MONTANA STATE UNIVERSITY

The role of behavior in the integration of a population of Aulocara elliotti (Thomas)(Orthoptera: Acrididae)

by Jerry Joseph Bromenshenk

A thesis submitted to the Graduate Faculty in partial fulfillment of the requirements for the degree of DOCTOR OF PHILOSOPHY in Entomology
Montana State University
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Abstract:
The role of behavior in the integration of individuals into a population of Aulocara elliotti (Thomas) was investigated in the field and in the laboratory. The effects of environmental factors, communicative signals, and individual movements and interactions on population structure and performance were examined. Both descriptive and experimental procedures were employed. A specially designed arena was utilized to study kineses and taxes. A wind tunnel facilitated olfaction studies, and an alternative humidity chamber was used to investigate response to different relative humidities. A sampling device to measure hatching rhythm also was designed and utilized.

The time of hatching of eggs of this species appeared to be determined by an increase in temperature. A preference for conditions of low (0-10%) relative humidity over high (95-100%) was generally demonstrated by nymphs and adults, but the moister conditions were preferred during each molt. A. elliotti increased activity and showed a downward movement in response to wind at low speeds (4-10 ft./sec.). Grasshoppers moved upwind in response to attractive odors, and unfed hatchlings displayed an inherent ability to find a suitable food source by odor alone. Receptors of the antennae are very important for the responses to odors. Light and temperature influenced general activity. Temperature responses appeared to be primarily kinetic; while responses to light sources (sunlight and artificial light sources) included both kineses and taxes. Low intensities of light inhibited locomotor and stridulatory activities.

A. elliotti primarily utilized visual and acoustic signals for communication. Several song types distinguished by differences in rhythm construction were identified. Loss of visual and/or physical contact with individuals of the opposite sex increased the number of songs produced by both males and females. Visual signals, especially those involving movement, were important to interactions between members of the species. Courtship behavior by males included simple and complex displays. Complex courtship involved prolonged sequences of mating behavior and were characterized by symmetric and asymmetric positions and movements of body parts. Groups of males often follow an ovipositing female. This behavior may be related to sexual selection by the female.

It is hypothesized that 'pottering' or intermittent wandering is a kinetic response controlled by environmental factors and the physiological state of the grasshopper and that pottering is a major factor in the displacements and distributions of individuals.

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in

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ABSTRACT

The role of behavior in the integration of individuals into a population of *Aulocara elliotti* (Thomas) was investigated in the field and in the laboratory. The effects of environmental factors, communicative signals, and individual movements and interactions on population structure and performance were examined. Both descriptive and experimental procedures were employed. A specially designed arena was utilized to study kineses and taxes. A wind tunnel facilitated olfaction studies, and an alternative humidity chamber was used to investigate response to different relative humidities. A sampling device to measure hatching rhythm also was designed and utilized.

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It is hypothesized that 'pottering' or intermittent wandering is a kinetic response controlled by environmental factors and the physiological state of the grasshopper and that pottering is a major factor in the displacements and distributions of individuals.

INTRODUCTION

Aulocara elliotti (Thomas) was first observed in Colorado and Wyoming in 1870 by Prof. Cyrus Thomas, United States Entomologist (Henderson, 1931). This species occurs on short-grass plains in the area west of the Mississippi River from southern Canada to Arizona (Pfadt, 1949; Brooks, 1958; Strohecker, 1968). It is primarily a grass feeder and attacks many species. Pfadt (1949) observed that the first two instars feed chiefly on sandberg bluegrass *(Poa secunda* Presl.*)*, while the older instars and the adults feed almost entirely on western wheatgrass *(Agropyron smithii* Rydb.*)*. Western wheatgrass appears to be the main food plant of both nymphs and adults in Montana (Anderson and Wright, 1952).

A. elliotti has become very abundant at times in parts of its range. Cooley (1904) reported heavy infestations of grasshoppers on rangelands in eastern Montana during 1901, 1902, 1903. The three most common grasshoppers were *A. elliotti*, *Melanoplus atlanis* (Riley) [*M. sanguinipes* (Fab.)], and *Camnula pellucida* (Scudder), with *A. elliotti* the leading species in abundance. Great numbers of *A. elliotti* occurred in Gallatin, Beaverhead, and Madison counties in 1919, and another outbreak occurred in parts of Montana in 1923 (Cooley, 1919; 1923). The short-grass ranges of Montana were again heavily infested with *A. elliotti* and *Melanoplus mexicanus* (Saus.) [*M. sanguinipes* (Fab.)] from 1934 to 1937 (Strand, 1937). An appearance of large

numbers of grasshoppers in 1949 was termed an outbreak by some workers (see Anderson and Wright, 1952). Montana has not suffered a major infestation of *A. elliotti* since 1949. However, large fluctuations of grasshopper numbers have occurred in localized areas (personal communication, Dr. Norman Anderson and Prof. Ellsworth Hastings of Montana State University).

Outbreaks of *A. elliotti* have been reported during the 1890's, 1930's, and 1940's in Wyoming, Colorado, Nebraska, Kansas, North and South Dakota, Utah, New Mexico, Arizona, and Washington (Pfadt, 1949). White and Rock (1945) stated that this species is economically the most important grasshopper on Alberta short-grass plains. Nerney (1954) and Ball *et al.* (1942) consider *A. elliotti* to be "one of the most injurious range grasshoppers in Arizona."

Dr. R. A. Cooley described the first organized studies of Montana grasshoppers in the First Annual Report of the State Entomologist of Montana (1903). Following the outbreaks in the early 1920's, research of an ecological nature, concerning egg and nymphal development and the effects of weather on grasshopper populations, was conducted (Parker, 1933; 1937). Extensive ecological studies of the factors suspected to be the underlying causes of grasshopper outbreaks were instigated by the Grasshopper Research Laboratory of the United States Department of Agriculture at Bozeman after its establishment in 1930 (Shotwell, 1941; Davis and Wadley, 1949). The Department of Zoology

and Entomology, Montana State College, organized a research program on rangeland grasshoppers in 1946 (personal communication, Dr. James H. Pepper of Montana State University).

Studies in the late 1940's and early 1950's conducted in the field revealed: (1) Grasshopper distribution on rangeland is not random; (2) Most grasshoppers have specific food preferences; (3) The amount of damage to vegetation is not necessarily proportional to the number of grasshoppers present; (4) Individual grasshopper species and not merely numbers of grasshoppers must be considered in studies of grasshopper damage; (5) Local movements of grasshoppers may be influenced by changes in environmental conditions; (6) Individuals from different species respond differently to similar environmental conditions. During the outbreak in southeastern Montana in 1949, some regions within the outbreak area were virtually grasshopper free or demonstrated a low incidence of grasshoppers. High populations of mixed species generally were found in transition areas between different habitats. The increase in numbers of one species did not necessarily coincide with the increase in numbers of another. (Anderson and Wright, 1952) It was concluded that the behavior of a grasshopper population (that is, the individuals which make up a population) is an expression of the environmental factors acting on the grasshoppers; grasshoppers respond to environmental factors through the mediation and interactions of biochemical and physiological systems. Infestations

by grasshoppers were thought to be composed of genetically different groups or subpopulations. Chromosomal studies to demonstrate genetic differences between wild populations failed to show differences in *A. elliotti*. (Personal communication, Drs. Stephan Chapman and Norman Anderson of Montana State University)

Physiological and developmental studies of the eggs and embryos of *A. elliotti* have been conducted in the Department of Zoology and Entomology at Montana State University from 1958 to the present (Van Horn, 1963; Roemhild, 1961; Wessel, 1973; and others). Nymphs and adults from wild populations were reared under laboratory conditions in an attempt to gain some insight into the manner in which a population responds to aspects of its environment. Factors such as temperature, light, humidity, food, and space requirements could be varied in the laboratory and their influence on the eggs and embryos of individuals from the experimental population could be observed. However, laboratory conditions may not be representative of the environment of a wild population. Solomon (1949) stressed that a "population functions in relation to a whole which includes itself." Only if an experimental group represents a 'population' can such studies have relevance to the wild population. The problem of how this is to be accomplished still remains.

Field studies of the structure and performance of a natural population of *A. elliotti* were initiated in 1970 in an attempt to

define a wild population. Distribution, density, and movements of the individuals in a field population were observed. Both wild and field-caged grasshoppers were used to measure survival, longevity, and fecundity and to identify behavioral patterns (Mussgnug, 1972). The behavioral investigations presented here were instigated in 1971 on the basis of the following hypotheses: (1) Communicative signals are vital to population integration and distribution, especially in adults; (2) Orientation to 'key' factors (Morris, 1959) is particularly important to population structure and performance in nymphs. Definitions and concepts utilized in this study are presented in Appendix A.

Literature Review

A review of the literature indicates that the integration of a population is established primarily through behavioral mechanisms.

For example, sensory stimuli initiate behavior. The environment contains many stimuli, some of which are not detected by organisms. Aspects of the environment which are not sensed may serve no useful purpose. This is not to say that undetected stimuli are unimportant. Some stimuli, such as X-rays, may even be harmful. If X-rays occurred naturally, those species developing the capability to detect the rays would have a better chance of survival. (Davis, 1966)

Response to stimuli in any organism only occurs if the stimuli are relevant. For example, honeybees utilize wavelengths of light and planes of light polarization for guiding their activities. Light

stimuli, on the other hand, are of minor importance to a flying bat, which relies on sound waves for guidance.

Davis (1966) presented the proposition that organisms respond only to those stimuli relevant to the species and the corollary that organisms ignore irrelevant stimuli and fail to discriminate among those not regularly encountered. This agrees with the hypothesis of Morris (1959) that 'key' factors largely establish population trends. Morris concluded that data on the major events influencing population dynamics should provide an understanding of the functioning of the life system of the subject.

Interactions between the genetically controlled 'blueprint' and the environment control the development of behavior in the individual (Thorpe, 1963). The expression of genes depends upon the environment providing stimuli or reinforcers necessary for the gene to be expressed in the phenotype (King, 1967). Often, several genes contribute to a particular trait. Combinations of genes show characteristic patterns (units) of behavioral response to changes in the environment. Selective pressures can operate on and may tend to fix patterns in the genotype. Through evolution, behavioral units may be modified and reshuffled and put to different uses. Comparative studies of behavior, based on behavioral units, can be used to demonstrate phylogenies. (Manning, 1967, Caspari, 1967)

Behavior is seen to develop since it depends upon morphological and physiological changes occurring during the development of an organism. Ultimately, behavioral development depends upon the maturational stage of the nervous system. As such, behavioral development should parallel overall and differential rates of morphological development. (King, 1967.)

King (1967) emphasized that behavior can be modified. Environmental conditions and especially previous stimuli and behavioral activities of an organism modify behavior. The phenotypic expression of a behavioral pattern is enhanced by reinforcement from the environment, by reinforcement from other responses, and by self-reinforcing properties of the responses themselves. King further stated that the development of behavior depends on the time when a response can first be expressed, or on the time when it is likely to be reinforced by the environment, and on the temporal relationship to other responses that may enhance or impede its further development.

The modification of behavior is important to the evolution of a species. Mayr (1958; 1970) regards behavior as "perhaps the strongest selection pressure operating in the animal kingdom." King (1967) concluded that slight behavioral deviations from the norm can affect: (1) the union of gametes in populations, (2) fecundity and viability, (3) gene flow between and within populations, (4) survival and continuance of gametes of each individual. Breeding patterns, assortative

mating, courtship, parental care, social tolerance, migration, shelter seeking, and agnostic behavior are patterns affecting changes in the gene frequency of populations. Mayr (1970) cites shifts into new niches or adaptive zones as an example of a change mediated by an alteration of behavior. Browning (1963) stated "the influence of the environment depends, often in a striking way, on the behavior of the animal." Wright (1949) divided adaptive characters and activities into three categories: viability, fertility, and fecundity. Speiss and Langer (from Caspari, 1967) added two more categories: rate of development and maturation for mating. Behavior may relate to any or all of the above categories. Manning (1967) presents numerous examples of the influence of mating behavior of insects on fertility and viability. Similarly, behavior patterns may produce sexual isolation and the establishment of mating systems (Perdeck, 1958). Assortative mating can cause rapid changes in gene frequency by departures from random mating, which contribute to differential fertility (King, 1967; Caspari, 1967). Genetically controlled mating and habitat preferences may be important factors in the formation of species (Caspari, 1967). This conclusion is supported by experimental studies of *Drosphila* species (Manning, 1963, 1967; Bastock, 1956; Merrell, 1949, 1953; Ehrman, 1964).

Caspari (1967) summarized the role of behavior. He stated that behavior not only integrates a population, it also is a major factor

influencing evolutionary processes leading to adaptation and speciation, both of which occur at the population level. From a taxonomic point of view, species differ in behavioral activities and potentialities just as much as they do in morphological and physiological characters. Mayr (1958) proposed that behavioral characters rather than morphological characters could be used as a basis for taxonomy, and in many cases behavioral analysis would give more refined and reliable results.

Behavioral characteristics may be classified according to the sense organs by which stimuli are received, one of which is usually emphasized, depending on the species. Senses responsive to auditory, visual, chemical, and tactile systems are particularly important. (Klopfer and Hatch, 1968.) Allee *et al.* (1949) added humidity and temperature to these systems. Davis (1966) classified sense organs according to the type of physical stimuli detected and lists six major categories: gravity, temperature, chemicals, energy, pressure, and electricity.

Behavioral patterns may also be arranged according to function such as aggregation, orientation, communication, habitat selection, and mate selection. King (1967) emphasized the contribution of behavioral patterns to temporal, spatial, and sex-age distributions in the subject population.

Behavioral analysis, ultimately, should provide information concerning: (1) population structure, (2) population performance, (3) major ecological events and processes influencing a population. This in turn should provide data on the major events determining population fluctuations and quantitative data on which to base an explanative and predictive model of the subject population. Pest management strategies, based on a better working knowledge of population dynamics and the life system of the subject population, could be formulated from such a model.

The present study attempts to define the role of behavior in population integration. A survey of the behavioral characteristics of *A. elliotti* attempts to answer several questions: (1) What are the major behavioral patterns responsible for population integration? (2) What are the major behavioral patterns influencing nymph, adult, and egg distribution? (3) What are characteristic patterns of behavior in a population? (4) Are changes in behavior observable as development proceeds from the time of hatching through maturation to the adult stage? (5) How does the behavior of caged laboratory grasshoppers compare to that of caged field grasshoppers and to that of a wild population? (6) What are the major environmental (ecological) stimuli responsible for population structure and performance as evidenced by behavioral responses?

This study was made as inclusive as possible, at the expense of more detailed investigations on any one aspect of behavior, because of a paucity of information about the behavior of *A. elliotti* either in the laboratory or in the field. A recognition of behavioral patterns of response is a prerequisite to comparative studies.

MATERIALS AND METHODS

The laboratory stock of nymphs of *Aulocara elliotti* was collected from a short-grass study site 5 mi. west of Billings, Montana. Mussgnug (1972) gave a detailed description of this area. He characterized the climate as hot, dry, and sunny. Occasional storms in the afternoon produced thunder, hail, and high winds. Observations of caged and wild individuals were conducted at this site, and the behavior of these grasshoppers was compared with that of animals in the laboratory at Bozeman, Montana.

Third and fourth instar grasshoppers were collected from Billings in mid-June of 1971 and 1972 and reared in a glass roofed room in the insectary at Montana State University. Rearing was conducted in wooden cages with clear plastic sides. Each cage consisted of a 1 x 2 in. fir frame, 34½ x 66 x 26½ in. high. A 3 in. high band of window screening at the base of each cage allowed air to circulate freely; while the 23½ in. high plastic sides above the screen prohibited climbing and jumping out of a cage. The top of each cage was left open in order to avoid filtering of sunlight and restriction of air flow. A grasshopper would jump out of a cage only if suddenly disturbed.

Vegetation and soil were transported from the study site and placed in the cages in an attempt to provide an environment that approximated the field conditions in soil and flora.

One hundred fifty male-female pairs of grasshopper nymphs were reared in the laboratory each summer. Mortality factors, especially those caused by handling, marking, testing, etc., reduced the original numbers collected to a stable population of approximately 100 pairs for each summer. Each year, two cages were maintained at a density of 15 pairs each, one cage at 30 pairs, and a fourth cage held the remainder as replacements. One cage of 15 pairs was utilized each summer primarily for behavioral observations, and these grasshoppers were not used for other experiments.

Rearing and observations of caged grasshoppers in the laboratory were performed in a glass-roofed, thermostatically controlled room. This room had been converted from a fiber glass to a glass roof, when it became apparent that the fiber glass tended to reduce solar radiation levels in the room. The conversion resulted in radiant energy fluctuations in the room beyond the capacity of the original heating-cooling system. Night temperatures were set at 15.6°C (10 p.m.-6 a.m.) and day temperatures were set at 29.4°C (6 a.m.-10 p.m.) on the thermostats. Air temperatures in the room ranged from a low of 11.7°C to a high of 18.9°C at night and from a low of 21.1°C to a high of 46.7°C during the day. Detailed weather data from the field study site for 1971 obtained by Mussgnug (1972) was used as a standard of reference for laboratory conditions for 1972. Air temperatures in the laboratory in July of 1972 averaged 30.6°C maximum, 15.3°C

minimum, with a mean of 23.1°C. Air temperatures in the field in July of 1971 averaged 39.1°C maximum, 11.1°C minimum, with a mean of 25.1°C. Air temperature in the field as well as relative humidity at 1 in. above the soil surface were measured by a continuous recording hygrothermograph (Bendix Aviation Company). Air temperature in the room was measured by a continuous recording thermograph (Taylor Instrument Company) with the temperature probe suspended 1 ft. above the soil in an open, draft free area between the cages. Air and soil temperatures in the cages were monitored by thermistors connected to a telethermometer with a range of -15° to 50°C (Yellow Springs Instrument Company). Thermistor probes placed ¼ in. above the soil in the cages often recorded temperatures ranging from 37.8°-43.3°C or higher, while the temperature probe measuring room air temperature registered 29.4°-32.2°C. Cage temperatures remained within 1°C of those of the room if measurements were made under similar conditions; i.e., temperature probes suspended at the same height above soil and shaded. The placement of temperature probes has a decided effect on temperature. The higher maximum air temperature average in the field as compared to that of the room is in part due to different placements of the temperature recording probes.

Thermistors connected to telethermometers (Yellow Springs Instrument Company) were used for temperature measurements in all observations and experiments of the present study. Soil temperatures

were determined by placing a banjo thermistor on the surface of the soil. Air temperatures were measured at ¼ in. above the soil unless otherwise specified. This height above the ground approximated the height of the body of a grasshopper above the soil.

Relative humidity readings were made from a hygrometer (The Chemical Rubber Company) suspended in the middle of a cage ¼ in. above the soil surface. Accurate control of humidity in the cages was impossible since each cage contained a large quantity of both dry and fresh vegetation and since the soil varied from wet to dry depending on the length of time from the last irrigation. Relative humidity varied from 0%-100% in the cages. Daytime levels averaged 20%-40%. Watering of the cages was scheduled to approximate the rainfall pattern in the field. As a result, vegetation in the cages became very dry by the end of each summer.

Solar radiation levels during July of 1972 were measured by two identical solar radiation meters (Weather Measure Company), one in the field and one in the glass-roofed room of the insectary. Maximum radiation levels at the two sites are compared in Table 1. Solar radiation levels in the field were only slightly higher than those in the glass-roofed room. A comparison of solar radiation in a fiber glass-roofed room and in the glass-roofed room of the insectary, obtained from recordings made in September, 1972, demonstrated a much lower level of radiation in the fiber glass covered room (Table 2).

TABLE 1. COMPARISON OF MAXIMUM SOLAR RADIATION LEVELS FOR THE FIELD AND THE GLASS-ROOFED ROOM OF THE INSECTARY, 1972. (Expressed in gm. cal./cm.^{2}/min.)

Date	Maximum Solar Radiation	
	Field*	Insectary
July 11	1.35	1.05
2	1.45	1.24
3	1.36	1.26
4	1.16	1.20
5	1.27	1.17
6	1.27	1.27
7	1.10	1.22
8	1.09	1.00
9	1.16	1.16
10	1.08	0.89
11	1.13	----
12	1.27	1.16
13	1.13	1.18
14	1.26	1.11
15	1.14	1.13
16	1.18	1.09
17	1.31	1.16
18	1.12	0.98
19	0.33	0.65
20	0.21	0.51
21	1.20	1.13
22	1.12	1.13
23	1.08	1.09
24	1.17	----
25	1.09	----
26	1.09	1.02
27	1.12	0.98
28	1.05	1.03
29	1.12	0.96
30	1.12	0.89
31	1.16	0.91
Aug. 1	1.25	0.88
2	1.23	0.95
3	1.09	0.88
4	1.27	0.88
Average Daily Maximum	1.12	1.04

*Field data collected by Mussgnug of Montana State University.

TABLE 2. COMPARISON OF MAXIMUM SOLAR RADIATION LEVELS FOR THE FIBER GLASS AND THE GLASS-ROOFED ROOMS OF THE INSECTARY, 1972. (Expressed in gm. cal./cm.^{2}/min.)

Date	Maximum Solar Radiation	
	Glass Roof	Fiber Glass Roof
Sept. 1	.93	.32
2	.91	.36
3	.99	.40
4	1.05	.40
5	1.01	.36
6	.29	.32
7	.96	.37
8		
9 Average Daily Maximum	.88	.36

However, solar radiation levels were often equal in the rooms, if not slightly higher in the fiber glass roofed room, on cloudy days. It is suspected that the fiber glass absorbs and reflects those wavelengths of light most likely to be absorbed and reflected by a heavy cloud cover. Therefore, the roof acts like an artificial cloud cover on sunny days.

Specialized equipment and techniques were utilized in several experiments. Appropriate descriptions of these are given in the details of the specific experiments to which they apply. Individual experiments are described in the Investigations section. Four major types of apparatus were developed and utilized in this study:

1. Tilt Table. (Figure 1). This apparatus was used to test grasshopper orientation to factors such as light, geotaxis, and visual signals. The test area consisted of a plate glass floor, 3 ft.

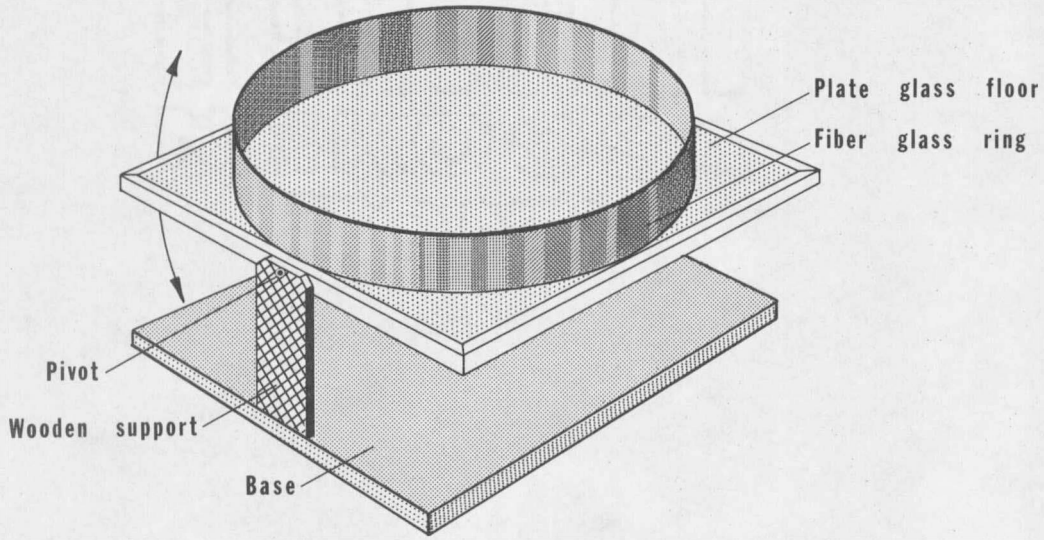


Figure 1. Tilt Table.

in diameter, with a fiber glass ring forming sides 5 3/4 in. in height. A removable clear plastic cover was used in experiments in which air currents were controlled. The entire device could be easily cleaned with ethanol or other solvents to remove odor clues from previous experiments. A 300 W., clear, incandescent bulb, 5 ft. above the center of the arena provided illumination. Heat effects from this bulb could be minimized by control of room temperature. White muslin shields surrounded the entire apparatus from floor to ceiling to eliminate distracting visual clues. The floor of the arena was supported on two vertical wooden pillars, 14 in. high, which could be replaced with taller supports to allow any tilt of the apparatus from 0°-90° above the horizontal. Lights, heaters, fans, screens, and the like permitted controlled introduction of many stimuli. A Y-tube olfactometer, patterned after Hocking and Lindsay (1958), was used with this arena for preliminary olfaction tests, but turbulent air currents, produced by the curved sides of the arena, limited the use of the olfactometer and necessitated the construction of a separate wind tunnel for olfaction tests.

The Tilt Table arena was similar in design to test arenas used by Ellis (1951, 1953) and Gillet (1972). It differed from other designs in its versatility, and it was larger than most other designs. Attraction to the walls was reduced by the large size of the arena in relation to the size of the grasshopper.

2. Wind Tunnel. A wind tunnel to test olfaction responses was constructed in 1972. The design of Haskell *et al.* (1962) was followed. Electric fences used to keep grasshoppers off the end filters were eliminated and four 250 W. GE infrared lamps were substituted for the three Philipps 375 W. infrared lamps of the original design. Low wind speeds of 1-4 ft./sec. were found to be the most effective for odor tests. Temperature in the tunnel was monitored by nine thermistors, six at the surface of the sand in the bottom of the tunnel, two ¼ in. above the sand for air temperatures, and one movable probe for spot measurements. Temperatures could be controlled within less than 1.0°C variation. White muslin shields were used to visually isolate the grasshoppers. The shields were removed for observations of hatchling nymphs, which proved to be very difficult to see against the sand. The apparatus was large enough that these first instar nymphs rarely approached the sides or ends of the tunnel and appeared not to notice the observer. However, adults rapidly reached the sides and would sit watching the observer if the muslin screens were not in place.

3. Alternative Humidity Chamber. An alternative chamber based on the design of Atkins and Wellington (1962) was constructed to test the effects of humidity on orientation and activity of grasshoppers. The major modifications from the original design included enlargement of the chamber and the use of wooden boxes lined with metal trays instead of battery jars. The apparatus was 24 in. square, 16 in.

high, and divided in the middle into two boxes 22 x 11 x 16 in. A window screening metal floor covered the inner boxes. A wooden box 24 in. square by 18 in. high surrounded the entire assembly. This outer box had a tight fitting Plexiglas cover, which was positioned 1½ in. above the screening floor. Illumination was by a single 200 W. bulb suspended 3 ft. above the center of the apparatus. All tests were performed at 32.2°C. Appropriate salts and solutions (O'Brien, 1946) provided a choice of relative humidities in excess of 95% on the wet side and less than 10% on the dry side. Equilibrium was achieved in 45-60 min. The assembly maintained the humidity gradients for 3-4 hr. or longer, with less than ½ in. transition zone between the extremes of humidity. Test grasshoppers were introduced to the choice chamber through a hole in the center of the Plexiglas cover.

4. Hatch Sampler. (Figure 2). This device was used to sample the number of grasshopper nymphs emerging from egg pods at any given time. Two samplers, each small enough to fit inside a G.E. Model 808 incubator, were constructed. Each sampler utilized a counterclockwise rotating drum obtained from an event recorder. Each drum completed a rotation in 24 hrs. An inverted, covered 9 in. pie pan was mounted on top of the drum so that it also rotated. The plastic cover of the pan was divided into 12 pie shaped sections and served as a collector for the emerging nymphs. A narrow opening was cut in the metal pan of the collector around the circumference. A second metal pie pan

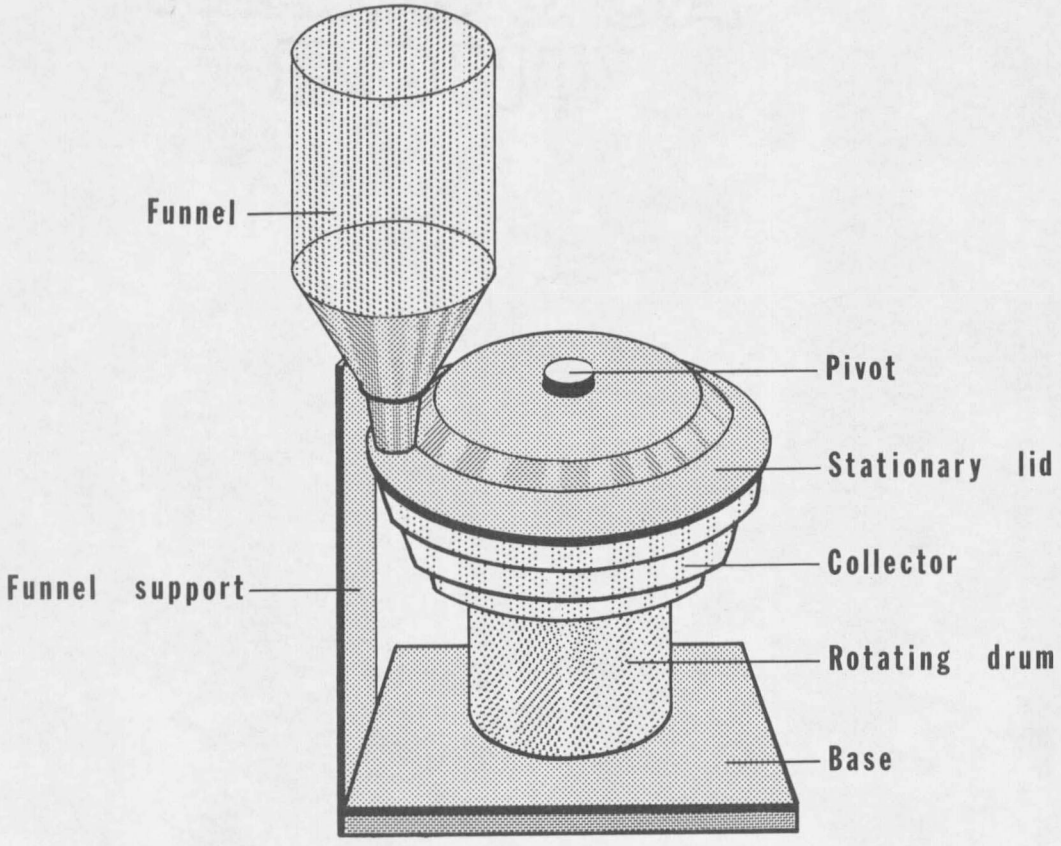


Figure 2. Hatch Sampler.

was inverted over the first as a cover. A 6 in. diameter plastic funnel was fastened to a wooden support and positioned over the assembly so that the apex of the funnel opened through a hole in the cover-pan directly over the slot in the collector-pan. The cover-pan acted as a lid to seal the apparatus and was stationary since it was affixed to the funnel. The collector rotated beneath the stationary lid. Grasshopper pods were suspended in the funnel so that when the nymphs emerged they would slide down the funnel and into one of the pie shaped divisions of the collector. The pods were first mounted in the funnel by pieces of plastic tape, but several nymphs became glued to the tape. This problem was eliminated by hanging the pods by means of individual fine copper wires from a ring in the top of the funnel. The entire assembly could be placed into an incubator and temperature and lighting could be varied to test their influence on hatching patterns. Concurrent replicate tests were performed, since two identical incubators were available. The 12 divisions of the collector sampled the number of nymphs emerging in any two hour period.

INVESTIGATIONS

I. Hatching Experiments

In September, 1972, *Aulocara elliotti* egg pods, laid by laboratory reared grasshoppers from Billings during the previous summer, were sifted from the soil and incubated in sand in 9 in. pie pans in the glass-roofed room of the insectary. The room temperature was regulated at 29.4°C during the day and 15.5°C during the night. Variations in the room temperature could be controlled within ± 2.0°C during the fall and winter months. The pods were exposed to a natural photoperiod. Egg pods also were collected from a field site near Townsend, Montana, which had had a high density (approximately 80 grasshoppers or more per square yard) population during the summer. These pods were treated in the same manner as the previous pods.

Hastings (1971) used a 60-day cold treatment at 5°C to terminate diapause in eggs of *A. elliotti*. Mussgnug (1972) reported that diapause was more successfully terminated by chilling the eggs at 3-5°C for 80 days than for 50 days. Both groups of pods used in the present study were placed in a cold room at 3-5°C on October 14, 1972, to terminate diapause. The pods were removed from the cold after 80 days and incubated in the insectary under fluctuating light (lights on at 6 a.m., off at 10 p.m.) and temperature (29.4°C from 6 a.m. to 10 p.m., 15.5°C from 10 p.m. to 6 a.m.).

Additional eggs were collected at Townsend, on January 16, 1973, and May 6, 1973. The pods collected in January were divided into two groups. Ninety pods were incubated in the glass-roofed room under the conditions described, without additional cold. One-hundred thirty pods were given an additional 80 days of cold (3-5°F). Pods collected in May were used in experiments to be discussed later.

Figure 3 summarizes data concerning hatching of the eggs collected in the laboratory and at Townsend in September, 1972, and from eggs collected from Townsend in January, 1973. The latter were incubated without further cold treatment.

The graph for the eggs collected from Townsend in January shows a typical laboratory emergence pattern. Numbers emerging rapidly increased to a maximum within 2-4 days of the initial emergence and then gradually declined, if all the pods in the experimental group received similar treatments of cold incubation.

The data are combined for eggs from three laboratory cages and from the Townsend field site, and a common pattern was observed. The hatch rate for all groups appeared to decline after an initial increase of emergence numbers; yet, only a relatively small percentage of the eggs had hatched. Noting that the sand in the pans had become compacted from top watering, the sand was loosened with a knife, which resulted in an immediate emergence of nymphs from all four pans and a high percentage of hatch through the day. Examination of the pods

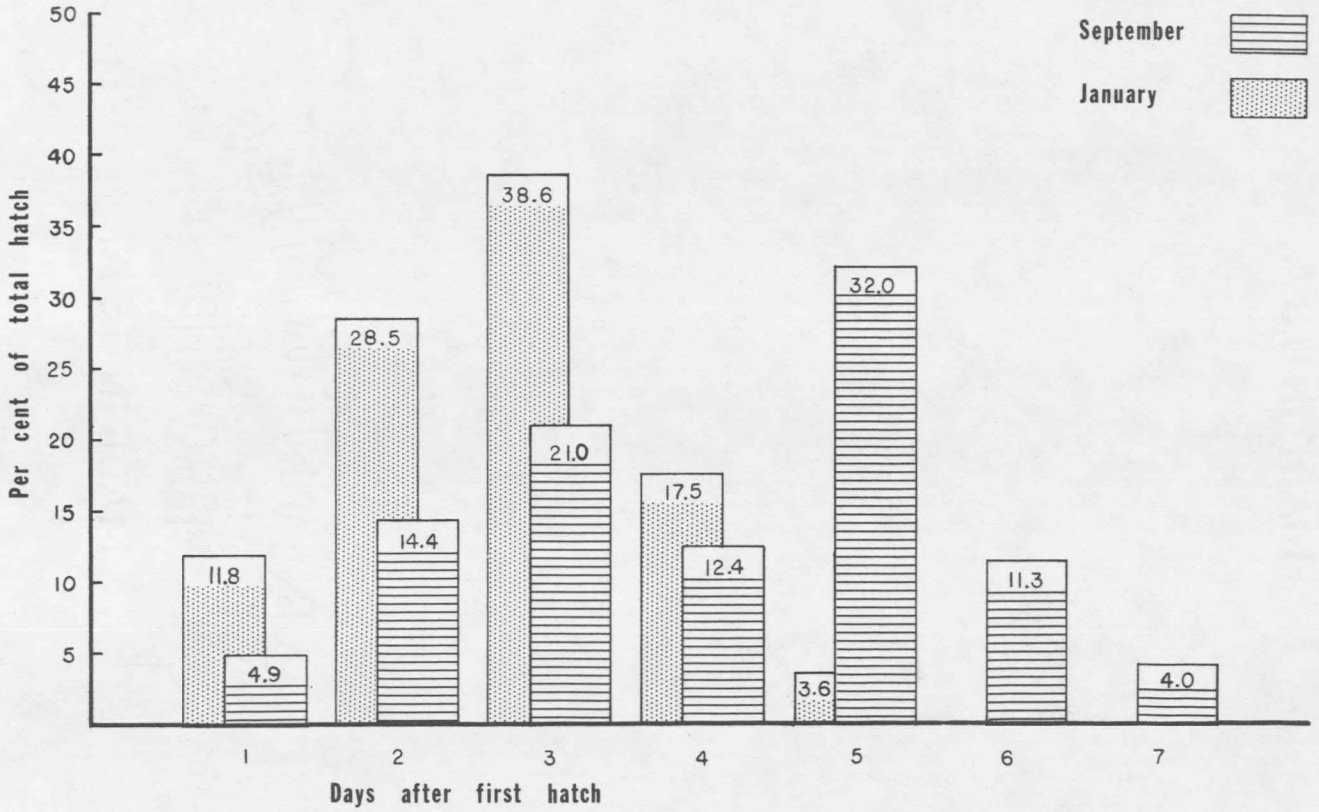


Figure 3. Hatching of eggs of *A. elliotti* in the insectary. Eggs were collected in September from the laboratory cages and from the Townsend field site; eggs collected in January were from Townsend and were maintained in loose soil. Soil around the eggs collected in September was compacted from top watering. On the fifth day after the first hatch, the hardened soil was loosened with a knife.

that failed to hatch in this and other hatching experiments revealed that occasionally nymphs emerge from the egg but are not successful in escaping from the pod, especially if the pods are in compacted soil or are very dry.

