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SURVIVAL AND FOOD DETECTION BY FIRST-INSTAR MELANOPLUS FEMURRUBRUM (ORTHOPTERA: ACRIDIDAE)

R. G. Bland¹

ABSTRACT

Newly hatched *Melanoplus femurubrum* (DeGeer) were evaluated for survival without food under various moisture, temperature, and light conditions. Although nymphs survived up to 113 h without food, they required food 48–60 h after hatching to ensure continued survival and growth. Olfactory food detection was very limited and feeding tended to occur on the first suitable food encountered. Food covered with a film of water and held within several millimetres of the palpi evoked palpal vibrations followed by antennal movements. The evidence suggests that hygroreceptors occur on the palpi and palpal stimulation is necessary before antennal olfaction occurs.

Grasshopper host selection and feeding behavior have been studied by numerous investigators and much of the research has been reviewed by Dadd (1963), Mulkern (1967), Gangwere (1972), and Chapman (1977). Nearly all work has been with adults or late instars because the major crop damage occurs at these stages, the insects display the greatest behavioral diversity, and their relatively large size makes them easy to manipulate and observe.

Investigations into feeding habits of 1st instars are uncommon even though this stage is relatively vulnerable to adverse environmental conditions and subject to high mortality (Pickford 1960, 1962). Williams (1954) included 1st instars of locusts and various grass-hoppers in his research on physical and biological factors affecting feeding behavior and host preferences. Bernays and Chapman (1970) used 1st instars and other stages of *Chorthippus parallelus* (Zetterstedt) to determine the role that physical characteristics of leaves have in food selection. The duration of survival of starved 1st instar *Camnula pellucida* (Scudder) and *Melanoplus sanguinipes* (Fabricius) was recorded by Smith (1960). Mulkern (1969) observed responses of nymphs (including 1st instars in some cases) and adults of eight acridid species to variations of light, visual patterns, food quality, and feeding extracts.

This study deals with the survival and food detecting ability of grasshopper hatchlings when confronted with suboptimum habitat conditions. The species chosen was *Melanoplus femurrubrum* (DeGeer), the redlegged grasshopper, a common mixed feeder found throughout most of North America (Vickery et al. 1974). The objectives were to (1) determine survival ability under varying food and moisture conditions, (2) evaluate the ability to detect food and moisture, and (3) observe the use of the antennae, mouthparts, and front legs for food and moisture detection.

METHODS AND MATERIALS

Egg cases were obtained from caged, field-collected adults in central Michigan and incubated in moist sand at 24°C for 30 days. After refrigeration for 6 months the eggs were incubated at 27°C on moist filter paper in a petri dish. Young leaves of dandelions (*Taraxacum officinale* Weber) and alfalfa (*Medicago sativa* L.) were used as food for hatchlings. Most experiments used five hatchlings and each test was replicated three times. Specific test conditions are described in the Results section.

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RESULTS

Egg Hatch. Hatching occurred 6–18 days after incubation, with 60% of the eggs hatching between days 15–18. Two percent of the eggs did not hatch and 11% of the hatchlings did not survive eclosion. The early hatching was probably due to eggs which were not in diapause within ca 2 weeks after oviposition and continued to develop until refrigerated.

Survival without Food. Hatchlings were maintained in a petri dish at 27°C and a 15 h photophase which approximate the average daytime temperature and photoperiod during the middle of June in Mount Pleasant when egg hatch occurs. Three moisture conditions were used: high (water droplets occupying ca 25% of the dish bottom surface), ambient (70–75% RH) without free water, and low (CaCl₂ covering the bottom surface beneath a false floor in the dish). A fourth condition consisted of keeping the hatchlings at 27°C during 15 h of light and 13°C for 9 h of darkness. The night temperature is the average that occurs during the middle of June. Moist filter paper lined the bottom of the dish in this test.

