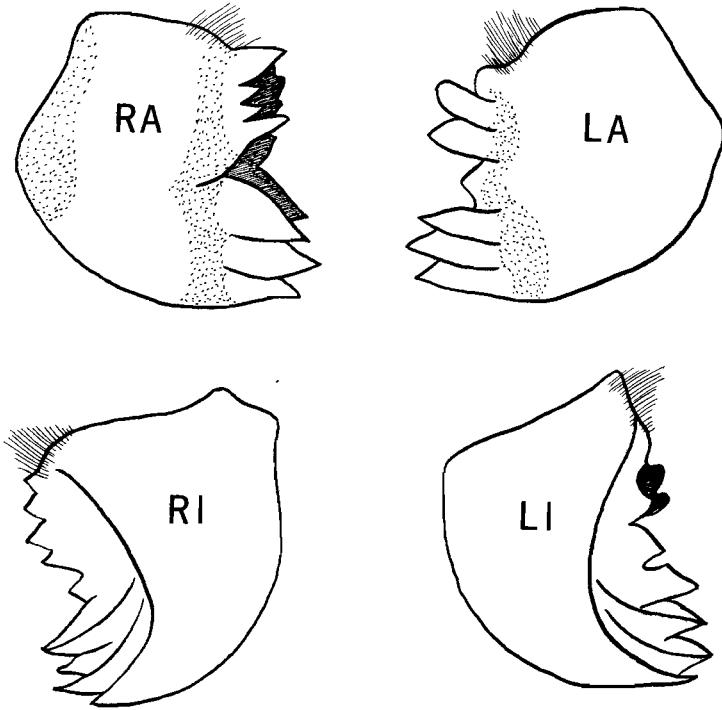


Fig. 3.—Mandibles of adult *Melanoplus borealis*. RA, right anterior; LA, left anterior; RI, right inner; LI, left inner view.

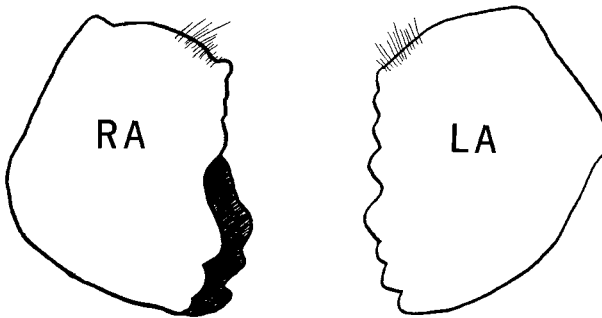


Fig. 4—Mandibles of old adult *Melanoplus borealis*. RA, right anterior; LA, left anterior.



## BEHAVIOR

The caged grasshoppers aggregated wherever it was warmest depending upon the position of the sun; when the sun was low, the insects were on the floor facing the sun, later they climbed up the cage wall on the same side as the sun rose higher, and finally rested on the cage ceiling when the sun was at the zenith. At night, when the ambient temperature fell below 20°C, the grasshoppers were found either on the cage wall away from the window (page 3) or roosted on the food plants, in which case horizontally spreading forbs were preferred to vertically standing grass blades. Crawling sometimes began at 16°C, but the insects were generally sluggish under 20°C. From 23° to 35°C, the animals became increasingly active with frequent spontaneous jumping and flying. At 38°C, some individuals would still bask in the sun but all avoided direct sunlight at 40°C and above. In the field when the ground temperature rose to an unusually high 46°C in July 1968, no grasshoppers were found on the ground in their usual short vegetation habitat (page 10), but in dense stands of tall grass. This temperature, however, is rather an exception in interior Alaska.

In rain the grasshoppers took refuge on vertical plants with their heads pointing skyward and thus exposing the minimum body surface to the rain. An artificial rain in the cage resulted in the same behavior; the insects immediately left the cage floor and climbed up vertical plants or cage walls where they remained with few movements until the "weather" cleared. After a rain, the grasshoppers "dried" themselves by stroking antennae, head, eyes, wings, and abdomen with their legs. Stomping in the field on rainy as well as on very windy or cold days did not cause the grasshoppers to jump out of their habitat.