It was decided to test if soil compaction could inhibit or delay escape from the pod. Two plastic bottles 2 in. in diameter by 2 in. deep were filled with sand to within ¼ in. of the top. Egg pods from Townsend, Montana, were inserted in a normal upright position in each jar. Each jar contained 30 pods. The pods in one jar were arranged in a loose layer of sand with the anterior ends of the pods slightly above the surface of the sand. Wet sand was packed firmly around the pods in the other jar, and ½ in. of wet sand was firmly packed over the ends of the pods. Less than ½ in. of hard, dried sand had covered the pods in the pie pans in which loosening of the sand appeared to contribute to emergence success. The pods used in the compaction test had been collected on May 6, 1973 and examination of a sample of the pods revealed that diapause had terminated. These pods were incubated, as before, in the insectary room without further cold treatments. Tables 3 and 4 present the emergence data for the pods in the loose and the packed sand. The nymphs in the loose sand emerged over a period of eight days, while those in the packed sand emerged over a period of four days. Emergence percentages were only slightly lower for the packed soil. Examination of the egg pods which failed to

TABLE 3. ECLOSION OF NYMPHS FROM PODS INCUBATED IN LOOSE SAND UNDER A NATURAL PHOTOPERIOD. (91.4% of total eggs hatched)

Date	Time of Day 8:30 a.m.	11:30 a.m.	5:30 p.m.	8:30 p.m.	Daily Totals
5-12	10	0	0	0	10
5-13	7	0	0	0	7
5-14	18	0	0	0	18
5-15	41	5	0	3	49
5-16	37	9	0	0	46
5-17	20	0	0	0	20
5-18	0	0	0	0	0
5-19	9	0	0	0	9
Time Period Totals	142	14	0	3	159

TABLE 4. ECLOSION OF NYMPHS FROM PODS INCUBATED IN COMPACTED SAND UNDER A NATURAL PHOTOPERIOD. (85.4% of total eggs hatched)

Date	Time of Day 8:30 a.m.	11:30 a.m.	5:30 p.m.	8:30 p.m.	Daily Totals
5-12	0	0	0	0	0
5-13	0	0	0	0	0
5-14	19	0	0	0	19
5-15	80	0	0	0	80
5-16	11	0	0	0	11
5-17	13	0	0	0	13
5-18	0	0	0	0	0
5-19	0	0	0	0	0
Time Period Totals	123	0	0	0	123

hatch did not reveal any pods in which the nymphs had hatched and failed to emerge from the pod. Some of the pods were filled with

dirt, indicating that they were probably old pods that had hatched in the field the year before. This accounts for the 25 pods reported in the data for the packed sand and the 28 pods for the loose sand, instead of 30 pods for each test. Parasitism, sterility, and arrested development accounted for the pods failing to hatch.

Observations of the hatch from the packed sand revealed that on May 14 nymphs from three pods broke through the sand in three places. All 80 nymphs that hatched on the morning of May 15, emerged before 8 a.m. Instead of numerous holes leading from each pod through the sand, the entire crust of hardened sand had been lifted and broken. Apparently, the combined pressure of a number of nymphs at one time was sufficient to break the surface layer of hardened sand. This in turn may have released the pressure on other pods, allowing them to hatch.

Frequently, during these and other hatching experiments, groups of nymphs were seen to hatch within a few minutes of watering either the pods or the soil. Hastings of Montana State University (personal communication, 1973) stated that he had performed some preliminary tests on the effects of water on hatching and found evidence that application of water could induce hatching, if the eggs had developed to the hatching stage. Whether water activates some types of hatching mechanism or facilitates opening of the pod is not known.

Mussgnug (1972) concluded that a diurnal pattern of emergence existed in *A. elliotti*. Numbers emerging in the laboratory in the present study were found to be greatest during the hours of 6 a.m. and 12 noon. Since both temperature and light cycled daily, experiments were designed to examine these factors separately.

The cold-treated pods collected in January, 1973, from Townsend were removed from the cold room on April 10, 1973. Thirty pods were placed in each of the two hatch samplers (Figure 2, p. 22). Seventy pods were placed in the greenhouse under fluctuating conditions, as in the previous tests, to serve as controls.

Table 5 presents the data obtained from 30 pods in a hatch sampler placed in an incubator under a fluctuating temperature regime (20°C from 12 midnight to 12 noon, 30°C from 12 noon to 12 midnight) and constant dark conditions. Pods were watered and emerged nymphs removed from the apparatus daily at 8 a.m. A 10 W. red, darkroom safelight was used in examination of the pods. Behavior tests indicated that nymphs and adults of *A. elliotti* could not orient to this light. The incubator was housed in a windowless room in order to eliminate extraneous light.

A greater number of nymphs emerged at the time of the temperature increase (12 noon) than at any other time. No eggs hatched at the time of the temperature decrease. A few nymphs emerged prior to the time of the temperature increase, but more hatched after the

TABLE 5. ECLOSION OF NYMPHS INCUBATED UNDER CONDITIONS OF CONSTANT DARK AND FLUCTUATING TEMPERATURE (20°C from 12 midnight to 12 noon, 30°C from 12 noon to 12 midnight).

	Time of Day												
Date	1-3 a.m.	3-5 a.m.	5-7 a.m.	7-9 a.m.	9-11 a.m.	11-1 p.m.	1-3 p.m.	3-5 p.m.	5-7 p.m.	7-9 p.m.	9-11 p.m.	11-1 a.m.	Daily Totals
4-20	0	1	0	2	15	25	17	5	1	1	0	0	67
4-21	0	0	0	1	0	5	5	2	1	0	0	0	14
4-22	0	0	0	0	1	14	2	1	0	0	0	0	18
4-23	0	0	0	0	0	0	0	1	1	0	0	0	2
Time Period Totals	0	1	0	3	16	44	24	9	3	1	0	0	101

increase than before.

Table 6 presents the data obtained from 30 pods in a hatch sampler placed in an incubator under a fluctuating light regime (fluorescent lights in the chamber on at 12 midnight, off at 12 noon) and constant temperature (25°C) conditions. Pods were watered and emerged nymphs removed from the apparatus daily at 8:30 a.m. The data suggests a random pattern of emergence, although a large number of eggs hatched at the 4 p.m. time period.

Table 7 presents the data obtained from 70 control pods incubated under fluctuating temperature and light in the greenhouse. The greatest numbers hatched between 6 a.m. and 12 noon. Previous tests demonstrated that few or no grasshoppers emerge between the hours of 10 p.m. and 6 a.m. under these conditions. Therefore, except for occasional spot checks, data for this time period were not obtained.

The time of first emergence and the duration of the hatch of the constant temperature pods varied greatly from that of the fluctuating temperature and control pods. The pods used in all three tests of pods in the hatch sampler were removed from the cold on April 10, 1973 after 84 days. On April 20, the nymphs in the incubator under constant dark and fluctuating temperature (20°-30°C) conditions began to emerge. The hatch began ten days after removal from the cold and was completed in four days. On April 26, after

TABLE 6. ECLOSION OF NYMPHS FROM EGGS INCUBATED UNDER CONDITIONS OF CONSTANT TEMPERATURE (25°C) AND FLUCTUATING LIGHT (lights on from 12 midnight, lights off from 12 noon).

	Time of Day												
Date	1-3 p.m.	3-5 p.m.	5-7 p.m.	7-9 p.m.	9-11 p.m.	11-1 a.m.	1-3 a.m.	3-5 a.m.	5-7 a.m.	7-9 a.m.	9-11 a.m.	11-1 p.m.	Daily Totals
5-4	0	0	0	0	0	2	1	1	0	0	0	0	4
5-5	8	28	0	0	1	0	0	0	0	0	0	7	44
5-6	0	4	3	1	0	0	3	0	0	1	4	0	16
5-7	0	0	0	0	0	0	3	0	1	0	0	0	4
5-8	0	0	0	0	0	0	0	0	2	0	1	0	3
5-9	3	0	0	0	0	2	0	0	1	0	0	0	6
5-10	4	1	0	0	0	0	0	0	0	9	3	5	22
5-11	4	3	0	0	0	9	0	0	0	0	0	0	16
5-12	0	0	0	0	0	0	0	0	0	0	0	0	0
5-13	0	0	0	0	0	0	0	0	0	0	6	2	8
5-14	0	0	0	0	0	1	2	0	0	0	0	0	3
Time Period Totals	19	36	3	1	1	14	9	1	4	10	14	14	126

TABLE 7. ECLOSION OF NYMPHS FROM EGGS INCUBATED UNDER FLUCTUATING CONDITIONS OF TEMPERATURE AND LIGHT IN THE INSECTARY (natural photoperiod).

	Time of Day						
Date	8:15-11:15 a.m.	11:15-2:15 p.m.	2:15-5:15 p.m.	5:15-8:15 p.m.	8:15-10:15 p.m.	10:15 p.m.-8:15 a.m.	Daily Totals
4-26	21	84	27	13	13	2	160
4-27	59	97	12	0	0	0	168
4-28	7	41	14	8	0	0	70
4-29	7	9	5	0	0	0	21
4-30	0	7	1	0	0	0	8
4-31	0	7	0	0	0	0	7
Time Period Totals	94	245	59	21	13	2	434

16 days, the nymphs from the control pods exposed to fluctuating temperature (60°-85°F, 15.5°-29.4°C) and light in the greenhouse began to emerge, and the hatch continued for six days. Lastly, on May 4, the nymphs in the incubator under constant temperature (25°C) and fluctuating light started to emerge. The hatch began 24 days after removal from the cold and lasted 14 days. Four pods, that had not hatched by May 14, were combined with pods used in a second identical test and these four hatched by May 18.

One hundred twenty additional pods were obtained from Townsend, Montana, on May 6, 1973, to further test the effects of temperature and light on hatching. Thirty pods were placed in each of the two samplers in the incubators, without further cold treatment. The remaining pods were used in the sand compaction tests, already

described (Tables 3 & 4), and they also served as controls for the environmental conditions of the insectary.

No definite pattern of emergence was discerned in the previous test of constant temperature and fluctuating light. This test was continued by the addition of 30 pods on May 6, 1973, to the sampler. All but four of the pods, that eventually hatched from the original test group, had emerged by May 14. On May 15, nymphs began to emerge from the second test group.

Table 8 presents the data obtained from the second test of pods incubated under constant temperature (25°C) and fluctuating light and summarizes the data from both tests. Again, more nymphs emerged during the 4 p.m. time period than at any other, although nymphs hatched during most time periods. The combined data from the two tests indicate the possibility of two periods of increased emergence, one early in the dark cycle, and one early in the light cycle.

The original test of the effects of fluctuating temperature under constant dark conditions indicated that a peak of emergence occurred at the time of temperature increase. However, the hatch began at the 6 a.m. time period and reached a maximum at the 12 noon time period. The control pods in the glass-roofed room of the insectary showed a pattern of emergence beginning at 6 a.m. and reaching a peak by 11 a.m. To eliminate the possibility that the 12 noon peak in the incubator resulted from a slightly shifted cycle

TABLE 8. ECLOSION OF NYMPHS FROM EGGS INCUBATED UNDER CONDITIONS OF CONSTANT TEMPERATURE (25°C) AND FLUCTUATING LIGHT (lights on from 12 midnight, lights off from 12 noon).

	Time of Day												
Date	1-3 p.m.	3-5 p.m.	5-7 p.m.	7-9 p.m.	9-11 p.m.	11-1 a.m.	1-3 a.m.	3-5 a.m.	5-7 a.m.	7-9 a.m.	9-11 a.m.	11-1 p.m.	Daily Totals
5-15	5	1	0	0	0	0	0	0	0	0	0	5	11
5-17	0	0	0	0	0	0	0	0	0	0	0	0	0
5-18	1	11	5	0	0	0	0	0	0	0	0	0	17
5-19	0	0	0	3	1	2	0	0	0	0	4	4	14
5-20	5	11	8	9	9	11	4	0	0	0	0	0	57
5-21	0	0	0	0	0	0	17*	2*	1*	—	—	—	20*
Time Period Totals	11	23	13	12	10	13	4	0	0	0	4	9	99 + 20* (119)

*Clock stopped.

Combined Totals of Tables 6 & 8	30	59	16	13	11	27	13	1	4	10	18	23	

of emergence, 30 pods were placed in the hatch sampler in the incubator on May 6, 1973, and conditions established as before, except that the temperature increased from 20° to 30°C at 12 midnight and decreased to 20°C at 12 noon. Pods were watered and emerged nymphs removed from the apparatus at 8 a.m. as before.

Table 9 presents the data from the second test of 30 pods incubated under constant dark and fluctuating temperature (20-30°C). The greatest number of nymphs again emerged at the time of the temperature increase. This was a shift of 12 hours from the previous test. Nymphs began to emerge as early as the 4 p.m. period and the peak of emergence occurred at 12 midnight. On May 16, nymphs began to emerge during the 4 p.m. period and continued until the midnight period, but the incubator failed to change to the high temperature cycle at midnight and no nymphs emerged at that time.

Grasshoppers were emerging in the field, by May 16, making it impossible to obtain sufficient numbers of pods to conduct further tests of temperature effects on hatching. The data obtained imply that temperature may be able to initiate emergence, if the embryo has developed to the definitive stage.

The pods in the constant dark and fluctuating temperature incubator were among the first to hatch from the May 6th groups. The first nymphs emerged on May 13, and the hatch continued for six days. The pods incubated in the insectary in loose sand, started to emerge

TABLE 9. ECLOSION OF NYMPHS FROM EGGS INCUBATED UNDER CONDITIONS OF CONSTANT DARK AND FLUCTUATING TEMPERATURE (20°C)from 12 noon to 12 midnight, 30°C from 12 midnight to 12 noon).

	Time of Day												
Date	1-3 p.m.	3-5 p.m.	5-7 p.m.	7-9 p.m.	9-11 p.m.	11-1 a.m.	1-3 a.m.	3-5 a.m.	5-7 a.m.	7-9 a.m.	9-11 a.m.	11-1 p.m.	Daily Totals
5-13	0	0	0	0	0	0	6	1	0	0	0	0	7
5-14	0	0	1	3	2	23	3	0	0	0	0	0	32
5-15	0	0	6	6	13	47	2	0	0	0	0	0	74
Time Period Totals	0	0	7	9	15	70	11	1	0	0	0	0	113

one day earlier, on May 12, and finished the hatch in eight days. The pods in the compacted sand emerged on May 4, and the hatch lasted four days. The pods in the fluctuating light and constant temperature incubator were the last to emerge. The first nymphs emerged on May 15, and the duration of the hatch was 12 days.

Discussion: Roemhild (1965) reported that diapause termination required a minimum of 50 days of cold at 9-10°C. Mussgnug (1972) found 80 days of cold at 3-5°C to be more effective than 50 days for diapause termination. He found that embryos completing blastokinesis but failing to hatch occurred in similar percentages for both groups and concurred with Roemhild (1965) that hatching and diapause termination may be controlled by two independent mechanisms.

It appears that hatching in *A. elliotti* may follow a circadian rhythm under natural conditions. Hatching was not observed in the field, but fluctuating temperature and light conditions in the insectary approximated those of the field. Hunter-Jones (1966) reported a circadian rhythm for emergence in *Schitocerca gregaria* Forsk, (Acrididae). The work of Mussgnug (1972) and the present study demonstrate a maximum of hatching numbers from 6 a.m. to 12 noon in the insectary.

Scott (1936) suggested that fluctuating environmental factors such as temperature, light, barometric pressure, relative humidity, electric potential, and electric conductivity of air may be

responsible for diurnal rhythms. He concluded that light and temperature, because of the magnitude of their daily changes, were the most important factors. Harker (1961) hypothesized that circadian rhythms may be endogenous, and that the rhythms are phased by environmental factors. Harker regards a change in light intensity as the most powerful phase setter in almost every case, and she reports that temperature-dependent rhythms have been shown to exist in *Drosophila*, *Ephestia*, *Ptinus*, and *Periplaneta*. She concluded, "temperature fluctuations do not appear to act as strongly or as generally as do light fluctuations."

Scott (1936) and Moriarty (1959) noted an increase in the eclosion of *Ephestia kühnrella* Zell. with a decrease in temperature. Scott induced a 16 hr. eclosion cycle in *Ephestia* which followed a 16 hr. temperature cycle. The cycle reverts to 24 hrs. under constant temperature; the timing of the rhythm determined by the time of the last temperature decrease (Moriarty, 1959). Both authors concluded that an external factor (a change in temperature or light intensity) regulates an endogenous rhythm to maintain a peak of emergence at the correct time of the day.

Temperature appears to be important in triggering the emergence of *A. elliotti*, although moisture, light, or other factors may be important. The occurrence of hatching before the temperature increase, suggests the existence of an endogenous rhythm phased by

the previous temperature increase. However, the lack of a peak of emergence, when the incubator failed to increase the temperature on May 16 suggests an initiating effect of temperature on emergence.

Light intensity may be important to *A. elliotti* in combination with temperature for timing hatching. Behavioral experiments indicate that fluorescent light is not as attractive to *A. elliotti* as other sources of light (see section of this paper on visual, photic, and thermal responses). It is possible that the fluorescent lights in the incubators are not of the proper intensity or wavelength of light to phase emergence rhythms. It is probable that only a minute amount of light reaches the eggs in a pod in the field, since the pods are about 1 in. below the surface of the soil. Although Pittendrigh and Bruce (1959) indicated that minute amounts of light could establish the time of hatching in *Drosophila*, it is probable that temperature is more important under field conditions than light for timing the emergence of *A. elliotti*.

The two increased periods of emergence early in the light cycle and early in the dark cycle of the constant temperature incubator may have been caused by light or temperature. It is possible that a change in light intensity can trigger an emergence cycle. It does not seem probable that either an increase or a decrease in light intensity should initiate a cycle of hatching. Under 'normal' conditions in the laboratory, grasshoppers do not hatch during the dark

hours as occurred in the incubator. The constant temperature of 25°C in the incubator is not accurate. The compressor of the incubator is needed to cool the interior of the cabinet during the lights on period since fluorescent lights generate heat. Heaters are often needed during the lights off period to maintain 25°C since a source of heat is removed when the lights are turned off. These changes cause temperature fluctuations at the beginning of each cycle, which may be responsible for the observed increases of emergence.

II. Humidity Experiments

Nymphs of *Aulocara elliotti* frequently were unable to shed the pro-nymphal exuvium when conditions in the laboratory were very dry. Some nymphs died within the exuvium; many were unable to free their metathoracic legs, which greatly hampered movement. Older nymphs occasionally experienced the same difficulties at each ecdysis. Riegert (1958) reported that nymphs of *Camnula pellucida* (Scudd.) often died in the field because they were unable to rid themselves of the pro-nymphal skins on hot, dry days. He also observed that exuviae were frequently piled in dense clusters under succulent weeds, where the microclimate is more humid than in areas of sparse or dry vegetation. His experiments on the humidity preferences of *C. pellucida* and *Melanoplus bivittatus* (Say) indicated that nymphs preferred dry conditions until the time of ecdysis, when a preference for moister conditions was manifested.

Laboratory hatched and reared nymphs and adults of *A. elliotti* were used as test subjects for humidity tests of the present study. These grasshoppers were kept in a room of the insectary 29.4 ± 2°C and 20-40 percent relative humidity. Grasshoppers were conditioned at 25 percent relative humidity and 24°C for four hours prior to testing. Newly emerged nymphs were tested immediately upon hatching without prior conditioning.

All tests were conducted in the humidity chamber described in the Materials and Methods section, p. 12. Nymphs of each of the five instars and adults of both sexes were exposed in groups of 15-20 to a choice of less than 10% and greater than 95% relative humidity. Riegert (1959) found that the index of reaction for *C. pellucida* increased as the difference between alternative humidities increased with a maximum at 0% and 90% relative humidity.

Groups of *A. elliotti* were introduced into the center of the apparatus and allowed to settle for five minutes. Preliminary observations indicated that within 20 min. the grasshoppers tended to settle in basking positions. Position records were made at 25 and 45 min. after the introduction of the animals. Tests were conducted at the beginning, middle, and end of each stadium. Nymphs that had molted within 12 hrs. of testing were considered to be representative of the earlier stadium. Nymphs tested 3-4 days after the previous ecdysis were categorized as mid-stadium. Each stadium

normally encompassed 6-10 days, although some third instar nymphs unexpectantly completed that stage in four days. Late stadium nymphs were determined by the length of time since the previous molt, by physical appearance, and by behavioral clues such as decreased feeding activities. These nymphs could usually be identified within 24 hrs. of the ensuing ecdysis. Some of the late stadium grasshoppers molted during the tests. Groups containing individuals which were observed to molt during a test are included in the category 'transition stage' in the tables.

The index of each reaction was calculated from the formula $\frac{100(D-W)}{N}$, in which D is the number of position records from the drier side, W is the number of position records from the wetter side, and N is the total number of observations (Bentley, 1944). This is a variation of the "excess percentage of reaction" of Gunn and Cosway (1938). Index values range from -100 to +100; 0 percent indicates no reaction; a negative value indicates a preference for the higher humidity; a positive value indicates a preference for the lower humidity.

A few *A. elliotti* were observed in the narrow transition zone between the dry and the wet side of the chamber during most tests. The number N is the total number of position records (wet + dry + transition). This value adjusts the index of reaction to account for grasshoppers in the transition zone.

Table 10 summarizes the humidity reactions of first instar

TABLE 10. DISTRIBUTION OF FIRST INSTAR NYMPHS IN THE ALTERNATIVE HUMIDITY CHAMBER (Temperature 32°C, relative humidities <10% and >95%, nymphs tested within 8 hrs. of eclosion, January 13, 1973).

Expt. No.	No. of Animals	No. of Animals in each Zone			$\frac{100(D-W)}{N}$ and $S_{\bar{x}}$
		Dry	Mid.	Wet	
1a.	17	6	-	11	-29.4
1b.	17	5	-	12	-41.2
1c.	17	4	2	11	-41.2
2a.	9	3	-	6	-33.3
2b.	9	4	-	5	-11.1
3a.	17	5	1	11	-35.3
3b.	17	5	1	11	-35.3
4a.	9	3	-	6	-33.3
4b.	9	2	1	6	-44.4
5a.	18	6	2	10	-22.2
5b.	18	7	1	10	-16.6
Total	157	50	8	99	-31.2 ± 3.23

nymphs within 8 hrs. of emergence from the pod. There appears to be a marked preference for the higher relative humidity.

Table 11 presents the data for the responses of first instar nymphs during the first half of the stadium. Whereas the nymphs preferred the higher humidity early in the stadium, this preference was not seen at 72 hrs. The humidity responses of nymphs between the first and the third days after hatching were variable.

A summation of responses to humidity by nymphs of each instar and by adults appears in Table 12. In general, a preference for

TABLE 11. DISTRIBUTION OF MID-STADIUM, FIRST INSTAR NYMPHS IN THE ALTERNATIVE HUMIDITY CHAMBER (Temperature 32°C, relative humidities <10% and >95%, nymphs tested at different stages after eclosion).

Hrs. after Eclosion	No. of Expts.	No. of Animals in each Zone			100(D-W)/N
		Dry	Mid.	Wet	
1- 4	8	42	9	94	-35.9
4- 6	8	26	5	58	-38.2
30	4	22	19	26	- 6.0*
48-50	4	27	2	28	- 1.7*
52-54	6	24	3	75	-49.0
72	2	25	5	14	+25.0

*Although the index value is negative, grasshoppers moved farther into the dry zone.

the drier environment was evidenced by adults and mid-stadia nymphs. About 20 hrs. prior to ecdysis, a preference for the wetter environment began to be manifested. This response continued through the molting period until approximately 12 hrs. after the molt. The responses of fourth instar nymphs to relative humidities demonstrated strong changes in movement direction at each of the three observed periods of the stadium. These movements were more pronounced than in earlier instars, both in regards to position numbers and to position distance from the transition zone.

Table 13 shows the changes in response to humidity conditions which occur if the grasshoppers were left in the alternative chamber for several hours without food. The initial response increased in intensity or reversed within 1-4 hrs. If the initial movement was

TABLE 12. DISTRIBUTION OF NYMPHS AND ADULTS IN THE ALTERNATIVE HUMIDITY CHAMBER (Temperature 32°C, relative humidities <10% and >95%, nymphs and adults tested at different periods in the ecdysial cycle).

Stage	Period	No. of Animals in each Zone			100(D-W)/N
		Dry	Mid.	Wet	
	Early	118	22	251	-34.0
First	Mid.	74	26	68	+ 3.6
Instar	Trans.	35	13	58	-21.7
	Early	49	5	95	-30.8
Second	Mid.	19	5	19	0.0
Instar	Late	15	5	26	-23.9
	Early	-	-	-	-
Third	Mid.	100	7	74	+14.4
Instar	Mid.-Late	34	5	37	- 3.9
	Late	52	6	61	- 7.6
	Early	9	3	16	-25.0
Fourth	Mid.	101	4	64	+21.8
Instar	Late	16	3	45	-45.3
	Early	16	2	32	-32.0
Fifth	Mid.	11	1	37	-53.0*
Instar	Mid.	25	3	20	+10.4†
	Late	18	3	78	-60.6
	Early	3	0	15	-66.6
	Mature	44	3	27	+22.97

*Food was very dry, same group ate fresh vegetation and reversed response (†).

TABLE 13. DISTRIBUTION OF NYMPHS AND ADULTS IN THE ALTERNATIVE HUMIDITY CHAMBER (Temperature 32°C, relative humidities <10% and >95%, nymphs and adults left in choice chamber for several hours).

Stage	Time after Introduction	Expt. No.	No. of Animals in each Zone			100(D-W)/N
			Dry	Mid.	Wet	
Adult	20 min.	1a.	6	1	5	+ 8.3
	40 min.	1b.	7	0	5	+16.7
	60 min.	1c.	8	0	4	+33.3
	120 min.	1d.	7	2	3	+33.3
Fifth	20 min.	2a.	4	0	12	-50.0
	40 min.	2b.	2	1	14	-75.0
	60 min.	2c.	5	0	11	-37.5
	120 min.	2d.	8	1	7	+ 6.3
Fourth	20 min.	3a.	10	1	10	0.0
	40 min.	3b.	9	0	12	-14.3
	240 min.	3c.	9	0	12	-14.3
	300 min.	3d.	5	0	15	-50.0
Third	40 min.	4a.	7	2	8	- 5.9
	60 min.	4b.	9	1	6	+18.7
	90 min.	4c.	11	0	6	+31.2
	20 min.	5a.	11	0	16	-29.4
	40 min.	5b.	15	1	11	-23.5
	240 min.	5c.	14	0	12	+12.5
Second	20 min.	6a.	3	2	10	-46.6
	40 min.	6b.	7	1	6	+ 7.1
	60 min.	6c.	9	2	3	+42.9
	20 min.	7a.	3	3	10	-43.7
	40 min.	7b.	5	1	9	-26.7
	120 min.	7c.	7	1	7	0.0

slight, continued exposure to the alternative conditions often induced a directed movement. If the initial movement was pronounced, the response frequently waned or reversed with continued stimulation.

Discussion: *A. elliotti* responds to a choice of relative humidity in a manner that closely parallels that reported for *C. pellucida* and *M. bivittatus* (Riegert, 1958; 1959; 1960). *A. elliotti* usually demonstrates a normal preference for drier conditions. A movement to areas of higher humidity conditions is seen at the time of ecdysis. The preference for dry conditions is not unexpected in view of the semi-arid areas that this species inhabits. Riegert (1958) suggested that a preference for a moist environment at the time of molting is a means of preventing rapid evaporation of the molting fluid. He concluded that the hygropositive response during the molting process appears to be a logical consequence of the physiological hyperactivity involved in this process.

Riegert (1958) demonstrated that deprivation of food and water induced a preference in adult grasshoppers for a higher humidity, probably as a result of desiccation. *A. elliotti* became hygropositive after being restricted to a diet of dry vegetation without access to additional water. This preference could easily be reversed by allowing the animals to feed on fresh vegetation (Table 12).

Ellis (1951) reported cessation of feeding one day or more before molting in *Locusta migratoria migratorioides* (R. and F.). This appears to occur in *A. elliotti* from observations during both the humidity and olfactory tests. Starvation, molting, and dry

vegetation can produce a hygropositive response in grasshoppers. A self imposed starvation period occurs before molting. It may be possible that a reduced intake of unbound water, normally obtained through feeding, may influence the movement to areas of high relative humidity during ecdysis.

A preference for conditions of higher relative humidity may insure a better chance to shed the exuvium by reducing evaporation of molting fluids. However, it is doubtful that this response is important in *A. elliotti* for removal of the pro-nymphal skin. Observations of *A. elliotti* in the laboratory indicate that the nymphs do not move away from the area of the egg pod before beginning the movements that free them from the pro-nymphal exuvium. Normally, these movements are instigated as soon as the grasshoppers have emerged from the pod. In fact, the grasshoppers seem to be incapable of walking until the old cuticle is shed or at least removed from the first two pairs of legs. The hygropositive response after molting may insure that the newly emerged nymphs are not desiccated too rapidly before the new cuticle has hardened and may benefit those nymphs which are not able to entirely shed the pro-nymphal exuviae during their initial efforts.

Observations of the humidity responses of *A. elliotti* in the alternative chamber suggested that the response may be a kinetic rather than a tactic response. Movement in the moist zone appeared

to consist mainly of random wandering. Activity and displacement distances in the moist zone appeared to be greater than in the dry zone, although no measurements of activity were made. Kennedy (1937) ascribed kinetic reactions to *Locusta migratoria*. Riegert (1959) concluded that humidity reactions in *C. pellucida* and *M. bivittatus* were composed of two types of responses: (1) a klino- or ortho-kinetic response resulting in increased movement in the moist conditions; (2) a klino-tactic response producing movement away from the moist environment.

An actograph is frequently used to investigate kinetic responses to humidity. The standard form of the apparatus is a box pivoted on a knife edge (Gunn and Kennedy, 1936). The assumption is made that animals usually travel round and round the box. The device only records movement along the longitudinal axis but not movements across the floor. The longitudinal movements are considered to be representative of the total movements of the animal. However, *A. elliotti* demonstrated great individual variation in response to a boundary such as the side of a box or a cage. Some individuals avoided contact with the sides of a container or turned away at the first contact. Others spent long periods trying to climb a barrier or remain sitting on or beside a barrier. Some grasshoppers became highly agitated when they encountered an unclimbable boundary such as the plastic sides of the cages. Repeated efforts to climb a

smooth surface appeared to subside only after reaching an apparent state of exhaustion. It was concluded that animal to animal variations in activity in the standard actograph would be difficult to separate from variations in activity induced by humidity.

A rotating ball actograph (Kerfoot, 1968) suspended on a column of air (Carrel, 1972) would eliminate the problem of walls or boundaries as stimuli. This apparatus consists of a freely rotating ball on which a tethered animal is placed. Movements of the animal cause the ball to turn. A brush mounted on a rubber diaphragm is deflected by rotation of the ball and touches a series of electrical contacts which activate pen recorders. This actograph, in theory, can produce a record of the movements of an animal through 360° of turning. This is accurate only if the animal always moved in a forward direction. Kerfoot (1968) reported that the apparatus was useful for monitoring cockroach activity. *A. elliotti* spent long periods walking backwards when placed on a ball. This animal frequently backs up when it encounters another grasshopper or an obstacle, but extended periods of backwards movements were not observed under natural conditions, such as in the field. Other species of grasshoppers are also reported to back up a few steps. Riegert (1959) reported that nymphs of *C. pellucida* and *M. bivittatus*, when about to enter the moister zone of an olfactometer, paused, extended and waved their antennae, and then backed up.

The backwards walking of *A. elliotti* on a ball appeared to be induced by the tether fastened to the thorax of the insect to insure that it remained in position on the ball. An insect lifted from the ball and placed on soil continued to pull backwards against the tether. Repositioning of the tether did not lessen this response.

The original apparatus (Kerfoot, 1968) used a tennis ball as the substratum on which a tethered insect walked. It was postulated that a ball with a larger surface area might be better to use with *A. elliotti* so that the insect would be sitting on the ball rather than be hanging over it. A 3 in. styrofoam ball was hollowed in the center to reduce weight and was tested as a substratum. The insects were able to maintain a firm grip on this substance and often sat quietly on the ball. Unfortunately, activity alternated between running forwards, backwards, and chewing on the ball. Consequently, actograph experiments on the kinetic effects of humidity were terminated.

Phipps (1963) reported good results monitoring insect activity in an activity apparatus which utilized narrow beams of infrared light focused on phototransistors to record movements in a test arena. Intersection of a beam of the infrared light activated a pen recorder, and the insects did not appear to be capable of perceiving the long wavelength (infrared) light. Edge or barrier effects could be minimized in this type of apparatus by enlarging

the arena, and a natural substratum such as soil could be used. Accuracy of position records depends on the number of intersecting light beams. The insect would not be tethered or hampered in its movements. Construction of such an apparatus was not within the scope of the present study, but undoubtedly it would be very useful for monitoring locomotor activity in response to controlled stimuli.

III. Olfactory Experiments

Many phytophagous insects lay their eggs on or near food plants or where random foraging will quickly discover food plants. However, many grasshoppers oviposit in arid areas with sparse vegetation (Dadd, 1963). *Aulocara elliotti* lays its eggs in areas of exposed ground surface (Mussgnug, 1972). An accurate method of food location would be advantageous to the newly hatched nymphs.

Attraction to food plants from a distance is probably a result of visual or olfactory clues. The response of grasshoppers to visual patterns and forms has been demonstrated by several workers (Mulkern, 1969). Evidence for the ability to locate food by olfactory responses has been contradictory for the acridids (Dadd, 1963).

Experiments by Haskell *et al.* (1962), Kennedy and Moorehouse (1969), and Moorehouse (1971) provide persuasive evidence that olfaction aids location of distant food plants by *Schistocerca gregaria* Forskal. Grasshoppers generally walked downwind in slow air currents in the absence of odor. Grasshoppers walked upwind in

the presence of an attractive odor or when highly excited (Kennedy and Moorehouse, 1969). Starvation for at least two hours was necessary to elicite an upwind movement in response to food odor by a basking nymph (Haskell *et al.*, 1962). All larval instars and adults moved upwind to bruised grass, but the response was greatest in the first half of each instar (Moorehouse, 1971).

Preliminary tests of olfactory responses of *A. elliotti* were conducted using a modified Y-tube olfactometer (Hocking and Lindsay, 1958) attached to the Tilt Table. Two air streams, directed towards each other from opposite sides of the circular arena, produced a diamond shaped pattern of air dispersal as shown in Figure 4. Phenothalein impregnated paper laid on the floor of the arena and subjected to air streams containing ammonia emitted from the vents produced a graphic representation of the air flow. A tightly fitted clear plastic cover over the arena eliminated extraneous air currents. Air was drawn into the apparatus by a vacuum pump. Air from the room was drawn into a ¼ in. tube and then passed through $CaCl_2$ drying salts, activated charcoal, and distilled water, and then into two separate lines which extended to the arena where each line terminated in a 25 ml. Erlenmeyer flask with an inlet and an outlet tube. Each outlet tube was connected to the arena wall and contained a needle valve to control the rate of air flow. Odor sources to be tested, such as whole grass stems, were placed in one of the two flasks and

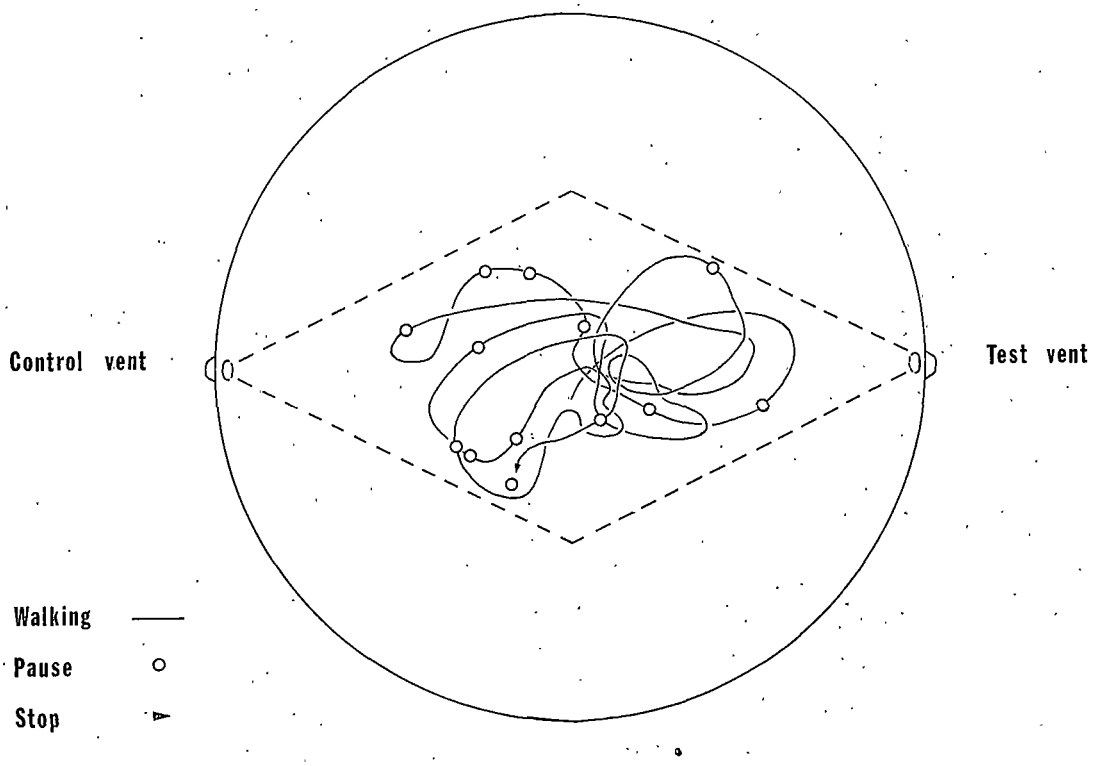


Figure 4. Movements of an adult female of *A. elliotti* in the Y-tube olfactometer. Air emitted by the control vent was filtered to remove odors; air from the test vent contained odors from fresh western wheatgrass *(Agropyron smithii)*. The dashed line indicates the boundaries of the air streams.

the other flask was left empty to serve as a control of odor-free air.