Survival results are shown in Table 1. There was no significant difference (Student's t-test, P > 0.05) in survival between high and ambient moisture conditions. Survival in low humidity and different day-night temperatures was significantly different (P < 0.05) from the high and ambient moisture conditions. Low night temperature extends longevity, low moisture reduces longevity, and moderate to high moisture levels appear to have little effect on survival in the absence of food. The minimum overnight (8 h) temperature at which 100% of 12-h-old instars will survive is -3 to -4° C.

Survival with Variable Food Conditions. Intact discs of soil with undisturbed plants were removed from the grasshoppers' habitat during the week of hatching. Discs were trimmed to fit into extra high petri dishes. The control consisted of intact soil, debris, and trimmed plants enclosed in a petri dish. The substrates were modified as follows: (1) all visible vegetation and debris removed, and (2) all visible vegetation removed except dry debris (primarily fine roots and bits of leaves). The substrates were oven dried until no further weight loss occurred and then separated into two groups; one group would remain dry and the other would have one-third of the soil surface moist. Hatchlings were placed in the containers and held at 27°C and a 15L:9D photoperiod.

Treatment	Mean Hours Survived \pm SD
Filter paper substrate	
Low moisture	60 ± 2
High moisture	86 ± 5^{a}
Ambient moisture	94 ± 5^{a}
27°/13°C, ambient moisture	108 ± 12^{b}
Soil substrate	
Control (with vegetation)	2nd instar
Dry debris only	
Moist	115 ± 7^{b}
Drv	93 ± 5^{a}
No debris or vegetation	
Moist	96 ± 4^{a}
Drv	84 ± 3^{a}
No debris or vegetation	
27°/13°C, ambient moisture	$113 \pm 5^{\mathrm{b}}$

Table 1. Survival duration with variable food and moisture conditions at 27°C or at a 27°C day and 13°night regime. A 15L:9D photoperiod was used.

^{a,b} Means with the same letter are not significantly different (P > 0.05).

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Grasshoppers in the control dishes all survived and developed into the 2nd instar (Table 1). When all vegetation and debris were removed, grasshoppers lived an average of 84 h (no moisture) and 96 h (moisture). The difference between these means was not significant (P > 0.05) nor were the means significantly different (P > 0.05) from the high and ambient moisture conditions on filter paper substrate. If dry debris was present the duration of survival increased slightly to 93 h (no moisture) and 115 h (moisture). The presence of moisture with dry debris caused a significant (P < 0.05) increase in longevity when compared to the absence of debris but grasshoppers were unable to survive to the 2nd instar. Reducing the night temperature also increased survival significantly (P < 0.05) even though debris was absent.

Survival and Moisture. Each hatchling was placed in a 1-oz clear plastic container within 30 min of eclosion. The small container allowed close contact with a leaf of alfalfa or dandelion under the following conditions: fresh leaf \pm water, dry leaf \pm water. Fresh leaves were replaced with new leaves every 12 h. Dry leaves were produced by air drying at 27°C for 2 days. Wet cotton was the water source. Containers were held at 24, 27, 30, 33 and 36°C.

Hatchlings did not begin feeding until nearly 3 h after eclosion. Those held at 24° C fed little or not at all and died after 3 days. Grasshoppers with fresh leaves \pm water and those with dry leaves + water survived and molted to the 2nd instar, taking 5 days at 27° C and 4 days at the higher temperatures. Individuals with dry leaves as food but without water did not survive past 3 days at all temperatures. These results show that 1st instars can survive and develop on fresh leaves without water or dry leaves with water if the temperature is high enough for feeding activity to occur.

Starvation Recovery. Hatchlings were starved 24, 36, 48, 60, and 72 h in 1-oz plastic containers held at 27°C and a 15 h photophase. A water droplet was present in each cup. Fresh alfalfa was placed in each cup at the end of a starvation period. All hatchlings fed and molted to the 2nd instar when given food after a 24–48 h starvation period. After 60 h without food they were alive but some were too weak to feed and others that fed nevertheless died by 72 h. Thus a 1st instar may survive 86–108 h under certain conditions (Table 1) but it must feed within 48–60 h to ensure continued survival and growth.