When approached by a human in the natural habitat, adult insects reacted by jumping or flying away, just once, 30-60 cm high above the vegetation for a short distance and then dropping to the ground. Further approaches would not cause the insects to reappear, for the moss-covered floor of the field offered the best protection against their possible predators not only because the color of the insect blended perfectly with that of the environment, but also the spongy texture of the moss provided numerous spaces for hiding. In the mowed area with the height of vegetation not exceeding several centimeters, the adult grasshoppers flew randomly 30-60 cm high above the ground for 50-150 cm at a time. Further approaches produced a repetition of the same escape pattern. This difference in behavior is evidently due to their ability to see the intruder. On exceedingly warm, dry, and windless days, some individuals of *borealis* flew about a meter high when approached and covered a distance of 3-6 meters. Thus, height and distance of flight may be affected by temperature, moisture, and presence or absence of wind.

## ECOLOGY

**HABITAT:** The type of field in which *M. borealis* is found in the Fairbanks area is a mixed grass-herb-moss association. The most abundant vegetation included *Calamagrostis canadensis*, *Arctagrostis latifolia*, *Equisetum arvense*, *Parnassia palustris*, *Epilobium angustifolium*, and *Salix padophylla* followed by *Trifolium pratense*, *Achillea sibirica*, and *Plantago rugellii*. Also present but less abundant were *Solidago multiradiata*, *Taraxacum officinale*, *Geum macrophyllum*, and *Petasites frigidus*. The ground was covered with moss. Within one field, no *Melanoplus borealis* was found where vegetation was tall (1 m and above) and dense, but individuals were concentrated in the area where vegetation was short (under 30 cm) and sparse enough to allow sunrays to penetrate to the ground surface. The preference for this microhabitat was very pronounced, for wherever vegetation became tall, the grasshoppers abruptly disappeared and appeared again when this condition gave way to a more suitable habitat. Consequently, the distribution of *borealis* even within one habitat was patchy depending upon the height and density of tall plants. In general, acridians are sun loving insects; *borealis* is no exception as it spends most of its time on or near the ground basking in the sun. From mid-June to mid-September, the surface of the ground freely exposed to the sun was 4-10°C higher than the ground covered with tall grass.

Moreover, arctic summer is brief and temperatures often fluctuate severely. Thus, effective utilization of the sunlight is vital for the development and reproduction of this insect.

Unexpectedly, in mid-July 1967, grass was mowed to within a few centimeters of the ground in approximately one-half of the observation site. Five days later, the percentage of the adult grasshopper population in the original part of the habitat did not differ greatly from that in the mowed area. However, 10 days later, the proportion had changed drastically as the population in the mowed area more than doubled. Finally, 15 days after the grass was cut the majority of the acridians had moved to and was concentrated in this artificial habitat where, due to the very short vegetation, the ground temperature was 2-3°C higher than in the natural habitat (Table 4).

Table 4. Movement of *M. borealis* adults from normal to artificially created habitat in the Observation Site.

Date	Normal Habitat		Mowed area*	
	ground temp. (C)	% acridians	ground temp. (C)	% acridians
July 20	20.5	53	23.0	47
July 25	26.0	30	30.5	70
July 30	21.0	12	24.0	88

\*One-half of the Observation Site was mowed on July 15, 1967 (see text).

Other open grasslands adjacent to the observation site had identical physical structures and vegetation. However, willows (*Salix padophylla*) in them were much taller and bulkier, and since this plant was abundant, microclimatic conditions on the ground were bound to be affected by their presence. Probably this is one of the main reasons why *Melanoplus borealis* did not occur in these fields. It also suggests that regular mowing of grasslands might help propagate *borealis* in the arctic for the reasons explained above.

**POPULATION:** The size of the population of *M. borealis* in any one habitat in and around Fairbanks was never large. Of a dozen open fields examined in 2 summers, only 1 had sufficient numbers of this species to enable this research.

Very young nymphs were always found concentrated in loose groups in places not far from where they had eclosed. However, as growth proceeded, accompanied by increasing physical strength, keener sense organs, and finally by the acquisition of wings, the grasshoppers dispersed into progressively wider areas. This often gave an impression of a drastically decreased acridid population especially when the habitat was large. Other factors for dispersal included height, density, kinds of vegetation, temperature, humidity, and weather conditions. In short and sparse vegetation, the grasshoppers (especially nymphs) travel more easily than through tall and dense vegetation. Also, stands of vertical grass offer less resistance for movement than horizontally spreading herbs and shrubs. Rain, wind, temperatures below 20° or above 40°C or any combination of these immobilized the acridians; while at 23-35°C, the adult insects flew so frequently that they covered wide areas in a relatively short period.

From the middle to the end of August, 1967, the observation site was completely covered by a few feet of flood water from the Chena River destroying not only the eggs which had already been laid but also many females before and during oviposition. Very probably due to this natural catastrophe, the numbers of *borealis* collected in the observation site in the 2 summers showed that the size of the *borealis* population of 1968 was approximately one-half that of 1967 (Table 5).