It soon became apparent that this apparatus had limited application. Grasshoppers, tested individually or in groups, demonstrated variable responses. Some grasshoppers assumed fixed positions on the screens over the vents, while others made repeated movements towards and away from the air vents. Final position data were of limited use because of these responses.

Movement scoring also proved to be of limited value. 'Pottering' or random wandering increased with time, probably as a result of saturation of the air in the arena with the test odor. Air turbulence at the point of contact of the two air streams and along the sides of the arena further complicated tests. However, individual adult grasshoppers starved overnight, placed in the arena, and continuously observed, showed a tendency to frequently approach a vent emitting western wheatgrass odor *(Agropyron smithii* Rydb.*)* and to remain within the diamond shaped pattern of air flow, turning whenever the boundary of the air stream was encountered (Figure 4).

A wind tunnel based on the design of Haskell *et al.* (1962) was constructed in order to more effectively pursue olfaction investigations. Air was drawn through a large rectangular box by an exhaust fan. Air flowed in across the entire width of the box at one end and exhausted in like manner at the other end, resulting in a highly

directional, relatively non-turbulent air flow. Odors were presented by placing the source of the odor (whole grass, filter papers impregnated with plant extracts, with distilled water, and with liquid chemicals; or dry chemicals on watch glasses) across the width of the tunnel.

Both individuals and groups of *A. elliotti* were tested in the tunnel. Unless otherwise specified, all experiments were conducted at sand and air temperatures of 30°-34°C, wind speed 2 ft./sec., and relative humidty 20-39 percent. Grasshoppers were starved 24 hrs., held at 20°C, and given free access to water. Unfed hatchlings were tested at 24 hrs. and 48 hrs. Individual grasshoppers were introduced into the center of the tunnel and allowed to come to rest. After remaining stationary for a minimum of 1 min., the grasshopper's position and orientation were recorded; the air flow was then initiated, and the responses recorded for a period of 20 min. Timing and position of all halts or changes in direction were noted. This technique differed from that of Haskell *et al.*. (1962) in that these workers terminated their observations of *Schistocerca* when the nymphs reached either the upwind or downwind screen or after 5 min. had elapsed. However, single grasshoppers of *A. elliotti* often sat for 1-2 min. or more before initiating movement. Also, individuals were sometimes seen contacting a screen, immediately turning, and then proceeding to the opposite screen, where they frequently remained.

This was especially true if a food odor was being tested and the downwind screen was the first encountered. Some individuals remained in a 'fixed' position on the first screen encountered for the duration of the test. Tests of single grasshoppers provided information about specific responses to wind and odor, but the 'screening' of substances for attraction or repulsion and the probability tests of upwind and downwind movements were more readily accomplished with groups of individuals. The long period of time involved in the testing of individuals precluded the testing of numerous substances or factors, especially for the instars.

Groups of 35-45 nymphs and 15-25 adults were tested. Nymphs were introduced into the center of the tunnel and allowed to settle for 15 min. If the group was used for more than one test without removal from the tunnel, the grasshoppers were herded to the middle of the apparatus and allowed to re-settle for 10 min. Herding was accomplished utilizing the visual evasive reaction of the nymphs to a moving hand. Kennedy and Moorehouse used this technique for herding *Schistocerca* (1969).

Scoring was done by counting the numbers of grasshoppers crossing the center line of the apparatus for 10 min. before and after application of the stimulus. Preliminary tests showed that movements across the center line were random in the absence of any experimentally introduced stimulus.

Groups of adults were handled in a slightly different manner. If allowed to settle for 15 min. and then scored for 10 min. prior to application of the stimulus, many of the grasshoppers were found perched on the screens. Therefore, two plastic cylinders 9 in. in diameter were set in the tunnel, one on each side of the center line. Equal numbers of adults were placed in each cylinder; a screen cover was placed over each cylinder, and the adults were allowed to settle for 15 min. Each cylinder was carefully lifted after 15 min., leaving the grasshoppers sitting on the sand. Usually only a few grasshoppers showed any signs of disturbance caused by removal of the cylinder. The lid of the tunnel was lowered and the stimulus applied after one minute. Scoring was again accomplished by counting numbers crossing the center line after application of the stimulus. If a group of adults was used for more than one test without removal from the tunnel, the grasshoppers were slowly herded to the center of the tunnel and allowed to re-settle for 2 min.

The method of handling nymphs and of scoring was based on that of Haskell *et al.* (1962). They counted numbers of nymphs crossing a center line every 30 sec. for 5 min. before and after initiation of the stimulus. Chi square (X^2) tests were applied to all tests to evaluate the significance of the results. The authors presented the following reasons for their method of analysis:

> This procedure had several advantages; it indicated whether a 'slight drift' was due to a few insects moving, with the majority standing still, or to much movement in both directions with a slight bias towards one. It also reduced the effects of 'apparatus bias' in the scores and removed from account those hoppers which had got into positions, e.g. on the end filters, or in corners, in which stimuli did not provoke movements...

Contingency X^2 tests were applied to the numbers of *A. elliotti* moving upwind and downwind before and after application of the stimulus. Simple X^2 tests of upwind and downwind movement numbers after presentation of a stimulus were utilized for tests of adults in which movements before initiation of the stimulus were not recorded.

Preliminary experiments revealed a tendency to move downwind, when wind was the only stimulus (Table 14). Figure 5 summarizes the data obtained from 47 unfed first instar nymphs one to two hrs. after emergence, 24 hrs. after emergence, and 48 hrs. after emergence. Movement in both upwind and downwind directions increased with the application of wind or with a rise in wind speed. The newly emerged nymphs appeared to be slightly less responsive, in terms of locomotor activity to the lower wind speeds.

At a constant air speed of 2 ft./sec., fourth instar nymphs and adults did not demonstrate a general inclination to move downwind in the absence of other stimuli. Tests of individual grasshoppers, both starved and unstarved, indicated that air speeds of 4 ft./sec. or greater were necessary to produce downwind movements in most adults and in the fourth and fifth instars. However, no tendency to move

TABLE 14. REACTIONS OF NYMPHS AND ADULTS TO WIND SPEEDS OF 2 FT./SEC. ALL TESTS CONDUCTED WITH GROUPS OF 30-40 GRASSHOPPERS, AIR AND SAND TEMPERATURES 30°C.

Expt. No.	Condition of Grasshoppers	Stimulus Presented	Movement Scoring: Up-wind	Movement Scoring: Down-wind	Probability
1	Unfed		12	20	Downwind
2	Hatchlings,		0	4	movement,
3	48 hrs.	Wind	4	6	$X^2=9.29$, df 1
4	after		0	11	$P<0.01$
5	hatching		3	2	
			19	43	
1	Fourth		3	3	Random
2	instar nymphs,		0	1	movement,
3	fed	Wind	2	3	$X^2=0.04$, df 1
4	Same,		6	4	$0.90<P<0.95$
5	starved 48 hrs.		2	3	
			13	14	
1	Adults		7	2	Random
2	fed		7	8	movement,
3	Same,		7	7	$X^2=0.35$, df 1
4	starved 48 hrs.		25	21	$0.50<P<0.70$

upwind in the absence of an attractive odor appeared, movements in both directions tending to balance or to show a downwind bias.

Dadd (1963) suggested that young *Schistocerca* nymphs may lack the facility to follow odor signals from some distance to their source, while the latter instars, fourth, fifth and adult, readily locate the source. Moorehouse (1971) showed that all instars of this species were equally adept at finding an odor source. The nymphs used in his experiments were fed to repletion, starved 17 hrs., and then tested

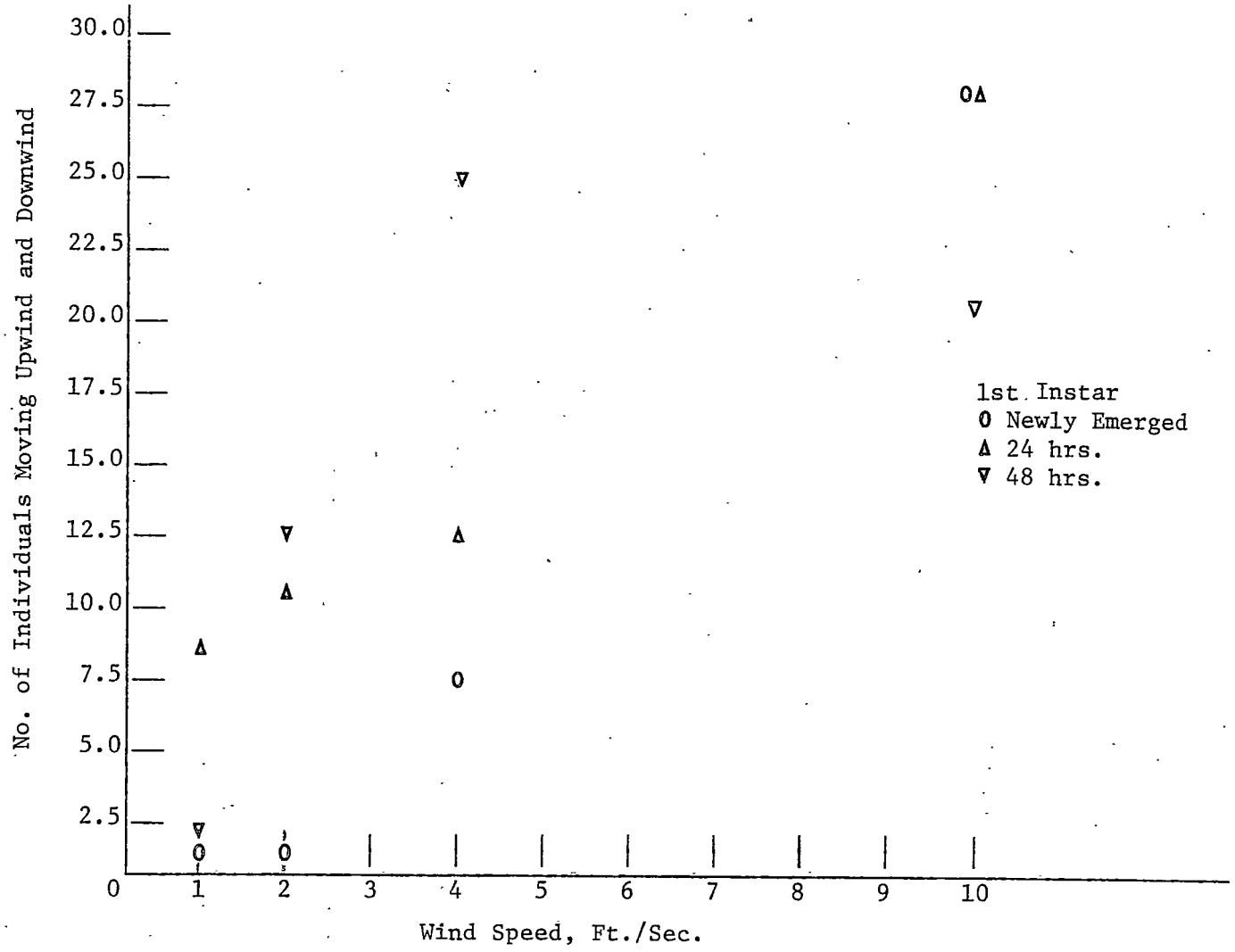


Figure 5. Responses of Unfed Hatchlings to Four Speeds of Wind.

for response to bruised grass.

Neither author tested the hypothesis presented by Dadd (1963) "As hatchlings have never fed, it may be envisaged that until they sample whatever is nearest to hand they may not learn the appropriate stimulus signalling food." Dadd based his idea on the observation that unfed hatchlings did not respond to bundles of grass wrapped in muslin and placed in a cage.

To test this hypothesis, *A. elliotti* nymphs, which had hatched during a 2 hr. period, were collected in groups of 35-45, held in a 9 in. circular cage on dry sand at 20°C without food, and given free access to water from a damp sponge. Response to food odors was observed at 24 and 48 hrs. after eclosion.

Western wheatgrass *(Agropyron smithii)* and *Poa* species, in particular sandberg bluegrass *(Poa secunda* Presl.*)*, appear to be the main food plants of *A. elliotti* (Anderson and Wright, 1952; Pfadt, 1949). In the laboratory, *A. elliotti* readily accepts and appears to thrive on a diet of Kentucky bluegrass *(Poa pratensis* L.*)* and domestic rye *(Secale cereale* L.*)*. Domestic wheat *(Triticum aestivum* L.*)* is eaten with reluctance and development is slower.

These grasses were grown in the insectary and were used to test the ability of unfed hatchlings to find a food source by odor clues. Grasses were clipped and bruised by beating with a pestle until each blade of grass was broken in 3-4 areas. The grasses were clipped and

bruised immediately before testing. Eight to ten whole stems of grass were used in all experiments, and fresh grass was used for each test. The bruised grass was spread across the full width of the air input to the wind tunnel for testing.

The nymphs showed little or no reaction to food odor 24 hrs. after hatching. Nymphs moved upwind to all the tested grass odors 48 hrs. after hatching. The response to domestic wheat odor was not as pronounced as in the other grasses (Table 15). Holding nymphs for 60 hrs. or more without food resulted in high mortality, probably due to starvation.

The effect of water vapor as a stimulus was included in these tests to see if changes in relative humidity produced by the moist grass or if effects of water as a constituent of the olfactory source accounted for the upwind movement. It can be seen from the data in Table 15 that no response to water vapor could be demonstrated. Haskell *et al.* (1962) reached the same conclusion after testing the effects of water vapor on *Schistocerca*.

Since starvation for 2 to 4 hrs. was necessary for the manifestation of the upwind olfactory response to food odors in *Schistocerca* unless the nymphs were agitated (Haskell *et al.*, 1962; Moorehouse, 1971; and Kennedy and Moorehouse, 1969), starvation effects on *A. elliotti* were investigated. The strength of the olfactory reaction depended on the degree of starvation. An olfactory response was

TABLE 15. REACTIONS OF UNFED HATCHLINGS OF *A. ELLIOTTI* TO ODORS FROM GRASSES AND TO WATER VAPOR. ALL TESTS CONDUCTED WITH 35-40 NYMPHS, AIR AND SAND TEMPERATURES 30°C, WIND SPEED 2 FT./SEC., 48 HRS. AFTER HATCHING.

Expt. No.	Stimulus Presented	Movement Scoring: Start Up-wind	Start Down-wind	Finish Up-wind	Finish Down-wind	Probability
1	Wind + Water Vapor	1	1	1	0	Random movement, X^2=1.05 df 1 0.30<P<0.50
2		4	3	5	6	
3		0	1	1	1	
4		7	4	14	20	
		12	9	21	27	
1	Wind + *Triticum aestivum* L.	2	1	15	13	Random movement, X^2=0.81* 0.30<P<0.50
2		2	2	9	4	
3		2	3	3	1	
4		2	2	8	3	
		8	8	35	21	
1	Wind + *Secale cereale*	3	5	9	3	Upwind movement, X^2=10.50 df 1 P<0.01
2		1	2	10	1	
3		1	2	14	2	
4		2	3	11	7	
		7	12	44	13	
1	Wind + *Agropyron smithii*	1	2	14	3	Upwind movement, X^2=8.00 df 1 P<0.01
2		2	2	15	0	
3		1	0	6	2	
4		2	3	10	4	
		6	7	45	9	
1	Wind + *Poa pratensis*	0	1	22	10	Upwind movement, X^2=6.78 df 1 P<0.01
2		3	4	13	1	
3		0	0	11	2	
4		2	3	7	5	
		5	8	53	18	

*Other tests indicated a slight upwind response.

manifested after 3 to 4 hrs. of starvation, and more insects responded as the period increased. An exception, as indicated before, occurred in unfed hatchlings in which the olfactory reaction was not manifested for 24 hrs. or more. It is possible that at 24 hrs. hatchlings may still be obtaining adequate nutrition from yolk reserves in the gut but that by 48 hrs. these reserves are depleted.

In view of the attraction produced by western wheatgrass and other grasses and reports of chemical attractants for other acridids (Haskell *et al.*, 1962, Barnes and McLellan, 1960; Skoog *et al.*, 1960; Slifer, 1954, 1955, 1956), several stimuli were tested with *A. elliotti*; the results are shown in Table 16.

Several of the above authors reported various forms of valeric acid to be highly effective repellants. In two series of tests with iso-valeric acid, the initial test for each series showed a tendency to move downwind ($P<.05$), but subsequent tests did not. However, the odor of the acid rapidly permeated the entire apparatus and the laboratory, even with exhaust fans in operation, and the sand in the tunnel had to be discarded because it had absorbed the odor. Therefore, it is probable that the entire apparatus acted as an odor source after the initial test. Since it took over a week to rid the laboratory and the apparatus of the valeric acid odor, the tests were not repeated.

TABLE 16. OLFACTORY REACTION OF NYMPHS AND ADULTS OF *A. ELLIOTTI* TO A VARIETY OF SUBSTANCES.

Stimulating Substance	Attraction	Repulsion	No Response
1. Grass (dry)	+ (slight)		
2. Grass (whole)	+ +		
3. Grass (bruised)	+ + +		
4. Grass (water extract)	+ +		
5. Grass (ethanol extract)			+
6. Grass (methanol extract)			+
7. Water vapor			+
8. Xylol			+
9. Ethanol			+*
10. Methanol			?**
11. Cedar Oil			+
12. iso-Valeric acid		?***	
13. Fecal material *(A. elliotti)*			+
14. Nymphs *(A. elliotti)*			+
15. Adult males *(A. elliotti)*			+
16. Adult females *(A. elliotti)*			+
17. Fecal material (cattle-dry)			+
18. Fecal material (cattle-wet)			+
19. Chloroform		+ + +	

*Very strong vapors repulse, can cause death.
**Very strong vapors cause biting motions of mouthparts
***First test indicated repulsion, succeeding tests did not.

Cattle feces was included in the stimuli examined, since it is not uncommon to find grasshoppers hollowing out cavities in dry droppings in the field. Fecal specimens that had been eaten by *Aulocara* were obtained for the tests, but no attraction could be demonstrated nor

would the grasshoppers chew or eat on the material in the laboratory cages. It may be envisaged that some factor missing in the diet of wild populations may be obtained from cattle feces, whereas this factor is present in the laboratory diet. Droppings may also be used for shade in the field.

Several extracts of grasses, in particular of *Agropyron smithii* and species of *Poa*, were prepared in an attempt to isolate an attractive principle. Extracts were prepared with room temperature solvents using 3.0 gm. wet weight of grass in 100 ml. of solvent. Methanol, ethanol, and distilled water were used as solvents. Four in. squares of filter paper were impregnated with the extracts and used as odor sources in the wind tunnel (two squares used for each test). The residue also were tested. In other insects, several attractants and some antifeedants have been identified in food plants. Hamamura (1970) demonstrated that mulberry leaves contained three important factors governing the feeding behavior of silkworm larvae *(Bombyx mori* L.): an attractive factor, a biting factor, and a swallowing factor. A methanol extract of mulberry leaves contained two biting factors, one ether soluble and one water soluble.

Methanol and ethanol extracts of grasses were not attractive to *A. elliotti*. Strong vapors of methanol (emitted immediately after soaking a filter paper in methanol) produced an alteration in the behavior of the grasshoppers. Pottering increased, antennae waving

increased, and mouth parts were rapidly moved in 'biting' motions.

In order to test if the different extracts contained a phagostimulant, filter papers were impregnated with the ethanol, methanol, and water extracts. Filter papers soaked in ethanol, methanol, and distilled water served as controls. These papers were tested in pairs and groups by placing them in a circle 12 in. in diameter on the glass floor of the arena of the Tilt Table and releasing groups of 20 grasshoppers in the center of the circle. Only the papers impregnated with distilled water and the distilled water extract showed any conspicuous attraction and biting of the edges.

It was considered desirable to locate the organs involved in the olfactory responses. In view of the work of Slifer (1955) and Haskell *et al.* (1962), the antennae were considered to be the most likely mediators of the reactions. Orientation to wind borne odors may be mediated by antennal chemoreceptors or by antennal mechanoreceptors. Haskell found that coating the antennae with Vaseline ® petroleum jelly suppressed but did not abolish the upwind response to grass odor, while restricting movement of the flagellum by cementing it to the pedicel did not affect the upwind response. As Kennedy and Moorehouse (1969) pointed out, this treatment does not rule out orientation to wind by some type of antennal mechano- reception. They cited work by Bayramoglu-Ergene (1968) on *Anacridium aegyptum* in which removal of the antennae resulted in depressed locomotor activity. Their experience

with *Schistocerca* also revealed a reduction of locomotor activity after antennectomy.

A. elliotti adults were antennectomized at the pedicel and vaseline applied to the wound area to cover any receptors not removed. Table 17 presents the results of these operations. Bilateral removal

TABLE 17. REACTIONS OF GROUPS OF *A. ELLIOTTI* TO WIND AND OLFACTORY STIMULI AFTER ANTENNECTOMY. ALL TESTS CONDUCTED WITH 20 GRASSHOPPERS, AIR AND SAND TEMPERATURES 30°C, WIND SPEED 2 FT./SEC.

Expt. No.	Condition of Grasshoppers	Stimulus Presented	Movement Scoring: Up-wind	Movement Scoring: Down-wind	Probability
1	Starved	Wind +	7	4	Upwind
2	48 hrs.:	grass odor,	8	3	movement,
3	unilateral	*Agropyron*	7	2	X^2=8.40, df 1
4	antennectomy	*smithii*	9	3	P<0.01
			31	12	
1	Starved		6	4	Random
2	48 hrs.:	Wind	4	6	movement,
3	unilateral		6	6	X^2=0.02, df 1
4	antennectomy		5	4	P<0.90
			21	20	

of the antennae suppressed the upwind response to western wheatgrass odor. A slight tendency to move upwind in grasshoppers starved 48 hrs. may have been due to chance (X^2=0.84; 0.30<P<0.40) or due to receptors other than the antennae mediating some response. Unilateral antennectomy did not suppress the upwind movement or result in 'circus movements' as reported by Haskell *et al.* (1962) for *Schistocerca*. As in

later tests of *Schistocerca* performed by Kennedy and Moorehouse (1969), unilaterally antennectomized *Aulocara* were more 'hesitant' and paused more often than unoperated controls, but did not move along noticably less direct upwind paths to the food odor. Typically, the *Aulocara* with one antenna pointed the intact antenna towards the odor source and whirled the antenna in a circular motion while walking, stopping occasionally with the antenna held momentarily motionless at different positions.

To further investigate orientation to food and odor, Haskell *et al.* (1962) blinded grasshoppers by applying black paint over the compound eyes or covering the head capsule with aluminum foil. These treatments abolished the downwind response to wind alone, but the nymphs performed circus motions and displayed signs of discomfort from the treatment. Therefore, further tests were discontinued with blinded nymphs, as the results were considered to be unreliable.

Adults of *A. elliotti* do not appear to be noticably disturbed by painting over the compound eyes and ocelli. Grasshoppers were 'blinded' by painting the entire head capsule with flat black enamel, being careful not to get paint on the antennae or the mouthparts. The initial response to the treatment consisted mainly of attempts to remove the fresh paint with the forelegs. These cleaning attempts were discontinued after a few minutes. The animals appeared to become well adjusted to the treatment after a few hours. Occasionally, a

grasshopper managed to get his antennae against the paint before it had thoroughly dried. This usually resulted in vigorous cleaning of the antennae. Circus movements were not performed by the blinded *A. elliotti*, although somewhat confused and hesitant locomotor activity was seen immediately after treatment.

Although electrophysiological experiments were not performed to determine if the grasshoppers were blind, the behavior of the treated grasshoppers indicated that they were effectively 'blind'. No evasive actions were taken to avoid capture by hand, unless an air current or some other clue disturbed the grasshoppers. They were capable of moving over rough terrain without much difficulty or hesitancy, even jumping and landing successfully. However, they frequently bumped into each other and other grasshoppers or sat within ½ in. of another grasshopper with no signs of recognition of the presence of the other.

Olfaction tests with the blinded grasshoppers showed a typical upwind response to food odor ($P<.05$, $X^2=4.94$). As in the case of the unilaterally antennectomized grasshoppers, movement upwind was more hesitant with more pauses than in the untreated controls, but movement was along a relatively direct path to the odor source.

In all tests of antennectomized and blinded grasshoppers, movement in the absence of an odor at a wind speed of 2 ft./sec. was essentially random or showed a downwind bias, as seen in the unoperated controls.

Although the antennae appear to be the principle mediators of the upwind responses to odor, other chemoreceptors and mechanoreceptors may be important.

Haskell *et al.* (1962), from concurrent electrophysiological experiments, concluded that at low wind speeds, the only receptors besides those of the antennae capable of responding to these wind speeds were a few of the long-hair sensillae on the cerci, a few hairs on the thorax, and some of the aerodynamic sense organ complex. Abolishing the response of these organs by petroleum jelly or severing of the ventral nerve cord between the metathoracic and first abdominal organ did not affect the upwind response to olfactory stimulus in *Schistocerca*. They did note a gradual decrease of locomotor activity in the cases of ventral nerve cord section. This latter operation, when performed in the present study on *Aulocara* reduced activity to such a level that results were considered unreliable.

Slifer (1954) demonstrated in *Romalea microptera* (Beauvois) the presence of chemoreceptors on the legs, except for the basal half of the femora. In the laboratory studies of *Melanoplus mexicanus mexicanus* (Saus.) and *R. microptera* (1954, 1955, 1956) she showed that grasshoppers could detect water, fresh or dried dandelion leaves, and wheat middlings from a distance of at least 40 cm. Grasshoppers with antennal flagella removed could still find certain foods at a distance, although with difficulty.

Occasionally a grasshopper in response to an odor appeared confused in trying to determine the source of the odor; i.e., the grasshopper was usually hesitant, paused frequently, and followed a rather circuitous route towards the source. The grasshopper would align its body more or less parallel to the direction of the wind flow and usually faced upwind. Next, one tarsus would be raised until it was over the body and parallel to the ground. The leg would be held in this position for several seconds, then the leg would be lowered, and the grasshopper would move forward or, as in one case in which a grasshopper was facing downwind, turn upwind. After advancing a short distance, the tarsus would again be raised and held quietly in the wind stream. A foreleg was raised by most grasshoppers; one grasshopper raised a metathoracic leg. A direct path to the source was pursued when near the source and no further leg raising occurred. This behavior was seen once during observations of an adult female in the Y-tube olfactometer. The behavior pattern was also seen in blinded and in unilaterally antennectomized males and females. No examples of this behavior were observed in the field or in the laboratory. This response may indicate the utilization of some type of chemoreceptor or mechanoreceptor on the leg for orientation towards the odor source.

Haskell *et al.* (1962) suggested that an olfactory stimulus might initiate locomotor activity that would continue in the absence of

the stimulus, being mediated by the effect of the wind on mechanoreceptors. Their tests of *Schistocerca* failed to support this hypothesis. Removal of an attractive odor suppressed the upwind movement of *A. elliotti* within one to four seconds and often produced downwind movement. Re-application of the odor resulted in an upwind movement. Haskell *et al.* (1962) reported that they could keep *Schistocerca* marching to and fro by merely inserting and removing an odor source; this response lasted for some time.

Kennedy and Moorehouse (1969), reported continued research on the orientation reaction of *Schistocerca* to wind borne grass odor. They discovered that 'agitating' nymphs, by handling them singly or by tumbling a crowd of nymphs in a large container just prior to testing, induced rapid upwind movement by both starved and fed hoppers even in the absence of grass odor.

Table 18 presents the data from one set of experiments on a group of *A. elliotti* adults to test the effects of agitation. All were starved 6 hours. From the report of Kennedy and Moorehouse (1969), it was expected that starved grasshoppers should show the strongest response. The reaction of the nymphs of *A. elliotti* was unchanged by agitation. In no case was an upwind movement attributable to agitation alone.

Since an upwind attraction to food odors was clearly demonstrated by *A. elliotti*, it was hypothesized that these grasshoppers may also

TABLE 18. REACTIONS OF GROUPS OF *A. ELLIOTTI* TO AGITATION IMMEDIATELY PRIOR TO TESTING RESPONSES TO WIND AND OLFACTORY STIMULI. ALL TESTS CONDUCTED WITH 20 GRASSHOPPERS, AIR AND SAND TEMPERATURES 30°C, WIND SPEED 2 FT./SEC. ODOR TESTED- *AGROPYRON SMITHII*.

Expt. No.	Condition of Grasshoppers	Stimulus Presented	Movement Scoring: Up-wind	Movement Scoring: Down-wind	Probability
1	Starved	Wind	7	8	Random movement;
2	24 hrs.		4	3	X^2= 0.14, df 1
			11	11	P=.99
3	Starved	Wind +	8	8	Random movement;
4	24 hrs.	Agitation	7	5	X^2= 0.14, df 1
			15	13	0.90<P<0.95
5	Starved	Wind +	9	3	Upwind movement;
6	24 hrs.	Grass Odor	10	3	X^2= 6.76, df 1
			19	6	P<0.01
7	Starved	Wind +	9	4	Upwind movement;
8	24 hrs.	Grass Odor	12	2	X^2= 8.34, df 1
		+ Agitation	21	6	P<0.01

orient to the smell of other grasshoppers. Lepiney (1930) and Volkonsky (1942) suggested that grasshoppers may have this ability.

In the field, aggregations of both nymphs and adults are seen. Males frequently follow ovipositing females, and the male courtship behavior frequently involves a complex sequence of antennal movements. Grasshoppers of both sexes, when encountering another grasshopper of the same species often cross antennae. Several females often oviposit in the same area, sometimes positioning as many as six egg pods side by side. Olfaction may be an important communicative channel in these

interactions.

In no instar and under no circumstances could a significant degree of attraction between grasshoppers be shown. Male-male, female-female, male-female, nymphs-adult, adult nymph attractions were tested. The source subjects were housed in groups of 20 in small screen boxes behind the filter on the intake end of the wind tunnel. Adults at various ages and physiological states (determined by behavior patterns such as mating, ovipositing, feeding, and stridulating) were tested. A minimum of four replicates was performed for each possible bombination. Ovipositing females and females that had demonstrated receptiveness to males immediately prior to resting were included as source subjects. In a few instances, a male that was sitting near the intake filter when the wind was applied, crawled onto the filter in the area directly in front of the screen box which held the source females, and the male remained in that position for the remainder of the test, often slowly raising and lowering his antennae to the surface of the filter. Whether this was merely a case of an animal moving up the filter and getting into a fixed position or whether it was a response to an olfactory stimulus that is only effective at close range is unknown. As in the tests of Haskell *et al.* (1962) on *Schistocerca*, no olfactory attraction at a distance to other grasshoppers could be shown.

Groups of grasshoppers often were observed marching upwind to an odor source or downwind in the absence of an attractive odor. Blinded grasshoppers did not march in groups. Presumably, marching groups are a result of visual 'nearest neighbor' reactions.

A few final points as regards interactions and stages of development in relation to olfactory stimulus should be reported. As in the studies of Moorehouse (1969) on *Schistocerca*, response to food odor declined at the time of ecdysis in *Aulocara*. Reaction to food odor appeared to be the same for all instars. Grass odor and wind elicited jumping in some first and second instar nymphs, but rarely produced this response in the older instars. Ovipositing females were unresponsive to food odor, although it was attractive after oviposition. Females searching for an oviposition site were not repelled by food odor as reported in *S. gregaria* by Norris (1968). Copulating males were unresponsive to grass odor, but copulating females often responded, carrying the male along. Courting males would approach females, even moving downwind, but often resumed an upwind approach to the odor source if the female was unresponsive.

Discussion: Host plant selectivity has been established for many species of grasshoppers (Pfadt, 1949; Anderson and Wright, 1952; Mulkern, 1969). Olfactory stimuli, visual clues, thermal alterations, and phagostimulants may orient and induce feeding in the grasshopper. Dethier (1953) found it convenient to consider the stimuli involved

in the selection of food by phytophagous insects under three categories: orientation stimuli, biting stimuli, and feeding maintenance stimuli.

In addition to the stimuli involved in the selection of food, general undirected activity enhanced by temperature, humidity, illumination, and the physiological state of the insect may bring an individual into contact with suitable host plants. Hunger, excitation, period of the molting cycle, oviposition, mating, etc. affect the arousal system's threshold for feeding (Moorehouse, 1969). It appears that the physiological mechanisms underlying certain behavior patterns and their interactions in *Aulocara* and other acridids are highly complex. It is not surprising, therefore, that field and laboratory work have produced variable and often seemingly contradictory results. Whereas, Hunter and Claassen (1914) Watson and Bratley (1940), and Slifer (1954, 1955, 1956), reported attraction to food at a distance by olfaction by several species of grasshoppers in the field and in the laboratory, other researchers such as Williams (1954), Chapman (1955), Kennedy (1939), and Dadd (1963) concluded that olfactory clues at a distance were not utilized, were secondary to visual signals, or were not utilized by young hoppers. Haskell *et al.* (1962), Kennedy and Moorehouse (1969), and Moorehouse (1971) provided persuasive evidence for the existence of a mechanism for finding food plants by air borne chemical clues in *Schistocerca*.

In discussing their findings in relation to those of Williams (1954), Haskell *et al.* (1962) stressed the importance of pre-experimental starvation and questioned the conditions of his 'choice chamber' experiment. Dadd (1963) observed that unfed hatchlings approached and fed on bundles of grass placed in their cage, but when offered bundles of grass or damp cotton wool enclosed in muslin, no conspicuous movement of nymphs to the bundles or difference between the numbers that eventually settled on the bundles could be discerned. Adults reared on an artificial diet, kept overnight without food, approached dishes of bran or of wheatgerm oil absorbed on cellulose powder. He suggested that nymphs may learn to follow odor clues after feeding.

In view of the experiments on *Aulocara*, it appears that unfed hatchlings have an inherant ability to locate a suitable host plant by olfactory clues, but that this response is manifested only after several hours of inanition. Observations of caged grasshoppers indicate that newly emerged nymphs often approach and climb vegetation but then sit on the plants for several hours before feeding. This may be due to visual and negative geotropic responses.

A series of experiments similar to the bundled grass tests of Dadd (1963) were conducted on both nymphs and adults of *Aulocara*. No conspicuous movement to bundles of grass nor difference between the numbers that settled on the bundles could be discerned. Living grasshoppers presented in the same manner also produced no discernable

response. Williams (1954) choice chamber experiment was similar to the bundle tests. Substances to be tested were placed below a screen which served as the floor of the chamber. Odors were propagated by diffusion and convection currents. Taken in conjunction with the observations that *Aulocara* is attracted at a distance to wind borne grass odor, the view may be hazarded that a directional air flow or steep gradient of odor is necessary for orientation to a distant odor source. This is in agreement with either the tropotactic (Haskell *et al.*, 1962) or anemotactic (Kennedy and Moorehouse, 1969) theories of attraction to an odor source.

Although agitation of *Aulocara* did not induce upwind movement, wind alone appeared to both initiate and stimulate movement, often in both directions. Downwind movement appeared to be influenced by wind speed. This suggests that temperature receptors detecting differential cooling of the body may be involved in the downwind movement of basking grasshoppers as reported by Haskell *et al.*, 1962. The lack of circus movements in blinded and antennectomized grasshoppers argues against a tropotactic response to food odor, as does the upwind response to odor by unilaterally antennectomized grasshoppers. However, the whirling of the remaining antenna, the hesitant approach, and the tarsi raising suggest the possibility of indirect orientation by interruption of regular deviations of parts of the body, a klinotaxis (Fraenkel and Gunn, 1961). Kennedy and Moorehouse (1969) seriously

question the existence of a significant gradient of odor concentration in the relatively short wind tunnel when the odor is admitted across the full width of the inlet. Without a steep gradient, tropotaxis and klinotaxis, by definition, are impossible.

The evidence from *A. elliotti* favors the classical theory of how a walking insect orients its path to a distant source of odor (Flugge, 1934; and Kalmus, 1942 on *Drosophila* spp.). According to this theory, as presented by Kennedy and Moorehouse (1969), the insect orients upwind towards the odor source by means of directional clues from the wind itself (anemotropotaxis). The olfactory stimulation serves to 'switch on' the orientation to wind or (Kalmus, 1942) to accelerate an anemotactic response that is already evident before the initiation of the olfactory stimulation. In their description of anemotaxis, Fraenkel and Gunn (1961) stated, "that the animal is stimulated to begin to orientate by the smell, and that the only way to reach the source of the smell is to go against the current with the aid of either mechanical or optical stimuli."