Food and Moisture Detection. Hatchlings were held in petri dishes either without food and water or with only water available for 8, 16, and 24 h in constant light. The tests were conducted at 30° C because the minimum temperature for good feeding activity was $25-27^{\circ}$ C. Below this temperature range the grasshoppers were relatively inactive and preferred to climb the sides of the container and/or move toward any light source where they remained with little additional activity. Fresh and air-dried (24 h at 27° C) dandelion and alfalfa and filter paper were used as food. Slivers of leaves and paper were cautiously presented to the side of a grasshopper through a hole in the side of the dish.

No measurable behavioral differences occurred between nymphs held with or without water and thus they are evaluated as one. Grasshoppers starved 8 and 16 h turned toward the fresh food or made slow semicircular movements that brought them to the leaves from a distance of ca 7 mm. Only 35% of the nymphs responded to dried leaves at that distance. Individuals starved for 24 h responded to fresh and dry leaves as well as filter paper up to a distance of ca 7 mm.

Both vision and olfaction may apparently cause the individual to turn toward the potential food since the filter paper presumably has no attractive odor. The grasshopper slowly waves its antennae as it approaches, not usually touching the food with the antennae, until the front tarsi contact the food enabling the insect to climb onto the surface. The antennae or mouth-parts do not have to touch the food before the tarsi make contact. Biting occurs on both leaves and filter paper but feeding proceeds only on the leaves. Feeding occurs immediately after biting on fresh leaves but the grasshopper takes longer to begin eating dry leaves because it moves about on the leaf biting various areas before feeding. One antenna (usually the same one) is lowered briefly every 8–12 sec to touch the leaf surface as the grasshopper initiates feeding and after 30–60 sec the frequency of antenna lowering decreases to once every 18–25 sec. When the grasshopper bites filter paper, the antennae are jerked upward rather than slowly lifted as if mechanoreceptors are strongly stimulated.

A second experiment exposed starved grasshoppers to fresh and dry alfalfa at 27° C and allowed them to select one for feeding. Two groups of hatchlings were starved for 24 h; one

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group had water available and the other lacked water. They were then introduced through a dark tube into one side of a petri dish. A light bulb was placed at dish level on the opposite side of the entrance at a sufficient distance so as not to act as a heat source. Fresh and/or dry alfalfa leaves were placed in the dish on the side opposite to the release hole so the insects would walk past the food as they moved toward the light.

The grasshoppers exhibited an extreme attraction to the light and would walk past the food without stopping unless they were within ca 5–7 mm of the alfalfa as they passed by it. At this distance nearly 75% of the nymphs would touch it with their antennae or front tarsi and then climb on the leaf to bite and feed. They exhibited a slight but not significant (P > 0.05) preference for fresh over dry alfalfa when the leaves were adjacent. The leaf that was touched first was the one fed upon. The presence or lack of water for 24 h did not cause a preference for fresh or dry leaves.

A third experiment exposed the grasshoppers to a 1-cm strip of wet filter paper under the same conditions as the second experiment. To move toward the light the insects had to cross the wet strip. Hatchlings without food and water for 24 h walked directly to the strip, stopped to drink, and then continued over the strip. Nearly two-thirds of those without food but with water for 24 h stopped 10–25 mm from the strip and slowly weaved side-to-side. Seventy-seven percent jumped over the strip without contacting it first and the remainder walked over the paper without stopping to drink.

Food Detection and Feeding in Darkness. Hatchlings were placed in darkness immediately after eclosion and starved without water for 0, 4, 16, and 24 h at 21, 24, and 27°C. Grasshoppers which would not have to search for food were each placed in petri dishes, after the appropriate starvation time, with pieces of alfalfa leaves scattered over ca half the bottom surface. Those needing to search for food were anesthetized with CO_2 and each placed in half of a petri dish which was separated from the other half by a vertical wall with two evenly spaced openings 10 mm wide and 15 mm high. Pieces of alfalfa leaves were scattered over ca half of the bottom surface on the side opposite the grasshopper.