**HIBERNATION:** *Melanoplus borealis* hibernates as eggs only. During midwinter, the eggs in the ground were exposed to -5° to -21°C under a few feet of snow cover. Depending upon the weather conditions of the year, from one to two months before eggs hatch in mid-June,

Table 5. The comparison of *M. borealis* population during the month of July in 1967 and 1968 in the Observation Site.

Date	No. of individuals caught in one hour	
	1967	1968
July 7	41	26
July 14	86	32
July 21	28	16
July 28	23	12
Total:	178	86

open fields in the Fairbanks area become marshy due to melting snow, and *M. borealis* eggs are literally soaked in water during this period. This actual immersion of the eggs in free water is probably necessary for viability.

The period of egg hibernation is from mid-September to mid-June of the following year. According to Kresky (1960), eggs of *borealis* hatched in the laboratory after 2 years' diapause in the soil. His specimens were collected in high altitude rangeland in the northern Rocky Mountain region. This was not observed in subspecies *borealis borealis* Fieber in the Fairbanks area during the 2 years of this investigation.

#### DISCUSSION

In the arctic as in desert areas, the matter of timing is essential to survival of the species. *Melanoplus borealis* eggs hatch only within a brief period of 10-15 days in June when the day consists of 22 hours of daylight and 2 of twilight. Because of this, during the development of this insect, never more than 4 (usually 2-3) different instars were observed in nature at one time (Table 3), and the time of adult emergence occurred also within 15-20 days. In contrast, *Zonocerus variegatus* in Ghana, West Africa (6°N) oviposited from December to March and the eggs hatched from July to October, respectively (Kaufmann, 1965a). Consequently, the nymphs of different stages and adults existed from July to December as the post embryonic development of this grasshopper covered 3 months. Finally, from December to March, there were only imagines (Kaufmann, 1965a). Thus, it had long been thought that *Z. variegatus* was multivoltine. This strong contrast between *M. borealis* and *Z. variegatus* in 2 entirely different geographical regions of the world well illustrates the responses of the acridians to their particular environments.

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## BOOK REVIEW

THE WASPS. Howard E. Evans and Mary Jane West Eberhard, with drawings by Sarah Landry. Ann Arbor: The University of Michigan Press, 1970. vi, 265 pp. Paper, \$3.45.

This pocket-sized book is indeed a high point in recent entomological literature. Concisely written, and including a remarkable amount of new or recently published information, *The Wasps* is essentially a comparative natural history of these fascinating animals. Only the "higher" or aculeate wasps are covered, a fact not clear from the title. After a brief survey of the Hymenoptera, five chapters follow: two on solitary species, two on social wasps, and a fascinating final chapter treating the diverse and often intricate biotic relationships of wasps. The book is generously illustrated, with 122 figures about equally divided between photographs and drawings; several photographs of tropical social wasps appear here for the first time. The University of Michigan Press is to be commended, as the book is virtually free of typographical errors, and the photographic reproductions are of the highest quality.

Many new or little explored areas of wasp behavior are discussed, including phoretic copulation, dual sex-linked mimicry, and the remarkable relationships of tropical social wasps with birds and ants. One interesting tidbit mentioned is the recent discovery that certain bats are important predators on some social wasp colonies. A major theme throughout *The Wasps* is the development of sociality among the Aculeata, and "the social ladder" presented here is of particular interest. A new and simplified classification of the nests made by wasps will also be welcomed by students who have struggled with the more cumbersome terminologies of other authors.

The enthusiasm and admiration for wasps shared by the authors is conveyed to the reader by the numerous delightful word-pictures sprinkled throughout; for example, there are the paper wasps that "terrorize housewives, ruin picnics, and build the large aerial nests that challenge fleet-footed stone-throwing boys the world over". A simplified, mostly non-technical terminology is employed throughout, but a two-page glossary is appended. It is somewhat distressing to find only a half page of suggested readings at the end, and an unfortunate omission is a bibliography of the numerous references cited in the figure captions and throughout the text.

Nevertheless, *The Wasps* achieves the rare distinction of being not only a highly readable popular treatise, but also being without doubt the best, and indeed the only synthesis of much recent literature on the comparative natural history of aculeate wasps. As such, it should be a required evening's reading for all students of insects, and a part of every entomological library. One hopes that it will not be long before the appearance of a similar well-organized, up-to-date synthesis treating that other half of the wasp world, the parasitic Hymenoptera.

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