Kennedy and Moorehouse (1969) concluded that the antennal chemoreceptors are very important for orientation to grass odor by *Schistocerca*, but decided that the behavioral role of the antennae is kinetic rather than tactic.

Otto (1951) working with *Drosophila melanogaster*, *Geotrupes silvaticus*, and *Vespa rufus* emphasized the importance of air currents

in chemo-orientation. *Drosophila*, under the influence of a stimulus, could find the source of odor about equally well with one as with both antennae. The behavior reported for these flies was similar to that seen in *Aulocara*. In a review of Otto's work, Fraenkel and Gunn (1961) concluded that the reaction closely corresponded to their definition of klinotaxis. It may be that the antennae have both a klinotactic and a kinetic function. Fraenkel and Gunn (1961) state that a striking feature of the chemical orientation of many animals is the change over from one method of orientating to another as the conditions make it possible for the more efficient methods to be manifested.

The changes in responsiveness in the molting cycle, and inhibition of the upwind response by activities, such as oviposition and courtship, demonstrate that inhibitory effects as well as excitatory effects such as starvation may change an arousal system's threshold. Also, Kennedy and Moorehouse (1969) demonstrated that food odor was only one of several types of stimulus that can switch an anemotaxis in locusts. They concluded that attractant or repellant odors probably determine the sign (positive and negative) of the response. The common effect of all these types of stimulus appears to be an excitation of locomotor activity.

IV. Photic, Visual, and Thermal Responses

Temperature and light frequently have been shown to be important factors affecting grasshopper movements. Photokinetic, phototactic,

thermotactic, and thermokinetic responses have been ascribed to grasshoppers. Fraenkel and Gunn (1961) summarized research of the light and temperature responses of *Schistocerca gregaria* (Forskal). Mulkern (1969) examined the responses of species of *Melanoplus* to these factors in relation to feeding behavior. Chapman (1955) considered light and temperature to be important kinetic factors to *Locusta migratoria migratoroides* (R. & F.).

Reactions to heat and light are difficult to separate in the field. Mussgnug (1972) reported that temperature appeared to play an important role in the determination of daily activity patterns of *Aulocara elliotti*. He decided that a response to light rather than to temperature appeared to be important for directing early morning movements. *A. elliotti* in the field moved into suitable areas for basking from depressions not receiving radiant energy at sunrise.

Observations of wild and caged *A. elliotti* in both the field and in the laboratory confirmed Mussgnug's report (1972). Grasshoppers approached areas illuminated by the sun before any thermal effects could be detected. Both nymphs and adults in the laboratory moved to the west end of the cages in response to sunlight. The first direct illumination from the sun occurred on the west wall of the glass-roofed room of the insectary. This room is on the second floor of the building, situated between two fiber glass roofed rooms. The roof covering the rearing rooms of the insectary faces to the south.

Individual rooms are separated by fiber glass walls. Heating and cooling vents and ducts surround each room on all but the north side. A redwood enclosure covers the ducts, forming an opaque wall to a height of 17½ in. above the laboratory tables. The cages in the glass-roofed room receive only diffuse light from the sun at sunrise. Light begins to appear on the west wall of the room above the cages as the sun climbs in the southwest. Sunlight spreads across the wall from south to north, down the wall, and out into the room from west to east. Direct radiation from the sun does not strike the cages until mid-morning (Figure 6).

Grasshopper movement towards the west end of each cage was initiated by bright illumination from the sun on the west wall of the room. This movement occurred before sunlight reached any of the cages. Grasshoppers moved to the west and crawled up the screen at the base of each cage. More grasshoppers moved onto the screens as the rays of light approached the base of a cage. Grasshoppers basked in the sunlight on the screens until the light rays had spread across the entire width of a cage and had spread into a cage to the east. Then they slowly disbanded, moving off the screen and out into the cage. This latter response may have been due to a general increase in activity induced by heat absorbed during basking rather than to a photo response.

Table 19 presents data obtained from position records of grasshoppers on the screens. Counts of grasshoppers on the screens at the

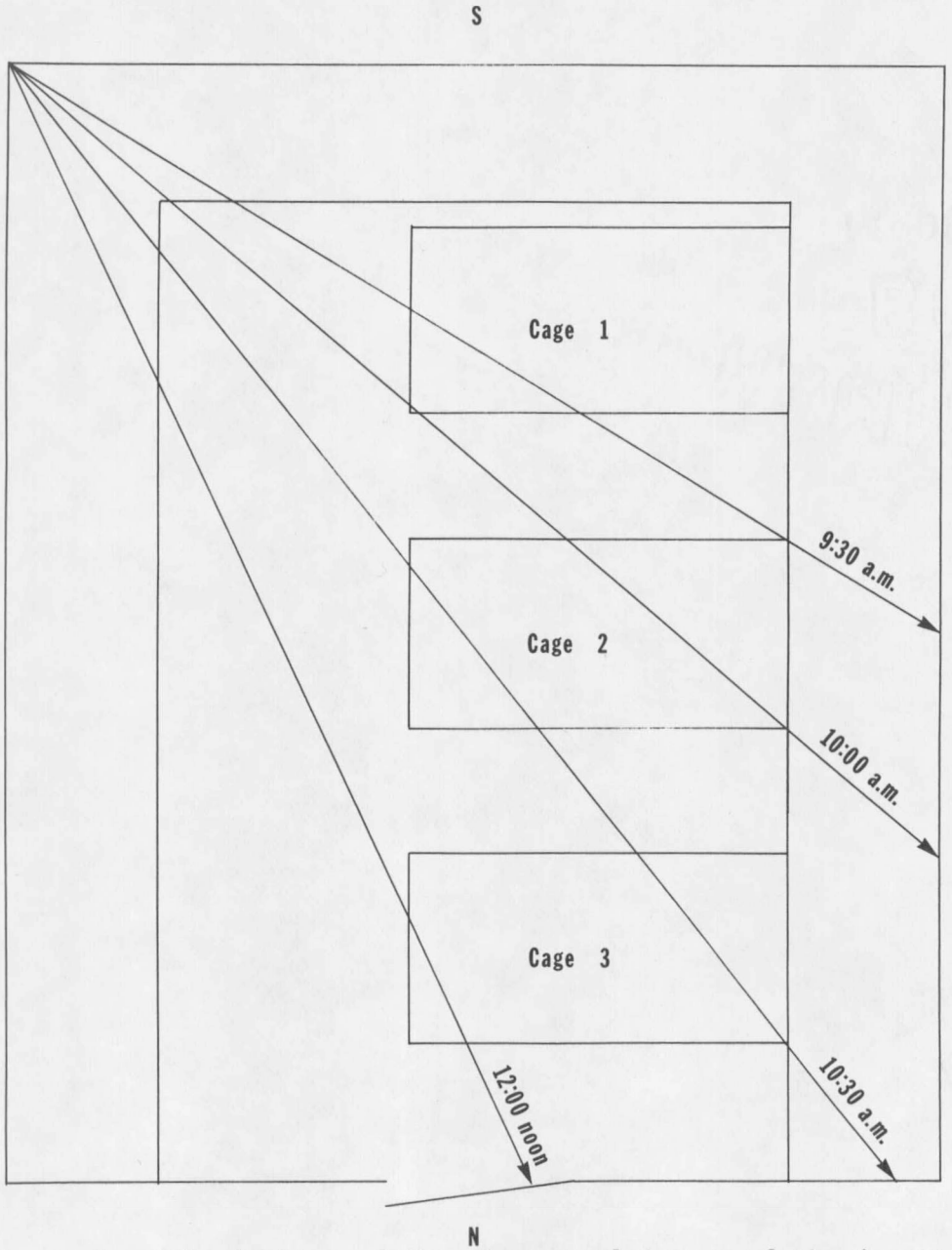


Figure 6. Illumination of the glass-roofed room of the insectary by sunlight. Each line indicates the point to which light has reached at the designated time. Arrows indicate the direction of light rays.

TABLE 19. POSITION RECORDS OF ADULT *A. ELLIOTTI* ON SCREENS IN CAGES IN RESPONSE TO SUNLIGHT. SUNLIGHT ILLUMINATES FIRST THE WALL AND THEN THE SCREENS AT THE WEST SIDE OF THE ROOM IN THE EARLY MORNING. DATA FROM THREE CONSEQUITIVE MORNINGS ARE SUMMARIZED.

Illuminated Area	Cage No. 2 Position Totals (10 min. intervals) East	West	Temperature °C East	West	Cage No. 3 Position Totals (10 min. intervals) East	West	Temperature °C East	West
Wall	--	--	--	--	6	27	24.4	23.9
Wall	6	31	24.4	23.9	5	33	23.9	23.3
Wall	1	32	24.4	24.2	1	37	24.3	24.4
Screen	0	40	24.4	25.0	3	44	24.2	25.6
Screen	2	42	24.4	25.0	2	53	25.2	26.2
Screen	0	34	24.4	26.9	2	57	25.7	27.2

base of each cage were made at 10 min. intervals from the time of the first appearance of sunlight on the wall across from a cage until the time of the disbanding of the basking grasshoppers. The data show that movements towards the illuminated area occurred before any temperature increase was noted in the cages. Cage temperatures varied from 23.3-24.4°C at ¼ in. above the soil before receiving direct light from the sun. Some grasshoppers walked about, fed, courted, copulated, and probed for oviposition sites, but only a small number of individuals were so engaged in activity at this temperature; the majority (70-80%) remained in resting positions or occasionally fed. Radiant energy from direct rays of the sun rapidly increased the air and soil temperatures of the cages. The initial temperature increase at the west end of the cages appeared to induce basking on the screens. Disbanding of the

basking groups occurred as temperatures rose above 28.3°C, and activities such as courtship, copulation, singing, and ovipositing increased.

Behavioral activities at different temperatures in the cages of the laboratory are summarized in Table 20. Mussgnug 1972) presented similar data for wild grasshoppers in the field. The temperature range in which *A. elliotti* were active in the laboratory was narrower than that reported for these grasshoppers in the field by Mussgnug (1972). *A. elliotti* were inactive in the laboratory at 12.8°C. They rarely moved at 15.5°C and could be captured easily by hand. Mussgnug (1972) reported that grasshoppers of this species assumed basking positions at 12.8°C in the field. He concluded that the daily activities of *A. elliotti* showed a diurnal pattern and presented data that indicated that each principal behavioral pattern, such as feeding, occurred at a preferred, narrow, temperature range (approximately 5.5°C). The present study of *A. elliotti* did not demonstrate a rigid dependence of a specific activity on time of day or temperature. The grasshoppers in the laboratory cages were exposed to a natural photoperiod as a result of sunlight being passed through the glass roof of the insectary. Basking occurred in the early morning and late afternoon in the laboratory. Resting occurred in shade or on vegetation early in the morning before direct illumination from the sun struck the cages and again in the late afternoon, when solar radiation levels were highest and temperatures were in excess of 35°C. Courtship, copulation, and oviposition were primarily

TABLE 20. DAILY ACTIVITY PATTERNS OF *A. ELLIOTTI* AND ASSOCIATED AIR TEMPERATURES. (Temperatures represent averages ± 1.5°C.)

Activity	Air Temperature, ¼ in. above soil in the laboratory cages °C	Air Temperature, 1 in. above the soil in the field (Mussgnug, 1972) °C
Resting (inactive)	27.7	-----
Resting (move if disturbed)	15.5	-----
Resting (some random movement)	17.2	-----
Resting (termination will move to light)	18.9	-----
Basking (includes strong light seeking)	23.9	11.6*
Disbanding of basking adults (initial)	26.7	-----
Disbanding (majority of adults)	28.3	-----
Courting (majority)	26.7-35.0	18.3
Copulation (majority)	26.7-35.0	23.9
Oviposition (probing)	26.7-35.0	-----
Oviposition (actual egg laying)	28.3	29.4
Sun avoidance (turn body parallel to sun, stilting, etc.)	>35.0	-----

TABLE 20. (Continued).

Activity	Air Temperature, ¼ in. above soil in the laboratory cages °C	Air Temperature, 1 in. above the soil in the field (Mussgnug, 1972) °C
Feeding	18.3-40.5	35.0
Roosting (Mussgnug's Resting) (initial)	35.0-40.0	40.5

*May include resting.

morning activities in the field (Mussgnug, 1972). These activities occurred throughout the day in the laboratory, although more individuals engaged in these activities during the period in which the cages were directly illuminated by the sun (9 a.m.-4 p.m.) than at any other times. All three activities could be observed at any one time or temperature during the day. Temperatures fluctuated as much as 26.7-42.0°C throughout a single cage, and active individuals, such as courting males and females searching for oviposition sites, experienced the entire range of cage temperatures during random wanderings. Courtship, copulation, oviposition, and locomotion were most evident over a range of temperatures of 23.9-35°C in the cages. Temperatures below or above this range appeared to result in a decrease of these activities. Riegert (1967) recorded temperature related activities for *Camnula pellucida* (Scudd.) and two *Melanoplus* species in the field. His

observations of activities of these species and of the temperatures at which specific activities occur are similar to data in Table 20 for laboratory reared *A. elliotti*.

Both sufficient light and temperature levels appear to be necessary for many of the normal daily behavioral patterns of *A. elliotti*. Low light intensities or sudden changes in light intensity, such as when a cloud passes overhead, often inhibited locomotor and singing activities. Time of day may not be as important as light and temperature to activity patterns. Courtship, copulation, and oviposition were observed in the test arena at 26.7°C at 10 p.m., during a series of tests conducted in the evening. Light was provided by a 250 W., clear, incandescent bulb 4 ft. above the center of the arena. Evening tests were performed on consecutive nights for a period of two weeks with one group of grasshoppers, and mating and egg laying activities appeared to increase by the second and the third nights. Numbers of individuals engaged in these activities were not quantized as the tests were concerned primarily with visual responses. It may be that some type of diurnal pattern of activity exists, which can be shifted a few hours by temperature or light applications.

The effects of temperature and light could be investigated separately in the laboratory. Grasshoppers on an opaque sheet of glass in the Tilt Table arena at a room temperature of 25°C congregated in a ring at a temperature zone of 35-45°C. The ring shaped heat zone

was produced by an infrared light bulb beneath the glass. The lamp produced a temperature gradient with maximum temperatures at the center of the arena. Fraenkel and Gunn (1961) employed this method of testing and obtained similar results with other insects.

Simple photoresponse tests using artificial lights were conducted with *A. elliotti* in the laboratory. Incandescent and fluorescent lights were used as light sources. Responses to different colors of light were tested by using G.E. 25 W. colored light bulbs. Large rectangular glass jars filled with cold water served as heat filters. Phototactic responses were analyzed using simple X^2 tests of position records.

A strong phototactic response was observed during the hatching experiments with newly emerged nymphs. Nymphs, after shedding their pro-nymphal exuvium, moved to an illuminated side of the pans in which they were hatched. This response was demonstrated to both diffuse light from windows 8 ft. from the pans and to a 200 W., clear, incandescent light bulb about 6 ft. away and 4 ft. above the pans. Very little heat was derived from these sources; none could be detected by temperature measurements of the pans receiving light from the window, and only 0.5-1.0°C higher temperatures on the sides of pans facing the light bulb could be discerned. The nymphs oriented to both light sources by aligning their bodies parallel to light rays from the sources. Rotating the pans by as little as five degrees from the source of light resulted in a consequent turning of the nymphs to again face directly

towards the light. This response declined but did not totally disappear 3-6 hrs. after emergence.

An opaque box (Figure 7) divided into three chambers was used as a choice chamber to further investigate this nymphal response. The floor of the box was covered with ½ in. of soil and three glass vials were inserted into each of the long sides of the box. The top of each small bottle was mounted at soil level and the bottles were bent downward at a 45 degree angle from the box. Each chamber had a pair of vials mounted on opposite sides. Water heat filters were placed between the box and lamps which served as light sources. Light sources were presented in pairs, one on each side of the box. Recently emerged nymphs in groups of 30-40 were placed in each chamber for a test, providing three replicates per test. Lights were introduced after the grasshoppers had settled for 15 min. Nymphs responsive to the lights in a phototactic manner entered the mouths of the bottles and fell to the bottoms of the bottles. Nymphs were unable to return to the box after falling into the vials. Counts of the numbers of nymphs in each vial were made after a 2 hr. exposure to the lights. The light sources were then reversed in position, and the test repeated with a new group of grasshoppers. All tests were conducted at a temperature of 26.7°C.

Table 21 presents the data from light tests with nymphs and adults. Tests of adults were conducted by placing light sources on opposite

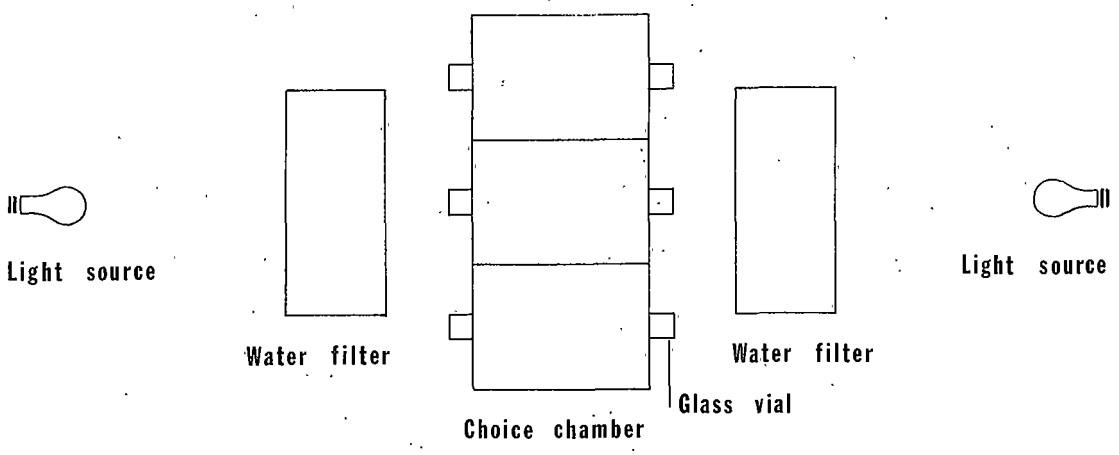


Figure 7. Choice chamber for testing the responses of *A. elliotti* to different colors and intensities of light. The water filter absorbed heat from the lights.

TABLE 21. RESPONSES OF NYMPHS AND ADULTS OF *A. ELLIOTTI* TO DIFFERENT LIGHT SOURCES. (Response determined by movement to a light source, final position records are presented))

Instar	Type of Light Source: Fluor.	Incand.	Wattage	No. Reps.	Position (No. of Animals): Color		Color		X^2	P
Adult	X		30	26	UV	125	CW	24	68.4	P<.001
First	X		30	18	UV	130	CW	105	2.6	P<.10
First		X	200, 25	6	LW	20	HW	82	37.6	P<.001
First		X	25	6	R	6	Y	56	40.4	P<.001
First		X	25	6	R	3	B	34	26.0	P<.001
First		X	25	6	B	60	Y	57	0.1	P<.50
First		X	25	6	G	33	Y	55	5.5	P<.02*
First		X	25	6	W	57	Y	21	16.6	P<.001

*Not confirmed by later tests.

UV = Ultraviolet
CW = Cool white
HW = Higher Wattage
LW = Lower Wattage
RR = Red
Y = Yellow
B = Blue
G = Green
W = White

sides of the rearing cages. Heat filters were not used and tests of fluorescent light sources with both nymphs and adults. Careful regulation of light placement and room temperatures minimized any heat effects. Fluorescent lamps produced less heat than the incadescent bulbs. Ultraviolet fluorescent bulbs were tested against cool white fluorescent bulbs to check the photoresponses to ultraviolet light. Ultraviolet light is absorbed by glass and water, and it was decided to omit the water filters for this reason.

Red light did not appear to be attractive to nymphs. Green, blue, and yellow were attractive but not significantly different in attraction from one another in most tests. White bulbs were more attractive than colored, but this may have been caused by higher light intensities from the white bulbs. Ultraviolet and cool white fluorescent bulbs were both attractive to nymphs, but not significantly different in attraction (X^2= 2.64; df 1; 0.10<P<0.20; 6 replicates; N=145). Photatactic responses increased with higher wattage bulbs which produced higher light intensities. A 500 W. movie photoflood lamp was the most attractive of the tested light sources to both nymphs and adults, approaching the response levels occurring in the cages to sunlight. Temperature effects probably accounted for some of this response, since the heat produced by this lamp could not be entirely removed by the water filters (temperatures increased as much as 5-10°C in 5 min. as compared to 0.5-1.0°C for other sources).

Adults demonstrated no response to red light, and preliminary tests indicated no difference in response to green, blue, and yellow lights; the results were essentially the same as for nymphs. However, responses of adults to an ultraviolet and a cool white fluorescent lamp (both lamps rated at 30 W.) indicated that the ultraviolet light was more attractive than the cool white light (X^2= 60.46, df 1, P<0.01, 13 replicates, N=149). Twenty-five adults, blinded by painting the head capsules with black enamel, appeared to be attracted to ultra-

violet light, although no attraction to any other source of light by the blinded grasshoppers could be shown. Figure 8 presents position records of both sighted and blinded grasshoppers after exposure for 30 min. to a 30 W. fluorescent, ultraviolet light source located at one side of the Tilt Table arena, 2 ft. from the center and 1 ft. above the glass of the arena. Tests were conducted in both a darkened room, except for the ultraviolet source, and with a 300 W. incandescent bulb illuminating the center of the arena. The UV light source was moved to the opposite side of the arena for half of the tests. Both normal and blinded adults of *A. elliotti* demonstrated a positive taxis to the ultraviolet source. Temperatures at the side of the arena near the source were the same as temperatures in the middle of the arena when the overhead incandescent bulb was on. The reaction appeared to be phototactic rather than thermotactic.

Blinded grassoppers were placed in the arena of the Tilt Table in groups of ten and allowed to settle in the dark for 15 min. An immediate increase in activity was demonstrated when the ultraviolet light source was turned on. Two 15 W. fluorescent bulbs at a distance of 2 ft. from the center of the arena were used as a light source. Quiescent grasshoppers often began to walk and to make short hops around the arena with the initiation of the light. Turning the ultraviolet bulbs off resulted in a quieting of activity within 30-60 sec. Switching the lights on and off at 1 min. intervals

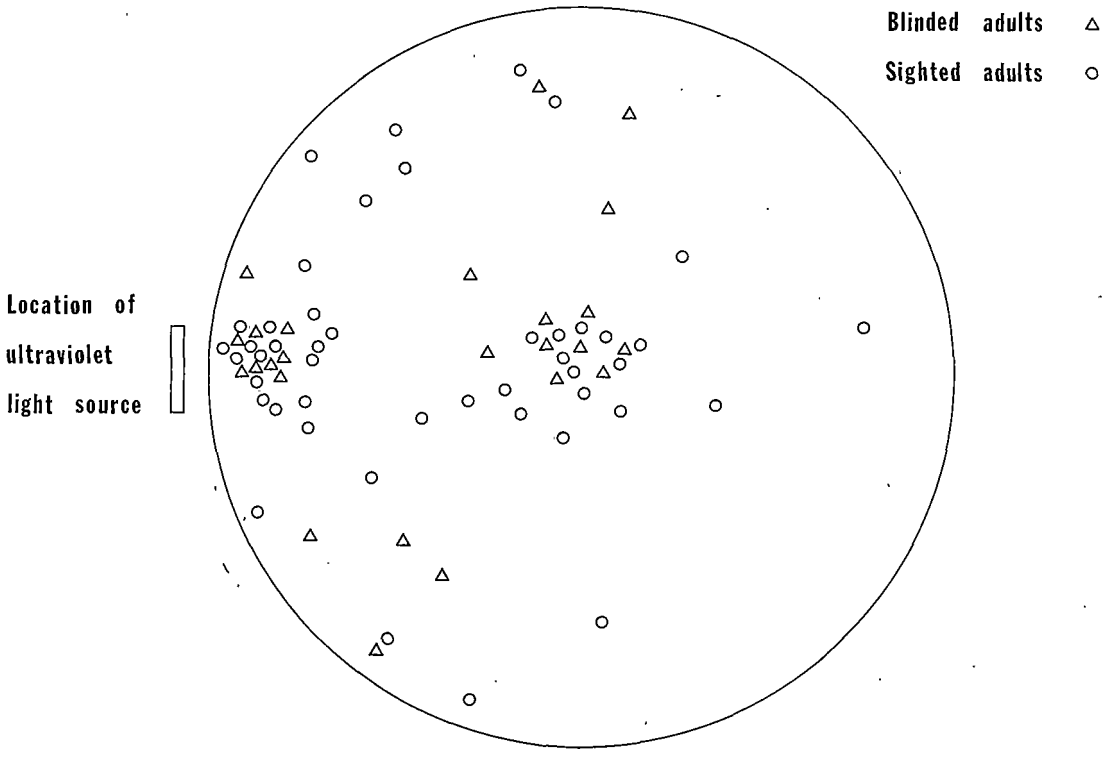


Figure 8. Responses of sighted and blinded adults of *Au elliotti* to a 30 W. ultraviolet light. The grasshoppers were released in the middle of the test arena and their positions were recorded after 15 min. exposure to the light.

continued to produce increases and decreases in locomotor activity for about 10 min. (based on 100 observations), after which time the grasshoppers became much less responsive and did not appear to be agitated by the light. Other light sources such as sunlight and incandescent bulbs did not induce activity changes in blinded animals. Whether ultraviolet radiation was transmitted to the ocelli and compound eyes through the black enamel or was affecting receptors on other parts of the body could not be determined.

Twelve blinded grasshoppers were placed in the middle cage of the glass-roofed room with 32 sighted animals. Observations of movements to basking areas were conducted each day for two weeks. Only once was a blinded grasshopper seen on the screen at the west end of the cage in the morning, while 75-85% of the sighted animals gathered there to bask in response to sunlight.

Responses to light by *A. elliotti* appear to be both phototactic, as evidenced by the attraction to light in nymphs and adults, and photokinetic, as evidenced by the responses of blinded grasshoppers to ultraviolet radiation. Mussgnug (1972) noted that the passing of a cloud's shadow over the field site would "immediately halt all activity of *A. elliotti* at any time during the day." The same phenomenon was frequently noted in the current field and laboratory observations. The passing of a cloud over the field might momentarily reduce the temperature in the field. Shadows other than clouds could

produce inhibition of activity as when the observer approached a grasshopper.

Laboratory observations indicated that light intensity changes do affect activities of *A. elliotti*. Both the wind tunnel odor tests and the acoustic signal recordings were made in the fiber glass roofed rooms of the insectary. Odor test sequences that continued from mid-afternoon through sunset showed a marked reduction of locomotor activity as the light intensity decreased in the room, although additional light and radiant energy were supplied from infrared bulbs. Sunlight was diffused by the fiber glass and distinct shadows were not produced in these rooms. Preliminary control tests of the wind tunnel indicated that no movements towards the sun occurred even in the absence of wind or odor stimuli. A lack of a directed light source as a result of diffusion by the roof probably accounted for the lack of a phototactic response to the sun. Temperatures could be well regulated in the fiber glass roofed rooms, and it is not likely that sunset was accompanied by a perceivable temperature drop, which might have accounted for the activity decrease during the odor tests. Observations of temperatures in the wind tunnel revealed that no recordable difference in temperature occurred at sunset.

Recordings of singing behavior in these rooms demonstrated similar responses to changes in light intensity. Overcast days, sunset, and the passing of a cloud's shadow all produced an almost total

cessation of all singing except for disturbance or aggressive songs. Again, little temperature difference could be discerned, especially during the short interval of time in which the rooms were shaded by a passing cloud. Overcast days did produce lowered room temperatures. Shadows from clouds over these rooms produced a general decrease in light intensity rather than a distinct shadow as occurred in the field. It is not likely that the cessation of singing in this instance was a response to a shadow such as a predator might produce.

Tests in the Tilt Table arena indicated that light could both initiate and stimulate activity. The reactions of adult grasshoppers to the turning on of a light in a dark room were observed by using a 10 W. red photosafe light bulb. The grasshoppers appeared to be unable to distinguish this light. Grasshoppers were allowed to settle in a dark room for 15 min. prior to testing. The red light allowed observations to be made on grasshopper activity, while in the dark room. Most grasshoppers settled into resting positions or moved only slightly. The response of these grasshoppers to clear incandescent bulbs of varying sizes from 10-500 W. and distances from 2-10 ft. from the light sources indicated that the introduction of light in all cases resulted in an increase of locomotor activity at 26.7-35.0°C. Temperatures below 15.5°C or above 35.0°C reduced the response to light. Lights directly above the center of the arena induced wandering around the arena, while lights to one side were attractive

to the grasshoppers.

It was thought that color might be an important visual stimulus to grasshoppers, since different colors of light produced different phototactic and photokinetic responses. Opaque 8 in. square sheets of plastic were presented to adult *A. elliotti* in sets of four sheets or in pairs of colors. Tests were conducted in both the cages and the arena of the Tilt Table. Colored squares were presented both lying flat and standing vertical on the ground or floor of the arena. Observations were made at irregular intervals in the cages. The colored squares were arranged about the perimeter of the cages and in a circle on the Tilt Table. Grasshoppers were introduced singly and in groups of 10 to the center of the Tilt Table under dark conditions. The animals were allowed to settle for 15 min. The overhead light was then turned on, and observations of grasshopper positions were made every minute for 10 min. *A. elliotti* frequently approached and sat on the squares in both the cages and the Tilt Table. No significant preference for green, red, yellow, blue, orange, beige, or violet colored squares was observed (simple X^2 tests were not significant). Temperatures at the surface of the cards were found to remain within ± 0.5 C during the tests. Black cards appeared to be relatively unattractive, while white cards were selected most frequently (X^2 = 10.8; df 1, $P<.01$; N=49; 28 observations in the cages) as determined by position records. Temperature differences were often less than 0.1°C when the

squares stood upright.

Ergene (1950) reported that *Acrida turrita* L. matched body color to areas of the cage of the same color as the body. Therefore, nymphs of *A. elliotti* from the Townsend field site were placed in a cage and given a choice of sand, soil from Townsend (grey color), or soil from Decker (red color). Two 12x18 in. bands of each soil type were presented in the cage. No preference for soil type as indicated by position records could be seen in first instar nymphs (N=376; Townsend=132, Decker=127; 5 replicates).

Many reports of grasshopper response to visual patterns or form perception have been made (see Mulkern, 1969). This area was briefly investigated with *A. elliotti*.

Figures were drawn on 3x5 in. index cards in India ink. Vertical lines, horizontal lines, square shapes, and asterisk shapes were presented in pairs. Alternating figures were arranged in upright positions around the inside of the wall of the Tilt Table arena. Grasshoppers were tested individually by placing an animal in the center of the arena, holding it so that the head faced between two figures, and after 10 sec. releasing the animal. The animal was then observed for 15 min., and its movements plotted on graph paper. Simple X^2 tests were applied to each pair of choices, using the first figure touched by the grasshopper as evidence of a choice. Both lines and shapes were attractive (Figure 9). Grasshoppers responded to vertical lines by attempting to

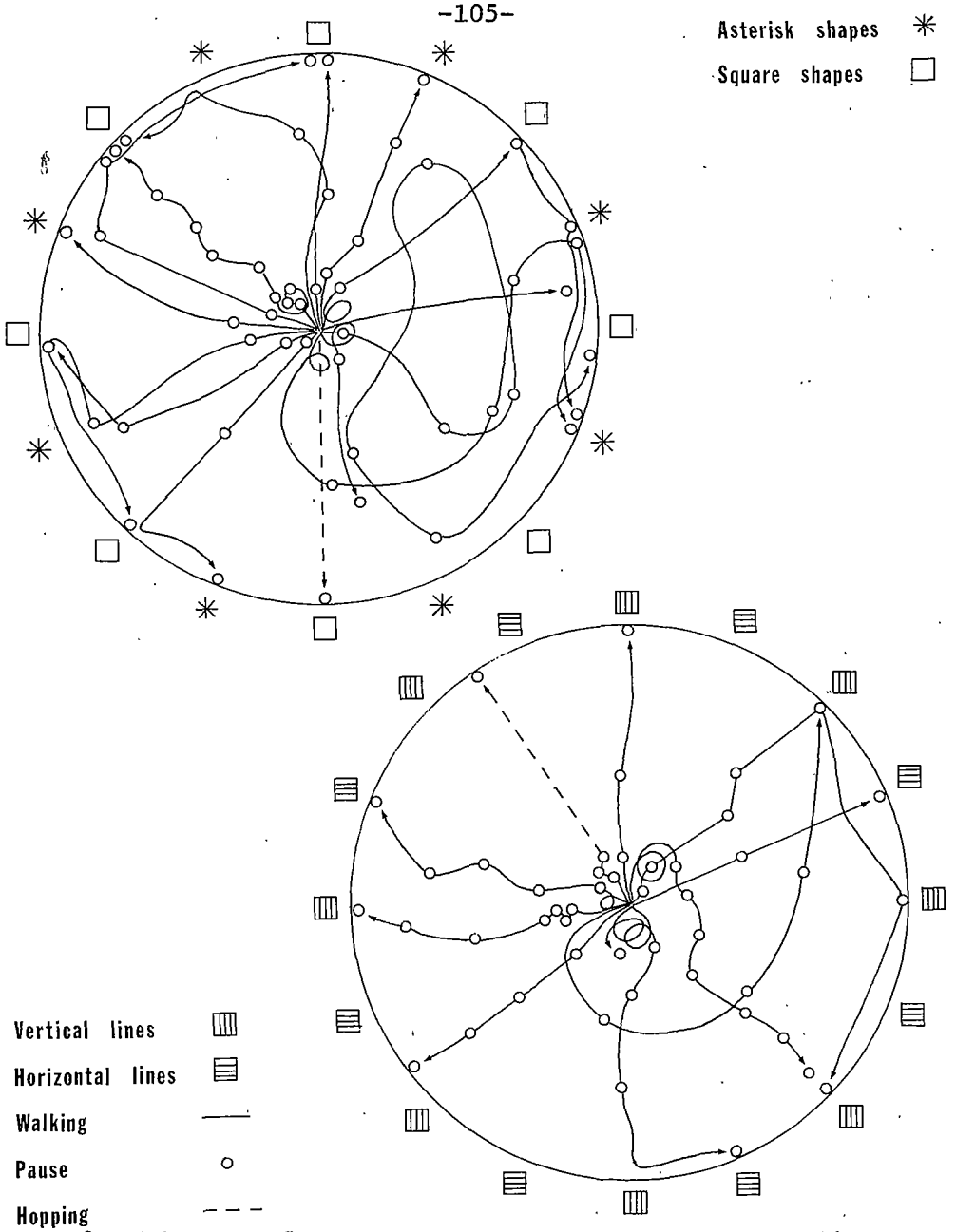


Figure 9. Diagram of pathways taken by adults of *A. elliotti* when presented with a choice of figures (shapes) painted in black on white cards. The figures tested are illustrated outside each circle. Each test involved the release of a single animal in the center of the arena and subsequent observations of its movements for 5 min.

crawl up the painted lines. Attraction to the edges of the cards and climbing of the edges was frequently observed. Horizontal lines were not as attractive as vertical lines ($X^2 = 6.24$; df 1; $P<0.02$; N=20), but occasional grasshoppers attempted to crawl along the edge of the horizontal lines.

Squares and asterisks were not as attractive as lines as indicated by circuitous approaches.

The first response of most grasshoppers upon release was a 'peering' reaction in which the fore part of the body and the head are moved from side to side to side by movements of the leg joints. Movement towards the cards usually included several pauses, with peering demonstrated during the stops. A final directed movement to a card occurred, in almost every case, as a grasshopper came within 4-8 in. of the card.

Discussion: Grasshoppers have an optimum range of temperature and humidity within which they are most active. Light also appears to influence activity. Positive reactions to temperature by *Schistocerca gregaria* have been reported (Bodenheimer *et al.*, 1929; Kennedy, 1939, 1945, 1951; Volkonsky, 1939; Fraenkel, 1929, 1930; and Fraenkel and Gunn, 1961). Phototactic and photokinetic responses of this species have also been observed (Fraenkel, 1929, 1930; Kennedy, 1939; Volkonsky, 1939). Azziz (1957) investigated the reactions of first and fourth instar *S. gregaria* to relative humidity, temperature, and light.

He investigated responses to each factor independent of the others and responses to the interactions of these factors. Increased light intensity resulted in greater activity as measured by duration of activity and speed of walking of the *Schistocerca* nymphs. Rising temperatures increased hopping and klinokinesis and orthokinesis. Light and temperature interactions produced responses similar to the responses for each independent factor. Both light and temperature increases resulted in greater activity at all humidity levels. Low or very high humidities produced agitation, and the speed of walking increased progressively with humidity.

The responses of *S. gregaria* to humidity, temperature, and light are fairly typical of the responses of other grasshoppers to these factors. The humidity reactions of *A. elliotti* and other acridids are discussed in the section on humidity reactions in this report. Positive phototactic responses to lights of varying intensities for three species of *Melanoplus* were observed by Mulkern (1969). Pielou (1948) postulated a photokinetic response to general illumination and a photoklinokinetic response that kept *Nomadacris septemfasciata* Serville out of the shade and in illuminated areas. He concluded that a phototactic response to directed light also occurred in this species.

Tests of *A. elliotti* demonstrated a positive phototactic response to most directed light sources. The greatest response occurred to lights of the highest intensity (500 W. photoflood lamp). Photokinetic

responses to general illumination were demonstrated in the test table area and in the fiber glass roofed rooms of the insectary. Locomotor and singing activities increased with a light intensity rise and decreased or ceased with a reduction of light intensity.