After 8 h in darkness all individuals at 24 and 27°C had fed on the alfalfa and continued to feed over the next 3 days they were monitored. Grasshoppers at 21°C did not feed and most rested on the sides of the vertical walls. These results indicate that 1st instars will move and feed in darkness if the temperature is sufficiently high for general activity. Based on their limited ability to locate food in light as shown earlier in this study, it's likely that they encountered the alfalfa by chance in their general movements rather than orienting to it by olfactory means.

Sensitivity of Antennae, Palpi and Tarsi to Food and Water. Hatchlings were mounted on tape so their ventral side was up and held without food or water for 24 h. Strips of fresh alfalfa and dandelion leaves and dry or wet filter paper were cut 1 mm wide and presented to the insects while observing them through a dissecting microscope.

Alfalfa and dandelion strips provoked similar responses. When the strips were moved close to but not touching the antennae, maxillary and labial palpi, or front tarsi, these appendages (including the mandibles) moved 0-11% of the time. When one antenna was touched briefly, it (and frequently the other antenna) was immediately raised and the mouthparts and front legs began moving which indicated an attempt to locate or sample potential food. If a food strip was moved toward the mouthparts after contacting the antennae, they were lowered as if to touch the strip but contacted it less than half the time even when held within reach of the antennae. When leaf contact ceased, antennal movements declined and generally stopped after ca 30 sec but could be restimulated by again touching one or both antennae.

When the maxillary and labial palpi were contacted they began palpating the leaf strip and the front legs were raised in an attempt to grasp the strip. Biting and a slight amount of feeding occurred regardless of whether or not the front tarsi grasped the leaf. Contacting only the front tarsi with a strip caused the palpi and labrum to move and the head to bend forward as the grasshopper attempted to touch the food with its mouthparts. The antennae were lowered and raised slowly during the head movement.

Dry filter paper strips evoked no response when held near the antennae, palpi, or front tarsi. When an appendage was touched, the grasshopper's response was essentially the same as the response to leaf strips except that only biting occurred and not feeding on the paper.

Wet filter paper strips held near the antennae and front tarsi did not stimulate movement

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of these appendages. When the appendages were touched the response was the same as to dry filter paper and leaf strips. However, when the wet paper strip was brought to within ca 0.5 mm of the maxillary and labial palpi, both vibrated rapidly, the mandibles and labrum moved, and one antenna was lowered although it did not touch the wet strip. Utilizing this information, alfalfa and dandelion strips were dipped in distilled water and held ca 0.5 mm from the antennae, palpi, and front tarsi. Again, only the palpi responded to wet paper strips. These results indicate that the maxillary and labial palpi contain olfactory hygroreceptors whereas the antennae, palpi, and front tarsi, which responded only to contact, bear mechanoreceptors and/or contact chemoreceptors and any hygroreceptors present are not functioning.

The above tests were repeated with an ink-white glue-water mixture covering the compound eyes of the grasshoppers to determine the importance of vision in antennae, mouthparts, and front tarsi responses. The reactions to dry and wet leaf and filter paper strips were generally the same as when the eyes were uncovered although the reaction speeds were more subdued.

DISCUSSION

A multitude of environmental components such as weather, food quality and quantity, habitat and natural enemies confront a population of grasshopper hatchlings. Newly hatched M. *femurubrum* did not initiate feeding until three or more hours after eclosion. The minimum temperature for feeding activity under laboratory conditions was 24°C. Smith (1960) noted that feeding did not start for 8 h at 30°C for M. sanguinipes and C. pellucida. During the prefeeding time, the strong negative geotaxis and even more vigorous positive phototactic response of M. femurubrum (Mulkern 1969) often causes them to climb nearby vegetation. By being above ground level for lengthy periods the risk of predation from geophilous arthropods (e.g., ants, carabid beetles, and certain spiders) is reduced. In addition, the drowning of hatchlings from excess rainfall or dew is less likely and the typically lower humidity above ground level may reduce the chance for fungal infections.