Blinded grasshoppers increased locomotor activity in response to light wavelengths in the shorter (UV) range. The receptors mediating this response are unknown. Medioni (1961) concluded that there was no evidence of sensitivity to light attributable to any integument sensilla other than the compound eyes and ocelli in grasshoppers. Ultraviolet light may have penetrated the enamel cap over the head of *A. elliotti*, but this seems unlikely due to the absorption characteristics of ultraviolet light.

Insect ocelli may serve as light intensity receptors. Investigations indicate that the ocelli do not form distinct or at least perceivable images, but they do react rapidly to fluctuations in light intensity. Ocelli are normally found in winged insects and appear to inhibit foraging in insects such as bees and wasps at definite threshold intensities of light. The ocelli may be considered in some respects to be similar to the pupil of the vertebrate eye. (Kerfoot, 1967.)

The relative strength of the phototactic turning tendency in locusts appears to be dependent on light intensity. Control by the ocelli (photoinhibition) appears to compliment control by the compound

eyes (photoexcitation). (Barry and Jander, 1968.) These workers concluded that interaction between the ocelli and the compound eyes appears to be a form of 'central light intensity adaptation'. The photokinetic and phototactic responses of *A. elliotti* may result from a similar interaction of the ocelli and the compound eyes. Low light intensities appear to inhibit some activities of *A. elliotti*, while a directed light source appears to excite and direct locomotor activity. Temperature effects may also be involved as seen in the disbanding of aggregated basking grasshoppers as air temperatures increased. Blinded grasshoppers did not react to most directed light sources and did not appear to react to most light intensity changes, ultraviolet wavelengths of light being the exception.

The reaction of *A. elliotti* to polarized light was not investigated. Jander (1963) was unable to demonstrate astrotaxis in locusts, implying an inability to perceive polarized light, although other insects possess this ability.

Circadian locomotor rhythms are entrained by environmental light in cockroaches. Removal of the ocelli has no effect on these rhythms, but entrainment is lost if the compound eyes are covered. This does not eliminate the possibility that light may still be perceived through the head capsule. (Roberts, 1965.)

Mussgnug (1972) concluded that a diurnal pattern of behaviors (basking, courting, copulation, oviposition, resting, and feeding)

occurred in adult *A. elliotti* and was most likely produced by temperature and/or light conditions. The present study indicates that light and temperature are very important to general locomotor activity. Experiments at night, conducted under artificial lights, revealed that courtship, copulation, and oviposition continued into the late evening given adequate light and temperatures. A lag of 1-2 days before these activities were frequently seen during the night tests implies that an entrainment of a new rhythm of activity may have occurred. However, observations of the laboratory cages indicated that temperature and light conditions, rather than time of day, were most important in regulating behavioral activities. Observations in both the field and the laboratory indicated that a male normally copulated no more than once and a female was incapable of ovipositing more than once a day. Mussgnug (1972) concluded that these were primarily morning activities. Early morning basking appeared to initiate most of the daily activities of *A. elliotti*, probably as a result of increasing internal body temperature and facilitating muscular contractions. It seems probable that activities that occur no more than once a day for any individual and that are initiated by basking would occur shortly after basking for the majority of the population; i.e., during the morning hours under natural conditions. Basking occurred between 9-10 a.m., since the walls of the room shaded the cages until 9 a.m. or later. Basking in the field occurred as early as 7:30 a.m. (Mussgnug, 1972). This could

explain observations of mating and courtship later in the day in the laboratory.

Not only light intensity but also wavelengths of light are important to insect responses to light. Responses to different wavelengths of light have been observed for a few species of grasshoppers. Mulkern (1969) reported maximum attraction to wavelengths at 4500-4750 Å with little response above 5000 Å in *Aeropedellus clavatus* (Thomas), *Arphia conspersa* Scudder, *Melanoplus bivittatus* (Say), *M. confusus* Scudder, *M. differentialis* (Thomas), and *M. sanguinipes* (Fabricius). Equal intensities of light of 4500-4750 Å and of white light produced similar responses. The response of these species to either of two wavelengths of light in a two-part response chamber was greatest in the blue-green to the ultraviolet range with the greatest response to a 3600 Å lamp. Uvarov (1966) cited research by Burt and Catton indicating that the eye of *Locusta* did not produce electrical responses to wavelengths greater than 6250 Å (red light). Responses up to violet (3900-4700 Å) and some ultraviolet wavelengths were recorded. Bennett (1966) reported that visual cells of *Locusta* demonstrated a high sensitivity in the blue and some of the green region of the spectrum. Crescitelli and Jahn (1939) demonstrated attraction of *Melanoplus* species at 5300 Å (green). Other workers such as Chauvin (1941, 1942) found that the responses to red wavelengths were weak and that responses to yellow, green, and blue were strong.

No response as indicated by activity or direction of movement to red light could be measured in *A. elliotti*. Yellow, green, and blue all were attractive. Ultraviolet light was particularly attractive to adults. Field-caged adults were tested using the same ultraviolet light source as that used in the laboratory, but no response to the light could be demonstrated. Mulkern (1969) reported the same lack of response in the field to an ultraviolet lamp that he had found to be highly attractive in the laboratory. He concluded that low night temperatures (13-16 C) in the field might have been partially responsible for the lack of a response, although even grasshoppers a few centimeters away did not respond. *A. elliotti* were tested in the field early in the morning at temperature and light levels similar to those of the laboratory under which a response was demonstrated. Placement of the lamp outside of the field cages resulted in the light farter from some of the grasshoppers in the cage than the distance from lamp to grasshoppers in the laboratory, since the field cages were larger than the laboratory cages. However, grasshoppers on the ground immediately in front of the lamp did not crawl onto the screen as occurred in the laboratory.

Tests of grasshopper responses to different colored squares of plastic were inconclusive. *A. elliotti* collected on the squares but frequently moved from one square to another. It is possible that the observed response was to the squares and not to the color.

Grasshoppers occurred on red squares in numbers not significantly different from those on other color squares, yet these grasshoppers did not respond to red lights. Comparing data from pairs of colors, only white versus black demonstrated a significant difference of attraction. It was suspected that this response may have been due to different temperatures at the surface of the cards, since white reflects light radiation and black absorbs radiation. The tests in the Tilt Table arena did not reveal any pronounced difference in temperature during the ten minute intervals for each test. Temperatures on the black cards rose to less than 0.2°C above the white.

Ergene (1950) reported that *Acrida turrita* with green or yellow bodies chose areas of a cage with the same color as the body. Light intensities and not color may be discerned, but green grasshoppers given a choice of grey or green backgrounds of the same intensity chose the green in 80 percent of the trials (Ergene, 1952). Observations of *A. elliotti* nymphs did not reveal any matching of body color to soil color.

From perception or response to visual patterns in grasshoppers has been studied by Williams (1954); Wallace (1958, 1959); Kaufmann (1965); Burtt and Catton (1962); and Mulkern (1969). The species studied oriented to and moved to vertical objects and shapes. Distance, form, and size can be discriminated. Wallace (1958) showed that nymphs of *Schistocerca gregaria* preferred simple forms in the visual

environment, preferring long, straight, vertical edges over short, vertical edges with wavey or serrated edges. More complex figures in the absence of straight vertical edges were chosen if the figures were of comparable size. Several workers have found that grasshoppers are very susceptible to movement in their visual field, and it is believed that peering, which consists of lateral swaying or moving of the head, produces a scanning of the visual field and movement of images across it (Wallace, 1958). It is also suggested that movements of the hind legs may be important in communicating distress, aggression, and mating response (Otte, 1970). Wing movements may be visual clues to some grasshoppers.

A. elliotti demonstrated the expected response to shapes, preferring straight vertical lines over horizontal lines and square and asterisk shaped forms. Little difference between asterisk and square figures could be discerned. An attraction to the edge of lines and of cards was seen in all tests. Mulkern (1969) reported that *Melanoplus keeleri* (Dodge) and *M. femurrubrum* (De Geer) nymphs responded to vertical lines projected on a screen by crawling along the edges of the lines. Horizontal lines inhibited upward movement except at the edge of the screen where grasshoppers moved upward, crossing horizontal lines. *A. elliotti* attempted to crawl along the edges of horizontal lines, but crossed the lines at the edges of the cards. Attraction to horizontal lines was low. Peering is frequently seen during the approach to shapes

by *A. elliotti*.

Leg movements appear to be important communication signals to *A. elliotti* and are discussed in the section on individual interactions.

Undirected activity by grasshoppers is stimulated by favorable illumination and temperature. Temperature is frequently used as an estimate of heat in a life system. Heat flow is a means of nonmechanical energy transfer.

Muscular contraction is affected by the internal temperature of an organism. The basking behavior characteristic of grasshoppers appears to be a means of raising internal body temperatures to facilitate muscular contractions.

The internal temperature of grasshoppers depends on additive and subtractive processes. Air temperature, radiant heat from the sun, vegetation, ground, and objects, and metabolic production of heat increase internal temperature. Convection, long-wave radiation from the body, and evaporation reduce internal temperature. (Uvarov, 1966.)

Solar radiation may be the most important source of heat gain by grasshoppers, causing rapid increases of internal temperature with exposure to the sun. Shading from the sun can cause rapid decreases in internal temperature (Uvarov, 1966). Digby (1955) found that the relation between radiation intensity and internal temperature excess (body temperature above air temperature) is practically linear in *Locusta*. Modification of radiation effects depends primarily on the

angle of incidence of the rays (Bodenheimer *et al.*, 1929) and on reflected radiation (Gunn *et al.*, 1948). Strelnikov (1936) found that the internal temperature of *Locusta* nymphs differed up to 6.7°C, depending on the angle of incidence of light rays. Gunn *et al.* (1948) found that up to 40 percent of the total radiant heat experienced by a grasshopper may be contributed by bare ground. The effect of this radiation decreases rapidly with height above the ground.

Fraenkel (1929, 1930) noted that *Schistocerca* formed dense aggregations on walls and slopes facing east and on the east side of vegetation in the early morning as temperatures increased to about 17-20°C. These aggregations may have been partly a response of one grasshopper to another. A nearest neighbor reaction would not explain grouping in areas exposed to the sun, nor was it probable that suitable temperature gradients to guide grasshoppers to basking areas existed, especially when a wind was present. It was concluded that *Schistocerca* wandered at random until the grasshoppers encountered a warm sunny spot, where they became immobile. Basking terminated at 28°C and the grasshoppers then began to migrate. A similar aggregation reaction to that of the morning occurred in the evening with aggregations forming on surfaces facing west.

Many species of grasshoppers orient their bodies at right angles to the sun during basking. This increases the surface area of the body exposed to the sun. An orientation parallel to the sun with only the

head exposed to direct rays from the sun is often seen when air temperatures exceed the normal activity range for a species. This greatly reduces surface area exposed to radiant energy. Climbing, shade seeking, and 'stilting' are other methods employed by grasshoppers to reduce absorption of radiant energy. Gunn *et al.* (1948) observed that *Schistocerca* adults adopted a stilting position by rising on the legs so that their bodies were held about 6 mm from the ground, where air temperatures were only 43°C as compared to a ground temperature of 56°C. Riegert (1967) reported that nymphs of *Camnulla pellucida* attempted to escape heat by climbing vegetation when temperatures exceeded 40°C. These nymphs often jumped straight up and down in rapid, unoriented, convulsive leaping until exhausted in areas in which vegetation was very short so that climbing did not permit escape from the heat. The presence of a wind appeared to prevent this hyperactive, erratic, thermokinetic behavior either as a result of convection cooling or direction of movement.

Fraenkel and Gunn (1961) commented that movements of locusts to radiant energy, such as turning of the body parallel or perpendicular to the source of radiant heat, often resulted in a state of akinesis and as such were not locomotory. Volkonsky (1939) suggested that facing the sun and broadside basking postures combine with heating effects in such a way as to produce a steady body temperature. He termed the two reactions tel-akinesis and men-akinesis, respectively. He also performed experiments on the mechanism of re-orientation to a source of radiation. Locusts oriented their bodies in response to head

movements induced by elevating a lamp. Re-orientation was not efficient or did not occur if the source of radiation emitted mainly infrared rays or if the compound eyes were made non-functional. The importance of the compound eyes to third instar nymphs or younger appeared to be less. It was suggested that visual orientation may be secondary to heat orientation. Visual orientation may increase precision and in adults may occur even when there is little or no heat effect.

The problems associated with discerning the mechanisms involved in these re-orientation responses are not resolved. Tests of *A. elliotti* indicated that a positive phototactic response directed movement to basking areas in the early morning. Blinded grasshoppers did not move to basking areas suggesting that the reaction was probably visual and not thermal. Blinding may have affected thermal as well as visual response if the hypothesis of Haskell *et al.* (1962) that the compound eyes may also serve as thermal receptors is true. Late afternoon aggregations of *A. elliotti* may also be a phototactic response to sunny areas, although this could not be easily tested. Observations of the responses of *A. elliotti* to solar radiation tend to support Riegert's (1967) conclusions concerning the early morning activities of *Melanoplus bivittatus*. A photokinetic response to sunlight probably caused the grasshoppers to move out into the sun and some to climb vegetation. Orientation to the sun and subsequent

turning of the body broadside to the sun for basking appears to be a direct phototactic response in order to rapidly increase internal body temperature. Once body temperature has been raised, an induced thermokinesis may reorient the grasshoppers to moderate photo effects. *A. elliotti* appeared to begin daily activities after basking, and orientation to the sun decreased in importance. Temperatures in excess of 35°C caused *A. elliotti* to reorient with the body parallel to sunlight, again probably a result of combined thermal and photic affects. Additional responses of *A. elliotti* to high temperatures included stilting postures, climbing of vegetation and objects, and avoidance of direct sunlight by shade seeking. Grasshoppers were also observed running rapidly over hot, bare ground, then stopping suddenly when encountering a shady area. It did not appear to be a directed movement to shade, but rather it seemed to be an erratic dash across hot areas and subsequent pauses when cooler areas were encountered.

The observations of the thermal responses of *A. elliotti* support the conclusions of Pepper and Hastings (1952). They investigated the effects of solar radiation on grasshopper *(Melanoplus* species) temperatures and activities. Body temperature was found to vary with air temperature and light intensity. Body temperatures in all cases were over that of surrounding air. The energy which results in raising the body temperature came mainly from the absorption of direct solar radiation. They also reported that *M. bivittatus* and *M. differentialis*

demonstrate movements and orientation to the sun. They concluded that this activity is motivated primarily by a temperature response. The present observations of *A. elliotti* indicate that light may in part direct this type of activity.

V. Acoustic Emissions

Dumortier (1963) concluded that acoustic messages represent the "most complete and efficacious mode of imparting information". Acoustic signals diffuse readily, are very resistant to screening disturbances, and permit a relatively great codification by variation of parameters of the emission. Busnel (1963) called attention to specific properties of sound waves which appear to be well adapted to communication. Acoustical signals have an easily locatable source, may attain a range of several miles (in vertebrates), are useful in the absence of visibility, are impermanent unless repeated, demonstrate a low loss of information due to background noise, and rapidly convey information. Reviews by Pringle (1956), Frings and Frings (1958), and Alexander (1957, 1960b, 1967, 1968) summarized evidence for short range and long range sound communication in insects.

Otte (1970) briefly described acoustic signals of *A. elliotti*. Audiospectrographs of a male and a female aggressive signals and of a male courtship song were published. Loher (1971) summarized acoustic behavior as related to sexual behavior in five species of grasshoppers including *A. elliotti*. Oscillograms, frequency spectrograms, and

sound intensity measurements were obtained for all five species in an attempt to identify parameters utilized for intraspecific recognition. Each species emitted several types of songs, each with a species-specific meaning. The rhythm patterns of songs were highly characteristic of a species. Loudness varied greatly within the various types of songs and probably is not characteristic of a species by itself. No obvious species-specific frequency differences could be determined. The distribution of sound frequencies for all five species included a range from 1 KHz to 50 KHz and beyond. The effects of rhythm and audiofrequency modifications of a male calling song were tested using males and females of the species *Chorthippus curtipennis* (Harns). A female response to the normal song included orientation and locomotion to the loudspeaker and performance of the responding song. These responses persisted even after modifications of song rhythm by more than 100 percent. Electronic filtering of different frequency bands and subsequent playback revealed that only the frequencies in the range from 3 KHz to 24 KHz were necessary to release a response in the female to the male calling song. Frequencies above or below this range did not release the female response.

Loher's (1971) observations are consistent with those of other workers. Haskell (1957) compared the stridulations of four closely related grasshoppers of the subfamily Truxalinae and found that the various types of songs performed by these species demonstrated inter-

and intra- specific differences, which consisted primarily of differing pulse repetition frequencies. Loher (1971) modified song rhythm by recording calling songs at different ambient temperatures. Temperature and song relationships have been shown for several species of Orthoptera. A rise in temperature increases both the chirping rate and the pulse rate while decreasing the duration of these emissions (Dumortier, 1963). Light in addition to temperature affects singing behavior in Orthoptera and Cicadidae (Hemiptera). Alexander (1960b) considered light to be "the most universally important single factor in determining the exact time on each day when different species begin to sing".

Acoustic signals of *A. elliotti* were recorded in the insectary for the present study. Tape recordings were made using a Robert's 1740X 4-track tape deck (frequency response 30-22,000 Hz ± 3 db at 7½ in. per sec. tape speed) and an Electro-Voice 664 Variable-D, dynamic cardioid microphone (frequency response, uniform from 60-16,000 Hz). Lack of a parabolic sound reflector negated the possibility of satisfactory field recordings with this equipment. Field and laboratory sound levels of background noise were measured with a General Radio Company Type 759 sound level meter. This instrument was not adequate for accurate measurements of the sound energy levels of songs. Grasshopper songs exhibit extremely rapid sound level transients which cannot be measured by ordinary sound level meters because of the

inertia of the meter movement (Loher and Chandrashekaran, 1970). Only an approximation of the sound energy of the songs of *A. elliotti* could be determined with the sound level meter available for the present study.

Analyses of sound emissions recorded on tape were conducted at the laboratories of the Department of Civil Engineering at Montana State University. A Keithley model 102B decade isolation amplifier was used to amplify low intensity recorded sounds. A Hewlett Packard 7100 B strip chart recorder produced a graphic representation of song rhythm as indicated by chirp interval. A Krohn-Hite model 3700 variable frequency filter was used to remove low frequency background noise from the recorded tapes. The insectary is not soundproofed and recordings made in the rearing rooms often were partially obscured by air conditioner and traffic noises. Cutting off frequencies below 600 Hz displayed a song waveform distinct from background waveforms. Comparison of the waveforms of filtered signals with those of unfiltered signals revealed little difference in the basic characteristics of the displayed signal (Figure 10). Stridulation waveforms were displayed on oscillographs. A Tektronix Type 561 A Oscilloscope with a Tektronix model C-13 polaroid oscilloscope camera and a Tektronix 434 Storage Oscilloscope (dual channel) with a Nikon F camera were used to display and photographically record the signals. Frequency analysis of sound emissions was performed by using tape

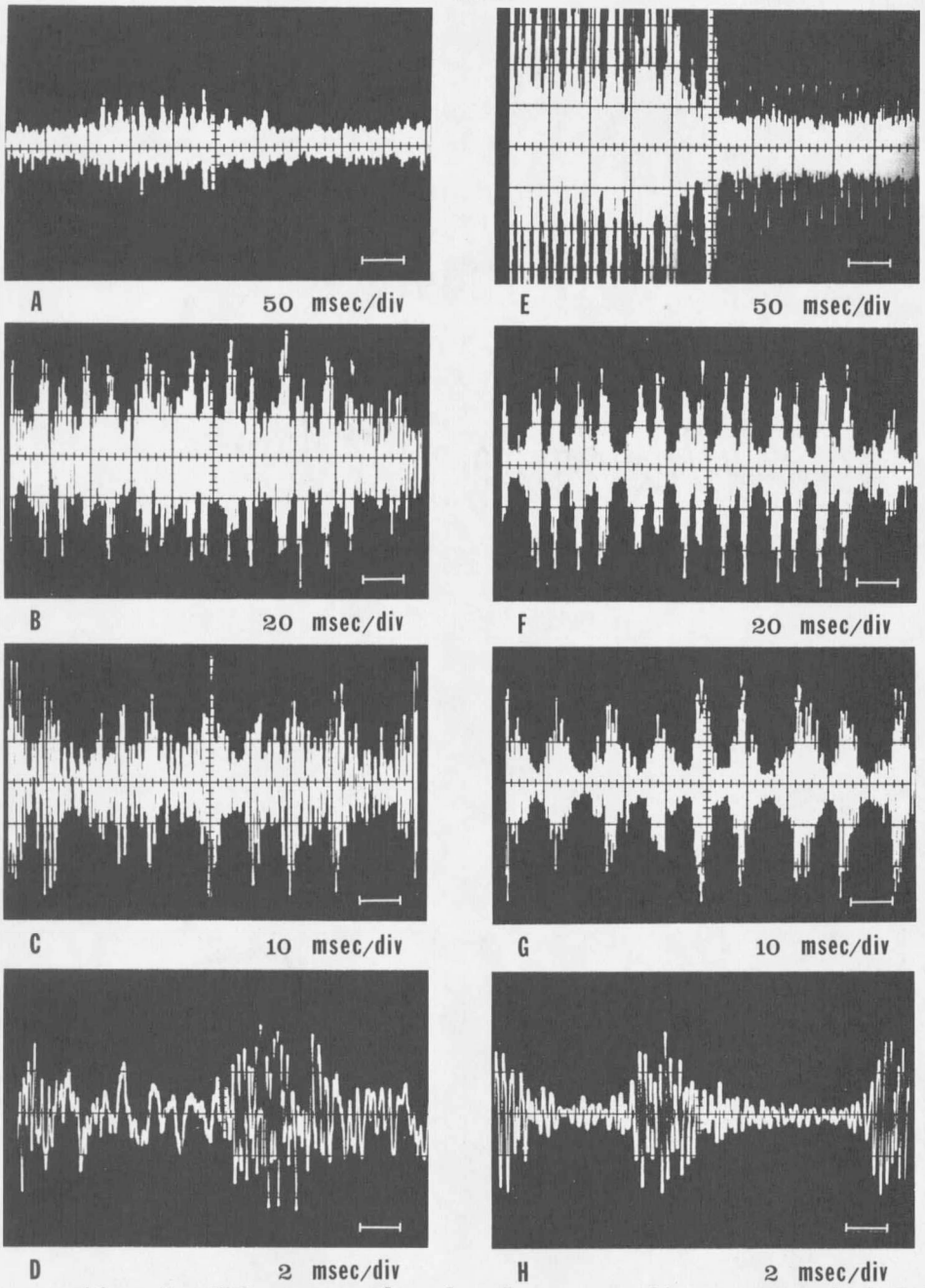


Figure 10. Oscillograms of a female responding song. A,B,C,D. Frequencies below 600 Hz were removed with a low band pass filter. E,F,G,H. Frequencies below 2 KHz removed. White bar in every case indicates one division. Vertical gain in A and E is not equivalent.

loops of recorded songs with a Hewlett Packard Wave Analyzer, Model 302 A.

Observations of the stridulations of *A. elliotti* were made in the field at Billings, Montana and in both the glass and the fiber glass roofed rooms of the insectary. Grasshoppers from six field sites in Montana were utilized to investigate populational differences in the singing behavior of this species. These grasshoppers were collected by Dr. Saralee Visscher from field sites at Simms, Decker, Trail Creek (S.E. of Bozeman), Townsend, Billings, and the O.W. Ranch (N.E. of Decker) in Montana for studies concerning embryogenesis. Grasshoppers were collected as nymphs and were reared in cyclindrical cages 9 in. in diameter by 20 in. high (see Visscher, 1971). Most of the cages contained a single male and female pair. A few cages contained groups of nymphs, adult males, or adult females. These cages were maintained in the fiber glass roofed rooms of the insectary.

Nomenclature describing the structure of the types of arthropod acoustic signals is confused. Broughton (1963) attempted to standardize bio-acoustic terminology, and his definitions have been utilized in the present study as follows:

Song: Sound of animal origin which is not both accidental and meaningless. Includes calls and call notes.

Chirp: The shortest unitary rhythm-element of a sound emission that can readily be distinguished as such by the unaided human ear.

Pulse: A unitary homogeneous parcel of sound waves of finite duration; a simple wave-train (i.e., one divisible into waves, but not into groupings of waves).

Syllable: Sound produced by one single cycle of contraction of the operating muscles.

Frequency: The rate of repetition of the cycles of a periodic quantity. The reciprocal of the period. The unit is the cycle per second (in Europe, the hertz: 1 c/s = 1 Hz).

Dominant Frequency: ... frequency of that harmonic which has the greatest amplitude.

An entire succession or sequence of chirps is termed phrase in the present study, although Broughton (1963) and Dumortier (1963) caution that workers use this term differently. Syllable applies to both sounds which are unipulsate and those which are monocyclic. Broughton (1963) prefers this term to pulse which is often defined in terms of a movement of the stridulatory apparatus. But, a pulse as it appears on paper or on an instrument such as an oscilloscope may consist of many physical pulses produced by the emitting apparatus. No attempt to relate wave-form to the mechanism of the stridulatory apparatus was made in the present study. Sound was investigated as a stimulus to certain behaviors in the receiving insect. Parameters likely to affect the efficacy of the signals were investigated. Loher (1971), Haskell (1957), and other workers have found that rhythm of the song, the waveform of chirps and pulses, the range of frequencies of which the waveforms are composed, and the loudness or intensity of the song may be important factors to the response of the receiving

grasshopper. Environmental factors such as temperature and light also may be important.

Terminology for types of sound phenomena according to the conditions under which the acoustic signals occur and to the behavior with which the emissions are associated has been presented by several workers. Alexander (1967) listed nine functional categories of arthropod signals. Faber (1929, 1932) recognized 12 different songs or phrases used by insects. Dumortier (1963) presented a classification of arthropod sound based on Faber's system. Loher and Chandrashekaran (1970) and Broughton (1963) critically reviewed behavioral terminology as applied to bio-acoustic signals.

The terminology applied by Loher (1971) to acoustic communication of *A. elliotti* and other species of Acrididae has been utilized in the present study where applicable. Songs performed by *A. elliotti* include the following: calling songs, responding songs, courtship songs, disturbance sounds, contact sounds, reflex cry sounds, and oviposition songs. The last two types of emissions were identified in the present study as additional to those sounds described by Loher. Also, disturbance sounds were observed in both sexes and not just males.

The principal songs of *A. elliotti* may be characterized on the basis of both physical and functional characteristics. Observations and recordings of the sound emissions of the grasshoppers from the six populations, reared in the insectary, did not reveal any

behavioral or physical differences which could be attributed to population source. Grasshoppers from all six populations sang in alternation with songs produced by males and females of any other population. Observations of the stridulatory behavior of each population indicated that each type of sound signal, performed by this species, served the same functions in each group. Frequency range, song rhythm, and the waveforms of pulses and chirps, as observed on an oscilloscope, were similar for all six populations. Interpopulational learning of singing types and patterns may have occurred, since grasshoppers from all six sites were in auditory contact with each other from the time of maturity. Grasshoppers in the cylindrical cages emitted calling and responding songs more frequently than grasshoppers in the larger rectangular cages used in the laboratory for the present study and more frequently than grasshoppers at the field site in Billings. The 200-250 adult grasshoppers in the three rectangular cages seldom performed calling or responding songs. Rarely were more than six calls heard in an 8 hr. observation period. One hundred seventy adults in male-female pairs in cylindrical cages in a single room at 32.2°C air temperature performed as many as 54 songs in a 15 min. interval. Six male-female pairs of blinded (head capsules painted with black enamel), adult *A. elliotti* frequently performed male and female calling and responding songs. Blinded males produced as many as eight calling songs in 2 min. Blinded females occasionally responded, singing in alternation and

after the termination of the male song. Calling and responding songs by the blinded grasshoppers were performed every day over a seven day period. No calling or responding songs by the 32 sighted grasshoppers in the same cage were observed during the same period. Sighted males and females, contained in groups of the same sex, in the cylindrical cages also performed frequent calling and responding songs. Female responding songs were observed on six occasions. Three virgin females contained in a cylindrical cage, since the time of molting to adult (2-3 weeks), performed responding songs for a period of 4 hrs. on two consecutive afternoons. Six adult females isolated from contact with males for one week performed calling and responding songs for a period of 20 min. during a conditioning period of starvation prior to olfaction tests of food odors. Individual blinded females in the cage in the glass-roofed room were observed performing calling and responding songs on three separate occasions. Twenty-four males in the same cage with no contact with females performed as many as 15 calling songs in 10 min. It appears that visual or physical isolation from members of the opposite sex increases the frequency of calling and responding songs.

Changes in light intensity appeared to influence the initiation and termination of calling and responding behavior. Low light intensities or sudden decreases in light intensity caused a complete cessation of singing in the insectary. (see section of this paper on

visual, photic, and thermal responses). Light intensity effects on song rhythm were not investigated. Air temperatures above 18-21°C appeared to be necessary before any singing could occur, but air temperatures as high as 43°C did not terminate singing by *A. elliotti*. The effects of other environmental factors on stridulatory activity were not observed.

Songs were recorded at air temperatures ranging from 35.6°C to 38.8°C. No relation between chirp or pulse repetition rate as well as chirp or pulse duration and temperature change was determined for any of the songs over this temperature range. Variation within a song was as great as variation between songs, over this temperature range. However, playback of songs recorded at these temperatures to grasshoppers at 31.0°C revealed that male calling and responding songs at 31.0°C demonstrated a longer chirp interval than that of the recorded songs. Males that sang in response to playback of a male calling song often sang in alternation with the recorded song but were slightly out of phase, usually lagging so that a responding chirp did not occur between every calling chirp. Males that responded more than once to playback of a calling song adjusted their stridulations to achieve accurate alternation. Analysis of alternation singing indicates that both the calling male and the responding male usually adjust their songs to establish true alternation; i.e., each produces a chirp in response to a chirp of the other and no overlap of the chirps of the

two grasshoppers occurs.

The principal song types identified for *A. elliotti* have both physical and functional characteristics. Table 22 compares the principal physical characteristics of the different songs. Physical characteristics were determined by analysis of recorded signals. Functional characteristics were determined by observations of the conditions in which the signal is emitted, of the behavior of the emitter, of the response of other grasshoppers at the time the signal is emitted, and of the response of other grasshoppers to playback of the signal without the presence of the emitter. The following song types were identified for *A. elliotti*. All time measurements are based on recordings made at 35.6-38.8°C; other temperatures, especially lower temperatures may alter temporal components of song rhythm.

a) Calling Song. (Oscillograms, Figure 11; chirp repetition oscillograms and graphs, Figures 12 and 13). The male song consists of a sequence of chirps emitted at a fairly regular rate of .53 to .64 sec. intervals. Each chirp has a duration of 120-175 msec. Calling songs are composed of as few as 3-4 chirps or as many as 37 chirps or more. A single chirp contains 17-20 closely spaced pulses at 8-10 msec. intervals.

Males were observed performing calling songs when alone, when with other males, and when in the presence of a sexually unreceptive female. The song may have a courtship function in the presence of an unreceptive

TABLE 22. COMPARATIVE SONG CHARACTERS OF MALE AND FEMALE EMISSIONS OF *A. ELLIOTTI*. (Frequency of all songs; 60-16,000 Hz and above; 16,000 upper range of microphone).

Sex	Song Type	Dominant Frequencies in KHz	Pulse Interval (msec)	Pulses per Chirp	Chirp Interval (sec)	Chirp Duration (msec)
Male	Calling	3.8, 5.8	8-10	17-20	0.56-0.81	120-175
	Responding	same	same	same	0.80-1. 0	150-200
	Courtship*	--------	----	-----	---------	-------
	Disturbance	4.8,6.0	10-14	23-30	0.46-0.53	250-350
	Reflex Cry	5.1, 6.4	8-12	14-17	0.31-0.40	150-170
	Copulation*	--------	-----	-----	---------	-------
Female	Responding	2.6, 3.2	10-16	17-20	0.80-1.00	200-230
	Disturbance*	--------	-----	-----	---------	-------
	Calling*	--------	-----	-----	---------	-------

*Recognized, but not recorded.

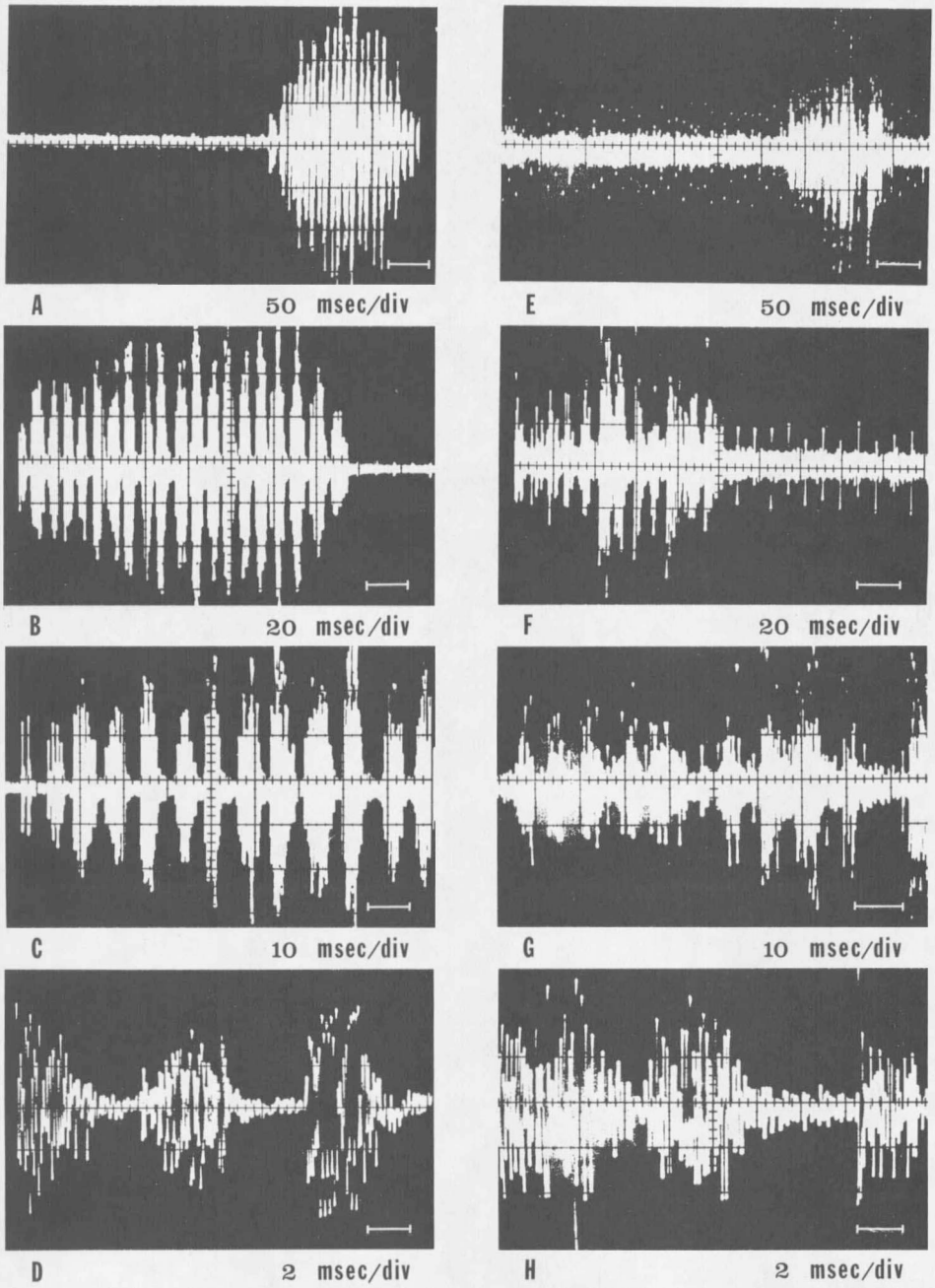


Figure 11. Oscillograms of male calling songs. A,B,C.D. Song produced using both legs. E,F,G,H. Song produced by male with only one leg. White bar in every case indicates one division.

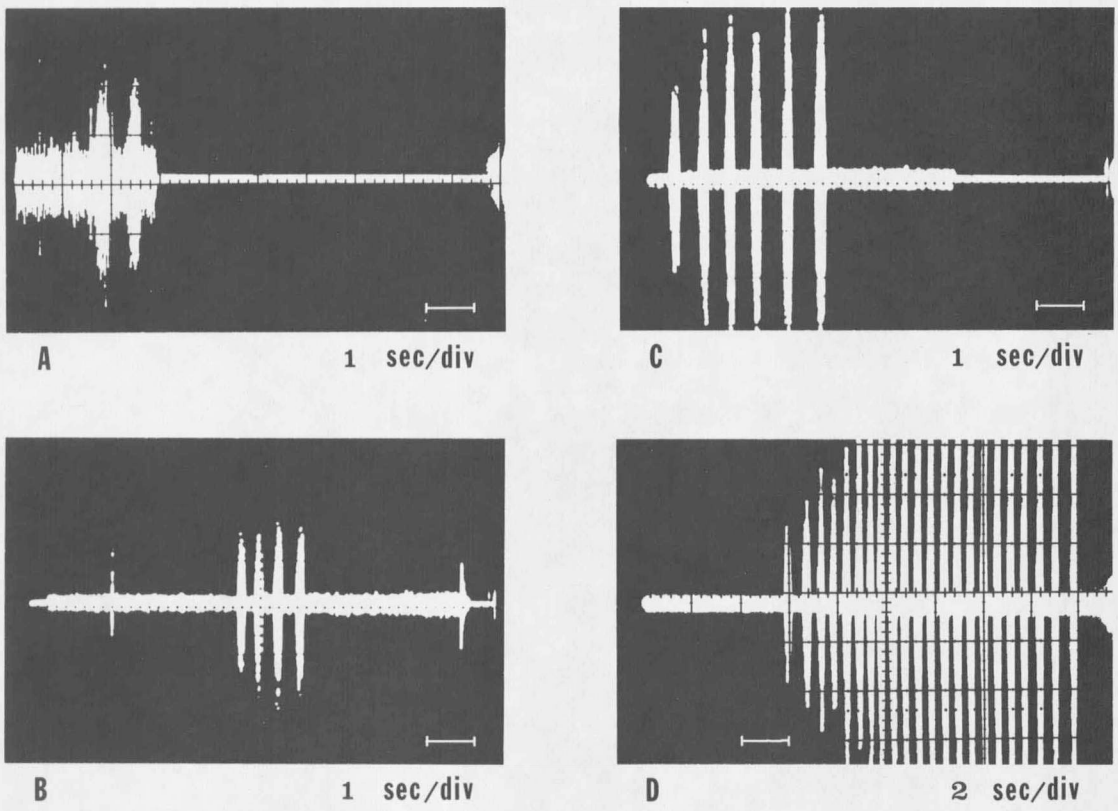
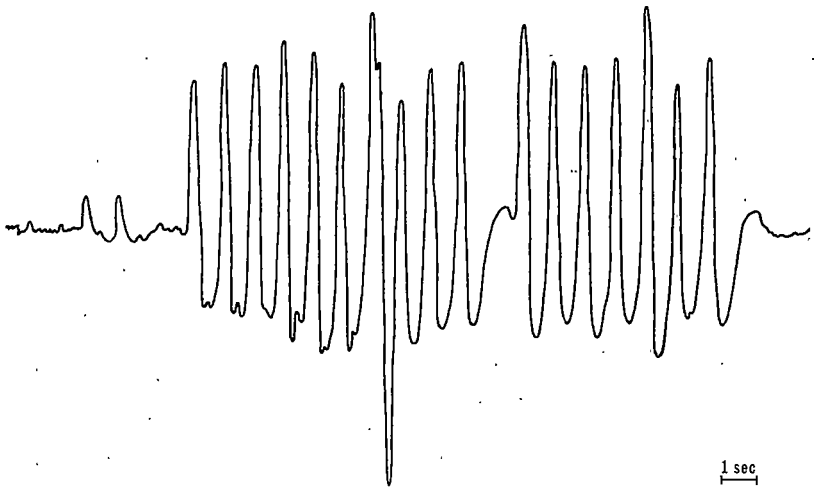
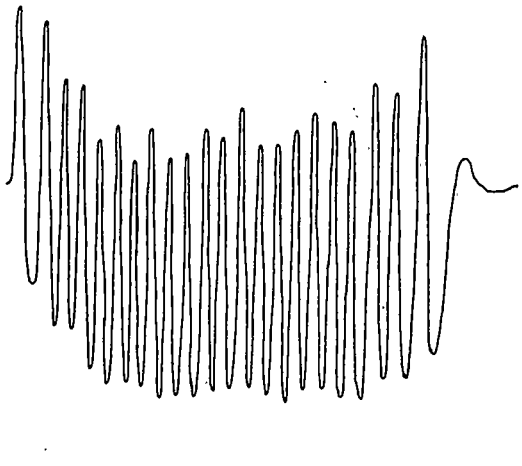


Figure 12. Oscillograms of male songs showing an entire sequence of chirps. A. Male disturbance song. B. Male reflex cry. C,D. Male calling songs. White bar in every case indicates one division.



A



B

Figure 13. Charts of the rate of repetition of chirps of calling and responding songs. A. Male and female responding songs, high peaks are chirps of female, slight peaks between female chirps and to the far left are produced by a male. B. Male calling song.

female, but it was primarily observed in the cylindrical cages where the male of necessity performed the song in the vicinity of a female regardless of any courtship connotations.

In the field, males pottered or wandered around on the ground, frequently stopped, and occasionally stridulated a calling song. Calling males frequently climbed onto small prominences such as rocks and lumps of dirt or up stems of grass before stridulating. Otte (1971) observed similar behavior by *A. elliotti* in the field. He also reported that these striculations were infrequent and sometimes were not observed in some populations. Tests in the insectary at Bozeman indicated visual or spatial isolation from other grasshoppers increased the frequency of performance of this song, whereas grasshoppers able to wander and make frequent contact with other grasshoppers, especially with females, seldom emitted a calling song.

Responsive females moved towards a singing male or towards a loudspeaker emitting a recording of the male calling song. Females that had been isolated from males for several days were much more responsive. Males occasionally oriented and moved towards the source of a calling song produced by a male or played through a loudspeaker. One male in the insectary first sang in alternation with a calling song emitted from 7 ft. away. The male terminated his response song, oriented and began to approach the loudspeaker before the recorded song was completed. He continued his approach after the loudspeaker

had stopped emitting the calling song. He stopped his approach and began to chew on a blade of grass after moving about 20 in. A second playback of the recorded song 30 sec. later was answered but no movement towards the source occurred. A third replay of the calling song was not answered, but the responding male again approached the source before the call ended. The speed of the approach increased as the song terminated. The male stopped about 10 in. from the silent speaker and emitted a calling song. He then continued towards the speaker and sat on the ground directly in front and about 1 in. from the speaker, which had been silent since the third replay. Additional replays of the calling song through the loudspeaker resulted in wandering in the area of the loudspeaker by the responding male with no responding stridulations. After 2 min., the male left the area of the loudspeaker. His approach had been along an almost straight line, with corrections made after each stop. His departure path was circuitous.

Both sexes, when approaching the source of a calling song, paused during the emission of the song, occasionally emitted a response song, oriented towards the source during performance of the calling song, and moved towards the sound source primarily between emission of calling songs. Stridulation of the calling song by a male appears to indicate sexual responsiveness on the part of the male and may have some territorial functions, indicating, at least, the location of the male.

b) Responding Song. (Oscillograms, Figure 10; chirp repetition graph, Figure 13). This type of song is emitted by males and females in response to a male calling song. Between males the calling song is modified and is usually performed in alternation between two males. One male initiates the stridulating, the other joins the first in alternation of the chirps of the song. Either male may terminate the song; the remaining singing male usually emits two or more additional chirps before discontinuing the song. Occasionally, a third male will alternate chirps with one of the duet singers, but only two males normally perform at the same time. Thus, one male will emit a calling song which may be answered by a second male. Whichever of these two males continues to sing after the other has terminated his exchange may be answered by a third singing male and again either male may terminate the song. Rarely were more than three males involved in alternation singing. Males often emitted a calling song within 1-2 chirp intervals of the completion of a calling or responding song of another male. These calling songs appeared to be in response to the previous singing, since they were initiated within 0.5-1.6 sec. of the termination of another male song.

Alternations between males were characterized by increased intervals and regularity of chirps (Table 22). Loher (1971) indicated that chirps become shorter, but the present study indicated that chirp duration may actually increase slightly. The waveform of the chirps of

the male calling song and of the male responding song differed primarily in the duration and intervals of the chirps. Responding songs emitted by males after cessation of stridulation by another male could not be physically distinguished from a calling song.

Calling and responding songs between males enabled males to locate one another and as such served as an 'aggregation' song as evidenced by movement of one male towards another as described under the calling song. Stridulation appears to trigger an approach and to serve as a navigational aid. Certain males consistently performed long calling and response songs and often sang last in alternations. Several workers have identified two types of male alternations - a responding song and a rivalry song, depending on the distance between males (Young, 1971). A responding song may change into a rivalry song as two male grasshoppers are brought together. Typically, the emission rate of the alternation song of some Acrididae increases as distance between the males decreases (Weih, 1951; Young, 1971; Loher, 1971). Young (1971) and Morris (1971) studied alternating songs of *Chorthippus brunneus* (Thumb.) and Conocephaline grasshoppers respectively and concluded that alternations between males, especially rivalry songs, provided evidence for a male hierarchial system in grasshopper social systems. Male dominance and maintenance of a territory may be associated with acoustic exchange.

The responding song of the female of *A. elliotti* is physically similar to that of the male, but the female song differs in some parameters. The female song has a dominant frequency of 3.2 KHz as compared to 5.8 KHz of the male. The interval between chirps and the duration of chirps of the female song is longer than that of responding songs between males (Table 22). The longer duration of a chirp in the female song is a result of a larger interval between pulses rather than an increase in the number of pulses in a chirp. Occasionally, a double chirp composed of two short chirps performed in rapid succession is emitted by a responding female. Short chirps also occur at the beginning or end of some responding sequences. The female song is usually sung in alternation with a male calling song or in reply to a male song. On one occasion, three females which had been isolated from physical and acoustic contact with males emitted a song very similar to the female response song. No recording of this song was obtained. It appears that a calling song may be emitted by females of *A. elliotti* and that the responding song is a variation of the calling song.

Responding songs performed between the sexes function in location of each individual by the other. Males will approach singing females from a distance of 6 ft. or more, females will approach from a distance of 4 ft. or more. Males approaching a singing female often sing in alternation or reply. Females usually silently approach a singing male. Females may remain stationary and repeatedly indicate their position by

emission of a calling or responding song. Responding songs between the two sexes have been termed agreement songs by some workers (Dumortier, 1963).

Females do not perform responding songs in alternation with other females. Synchronous stridulatory movements by two females were observed in one recording of the female response song. The two females were within 3 in. of each other and were moving their legs in what appeared to be almost absolute synchrony, while a female responding song was emitted. Analysis of the waveform produced did not reveal any overlapping or lurring of the oscillations in each pulse, indicating that probably only one of the females was emitting an audible chirp. Silent stridulatory movements by females were occasionally observed.

c) Courtship Song. No elaborate courtship songs were observed in *A. elliotti*. Loher (1971) did not observe any specialized courtship song in this species. Otte (1970) published an audiospectrograph of a male 'courtship' song for *A. elliotti*. He reported that males usually approached and attempted to mount a female with no courtship song performed but that in two approaches of 13 observed in one population, the males also stridulated before mounting in a series of short, more or less regularly spaced pulses of sound. The song identified by Otte (1970) as a courtship song appears to be the song referred to as a reflex cry in the present study.

A courtship song, when present in a species, usually involves emission of a song by a male in proximity to a female and is accompanied by strong visual stimuli. The primary function of the song appears to be to stimulate the partner to induce a state of sexual responsiveness. Some self-stimulation of the male also may occur (Loher, 1971).

In the present study, a calling song was occasionally emitted by a male in visual contact with a female in the laboratory and field cages, but this was not observed in the wild population. This calling song may perform a courtship function in synchronizing sexual responsiveness, but most courtship sequences of behavior were silent with no stridulation of a calling or courtship song after visual contact between the male and female had been established. Jacobs (1953) distinguished four groups of courtship in Acridinae (Gomphocerinae). The groups demonstrate a gradual development of courtship behavior, starting with a complete lack of a courtship song, continuing through slight variations of the calling song for a courtship function, and ending with a highly structured courtship song consisting of a long emission often broken with various short elements.

d) Disturbance Song. (Oscillograms, Figure 14; chirp reception oscillogram and graph; Figures 12 and 15). The male song is composed of a short series of chirps of relatively long duration. The number of pulses in the chirp and the interval between chirps is greater than for

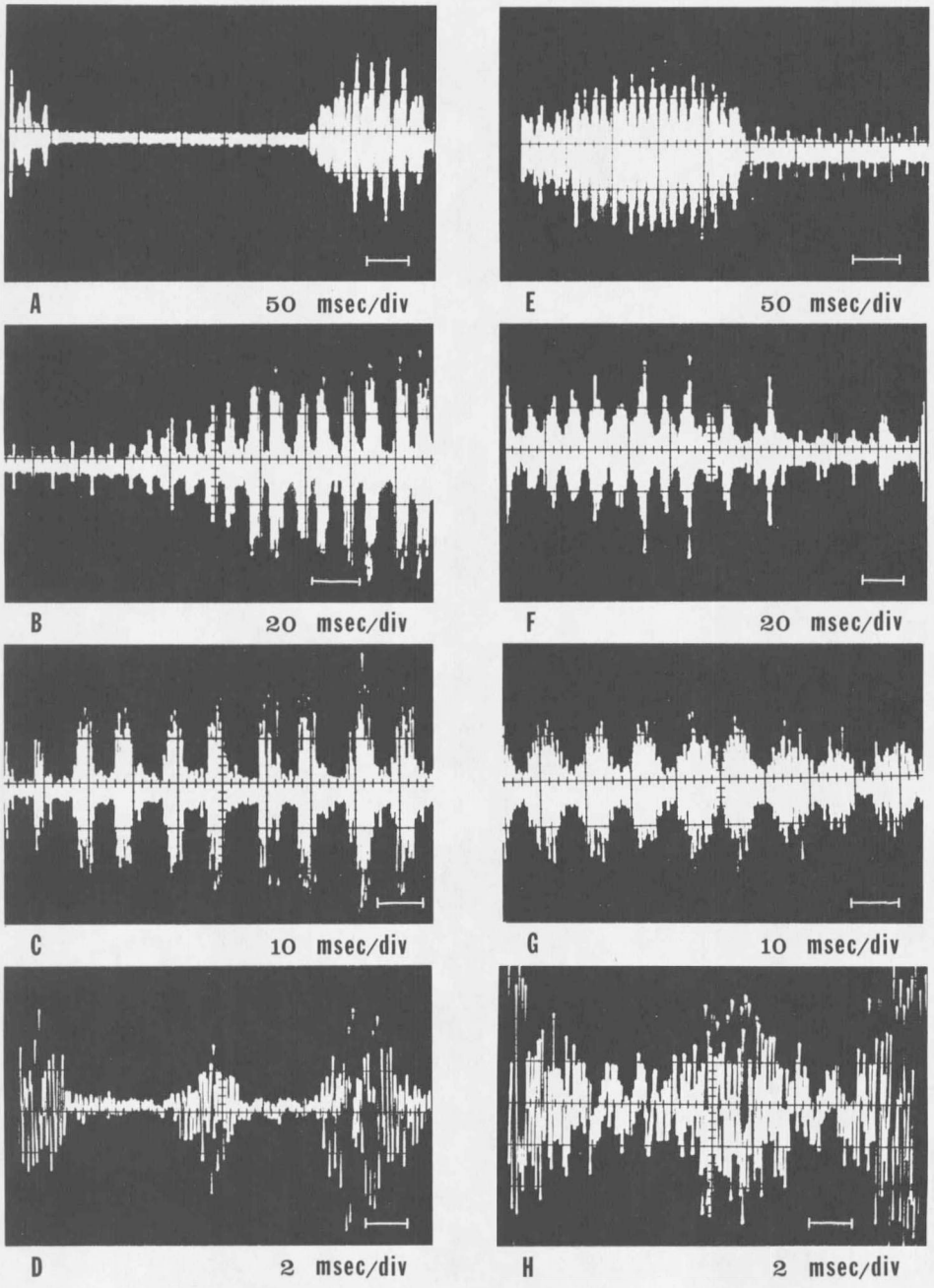
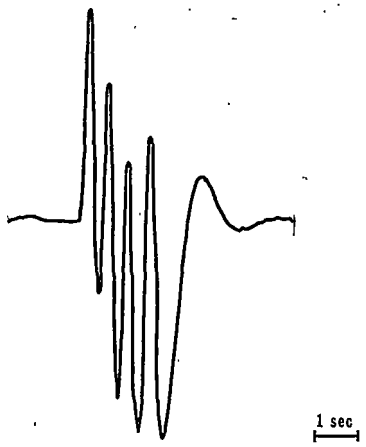
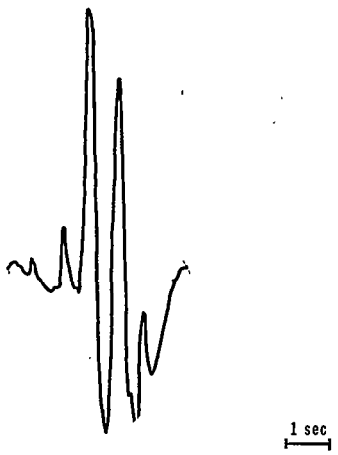


Figure 14. A,B,C,D. Male reflex cry. E,F,G,H. Male disturbance song. White bar in every case indicates one division.



A



B

Figure 15. Charts of the rate of repetition of chirps of male disturbance and reflex sounds. A. reflex cry of male. B. Disturbance song of male.

any other male song. Seldom are more than four chirps emitted. The song has a distinct buzzing sound for each chirp.

The disturbance song is performed by a male when approached, touched, or in the proximity of another member of the species, usually of the same sex. Stimuli such as the passing of a fly or being touched by the observer also elicited this response. Otte (1970) termed this song an aggressive song. Loher (1971) characterized the disturbance song as "short, sharp sounds stridulated in a rhythmical fashion between males". He reported that the consequence of such duets was dispersal in all cases. Duet performance of the disturbance song was not observed in the present study. Loher's description is brief and it was not possible to determine if he was describing the same song as that identified in the present study. Duet performance by males in close proximity is specifically termed a rival's song, while performance of a song by one individual caused by the proximity of another individual of the same species is properly termed a disturbance song (Dumortier, 1963). Dumortier includes the copulation song produced by some male Acridinae when disturbed while mating among the disturbance songs. *A. elliotti* males emitted a disturbance song when disturbed while mating by another male. The song also was emitted when a female began to walk around or tried to dislodge a copulating male. Recordings were not obtained of these songs, but they all exhibited the characteristic short series of buzzes associated with the disturbance song

of this species.

The disturbance song appears to establish the sexual identity of the disturbed male to deter copulatory attempts by other males. The song also dispels intruders, especially other males. It is probably indicative of territorial behavior. The disturbance song of a copulating male appeared to be very effective in promoting the withdrawel of an intruder. In almost every observed approach of a male towards a mating pair, performance of the copulating song by the mating male was followed by a termination of the approach of the other male and a subsequent turning away by the intruder. The copulatory song also may serve a copulation-facilitating or pair-maintaining function when produced in response to activity of the female as suggested by Alexander (1967) as the function of a copulatory song.

A disturbance song produced by a female in response to being approached or touched by another member of the same species was occasionally heard. The song was most frequently observed in response to courtship or copulatory attempts by males. A silent stridulation in response to male mating behavior was also seen. Otte (1970) published an audiospectrograph of a female 'aggressive' song. The song demonstrated a dominant frequency in the range of 2-4 KHz, whereas the male song showed a dominant frequency at approximately 7.8 KHz. Recordings of a female disturbance song were not obtained in the present study because the song was only heard infrequently. However,

the frequency appeared to be lower than that of the male song. The female song also demonstrated a relatively long duration of each chirp resulting in a buzzing sound. The female disturbance song was composed of only 1-2 chirps in most instances. The song appeared to indicate a non-responsive sexual state of the female.

e) Contact Sounds. These sounds were observed only by Loher (1971) in *A. elliotti*. He described these sounds as soft, short signals emitted by a male after an unsuccessful copulatory attempt as the female walks away and the male follows her. The male can perform the song while walking and with only one leg.

Males of *A. elliotti* as well as females occasionally make stridulatory movements without audible sound production. It is possible that contact sounds were not observed during the present study due to background noise or inadequate microphone sensitivity.

f) Reflex Cry. (Oscillograms, Figure 14; chirp repetition oscillogram and graph, Figures 12 and 15). This sound is performed by males in response to strong stimuli, usually not produced by other members of the species. A series of chirps of short duration composed of fewer pulses than any other song are emitted at rapid rate of repetition. Intervals between pulses are short. The sound may be produced in response to another grasshopper just as the disturbance song is occasionally emitted in response to stimuli other than another member of the species. The reflex cry has only been observed in males. The sound

may be a displacement activity produced by intense nervous activity in response to stimuli. Dumortier (1963) prefers the term reflex cry to protest song to describe this type of song in arthropods, since the sound appears to be an outlet for intense nervous discharges in situations of constraint or excitation.

The 'courtship' song presented in the audiospectrographs of the songs of *A. elliotti* in the paper by Otte (1970) appears to be composed of short pulses emitted at a rapid rate of repetition and may be an example of the reflex cry observed in the present study.

g) Oviposition Songs. This category has been conceived for the present study to include songs performed by males of *A. elliotti* while accompanying a female demonstrating oviposition behavior. Males were frequently observed in both the laboratory and in the field following a female searching for an oviposition site, remaining with a female while she oviposited, and chasing after a female that had recently completed oviposition. Usually several males accompany a female at this time with some males joining the group and other males leaving at any time. Occasionally, a male will stop and stridulate a short song, normally composed of 2-6 chirps. Buckell (1922) probably observed this type of behavior in his note on the behavior of *A. elliotti* males in British Columbia: "On several occasions from three to five males were observed following a female. In each case the female was hopping while the males were running rapidly behind, stopping

occasionally to stridulate." The present study indicated that the only time a female normally rapidly ran and hopped about was during a 15-20 min. period immediately following oviposition. At this time, males were strongly attracted to the female, probably as a result of strong visual stimuli from the moving female.

Oviposition songs were emitted before, during, and after oviposition of the female. Recording attempts to obtain this signal were unsuccessful because the males actively moved about the female making it impossible to bring the microphones close enough to the males to receive a signal. Occasional disturbance songs were stridulated by males, probably in response to the presence of other males. The oviposition songs appeared to be modified calling songs and varied in rhythm, at times closely resembling a short calling song and at other times approximating the rapid repetition rate of the reflex cry. The function of the oviposition songs in unknown. Females are totally unreceptive to sexual advances at the time of oviposition and remain so until 15-25 min. after oviposition has been accomplished. Males rarely try to copulate with a female during the period preceeding completion of oviposition. Males appear to be very excited during this time, actively moving about and performing frequent leg movements. It is possible that the oviposition songs represent displacement activities.

Sounds other than stridulatory emissions may impart information among grasshoppers. Mandible-snapping may influence aggregation for

feeding, may indicate disturbance, and may serve a calling function in a few genera of Acrididae (Alexander, 1960a). Audible sounds are produced by *Aulocara* chewing. Movements of the empty mandibles produced faint sounds, but these did not appear to operate as intraspecific communicative signals. Recorded feeding sounds were played through a loudspeaker placed in the center of each cage in the glass-roofed room of the insectary. The sounds were played 25 times at 30 sec. intervals in each of three cages. Two cages contained 30-35 grasshoppers; the third cage contained 64 grasshoppers. No grasshoppers approached the loudspeaker during these tests, either while sounds were being played or during the interval between playback of sounds. Playback of chewing or feeding sounds did not appear to induce any attraction to the sound source. These tests were rudimentary and did not investigate the effects of prior conditioning such as starvation on the response of grasshoppers.

Wing-produced sounds are probably not important communicative signals for *A. elliotti*. Flight sounds have not been observed and the species rarely flies. Occasional spreading flaps of a single wing were performed by a stationary grasshopper and a soft sound was produced, but the movement was performed by solitary individuals as well as individuals in groups and did not appear to have either a visual or an acoustic signalling function.

Sounds were produced by both sexes by percussion of the substratum usually accompanied by stridulation. Stridulating males and females placed on a screen produced an audible resonance sound by vibration of the screen. The resonance is apparently produced by contact of the tarsi of the hind legs with the substrate. Dumortier (1963) postulated that a noise produced by percussion on a substratum may act as a communicative signal for a partner or a rival. The signal, if a signal exists, may be received by mechano-receptors sensitive to vibrations transmitted by the substrate as well as by auditory receptors. It is also possible that the striking of the ground is incidental to visual stimuli (movement of the legs) or other acoustic stimuli (stridulatory sounds). It was not discerned whether the 'silent' leg movements produced by males and females of *A. elliotti* produced a sound by a striking of the substratum.

Stridulatory emissions of *A. elliotti* are produced by a relatively low-amplitude, rapid passage of the femora across the forewing. Removal of the tibial spines did not affect sound emission nor did removal of the tibia. Both femora are moved synchronously during stridulation. Sound emissions produced by males with only one hind leg could not be distinguished from those produced by males with both hind legs in terms of pulse waveform. A ridge on the inside of the femur is apparently struck against a raised vein of the forewing. Detailed analysis of the mechanism of sound production was not attempted.

Stridulatory movements were observed in hatchlings less than 24 hrs. old in response to other members of the species in close proximity. No audible sounds were produced by stridulatory movements of any instar nymph because the wing portion of the stridulatory apparatus had not developed. These silent stridulatory movements may have had a visual communicative significance. It is also possible that percussion of the substrate may have occurred and may have been of communicative value.

Discussion: Dumortier (1963) grouped sound phenomena under two categories according to the behavior with which sound emissions were associated and the situations under which they occur. The first category includes sounds that establish a situation which satisfies a need or tendency such as calling and mating songs. The second category includes sounds that are associated with a defensive or "hostile" attitude such as the disturbance and rival's songs.

Alexander (1967) recognized nine functional categories of arthropod acoustic signals:

1. Disturbance and alarm (predator-repelling and conspecific alarming) signals.
2. Calling (pair forming and aggregating) signals.
3. Aggressive (rival-separating and dominance-establishing) signals.
4. Courtship (insemination-timing and insemination-facilitating) signals.
5. Courtship interruption (pair-reforming?) signals.
6. Copulatory (insemination-facilitating and pair-maintaining) signals.
7. Post-copulatory or intercopulatory (pair-maintaining) signals.
8. Recognition (pair- and family-maintaining) signals. (limited to subsocial and social species)

9. Food and nest site directives (limited to social species).

Number nine was deleted later by Alexander (1968) and he added aggressive mimicry "prey attraction by production of pair-forming signals of prey species".

Evidence from the present study and those of Loher (1971) and Otte (1970) indicate that the first seven categories may be present in *A. elliotti*. The functions ascribed to sounds of this species in the present study closely agree with those identified by Loher (1971). Aggressive signals are referred to as disturbance signals by Loher (1971) and in the present study. In addition to the categories presented by Alexander, it appears that some sound emissions of *A. elliotti* may function as displacement activities and may not have a communicative function.

The stridulatory emissions of this species appear to be derived from the calling songs of the respective sexes. The waveform of each pulse varies within a song as much as between songs for all of the sounds recorded in the present study. The male and female pulse waveforms closely resemble each other in shape. Songs differ physically primarily by rhythm changes produced by varying the number of pulses in a chirp and the interval between pulses and chirps. The disturbance sounds of the male and possibly that of the female are very stereotyped. The other songs are somewhat variable in rhythm, and gradation from one song type to another is demonstrated. The

responding songs of both sexes appear to be a modification of a calling song; the calling song of the initial stridulating individual changing to a response song when another individual answers. The reflex cry of the male often continues into performance of a calling song by a slowing of the rhythm of the chirp sequence.

A. elliotti has not developed the highly differentiated acoustic displays for courtship that are demonstrated by some members of the sub-family Acridinae. Jacobs (1953) proposed a classification of the courtship of the Acridinae (Gomphocerinue) composed of four classes progressing from a group in which no courtship song is performed through groups with a courtship song like the calling song to a group in which a real and complex courtship song is emitted. A courtship song may occur in *A. elliotti*, but most courtship displays do not include emission of a courtship song. Visual signals, tactile signals, and possibly olfactory signals appear to be important components of courtship behavior (described in the section of this paper on behavioral patterns and social interactions).

The production of acoustic emissions depends in part on the degree of isolation of the members of a population. Otte (1970) noted that members of some populations rarely stridulated in the field. Stridulations were seldom heard in the field at Billings, Montana. Visual isolation by blinding or caging of individuals increased emissions of calling and responding songs, especially if individuals were separated

from members of the opposite sex. Internal biological factors such as the sexual state of the individual appear to be important for the initiation and maintenance of stridulatory activity.

Observations on the effects of temperature and light on song parameters support the conclusions of Dumortier (1963) that heat is a limiting factor, that singing can only occur at or above a particular temperature level, but that temperature does not directly initiate singing, and that light has a dual function. It may regulate daily activity rhythms; the distribution of stridulatory activity over 24 hrs. is quite characteristic for families of Tettigoniids and Acridids. It may interrupt or disturb singing if light intensity changes suddenly. Other physical factors such as atmospheric pressure, humidity, ionization of air may influence stridulatory activity or associated behavior.

Phonotaxis towards both natural and artificial acoustic signals was demonstrated by both male and female *A. elliotti*. An "acoustic directional memory" exists in both sexes of this species. Dumortier (1963) discussed this ability to continue to move towards the source of sound emission, even if the sound is interrupted, by females of the species *Ephippiger* (Orthoptera, Tettigonioidea). This "memory" is probably only an ability to temporarily continue a state of excitation created by an acoustic stimulus.

Dumortier (1963) distinguished insect phonotaxis from tropism based on characteristics of tropisms taken from work by Viaud (1956).

Dumortier's concepts of tropisms are presented here. Phonotaxis resembles tropisms in a broad sense, but differences are more numerous than similarities. The stimulus for a tropism is usually produced continuously; the stimulus for phonotaxis is usually emitted discontinuously as a natural consequence of the sound apparatus. The stimulus responsible for a tropism acts as a whole and individual factors do not appear to trigger a response. Individual factors of phonotaxis such as pulse rate, signal form, etc. can be extracted from the sound signal and are effective releasers (sign-stimuli) of a response. Finally, the stimulus for a tropism usually has an origin outside of the species from the inanimate environment, while the stimulus for phonotaxis normally has a biological origin from another member of the species.

In terms of behavior, three basic differences are seen in a comparison of phonotaxis and tropisms. First, tropism is not linked with motivation, while phonotaxis depends on certain physiological conditions in the receiver, often depending on the sexual state. The effectiveness of a trigger stimulus of a sound signal depends on the level of motivation of the receiver. This level actuates the I.R.M. (innate releasing mechanism, Tinbergen, 1951) which releases instinctive motion. Second, a tropism is an end in itself. A phonotaxis, on the other hand, is a link in a complex behavior pattern, the result of which is the establishment of a situation in which the motivation,

such as mating, can be satisfied. Third, in tropism, the source and the stimulus cannot be dissociated. The source may even be indefinable such as rheotropism or inaccessible such as phototropism and geotropism. Phonotaxis leads to a meeting with the source of the stimulus and new forms of stimulus (olfactory, tactile, visual) from the source create a second behavior sequence such as mating. It should be noted that phonotaxis is used here as defined by Busnel (1963) as movements directed towards the source of the acoustic emission, produced by a natural or artificial sound signal.

Tactic responses to acoustic signals can also result in dispersion as seen in the disturbance reactions of *A. elliotti*, and phonotaxis is not restricted to members of the opposite sex in this species since males are seen to approach other calling males. Alexander (1960) concluded that the primary function of male calling songs in Orthoptera and Cicadidae is to bring the sexes together, but that these sounds may have a greater variety of effects on other males which receive them than on females. The singing of one male may "cause another male to become more active, to become less active, to move toward him, to move away from him, to start singing, to stop singing, or to sing at a different rate or rhythm than he would if he were unable to hear the first male's song". Sound communication in adult *A. elliotti* affects the entire social organization of the species. Hierarchial relationships, territorial establishment, aggregation and dispersal, species-

specific recognition, synchronization of physiological states and possibly self-stimulation, maintenance of a population in a particular area, and location of other individuals of the species are some of the functions performed by acoustic signalling, which is very effective at both short and at long range. Alexander (1960) concluded that arthropod sound signals realize a high degree of intricacy and efficiency and in the complexity and multiplicity of functions as an intraspecific communicative device are probably only exceeded by combinations of tactile responses and by visual responses associated with rhythmic "dances."

VI. Behavioral Patterns and Individual Interactions

Mussgnug (1972) characterized six principal behavioral patterns of activity for *Aulocara elliotti:* a) resting, b) basking, c) feeding, d) courting, e) copulating, f) ovipositing. The last three categories are restricted to activities of the adults. Additional patterns of behavior were recognized in the present study: g) social interactions, h) pair formation, i) locomotion, j) stationary movements.

Published accounts of patterns of activity of *A. elliotti* are very incomplete. Feeding and vegetational relationships (Pfadt, 1949; Anderson and Wright, 1952; Anderson, 1961, 1964), aggregations and movements (Mussgnug, 1972; Anderson, 1964), mating behavior (Ferkovich *et al.*, 1967; Otte, 1970; Mussgnug, 1972; Anderson and Hastings, 1966), oviposition behavior (Nerney, 1954; Anderson and Hastings, 1966;

Mussgnug, 1972), and acoustic signals (Otte, 1970; Loher, 1971) have been described for this species, but many activities were not described in detail.

Observations of behavioral patterns of *A. elliotti* were conducted in the field and in the laboratory during the present study. Photographs of activities were made using a Nikon F, 35 mm camera with a Micro-Nikkor-P Auto 1:3.5 f=55 mm lens and a Bell & Howell model 374 Super 8 mm movie camera. Vocal descriptions of behavior were recorded on magnetic tape using a Sony TC 4-track tape recorder in the laboratory and a Panasonic RQ 420 S cassette recorder in the field. Individual grasshoppers were observed for periods of 20 min. or until a pattern of activity was completed. The magnetic tapes and the movie films were analyzed for temporal and sequential patterns of activity. A timing signal recorded on the magnetic tape facilitated temporal analysis, and a film editor was used to examine individual frames of the movie films.

Descriptions and analyses of the principal behavioral patterns of *A. elliotti* were obtained from 24 hrs. of tape recordings, 500 35 mm photographs, 1½ hrs. of movie film, and hundreds of written notations from observations. The behavioral patterns listed are displayed in both the field and the laboratory, unless stated otherwise. Sequences of activity often included rapid events; a grasshopper might start, alter, or terminate a movement in less than 0.1 sec. Movements by the

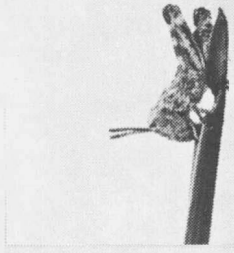
observer disturbed the grasshoppers, but vocal sounds did not appear to disrupt activities. Sharp clicks or noises and buzzing sounds produced by the Bell & Howell movie camera were discerned by *A. elliotti* and were sometimes disruptive to patterns of activity. The various activities observed in this species included communicative and non-communicative signals. Signals can be defined according to the function that they serve or according to the patterns of movements of the display. The function of a specific display is not always known, and unless a function can be demonstrated, naming the display according to the pattern of movement avoids functional implications. Functional names have only been used in cases where the function of the signal is evident, such as "calling" by the male. The following is a description of the principal behavioral patterns of *A. elliotti*.

a) Resting. (Figure 16). A resting grasshopper sits with the hind legs folded close to the abdomen, holds the thorax just above the surface on which it is resting, and often lays the abdomen on the surface. Members of this species usually rest on the ground, although they may rest on plants, sticks, rocks, and low objects. Resting off the ground is termed "roosting" in accordance with the usage of Ellis and Ashall (1957) in describing activities of *Schistocerca gregaria*.

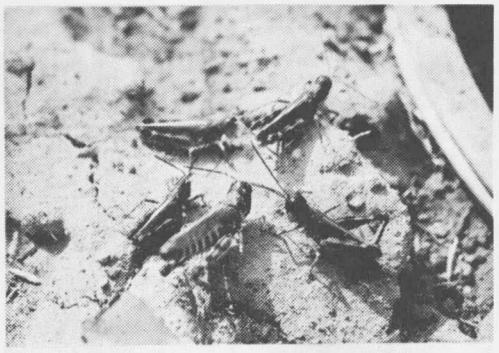
A. elliotti rest at night, unless air temperatures exceed 15.5°C, and during the day when air temperatures exceed 38.0°C, although individuals rest for short periods throughout the day. Short periods of



A



B



C

Figure 16. Feeding and basking positions of *A. elliotti*. A. Feeding by copulating female. B. Feeding by nymph in inverted position. C. Basking grasshoppers in resting positions.

resting (a few seconds to a few minutes) are interspersed among other activities such as feeding, wandering, and marching. The amount of time spent resting appears to depend on environmental conditions such as temperature and on individual differences in response. Adult males seldom rested during the day for more than short periods (5-15 min. maximum) unless environmental conditions prohibited activity. Adult females frequently rested for periods of 30-60 min. during the day. Observations of marked individuals of both sexes revealed that some grasshoppers are very active throughout their adult life whereas others are relatively sedentary.

Members of this species rest in groups or individually. Groups of resting grasshoppers often occur in response to environmental factors. Aggregations of grasshoppers bask in areas exposed to sunlight, sit in the shade or on objects to escape high soil temperatures, and rest at feeding and ovipositing sites. Visual stimuli appear to play a role in establishing and maintaining aggregations of grasshoppers. A group of resting grasshoppers appears to attract other grasshoppers of the same species. Movement occurs within a resting group; individuals enter and leave the group, others shift position and clean their eyes and antennae, some stridulate or perform leg movements, while others examine each other with their antennae and palps. The totality of these movements provides numerous visual signals to grasshoppers within and outside of the group

b) Basking. (Figure 16). Basking grasshoppers rest in areas exposed to radiant heat from the sun. *A. elliotti* also bask in warm areas near light bulbs and radiant heaters. Grasshoppers of this species frequently turn their bodies broadside to the sun while basking. Basking occurred during the early morning and late afternoon at low air and soil temperatures (see section of this paper on photic and thermal responses).

c) Feeding. Food preferences and the distribution of *A. elliotti* in relation to vegetation have been reported in detail by Pfadt (1949), Anderson and Wright (1952), Anderson (1961, 1964), and Mussgnug (1972).