Cleanly tilled soil, continuous rain, or abnormally cool temperatures at the time of egg hatch require the hatchlings to survive until seedlings emerge, or dispersal takes them to nearby food, or the weather improves to allow for food-searching activity. In the laboratory M. *femurubrum* survived an average of 60 h (2.5 days) at low humidity and constant temperature to 113 h (4.7 days) with moderate humidity and low night temperature (Table 1). Moisture lengthened survival duration on soil with debris but had no effect on bare soil. Under constant temperature conditions 1st instars must locate food within 2.5 days or become too weak to feed and utilize available food. Smith (1960) showed that M. sanguinipes and C. pellucida would survive 4 days at 30°C and 5 days at 25°C constant temperature which averages about 0.5 days longer than M. femurubrum under similar conditions. He did not check for their ability to resume feeding and survive during this time.

If negative geotactic and positive phototactic responses have not caused the hatchling to climb onto a suitable host then the grasshopper must search for food. Hunger stimulates random movements until the nymph perceives a vertical object for orientation (Williams 1954, Kaufmann 1968, Mulkern 1969). Color appears to have no effect on food selection (Williams 1954, Mulkern 1969). In this study *M. femurrubrum* was found to move toward and contact food only when within ca 7 mm of the food. The nymphs showed no long distance olfactory ability to recognize food and fed on whichever suitable source they first encountered. Mulkern (1969) reported that adult and last instar *M. femurrubrum* had to be within 3–4 cm of fresh or dried vegetation to locate it and Dadd (1963) has also referred to the limited olfactory guidance of grasshoppers. Riegert et al. (1954) found that 2nd instars of *C. pellucida* and *M. sanguinipes* released in a bare field were unable to orient themselves and move toward a food supply several hundred metres distant. Second-instar *C. pellucida* moved up to 82 m in 8 days and the direction was primarily downward. However they would have been feeding during this time or otherwise the nymphs would not have survived so long.

Pruess (1969) and Bernays and Chapman (1970) cited evidence that a grasshopper's diet is

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generally determined by its acceptance or rejection of the plant it is perched on when ready to feed. In this study, *M. femurrubrum* 1st instars had a slight but statistically insignificant (P > 0.05) preference for fresh alfalfa over dry alfalfa. Nymphs required free water in order to survive on dry alfalfa indicating that if the habitat contains food that is palatable and nutritous but in a dry condition, the grasshopper will feed on the dry food and develop at least to the 2nd instar as long as a moisture source is available and the temperature is sufficiently high for feeding activity. Williams (1954) found that food with a higher moisture content was preferred by grasshoppers he studied, but Bernays and Chapman (1970) observed that moisture was not important in the differential selection of fresh leaves in *C. parallelus*. They noted that the leaves used by Williams (1954) were probably much drier than the more controlled moisture levels they tested. Kaufmann (1968) and Lewis (1979) observed that *M. differentialis* (Thomas) preferred dried or wilted tissue in the presence of fresh plants. Lewis (1979) related this preference to nutrient or chemical defense changes or that the leaf is easier to chew. Other studies on the role of water content were reviewed by Gangwere (1972).

If environmental conditions such as rainfall, low temperatures, or wind prevent *M. femurrubrum* hatchlings from feeding during the day, night feeding can occur as long as the temperature is high enough (> 24°C) for general locomotor activity that results in encountering food. Williams (1954) observed that the adults of *Locusta migratoria* (L.) fed at a reduced level when their eyes were blackened and Blaney et al. (1973) reported that 5th instars of this species fed in darkness with the only change being a longer interfeed period than in the light. Mulkern and Mongolkiti (1977) noted that grasshoppers probably feed at night if hungry and the temperature is high enough to stimulate activity.