The present study of feeding by *A. elliotti* indicated that feeding consists of three phases: 1) searching, 2) biting, 3) ingesting. 1) Searching: A grasshopper performs wandering movements, often sweeping the ground with the antennae and the mouthparts. The palpi are frequently waved in the air and brushed over surfaces. Searching appears to be induced by hunger and increases with starvation. Searching and other phases of feeding are inhibited by some behavioral activities. Adult females do not feed while ovipositing, and males may interrupt feeding to mate with nearby females or to stridulate. Environmental conditions such as low light intensities and unfavorable temperatures also inhibit feeding.

Searching movements continue until the animal is brought into contact with attractive olfactory stimuli and/or attractive visual

stimuli such as vegetation or vertical objects (see sections of this paper on olfaction and on photic and thermal responses). The animal then orients towards the source of the stimuli and approaches them, usually climbing and biting visual sources.

2) Biting: Biting appears to be a relatively indiscriminate tasting of potential food sources. Food odors and starvation increase the frequency of biting, which continues until a suitable food source is encountered. Mulkern (1969) concluded that Acrididae select host plants for ingestion by the presence of the proper phagostimulants and by the physical characteristics, such as texture of the plant. The absence of a phagostimulant or the presence of a deterrent causes the animal to resume searching and biting.

3) Ingesting: (Figure 16). *A. elliotti*, having chosen a suitable food plant by searching and biting, often assumes a particular position prior to ingesting food. The grasshopper inverts its body and hangs head down while eating. Adult females may ingest food for 20 min. or longer; ingestion continues until the grasshopper is satiated or is disturbed. The animal may occasionally select a new food source while feeding. Adult males appear to ingest food for shorter periods than females, seldom eating for longer than 10 min. at a time, although males may feed more frequently than females or at different times of the day. Observations on feeding were made during the mid-morning and mid-afternoon when males were engaged in searching activities for mates.

It is possible that males may feed for longer periods during the early morning and late afternoon. Males may feed while searching for mates, but do not feed while copulating. Females do not feed while searching for an oviposition site but often do feed while copulating.

d) Locomotion. Grasshoppers are continually moving in any grouping of this species unless environmental conditions such as temperatures above or below the thresholds of activity inhibit movement. All displacements of these grasshoppers normally occurred by walking or jumping. *A. elliotti* were never observed to fly unless disturbed by the observer or suspended by a thread attached to the dorsum of the thorax. Mussgnug (1972) noted that *A. elliotti* did not fly unless disturbed by the observer. Uvarov (1966) reviewed evidence from several workers that indicated that flight initiation and orientation in locusts is controlled in part by wind sensitive receptors on the head, body, and wings.

Adults of *A. elliotti* usually jump when disturbed, and they often jump down from objects upon which they have climbed. Short outbursts of jumping occur in groups of first and second instar nymphs, but this type of jumping rarely occurs in adults. Both nymphs and adults, individually or in small groups, make long jumps when disturbed by other animals or by quick, unidentified movements. A leaf blown by the wind or a rock tossed overhead can induce a long jump. Generally, the grasshoppers jump away from the direction of the disturbance and remain

low to the ground. Seldom did a grasshopper jump as high as 28 in., the height of the cages in the laboratory. These animals usually only jump once when disturbed. Upon landing, the grasshopper either remains quiet or runs along the ground until it reaches a hiding place in a depression or under vegetation. Grasshoppers, disturbed by the observer, jumped away and then often sat 'peering' in the direction of the observer. If again approached by the observer, the grasshopper either ran away or sat quietly, jumping only if the observer made a sudden movement or came within 2-3 ft.

A. elliotti frequently climb vegetation and low objects. Adult males often pause during their wandering activities on top of small prominences and appear to survey the area. Climbing may reflect a negative geo-taxis or a postural reflex. *A. elliotti* tested in the Tilt Table arena showed a tendency to move up an inclined plane at 17.5° or more from the horizontal. The angle of movement up the plane increased as the angle from the horizontal increased (Figure 17). Climbing is partially controlled by temperature. Different air and soil temperatures may either inhibit or stimulate climbing (see section of this paper on photic and thermal responses).

Horizonatal displacements of this species usually occur by walking, which includes 'pottering' (see Kennedy, 1945) and 'marching' (see Ellis and Ashall, 1957).

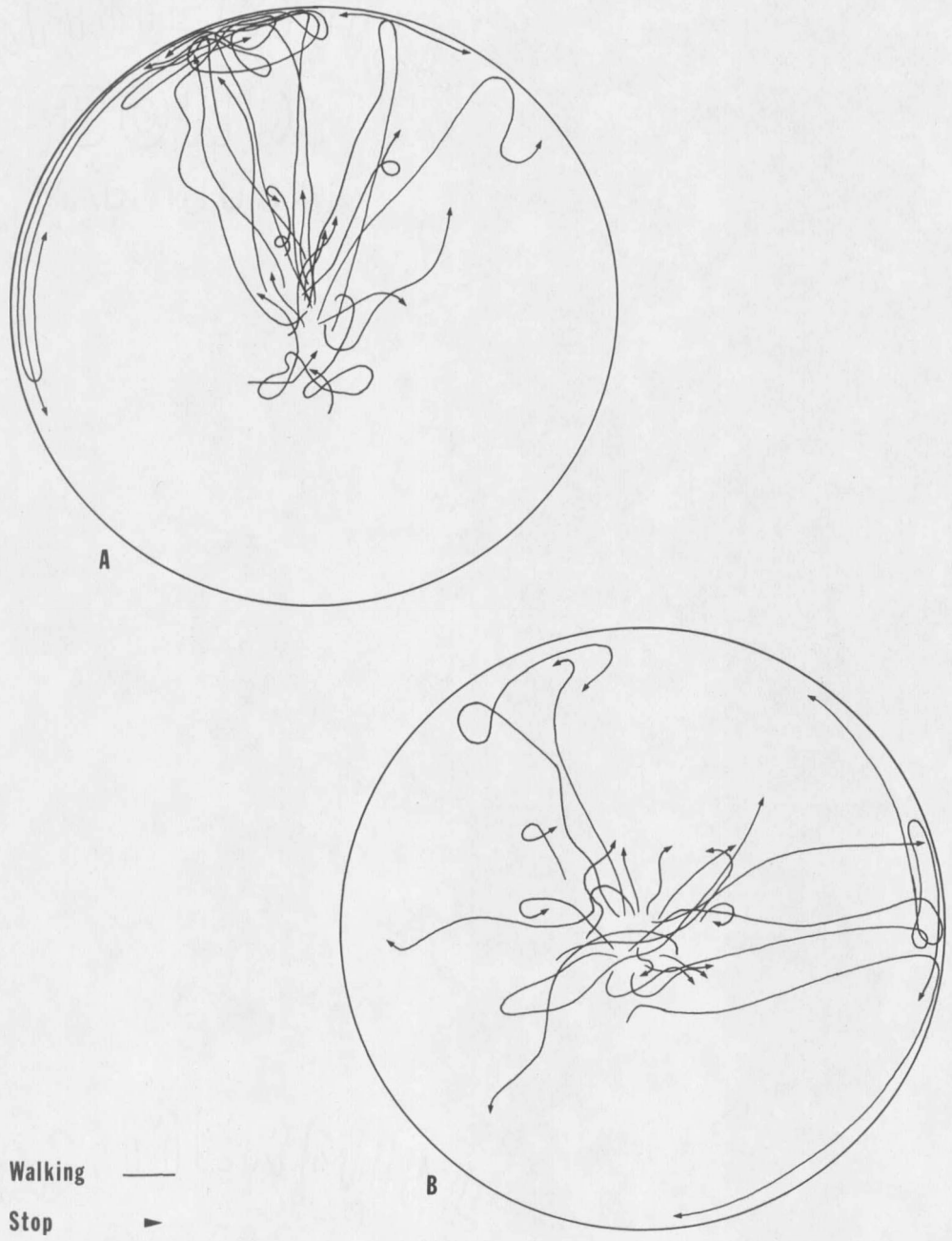


Figure 17. Movements of adult *A. elliotti* on an inclined plane. A. 35° from the horizontal. B. 17.5° from the horizontal. Top of each circle is the highest point above the horizontal.

Pottering is intermittent wandering, characterized by frequent changes in direction. The antennae and palpi frequently sweep the ground or surface on which the grasshopper is moving. Movements are generally slow, although adult males generally move faster and change direction more often than adult females. Under conditions of light and temperature conducive to activity, most males walk about, stopping frequently to examine the area. The antennae are frequently cleaned and are often used to examine objects. The male pauses on low elevations such as sticks, stones, and lumps of dirt and visually scans the area. During these pauses, the head and thorax are held well clear of the ground and the antennae carried erect. Pottering males have been observed to change direction, pause, or otherwise alter activity 367 times during a 20 min. observation. Pauses were generally short; many males paused less than 45 sec. at a time. Occasionally, a male rested or fed for 5 min. or longer, but usually for not more than 15 min. A few males were sedentary, seldom pottering and often resting for 30 min. or longer during the day. Individual members of both sexes demonstrated characteristic levels of general activity throughout their adult life. Some were usually very active while others were very inactive. Nymphs were not examined for individual variations in general activity levels, although nymphs demonstrate pottering.

Adult females spend less time pottering than do the males. Females frequently rest or feed for periods of 30 min. and occasionally

sat for as long as 60 min. during the day. Females tend to pause or rest in depressions, holding the body near the ground and the antennae low. Rarely do females assume the erect position on top of a prominence that is typical of a male. Pottering females frequently pause for 1-2 min. Seldom did a female alter activities more than 150-200 times during a 20 min. observation.

Searching for food, oviposition sites, and mates appear to be modified pottering activities. An ovipositing female pauses frequently to probe the soil, a male searching for a mate frequently pauses to scan the area, and grasshoppers searching for food continually examine the area with their antennae and palpi.

Marching differs from pottering in that the grasshopper moves more or less continuously, making few changes in direction. Individuals and groups of *A. elliotti* march in response to directed stimuli such as light, sounds, air currents, and odors. Both adults and nymphs march. Groups of marching grasshoppers apparently are held together by visual stimuli from their marching associates. Marching grasshoppers hold their bodies well off the ground and carry their antennae upright. Observations of *A. elliotti* indicated that these animals usually march short distances (5-10 ft.) and for short periods (5 min. or less). Displacement of groups of populations of this species may occur by marching, and marching may be initiated by undirected stimuli such as food depletion, but this was not observed in the present study.

e) Stationary Activities. *A. elliotti* perform several activities that do not involve locomotion. Many of these activities involve movements of the appendages and may serve communicative functions. These activities include:

1) Peering: The head and thorax are lifted well clear of the ground by extending the prothoracic legs and are moved slowly from side to side (see Kennedy, 1945). *A. elliotti* frequently stop and peer while approaching distant objects and grasshoppers. Peering also occurs in response to movements in the visual field of the grasshopper.

2) Stilting: (see Gunn *et al.*, 1948). The grasshopper raises its entire body clear of the ground by extension of all three pairs of legs (Figure 18). Stilting occurs in response to high soil temperatures, and it results in the body being raised as high as possible off the ground. Grasshoppers on hot surfaces may also shift positions of their feet, lifting one or more feet slightly for short periods.

3) Fidgeting: (see Ellis and Ashall, 1957). Fidgeting includes movements of the appendages without movement of the body as a whole. Eyes and antennae may be cleaned with the forelegs; legs may be moved; other grasshoppers may be examined with the antennae and palpi. In the present study, the term is applied to an assemblage of more or less unrelated movements performed by a stationary grasshopper.

4) Cleaning of the Antennae: This activity appears to be a fixed action pattern in *A. elliotti*. The antennae are frequently cleaned,

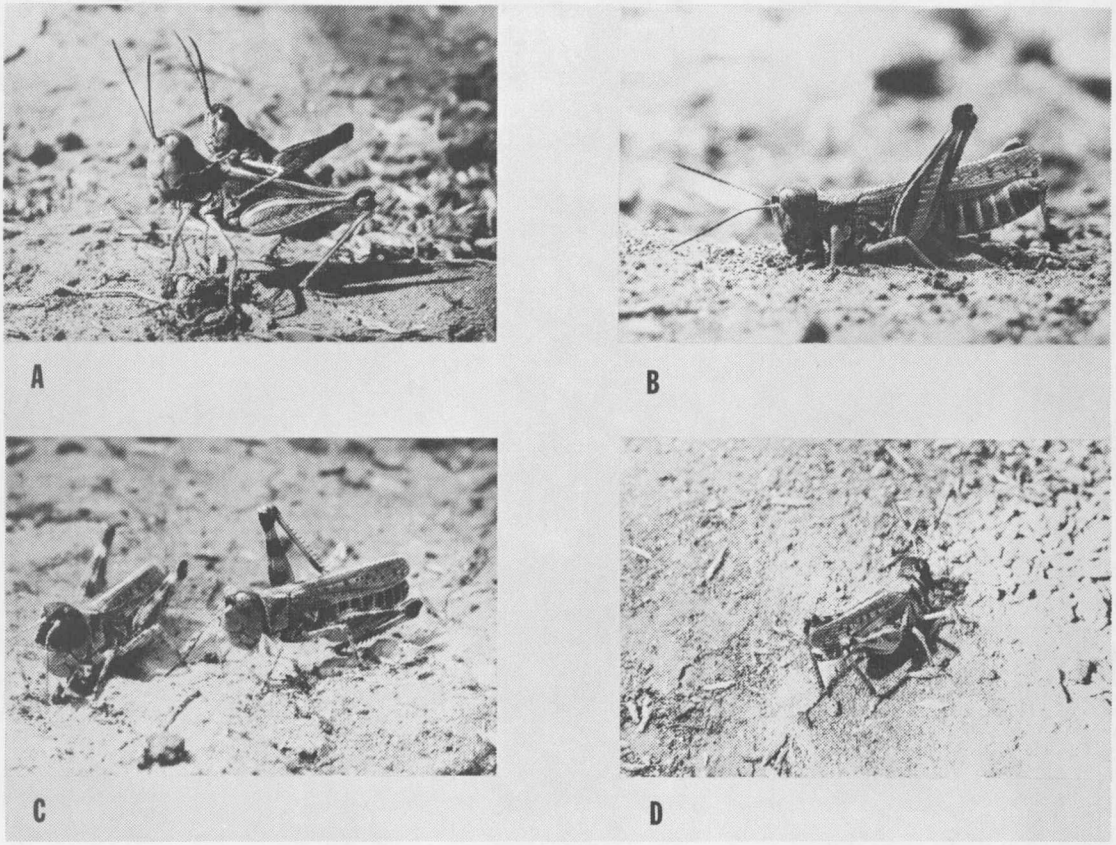


Figure 18. Typical positions and leg movements of *A. elliotti*. A. Copulating pair, female is stilting. B. Femur-tipping of near leg; low amplitude movement. C. Femur-raising in response to another grasshopper. D. Rejecting posture of female.

especially if food odors are present (antennal cleaning was observed in response to odors in the wind tunnel) or if the animal encounters unfamiliar situations or surroundings. Cleaning may function at times as a displacement activity. Each antenna is cleaned individually, and cleaning is repeated 1-3 times for each. The grasshopper may clean one or both antennae during a cleaning sequence.

Cleaning of the antennae follows a fixed order of movements. The foreleg, nearest the antenna, is lifted above the head, and the tarsus is placed above the base of the antenna. The tarsus is then brought forward and down, engaging the antenna in a groove near the base of the tarsus. The antenna is forced downward by the pressure from the tarsus, and the head is tilted so that the base of the antenna is brought close to the ground. The tarsus slides down the antenna until the foot rests on the ground. The terminal portion (about 1/2-2/3 of the length) of the antenna is then drawn through the cleaning groove by holding the tarsus firmly on the ground and simultaneously lifting the fore part of the body and straightening the head. This sequence may be repeated. Removal of the antenna by clipping at the base does not terminate this response. All of the movements are conducted in their proper order and in their entirety. Cleaning movements were observed several hours after antennectomy. It is possible that the cleaning response may disappear after longer periods, but observations were discontinued after 24 hrs.

5) Leg Movements: Leg movements include stereotyped and non-stereotyped movements. Otte (1970) classified movements of North American Acridoidea, and his terminology and definitions are utilized in the present study unless otherwise indicated. Stereotyped movements of the legs include stridulation, femur-tipping, and femur-shaking. Non-stereotyped movements include femur-jerking, femur-raising, kicking, femur-forward-swinging, sparring, and presenting.

Stridulations of *A. elliotti* are produced by rapid, low-amplitude movements of the femora. Almost all stridulations are performed while the animal is sitting. Stridulatory movements that do not produce sounds are occasionally performed by both sexes (see section of this paper on acoustic signals). Otte (1970) included 'ticking' under stridulation. Ticking consists of raising of the hind femur and then kicking out with the tibia so as to strike the end of the forewing. This was not observed in *A. elliotti*, but a similar movement was used to kick away fecal pellets.

Femur-tipping (Figure 18) is a common movement of males of *A. elliotti*. It consists of a single raising and lowering of the femora from about 45° to nearly vertical. The movement is usually rapid, and it may be performed by one or both femora. Tipping is silent and functions as a visual display.

Most communicative leg movements display conspicuous colors on the tibiae and on the inside of the femora. One insectary cage

contained 30 adult *A. elliotti* females, 10 of which had their femora and tibiae painted red, yellow, or orange with enamel. *A. elliotti* males approached and mated with these females, yet males in both the laboratory and the field often approached but did not attempt to mate females of other species. Atypical leg colors did not prevent species recognition of the *A. elliotti* females by males.

Tipping by courting males was faster (duration 0.15-0.3 sec.) and more stereotyped than that of male-male encounters. Tipping movements of solitary males appeared to become more pronounced as a female was approached. Tipping was repeated 1-3 times during momentary stops, and tipping of the femora was synchronous by courting males. Tipping of one femur while walking was occasionally performed. The courtship function of tipping by males is unknown, but it appears to display sexual excitation of the male.

Tipping during male encounters is relatively slow (duration 0.4-1.0 sec.). The femora are often moved asynchronously. Males may produce fast, synchronous tipping as they first approach other males and then switch to the slower, asynchronous type of tipping in response to displays by the male being approached. Femur-tipping during male encounters usually causes the males to separate before they touch one another.

Females also perform femur-tipping movements of the hind legs. Tipping by females resembles the male-male encounter type of tipping

and is usually performed in response to the approach of other members of the species. The leg nearest the approaching grasshopper is tipped in a slow, graded, non-repetitive movement. The movement functions to dispel the approaching individual.

Femur-shaking is only rarely seen in *A. elliotti*. Otte (1970) described this movement as shaking of the femora, which may include striking of the femora against the forewings or of the tibia against the ground. He reported that this movement is performed by both males and females (mainly of the Oedipodinae) and dispels individuals. The few times that this movement was observed in *A. elliotti* during the present study, it was performed by a solitary individual.

Femur-jerking is performed by members of both sexes of *A. elliotti*. The hind femora are jerked upwards in response to being touched or mounted by other grasshoppers. The femora may be jerked upwards only a few degrees or may be jerked to a vertical position. The tibiae may also be kicked out at the intruder. The intensity of the response appears to depend on the nature of the disturbance. Otte (1970) concluded that this response demonstrated a graded response that depends on the degree of disturbance.

Femur-raising (Figure 18) consists of raising one or both hind femora to a nearly vertical position. The femora may be tilted forward from the vertical, and the tibiae may be extended away from the femora and are sometimes held in a horizontal position above the back. The

tibiae may be moved in short up and down movements or may be quickly thrust out towards an intruder. Femur-raising is a graded response, indicating disturbance, and increasing in intensity with the degree of the disturbance. It occurs in response to the approach of other grasshoppers and becomes particularly intense if the displaying grasshopper is touched or mounted. Physical contact by another grasshopper usually releases kicking with the hind tibiae. Both sexes perform femur-raising. Femur-raising occasionally is performed in response to disturbances other than those produced by other grasshoppers. Touching of the grasshopper by the observer often elicited femur-raising. A copulating male often raised his hind femora and held the tibiae horizontal when approached by another male or when the female with which he was copulating began to move. The moving may convey sexual unreceptiveness in the female.

Kicking with the hind tibiae is performed by members of both sexes in response to physical contact. Kicking appears to discourage mating attempts by most males, but some males persist even after being kicked away. The female can kick with enough force to dislodge a male that is attempting to mount.

Femur-forward-swinging as described by Otte (1970), occurs chiefly in members of the Catantopinae and consists of swinging the hind femora from the resting position all the way forward to the head and back in a single rapid movement. The movement occurs in response

to being touched on either side or from the front and normally only the leg nearest the intruder is swung forward. Solitary males and females of *A. elliotti* perform a different forward swing. One hind femora is swung forward until it almost touches the head. Simultaneously, the tibia is extended until the femur and the tibia form almost a straight line extending forward over the head. The femur and tibia are then returned to the resting position. The action is usually only performed once, and the movement is slow and sterotyped.

Sparring consists of striking out at another grasshopper with the forelegs and occasionally with the middle legs. *A. elliotti* also lashes out with the antennae. Sparring usually occurs when two grasshoppers directly approach each other from the front and touch. Sparring occurs for only a few seconds and then the grasshoppers separate.

Presenting is performed by the female. The hind femur nearest an approaching male is lowered and the tip of the abdomen may be turned towards the male. The movement appears to indicate sexual responsiveness of the female and may attract the male and facilitate coupling. Otte (1970) reports that presenting females always allow males to mount and to attach their genitalia. He also reported that the response occurs mainly in females of the Oedipodinae. The present study indicated that females rarely presented, and a presenting female did not always allow a male to mount or to attach his genitalia.

Rejecting (Figure 18) is performed by sexually unresponsive females of *A. elliotti*. The female elevates the terminal portion of her abdomen, either as a male approaches or after a male has already mounted. The position makes it almost impossible for the male to attach his genitalia since the tip of the abdomen of the female is turned upwards and away from him. The male also appears to have difficulty maintaining a grasp on the female. Ferkovich *et al.* (1967) reported that males often became disorientated and reversed their position, when a female assumed the rejecting position. Otte (1970) did not report this signal.

6) Miscellaneous Movements: Activities such as wing flapping, antennal whirling, antennal tapping, and regurgitation are included here.

Solitary adults of both sexes of *A. elliotti* occasionally flap one or both wings, extending the wings horizontally until they are perpendicular to the body. The movement produces a fluttering noise. No communicative function could be determined for this movement since it usually occurred in the absence of other individuals.

Antennal whirling includes the various waving motions performed by the antennae. *A. elliotti* frequently point the antennae towards objects being examined. The antennae may also be waved up and down or whirled in circular motions. Movement of the antennae may be synchronous or asynchronous. Members of this species frequently meet face to face and cross their antennae. Antennal movements occur while moving and while stationary.

Antennal tapping consists of gently striking another grasshopper with the antennae. Otte (1970) reported that in many species the male sometimes taps the female with his antennae as he mounts. He concluded that tapping probably serves merely to orient the male as he mounts. Antennal tapping by males of *A. elliotti* appears to serve additional purposes. Males tap females during mounting, but also tap and stroke sexually unreceptive females prior to a mounting attempt. A mounted or copulating male will vigorously tap a rejecting or moving female with both of his antennae. The action appears to quiet the female. Stroking with the antennae also appears to subdue resistance of the female to mating attempts.

f) Oviposition. Nerney (1954) described oviposition by females of *A. elliotti* in detail. He identified three phases of oviposition: 1) drilling, 2) egg laying, 3) covering of the egg pod. Observations of the present study were consistent with those of Nerney.

Nerney (1954) reported that during the final phase of oviposition 1-5 males sat within 2-5 in. of the female and intently watched her. They "cocked up on their hind legs in unison" as she withdrew her abdomen from the soil. The female then covered the pod with soil by movements of her hind legs. As she walked away, the males took after her in pursuit.

Males observed in the present study followed and watched ovipositing females during all three phases. The males rarely made any

movements towards the female or tried to mount her. Occasionally, a male stridulated. During the egg laying phase, a male occasionally stroked or tapped the female with his forelegs and antennae (Figure 19). Some males accompanied a female throughout oviposition, others joined and left a female after a few minutes.

The males always assumed an alert position as the female began to cover the egg pod. The female covered the pod with her tarsi by alternately tamping the soil with fast, vertical movements of the hind femora and extending the hind legs horizontally and to the sides to sweep soil over the pod. During the initial covering of the egg pod, the female frequently lowered one hind tarsus into the cavity above the pod to pack soil securely around and over the top of the pod. A female disturbed while covering an egg pod usually ran away, but would frequently resume the covering movements wherever she happened to stop. The action appears to be stereotyped. It also appears to stimulate the males. The female normally pauses momentarily after completing the covering of the egg pod. She then dashes away, running and hopping over the ground with the males in pursuit. She often succeeds in escaping from the males by breaking visual contact with them. The female appears to be highly excited at this time and will continue to demonstrate periods of running and hopping for 15-30 min. after covering the egg pod. This activity continues even in the absence of pursuing males. The female frequently feeds for periods of a few

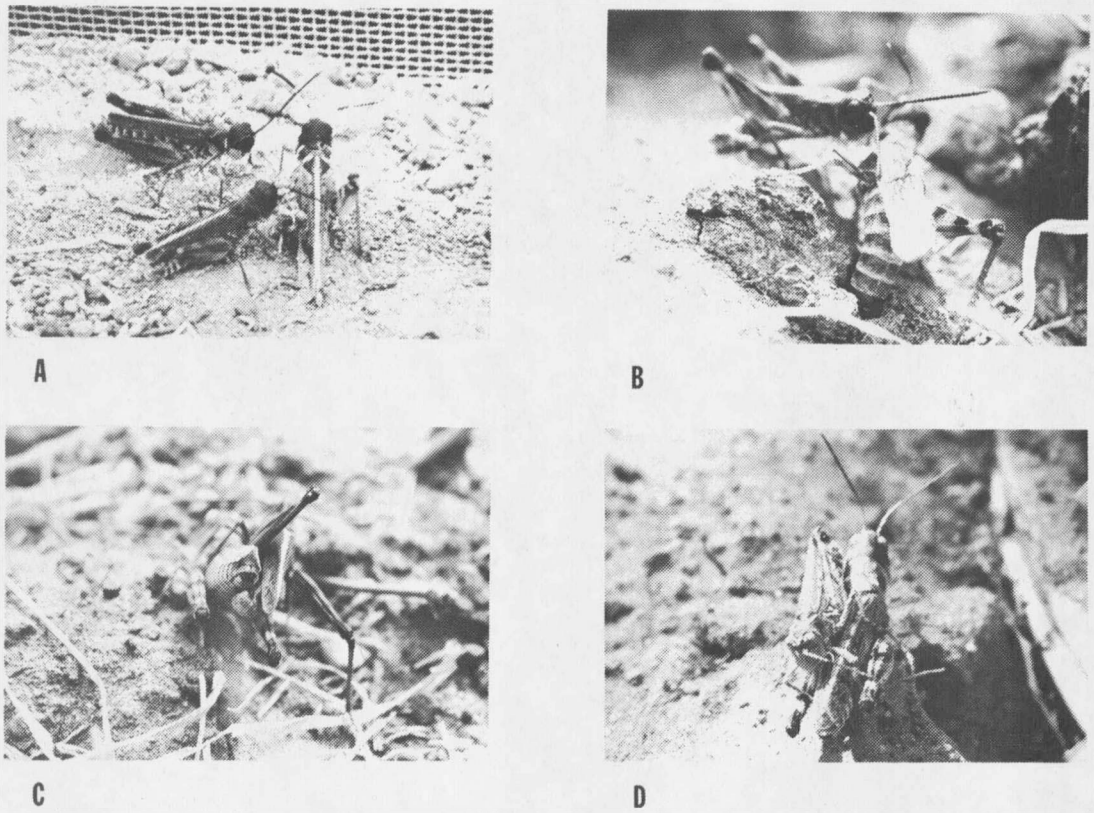


Figure 19. Oviposition and copulation of *A. elliotti*. A. Blinded males attending ovipositing female. B. Male stroking ovipositing female. C. Male attempting to attach his genitalia. D. Male in reversed position after mounting from the front of the female.

minutes. She is usually unreceptive to males at first, vigorously kicking them away or running and hopping excitedly if a male tries to mount. But, a persistent male usually succeeds in copulating with the female 13-30 min. after she has finished ovipositing, although the female may vigorously reject his first mating attempts. Most males made 1-2 tries at mounting a female during this postoviposition period. One male made five mounting attempts and was kicked away each time. He succeeded in mounting on the sixth try, but the female jumped around trying to dislodge him, and she assumed a rejecting position. After 30 sec. the female began to quiet down, and after two min. the male was able to attach his genitalia. No other male made more than three mounting endeavors in 50 observed mating sequences. Females that did not mate within one hour of ovipositing usually did not mate until the next day.

The excited running and hopping of the female appears to be a strong visual stimulus to males. Males rapidly approach small moving objects. Males would approach moving females contained in a glass bottle with a tight lid that eliminated odor clues. Stationary females were seldom attractive to males. Cardboard silhouettes of *A. elliotti* were used as models to test for attraction to males. These were not attractive to males. Pulling the cardboard models by a thread to produce movement attracted a few males. One inch lengths of wooden matchsticks were not attractive to males if the sticks were stationary, but

they became very attractive if they were pulled along the ground by a thread at a speed approximating that of a running grasshopper. Males would rapidly pursue a small moving object until they came within 1-2 in. of the objects. They then apparently were able to identify the object as not being a female and discontinued pursuit. Moving grasshoppers of other species also attracted *A. elliotti* males. Size was not greatly important to attraction. Even grasshoppers as large as *Brachystola magna* and *Melanoplus bivittatus* attracted males of *A. elliotti*. Again, the males discontinued their pursuit when they approached within a few inches of these other species.

Females of *A. elliotti* often attracted males by movements such as walking, climbing, or jumping. Sexually unreceptive females frequently avoided mating attempts by males by stopping and remaining stationary when approached by a male. The male often passed within 2 in. of the female, apparently unable to detect her presence.

g) Pair Formation. Pair formation is the initial phase of mating behavior. Mating behavior (summarized in Figure 20) is here defined as the cumulative events associated with the insemination of the female by the male. This involves a sequence of events including pair formation, courtship, and copulation. Pair formation consists of the coming together of a male and a female in connection with mating activities; courtship includes interactions of the male and the female after pair formation and before coupling, and copulation consists

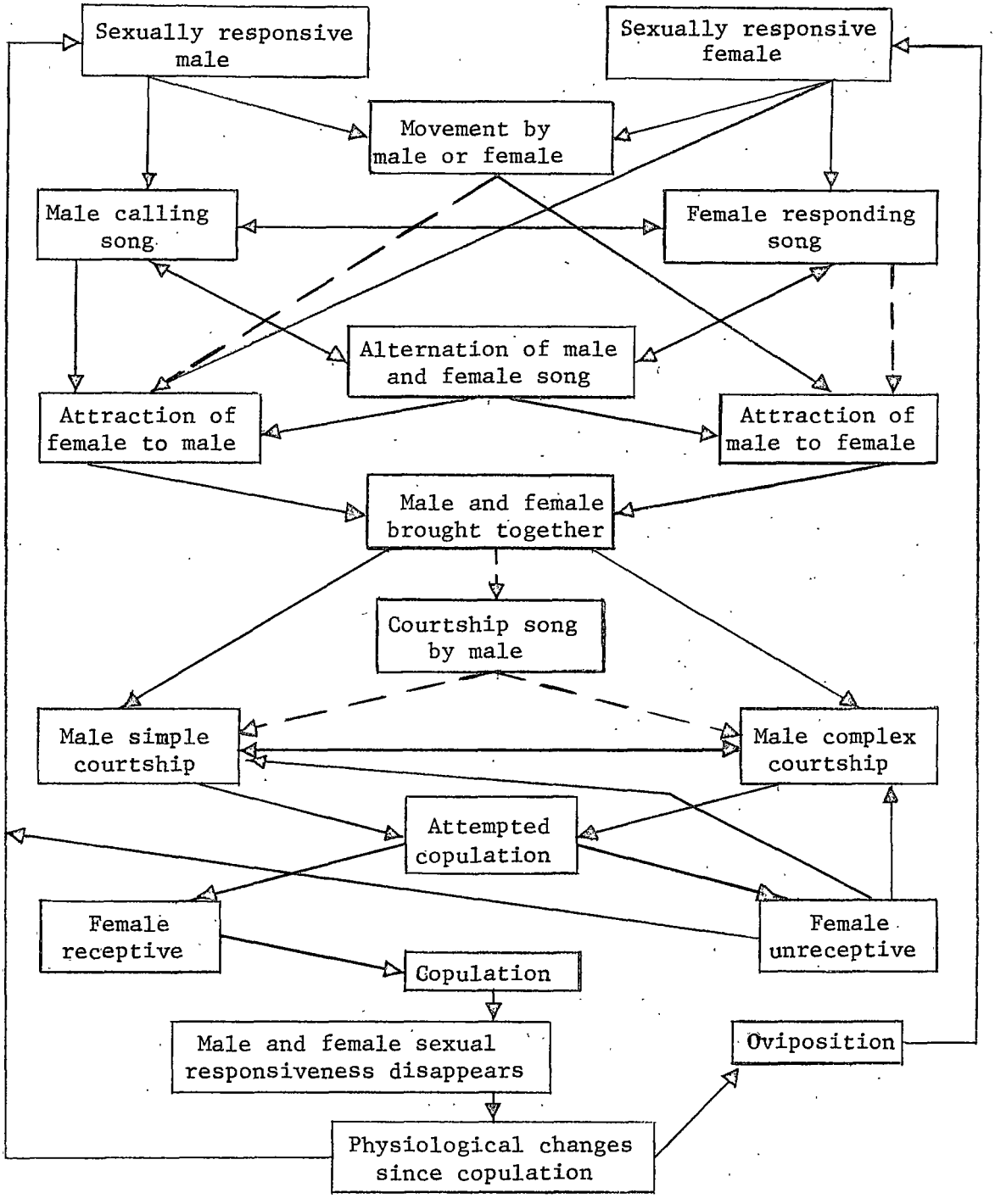


Figure 20. Mating behavior of *A. elliotti*. Dashed lines indicate less frequent interactions.

of coupling (attachment of the genitalia of the two sexes) and subsequent insemination. These events, especially pair formation and courtship, are not always clearly separable, but it is convenient to describe them separately. The ability to differentiate between them is not important, if the mating behavior is studied in its entirety.

Mating behavior necessitates the use of signals over considerable distances and at close range. Visual, acoustic, and probably chemical and tactile stimuli are important factors relative to mating behavior. These signals act alone and in combinations, although all need not be present for successful mating sequences.

Pair formation between distant *A. elliotti* usually involves sound production by either or both the male and the female, although stridulations by the male are more common. Sexually responsive individuals of the opposite sex are attracted by the calling, or stridulating, individual (see section on acoustic signals in this paper). Olfactory attractants, if present, do not appear to cause attraction at a distance. Vision appears to be very important to pair formation and to courtship, although it is not essential. Males and females,'blinded' by painting over their head capsules with black paint, successfully mated with sighted and blinded partners. Pair formation by the blinded grasshoppers appeared to occur in part by chance. Blinded grasshoppers often sat or walked within 2-3 in. of an individual of the opposite sex and appeared to be unaware of the other's presence.

Blinded grasshoppers frequently stridulated and may have attracted mates. Some were observed bumping into other grasshoppers during their wanderings and in a few cases mating followed physical contact. It is possible that sounds or odors emitted by a nearby (1-2 in.) grasshopper may have directed pair formation by the blinded individual. Sighted grasshoppers are sensitive to movement, and males orient towards and approach moving individuals. Visual orientation and approaching appear to occur in the final stage of pair formation. Pair formation by *A. elliotti* often occurs when visual contact between a male and a female is established, and pair formation frequently occurs in the absence of any stridulatory signals. Pottering by the male, which increases the probability of encountering females, apparently was responsible for the initiation of pair formation in many of the mating sequences observed in the cages and in the field. Pottering brought males into visual contact with females. Aggregations of grasshoppers in feeding, basking, or resting groups also increased contact with members of the opposite sex and consequently the number of pair formations.

h) Courtship. The final approach of a courting pair usually consists of the male walking rapidly towards the female. The male frequently stops momentarily and tips his hind femora. The approach is usually silent. The antennae of the male may be raised and lowered rapidly and repetitively as the female is approached. The male normally approaches to within ½-1 in. of the female, pauses briefly (0.2-0.5

sec.), and then either continues courtship behavior or terminates his approach. The response of the female to the approach of the male partially determines whether the courtship sequence is continued by the male. Females frequently perform slow tipping movements of the hind femora during the initial approach of the male. Sexually unreceptive females may perform one or more visual displays as the male comes nearer. Several different movements may be performed in succession, and the intensity of the responses often increases if the male attempts to mount. Females indicate sexual unresponsiveness by: 1) raising the hind femur closest to the male to the vertical, 2) raising both hind femora to the vertical, 3) jerking both hind femora from the resting position to nearly vertical, 4) rapidly vibrating the hind femora, which was usually silent but occasionally produced a stridulatory sound, 5) assuming the rejection position with the abdomen elevated, 6) kicking at the male with the hind legs. Femur-tipping and femur-raising are performed as the male approaches from a distance. The other movements occur as the male approaches within approximately one inch of the female or as the male attempts to mount. These displays often caused a male to discontinue a mating attempt. Some males discontinued their approach towards a female in the absence of any visible display by the female. Other males continued their approach and attempted to mount females that were vigorously displaying their rejection of the male.