Nymphs of *M. femurrubrum* that have had water but not food available will generally jump over a wet paper strip as they move toward a light. They do not need to contact the paper and may weave side-to-side before exhibiting avoidance behavior, indicating a reception of olfactory and/or visual signals. Kendall and Seddon (1975) showed that hydrated *L. migratoria* avoid a wet paper strip but they point out that humidity differences also occur as the insect approaches the strip. Early instars of grasshoppers and locusts select low humidity (Kennedy 1937, Riegert 1959) unless they are close to the time of molting (Riegert 1958) or have been deprived of food (Aziz 1957).

A wet paper strip held at various distances from the antennae and front tarsi of mounted *M. femurrubrum* maintained without food and water elicited only an occasional antennal or mouthpart response. However when moved to ca 0.5 mm of the maxillary or labial palpi, both pairs of appendages vibrated which indicated that hygroreceptors were present, and the antennae, labrum, and mandibles began to move. This study does not explain why nymphs were able to detect and avoid a wet paper strip from greater distances as previously described. Slifer (1955), Riegert (1960) and Waldow (1970) had evidence that grasshopper and locust antennae contain hygroreceptors. Neither these workers nor those dealing specifically with locust mouthpart function have reported the response of palpi to moisture, but the palpi have been proven without doubt to be contact chemoreceptors (Haskell and Mordue 1969, Haskell and Schoonhoven 1969, Blaney and Chapman 1970, Blaney 1975).

Fresh alfalfa and dandelion leaves and dry filter paper did not elicit a response from 1st instars when these items were held up to but not touching the antennae, mouthparts, and front tarsi. The lack of response to the leaves was unexpected since nymphs in a petri dish are attracted toward a leaf when it is brought to within ca 7 mm of the grasshopper. However, vision may play a major role in attracting the grasshopper especially if the potential food contrasts greatly with the background as it does in a petri dish. In addition, individuals were unrestrained in petri dishes rather than mounted dorsally, and the more natural position and environment may allow greater sensory activation and coordination. When the leaves and paper were dipped in distilled water and again offered to the mounted grasshopper, the palpi responded by vibrating followed by attempts to feed. These results indicate the presence of palpi olfactory receptors more responsive to water vapor (hygrore ceptors) than phagostimulatory odors that are presumed to eminate from the cut leaves.

Touching the antennae, mouthparts, or front tarsi with leaves and filter paper caused all of

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these appendages to move in a predictable fashion indicating that contact chemoreceptors and/or mechanoreceptors are present. The likely mode of food selection is through chance contact with plant material followed by exploratory biting. The antennae generally did not contact the proferred food once it had touched the palpi, and instead usually one antenna was intermittently waved up and down. This movement suggests that important olfactory reception occurs while the palpi palpate the food and during exploratory biting, and that chemotactic sensilla on the palpi must be stimulated before olfactory sensilla on the antennae are receptive. The antennae may then respond to food odors and/or moisture. The front tarsi also produce the same antennal response and may serve the same initiation function as the palpi or act simultaneously with the palpi to activiate the antennal olfactory system. As mentioned earlier, antennal movement does not occur in the presence of water vapor until the palpi begin to vibrate, presumably stimulated by their hygroreceptors. Perhaps antennal olfaction and palpal chemotactic or hygroreceptive activity are needed simultaneously for exploratory biting to proceed to actual feeding.

The antennae of grasshoppers are assumed to be the major olfactory site by virtue of the abundance of thin walled, multiporous basiconic sensilla (Slifer et al. 1959). Numerous studies have demonstrated olfaction in foodfinding with detection ability ranging from a few centimetres to over 1 m (Williams 1954, Slifer 1955, Dadd 1963, Mulkern 1967). However, adult or late instar grasshoppers have been used in these sense organ studies and perhaps the weak olfactory response of 1st instar *M. femurrubrum* occurs because they have not developed full innervation of the basiconic or coeloconic sensilla on the antennae or have not learned to recognize the appropriate olfactory stimuli that signal food.

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