Males approached females from the side or from the rear and occasionally from the front. The male usually mounted by dashing quickly to the female, grasping her pronotum with his forelegs, placing his mesothoracic legs on her mesothorx, and swinging his abdomen into position parallel to her abdomen and between it and her near hind femur. The hind leg of the male nearest to the female rested lightly against the forewing of the female or was held slightly above the wing. The far hind leg of the male remained braced against the soil until the male obtained a firm hold on the female. The male then lowered his abdomen below that of the female and curled the terminal portion upwards, bringing his genitalia into contact with the female's genitalia (Figure 19). Following coupling, the male moved slightly forward, pulling the terminal portion of the female's abdomen sideways and allowing the male to partially straighten his own abdomen. The tibia of the far hind leg of the male was drawn up close to the body and rested lightly on the outer surface of the female's hind femur. These observations agree closely with those of Ferkovich *et al.* (1967) on couplings of *A. elliotti* obtained from a population near Wheatland, Wyoming.

Females often rejected mounting attempts by males. A male that was not successful in attaching his genitalia after 5-6 sec. usually terminated his mounting attempt. Many males were kicked away as they tried to mount. Males often lashed rejecting females with their

antennae during mounting attempts.

Courtship characterized by a rapid approach of the male and mounting after only a momentary pause or in the absence of any pause is termed 'simple courtship'. The male performs a minimum of courtship signals, usually only tipping the femora and sometimes tapping the female with his antennae before mounting.

Some males, when rejected by females, began elaborate patterns of courtship behavior. These 'complex courtship' (Figure 21) patterns were characterized by slow, cautious approaches towards the female accompanied by diverse antennal movements. Complex courtship displays were performed for several minutes (2-10) by some males, and one male (100 mating observations) repeated complex displays for 20 min. Occasionally a male performed complex courtship movements during the initial approach towards a female. The male usually approaches the female and assumes a courtship position to the side and slightly ahead of the female. The male faces the female and sits with his body perpendicular to that of the female or turned slightly forward or backwards. If the male approaches from the front, he often stops momentarily and taps the antennae of the female with his own, before moving to the courtship position. The male then waves one or both antennae in front of the face of the female. Usually, one of the male's antennae is extended forward from the head and is waved in front of the female. The other antenna is held at an angle of 90° to the first and parallel

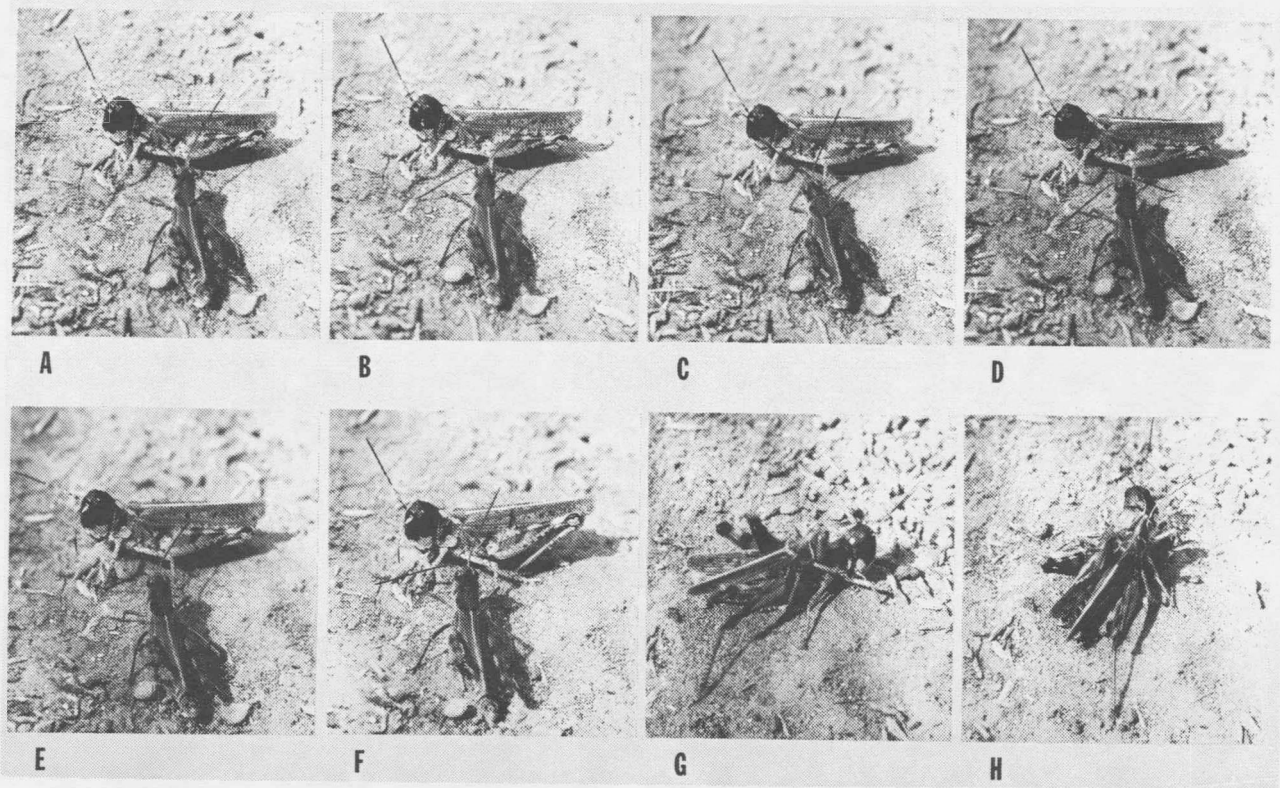


Figure 21. Complex courtship of *A. elliotti* performed by a male with a blinded female. Continuous sequence of movements.

to the body of the female. This antenna may perform small waving movements or be held fairly still without touching the female (Figure 21). The waving of the antennae in front of the face of the female is sometimes omitted and the action is not repeated at any later phase of the courtship. After waving the antennae in front of the face of the female, the male slowly moves slightly posterior from the head of the female. He then begins a sequence of varied antennal movements. Both antennae may be extended over the back of the female and simultaneously lowered until they rest on the female. The antennae are rested momentarily and then lifted. This movement may be repeated 2-3 times. The antennae may also be held so that one antenna is extended over the female and the other is held at a 90° angle to the first, parallel to the body of the female, but not touching her. The extended antenna is lowered onto the back of the female and slid along the top of the thorax and of the wings. It may also be moved up and down in slow, soft, tapping motions. The other antenna is held motionless. Additionally, both antennae may be held parallel to the body of the female and at an angle of 180° to each other. The antennae do not touch the female and are held motionless. All three antennal movements are usually performed by the courting male; they may occur in any sequence; and one or more of the movements may be repeated several times. The antennae may be held in a motionless position without touching the female for 20-30 sec. Eventually, the male steps forward and places

one foot on the thorax of the female. The movement is again slow, unlike the movement associated with mounting during simple courtship. The male will usually mount at this time, if the female does not perform a rejection display.

The complex courtship of the male is usually silent and visual displays of the legs such as femur-tipping are not performed. Neither are the palpi moved, although they are occasionally brushed against the thorax of the female as the male mounts. The female is usually quiescent and does not perform rejection or disturbance displays prior to mounting, although vigorous rejection movements usually initiate complex courtship by the male. If the female is disturbed or approached by other males during a complex courtship sequence, she will perform disturbance or rejection movements. These will cause the courting male to either leave or to begin again the courtship movements. Complex courtship appears to pacify the female and to make her more receptive to copulation with the courting male.

Some males, when vigorously rejected by the female, will repeat the simple courtship procedure one or more times. This does not appear to be as effective as switching to the complex courtship in regards to making the female more responsive.

Males occasionally mounted a vigorously rejecting female from the front (Figure 19). The grasshopper would mount from in front of the thorax and then turn 180°. This did not appear to make the female

any more receptive to copulation, but it enabled the male to avoid being kicked by the hind tibiae of the female.

i) Copulation. Copulating pairs remained coupled for 40-70 min. The female frequently fed during copulation, carrying the male with her. Copulation terminated either by the genitalia being suddenly released and the male hopping off or by the female beginning to move around vigorously in apparent efforts to dislodge the male.

Males stridulated while copulating if approached by other males. They also stridulated when disturbed by movements of the female. Males would vigorously tap the female on the head with their antennae if the female began to kick or move while they were copulating. The males would also raise the hind femora to the vertical in response to disturbances by the female.

Males demonstrated differences in mating behavior and in the frequency of copulations. One male in the laboratory copulated each day for two weeks. He was in a cage containing 20 males and 15 females. Other males in the same cage copulated once every 2-3 days. Most males in the cages made a maximum of 2-5 mating attempts during a 20 min. observation period, but the male that copulated daily made 27 mating attempts in one 20 min. observation period. This male was very active, almost constantly engaged in pottering activities, and he was the last male to die in the laboratory in 1972. All individuals in this cage were marked with enamel paint on the thorax for identification.

j) Social Interactions. Social interaction is here defined as the interstimulation and response occurring between individuals and between groups of the same species. It includes all activities that directly or indirectly influence the behavior of other grasshoppers. Interactions between individuals include mating behavior, disturbance or aggressive displays, male-male encounters, and other encounters. Group interactions include basking, feeding, resting, and marching. Visual, acoustic, tactile and probably chemical signals are important in social interactions.

Aggregations of *A. elliotti* nymphs and adults were frequently seen. Aggregations are formed by grasshoppers, especially males, approaching moving individuals, by adult grasshoppers approaching stridulating individuals (includes males attracted to females, females attracted to males, and males attracted to males), by physical factors such as humidity, temperature, sunlight, vegetation, and odors influencing movements, and possibly by grasshoppers being attracted by other biotic stimuli such as scents from other grasshoppers, feeding noises, and sounds produced by group activities. Physical factors of the environment produce more or less accidental congregations, but interactions between grasshoppers appear to play some role in the maintenance of these groupings.

The various sound and visual signals performed in aggression, disturbance, and mating behaviors of adults are also performed by

nymphs, although the signals may not be totally functional or produced in the proper context. Stridulatory movements are performed without sound production as early as first instar and occur primarily as disturbance signals. All of the femoral displays, except presenting by the female, performed by adults are observed in each of the instars. Nymphs also examine and tap each other with the antennae. Movement by a nymph attracts other nymphs. Disturbance and aggressive signals are essentially the same in nymphs as in adults.

Adults of *A. elliotti* appear to recognize members of the opposite sex primarily by differences in movements and possibly by odors. When two males encountered, they tipped their femora, occasionally crossed antennae, and then separated. Attempts by one male to mount another were protested by vigorous femoral displays, stridulations, or kicking. When a male approached a female, pair forming and courtship displays were often involved, and the female performed visual displays which differed from those of a male. Both sexual and species recognition by males often occurred after the male had almost made physical contact with the grasshopper being approached. Males approached to within 1-2 in. of moving grasshoppers and sometimes touched the other grasshoppers with their antennae before separating. It appears that the initial approach is a rather non-specific attraction to movement and at close proximity to another grasshopper, sexual and species recognition occur. The tapping of other grasshoppers with the antennae suggests that odors

may be involved in recognition; however, the absence of antennal contact in many encounters indicates that visual factors are the chief means of identification.

Species recognition over long distances is accomplished by sound signals. *A. elliotti* appears to be highly species specific in response to stridulatory behavior. *A. elliotti* did not answer or approach singing grasshoppers of other species, although they responded to playback of recorded songs of their own species. A male of the species *Ageneotettix deorum* (Scudder) sang in alternation and approached a speaker emitting a recording of the calling song of a male *A. elliotti* during a field test. The isolating value of calling songs apparently varies according to the species being studied.

Discussion: Ellis (1963) concluded that marching and pottering activities were aspects of general activity in locust nymphs. Light and temperature changes affected pottering and marching activities, and air currents specifically increased marching.

General activity levels of *A. elliotti* were influenced by several environmental factors, although sufficient light illumination and an optimal temperature range were prerequisites for locomotor activities. Marching occurs infrequently in this species and appears to be usually in response to some type of directed stimuli such as air currents, wind borne odors, sunlight, and stridulations. Marching appeared to be a type of taxis in this species, although it may also involve

kinesis. Pottering appears to be a kinesis. It is possible that pottering activity must occur before marching can be initiated. Pottering is an important component of many of the principal behavioral patterns of activity of *A. elliotti*. Pottering is performed in searching for food, mates, oviposition sites, resting sites, and other members of the species. Mulkern (1969) proposed a general hypothesis of the feeding behavior of *Melanoplus* species that describes the pottering activities of *A. elliotti*. According to Mulkern's hypothesis, a general type of orthokinesis causes grasshoppers to concentrate in areas of attractive host plants. The hypothesis applies to a grasshopper in a grassland situation, one in which stress conditions that might exert overiding influences are not present. A grasshopper that is not in contact with a suitable host plant is stimulated by hunger and by environmental conditions, including sufficient intensities of light and favorable temperatures, into random movemements (pottering). Pottering continues until the grasshopper is brought into visual contact with a vertical object on which it then orients, approaches, and climbs. A biting response may occur, and if the physical structure of the object is conducive to feeding and the proper phagostimulants are present, the grasshopper initiates ingestion. The animal resumes pottering activities if the proper stimulants are absent or if some deterrent is present. The grasshopper will likely move directly from one plant to another in a densely vegetated area and will wander until he encounters

another plant in a sparsely vegetated area. This response tends to keep a grasshopper moving through a sparsely vegetated area or an area of unsuitable plants and to remain in areas of suitable host plants. Feeding behavior in *A. elliotti* appears to occur in much the same manner. Olfactory guidance to food plants as well as visual guidance occurs in this species.

Pottering of *A. elliotti* appears to be a general kinesis controlled by environmental factors and the physiological state of the grasshopper. Hunger, sexual responsiveness, oviposition readiness, social needs, and other internal stimuli influence pottering activities; while environmental stimuli interact with the internal state of the grasshopper and may inhibit or enhance activities. Pottering appears to function as a general searching activity, the grasshopper remaining in areas of favorable conditions by orthokinesis and/or klinokinesis. Resolution of pottering depends on the presence of the proper stimuli and the absence of deterrents. Low light intensities and certain temperatures appear to produce akinesis (see section of this paper on photic and thermal responses). An ovipositing female of this species is affected by soil source and texture (Anderson and Hastings, 1966). A male searching for a mate orients towards pair forming displays and to visual contact with a moving individual.

The highly agitated running and hopping of the female of this species, after oviposition, may be a very intense kinetic reaction

produced by physiological changes occurring during oviposition. The movements of the female are highly attractive to males of the species, but the female usually only mates with a male that makes repeated mounting attempts at this time.

Two types of mating behavior appear to increase the probability of copulation by a male: 1) repetitive or vigorous mating attempts, and 2) prolonged or complex courtship. Otte (1972) analyzed the courtship behavior of *Syrbula admirabilis* (Uhler) and *S. fuscovitta* Thomas, and he described elaborate courtships by these two species that were performed by males in the presence of sexually unreceptive females. These elaborate courtships involved a number of body parts and a number of movements in signalling. The movements of the appendages were mostly synchronous, but some asymmetry of movements existed. The appendages on the two sides of the body of the male assumed different positions and could be moved out of phase with one another. The appendages near the female performed one set of movements, and the appendages away from the female performed another set. Each side of the body can perform the other set of movements if the male repositions himself on the opposite side of the female. Otte concluded that at least two commands travel down the neural connectives, one governing motor patterns, and one governing the position of the appendages.

The complex courtship behavior of *A. elliotti* resembled that of the *Syrbula* species. *A. elliotti* did not utilize as many body parts as

Syrbula spp. in signalling, and the movements were different, but complex courtship was performed in the presence of an unreceptive female; a number of movements were performed; asymmetry of movements and position of the appendages occurred; the near and far appendages performed different movements, and each side of the body can perform both sets of movements.

Otte (1972) suggested possible explanations for the evolution of elaborate courtship behavior: 1) Elaborate behavior is more conspicuous; 2) The female is made fully receptive; 3) Males which display more elaborately, more vigorously, or for longer periods have (or had in the past) greater fitness; 4) Elaborate behavior promotes interspecific recognition and reduces interspecific sexual interactions. Since males of *A. elliotti* begin courtship when they are very near the female, the first explanation probably does not apply. Otte (1972) found no evidence for the last explanation in any species. The second and third explanations may apply to both the complex courtship and the repetitive mating attempts performed by males of *A. elliotti*.

Visual, acoustic, and possibly olfactory and tactile signals appear to be important to mating behavior and other social interactions of *A. elliotti*. These signals may act independently or in combinations. Visual responses to movement are probably most important, but mating and other interactions were observed in blinded grasshoppers. Olfactory

attractants from other members of the species could not be demonstrated, although olfactory signals may occur at close range. Tactile signals may be important since grasshoppers examine each other with their antennae and palpi (olfactory stimuli may be involved).

The movements of *A. elliotti* included both communicative and non-communicative signals. Communicative movements included movements of the appendages and sound production. Non-communicative movements included approaching, mounting, some antennal waving, and peering.

The principal behavioral patterns of activity of *A. elliotti* are an active means of adaptation to the environment through active selection of habitat, escape from predators, and population integration. Communicative signals are essential to this integration. Environmental factors play an important role in the control of behavioral patterns and in population integration and performance.

SUMMARY AND CONCLUSIONS

The role of behavior in the integration of individuals into a population of *Aulocara elliotti* (Thomas) was investigated in 1971, 1972, and 1973. Observations and experiments were performed in the laboratory at Bozeman, Montana and at a field site 5 mi. west of Billings, Montana. Responses to environmental factors, communicative signals, intraspecific interactions, and principal behavioral patterns were examined. A specially designed arena was utilized to study kinses and taxes. The major findings and conclusions are listed below:

1) Hatching of eggs of *A. elliotti* occurred primarily in the morning under insectary conditions. The time of emergence appears to be random under conditions of constant temperature (25°C) and alternating periods of darkness and light. Eggs exposed to conditions of constant darkness and alternating temperatures (20°C and 30°C for 12 hr. periods) demonstrated a peak of hatching at the time of the temperature increase.

2) Adults and mid-stadia nymphs exposed to conditions of 0% and 95% relative humidity in an alternative choice chamber generally demonstrated a preference for the drier conditions. Hatchlings, given the same choice, chose the wetter conditions. A preference for the moister conditions was evidenced during each molting period. Access to dry food only and deprivation of access to water caused mid-stadium, fifth instar nymphs to

seek areas of high relative humidity. It is hypothesized that moist conditions during the molting period reduced desiccation of the newly molted grasshopper and facilitated shedding of the exuvium.

3) The responses of *A. elliotti* to wind and to various olfactory stimuli were tested in a wind tunnel. Locomotor activity increased and a general tendency to move down-wind in response to wind at low speeds (4-10 ft./sec.) was demonstrated. Grasshoppers moved up-wind, singly or in groups, in response to attractive odors. Attraction to odors from other members of the species, if present, only occurs at close range (1-2 in.). Starvation, for 4 hrs. or more, increased the intensity of response to odors from food plants. Unfed hatchlings, 48 hrs. after emergence from the pod, moved up-wind in response to odors of specific grasses commonly utilized as host plants by this species. At 24 hrs. after hatching, these nymphs did not respond to food odors. It was suggested that yolk reserves in the alimentary canal provided sufficient nourishment at 24 hrs. after hatching, but that yolk reserves may be depleted after 48 hrs.

4) The antennae are the primary mediators of responses to windborne odors. Bilateral antennectomy eliminated the response to odors, but unilateral antennectomy and blinding by painting

over head capsules did not reduce the competency to move upwind towards an odor source, although movements were hesitant. Agitation of grasshoppers prior to testing in the wind tunnel did not alter responses to wind or to wind borne odors. The response to wind carried odors appeared to be an anemotropotaxis. The antennae probably are involved in kinetic and possibly tactic effects.

5) Phototactic and photokinetic responses were shown to natural and artificial sources of light. Low intensities of illumination or sudden changes of light intensity inhibited or disrupted general activities.

6) Responses to different colors of light indicated that red light is not perceived by *A. elliotti*. Ultraviolet light produced both kinetic and positive phototactic movements in sighted and blinded (head capsules painted over) grasshoppers. Grasshoppers presented with a choice of different colored squares of plastic did not demonstrate a statistically significant preference for any of the tested colors, except for black and white. Position records of grasshoppers on the black and on the white cards demonstrated a significantly greater attraction to white ($P<.01$, X^2)

7) Visual responses to black figures on white cards indicated that vertical lines were more attractive than horizontal lines,

and lines were more attractive than squares or asterisks. Grasshoppers typically peered when presented with a choice of figures and frequently tried to crawl the edges of the painted lines and of the cards on which the figures were presented.

8) Temperature produced both kinetic and akinetic effects. Temperatures below 12.7°C or above 40-45°C inhibited activity. Basking appears to be an akinetic response to radiant heat. Temperature and light appear to be the primary environmental determinants of general activity patterns.

9) Stridulations of *A. elliotti* were recorded on magnetic tape and analyzed by an audiospectrometer and by oscillograms. The principal acoustic signals of this species included: calling songs, responding songs, disturbance songs, reflex crys, and oviposition songs. The first three types of songs are performed by both sexes; the last two are produced by males. Adults of both sexes also produce sounds by striking the substratum with their tarsae, and both nymphs and adults perform some stridulatory movements without producing audible sounds.

10) The different songs seem to consist of modifications of the rhythmical construction of the calling songs of the respective sexes. Rhythms may be altered by varying the number of pulses per chirp, by changing the interval between chirps, and to some extent by modifying the duration of the pulses.

Phonotaxis and other functions of the various sounds are discussed.

11) Loss of visual and/or physical contact with members of the opposite sex increased the number of performances of calling and responding songs. Light intensity may control the initiation and termination of singing.

12) Ten major behavioral patterns of activity were characterized: 1) resting, 2) basking, 3) feeding, 4) locomotion, 5) stationary movements, 6) pair formation, 7) courting, 8) copulating, 9) ovipositing, 10) social interactions. It was hypothesized that pottering is a kinetic response controlled by environmental factors and the physiological state of the grasshopper. Pottering appears to be a major factor in the displacements and distributions of individuals.

13) Communicative and non-communicative signals are discussed. Visual signals, especially those involving movement, are important to social interactions. Acoustic signals are effective over longer ranges than visual signals; while olfactory signals, if present, are effective only at close ranges. Tactile signals, as evidenced by the use of the palpi and the antennae for examining other grasshoppers, may affect social interactions.

14) Mating behavior involves both simple and complex courtship sequences, which are performed by males. Complex courtship involved prolonged sequences of mating behavior, characterized by several movements of the appendages. Synchronous and asynchronous movements were performed with the appendages, and symmetrical and asymmetrical positions of the appendages were assumed.

15) Groups of males were frequently observed near an ovipositing female. The implications of this behavior in regards to mate selection by the female are discussed.

APPENDIX A

Definitions and Concepts of Terms as used in this paper

Kineses are undirected reactions or movements. The body is not oriented with respect to the source of stimulation. Locomotion is random in direction (Fraenkel and Gunn, 1961).

Klinokinesis involves reactions in which the rate of turning is affected by the intensity of stimulation (Hinde, 1970).

Orthokinesis includes reactions in which the speed or frequency of locomotion depends on the intensity of stimulation (Fraenkel and Gunn, 1961).

Taxes are directed reactions or movements. The animal's body takes up a particular direction with respect to the source of stimulation. Taxis may be combined with locomotion so that the animal moves towards, away from, or at a fixed angle to the source (Hinde, 1970).

Anemotaxis refers to movements which are directed by air currents (Fraenkel and Gunn, 1961).

Geotaxis includes movements in which orientation is along the lines of gravitational force (Fraenkel and Gunn, 1961).

Klinotaxes are reactions in which orientation depends on successive comparisons between the stimulation on the two sides of the body or of a part of the body. Deviations of the body or of a part of the body are necessary for comparisons of stimulation; orientation is indirect (Fraenkel and Gunn, 1961).

Phototaxis refers to movements which are directed to light (Fraenkel and Gunn, 1961).

Telotaxes are reactions in which the attainment of orientation is direct, without deviations. Orientation

APPENDIX A
(Continued)

to the source occurs as if the source were a goal. Fraenkel and Gunn restrict this term to responses to light. Hinde includes configurational stimuli in this category (Fraenkel and Gunn, 1961; Hinde, 1970).

Tropotaxes — are reactions in which orientation depends on simultaneous comparisons between the stimulation on the two sides of the body or of a part of the body. Attainment of orientation is direct; no deviations are required (Fraenkel and Gunn, 1961).

Circus Movements — are continuous turning movements. They are indicative of tropotaxis (Fraenkel and Gunn, 1961).

Population — "... a number of organisms of the same species forming a more or less frequently interconnected group, separated more or less clearly from other groups of the species." (Solomon, 1949).

Environment — "... for the most part we are faced with an intricately combined action by population and environment together. Hence any idea that the environment can be clearly distinguished from the population on a functional basis is illusory... the population functions in relation to a whole which includes itself. It is therefore better to think of the population as an integral part of the ecosystem." (Solomon, 1949).

LITERATURE CITED

Alexander, R. D. 1957. Sound production and associated behavior in insects. Ohio Jour. Sci. 57: 101-113.

_____. 1960a. Communicative mandible-snapping in Acrididae (Orthoptera). Science. 132: 152-153.

_____. 1960b. Sound communication in Orthoptera and Cicadidae, p. 38-92. In W. E. Lanyon and W. N. Tavolga (Eds.). Animal Sounds and Communication. Am. Inst. Biol. Sci. Publ., Washington, D. C. 443 p.

_____. 1967. Acoustical communication in arthropods. Ann. Rev. Entomol. 12: 495-526.

_____. 1968. Arthropods, p. 167-216. In Thomas A. Sebeok (Ed.). Animal Communication. Indiana University Press, Bloomington. 686 p.

Allee, W. C., A. E. Emerson, O. Park, T. Park, and K. P. Schmidt. 1949. Principles of Animal Ecology. W. B. Saunders Company, Philadelphia. 837 p.

Anderson, N. L. 1961. Seasonal losses in rangeland vegetation due to grasshoppers. J. Econ. Entomol. 54(2): 369-378.

_____. 1964. Some relationships between grasshoppers and vegetation. Ann. Entomol. Soc. Am. 57(6): 736-742.

_____., and E. Hastings. 1966. Some notes on rearing *Aulocara elliotti* (Orthoptera:Acrididae). Ann. Entomol. Soc. Am. 59(4): 718-719.

_____., and J. C. Wright. 1952. Grasshopper investigations on Montana rangelands. Mont. Agr. Exp. Sta. Tech. Bull. 486. 46 p.

Atkins, M. D. and W. G. Wellington. 1962. A versatile alternative chamber for insect behaviour studies. Can. Entomol. 94: 428-433.

Aziz, S. A. 1957. The reactions of the Desert Locust *Schistocerca gregaria* (Forsk.), (Orthoptera, Acrididae) to physical factors, with special reference to relative humidity. Bull. Ent. Res. 48: 515-531.

Ball, E. D., E. R. Tinkham, Robert Flock, and C. T. Vorhies. 1942. The grasshoppers and other Orthoptera of Arizona. Ariz. Agr. Exp. Sta., Tech. Bull. 93.

Barnes, O. L., and C. W. McLellan. 1960. Progress in tests of repellants against grasshoppers. USDA Agr. Res. Service Special Report Z-120.

Barry, C. K. and R. Jander. 1968. Photoinhibitory function of the dorsal ocelli in the phototactic reaction of the Migratory Locust *Locusta migratoria*. Nature, Lund. 217: 675-677.

Bastock, M. 1956. A gene mutation which changes a behavior pattern. Evolution. 10: 421-439.

Bayramoglu-Ergene, S. 1968. Untersuchungen über die dynamogene Funktion der Antennen bei *Anacridium aegytium*. Z. vergl. Physiol. 52: 363-369.

Bentley, E. W. 1944. The biology and behaviour of *Ptinus tectus* Boie (Coleoptera, Ptinidae), a pest of stored products. V. Humidity Reactions. Jour. Exp. Biol. 20: 152-158.

Bodenheimer, F. S. *et al.* 1929. Studien zur Epidemiologogie, Ökologie und Physiologie der afrikanischen Wanderheuschrecke *(Schistocerca gregaria* Forsk.). Z. angew Ent. 15: 435-557.

Brooks, A. R. 1958. Acridoidea of southern Alberta, Saskatchewan, and Manitoba (Orthoptera). Can. Entomol. Supplement 9 (accompanying volume 90, 1958). 92 p.

Broughton, W. B. 1963. Method in bioacoustic terminology, p. 3-24. In R. G. Busnel (Ed.). Acoustic Behaviour of Animals. Elsevier Publ. Comp., New York. 933 p.

Browning, T. O. 1963. Animal Populations. Harper & Row, Publishers, New York. 127 p.

Buckell, E. R. 1922. A list of the Orthoptera and Dermaptera recorded from British Columbia prior to the year 1922, with annotations. Proc. ent. Soc. Br. Columb. 20: 9-41.

Burtt, E. T. and W. T. Catton. 1962. A diffraction theory of insect vision. I. An experimental investigation of visual acuity and image formation in the compound eyes of three species of insects. Proc. Roy. Soc. B. 157: 53-82.

Busnel, R. G. 1963. Acoustic Behaviour of Animals. Elsevier Publishing Company, New York. 933 p.

Carrel, J. S. 1972. An improved treading device for tethered insects. Science. 175: 1279.

Caspari, E. W. 1967. Introduction to Part I and remarks on evolutionary aspects of behavior, p. 1-9. In Jerry Hirsch (Ed.). Behavior-Genetic Analysis. McGraw-Hill Book Company, New York. 522 p.

Chapman, R. F. 1955. A laboratory study of roosting behaviour in hoppers of the African Migratory Locust *(Locusta migratoria migratorioides* R & F.*)*. Anti-locust Bull. 19: 41 p.

Chauvin, R. 1941. Variations du phototropisme du criquet pélerin *(Schistocerca gregaria* Forsk.*)* suivant différentes longueurs d'onde. Bull. Soc. Zool. Fr. 66: 27-32.

_____. 1942. Notes sur la physiologie comparée des Orthoptères. I. Sur le phototropisme des Orthoptères. Bull. Soc. Ent. Fr. 46: 150-154.

Cooley, R. A. 1904. Grasshoppers. Mont. Agr. Exp. Sta., Bull. 51: 232-242.

_____. 1919. Seventeenth annual report of the state entomologist of Montana. Mont. Agr. Exp. Sta., Bull. 133: 15 p.

_____., J. R. Parker, and A. L. Strand. 1923. Improved methods of controlling grasshoppers. Mont. Agr. Exp. Sta., Circ. 112: 20 p.

Crescitelli, F. and T. L. Jahn. 1939. The electrical response of the dark-adapted grasshopper eye to various intensities of illumination and to different qualities of light. J. Cell. Comp. Physiol. 13: 105-112.

Dadd, R. H. 1963. Feeding behaviour and nutrition in grasshoppers and locusts. Advanc. Insect. Physiol. 1: 47-109.

Davis, E. G. and F. M. Wadley. 1949. Grasshopper egg-pod distribution in the northern Great Plains and its relation to egg-survey methods. U.S.D.A. Circ. 816.

Davis, D. E. 1966. Integral Animal Behavior. The Macmillan Company Limited, London. 118 p.

Dethier, V. G. 1953. Host plant perception in phytophagous insects. Trans. IXth Int. Congr. Ent., Amsterdam. 2: 81-88.

Digby, P. S. B. 1955. Factors affecting the temperature excess of insects in sunshine. J. Exp. Biol. 32: 279-298.

Dumortier, B. 1963. Morphology of sound emission apparatus in Arthropoda, p. 277-345; The physical characteristics of sound emissions in Arthropoda, p. 346-373; Ethological and physiological study of sound emissions in Arthropoda, p. 583-654. In R. G. Busnel (Ed.), Acoustic Behaviour of Animals. Elsevier Publ. Comp., New York. 933 p.

Ehrman, L. A. 1964. Courtship and mating behavior as a reproductive isolating mechanism in *Drosophila*. Amer. Zool. 4: 147-153.

Ellis, P. E. 1951. The marching behaviour of hoppers of the African Migratory Locust *(Locusta migratoria migratorioides* R. & F.*)* in the laboratory. Anti-Locust Bull. 7: 46 p.

_____. 1953. Social aggregation and gregarious behaviour in hoppers of *Locusta migratoria migratorioides* (R. & F.). Behaviour. 5: 225-260.

_____. 1963. An experimental study of feeding, basking, marching, and pottering in locust nymphs. Behaviour. 20: 281-310.

_____., and C. Ashall. 1957. Field studies on diurnal behaviour, movement, and aggregation in the Desert Locust *(Schistocerca gregaria* Forskäl). Anti-Locust Bull. 25: 94 p.

Ergene, S. 1950. Untersuchungen über Farbanpassung und Farbwechesel bie *Acrida turrita*. Z. vergl. Physiol. 32: 530-551.

_____. 1952. Erkennen homochrome Heuschrecken die Farbe oder die Graustufe ihrer Umgebung? Rev. Fac. Sci. Univ. Istanbul B. 17: 305-314.

Faber, A. 1929. Die Lautäusserungen der Orthoperen. (Lauterzeugung, Lautabwandlung und deren biologische Bedeutung sowie Tonapparat der Geradflügler). Verglich. Untersuch. I. Ztschr. f. Morph. u. Okol. der Tiere. 13: 745-803.

_____. 1932. Die Lautäusserungen der Orthoperen. II. (Untersuchungen uber die biozönotischen und vergleichend-physiologischen Probleme der Orthopteren-stridulation. Methodik der Beareitung und Auswertung bon Stridulationsbeobachtungen. Einzeldarstellungen). Ztschr. f. Morph. u. Ökol. der Tiere. 26: 1-93.

Ferkovich, Stephan, S. G. Wellso, and W. T. Wilson. 1967. Mating behavior of the Big-Headed grasshopper, *Aulocara elliotti* (Orthoptera: Acrididae), under caged conditions in the greenhouse and outdoors. Ann. Entomol. Soc. Am. 60(5): 972-975.

Flügge, C. 1934. Geruchliche Raumorientierung von *Drosophila melanogaster*. Z. vergl. Physiol. 20: 463-500.

Fraenkel, G. 1929. Untersuchungen über Lebensgewohnheiten. Sinnesphysiologie und Sozialpsychologie der wandernden Larven der afrikanischen Wanderheuschrecke, *Schistocerca gregaria* (Forsk.). Biol. Zbl. 49: 657-680.

_____. 1930. Die Orientierung von *Schistocerca gregaria* zu strahlender Wärme. Z. vergl. Physiol. 13: 300-313.

_____., and D. L. Gunn. 1961. The orientation of animals. Kineses, taxes, and compass reactions. Dover Publ., Inc., New York. 376 p.

Frings, H. and M. Frings. 1958. Uses of sounds by insects. Ann. Rev. Entomol. 3: 87-106.

Gillet, S. D. 1972. Social aggregation of adult *Schistocerca gregaria* and *Locusta migratoria migratorioides* in relation to the final moult and ageing. Anim. Behav. 20: 526-533.

Gunn, D. L. and C. A. Cosway. 1938. V. Humidity preference of *Blatta orientalis*. J. Exp. Biol. 15: 555-563.

_____., and J. S. Kennedy. 1936. Apparatus for investigating the reactions of land arthropods to humidity. J. Exp. Biol. 13: 450-459.

_____., F. C. Perry, *et al.* 1948. Behaviour of the Desert Locust *(Schistocerca gregaria* Forskal*)* in Kenya in relation to aircraft spraying. Anti-Locust Bull. 3: 70 p.

Hamamura, Yasuji. 1970. The substances that control the feeding behavior and the growth of the silkworm, *Bombyx mori* L., p. 55-80. In D. L. Wood, R. M. Silverstein, M. Nakajima (Eds.). Control of insect behavior by natural products. Academic Press, New York. 345 p.

Harker, J. E. 1961. Diurnal rhythms. Ann. Rev. Entomol. 6: 131-146.

Haskell, P. T. 1957. Stridulation and associated behavior in certain Orthoptera. I. Analysis of the stridulation of, and behaviour between males. Brit. Jour. Animal Behaviour. 5: 139-148.

_____., M. W. J. Paskin, and J. E. Moorehouse. 1962. Laboratory observations on factors affecting movement of hoppers of the desert locust. J. Insect Physiol. 8: 53-78.

Hastings, E. 1971. Laboratory studies of compatability of males and females of two populations of *Aulocara elliotti* (Orthoptera: Acrididae). Ann. Entomol. Soc. Am. 57(2): 216-220.

Henderson, W. W. 1931. Crickets and grasshoppers in Utah. Utah Agr. Exp. Sta., Circ. 96, 38 p.

Hinde, R. A. 1970. Animal Behaviour. McGraw-Hill, Inc., New York. 876 p.

Hocking, B. and I. S. Lindsay. 1958. Reactions of insects to the olfactory stimuli from the components of an insecticidal spray. Bull. Ent. Res. 49: 675-683.

Hunter-Jones, P. 1966. Studies on the genus *Schistocerca* with special reference to development. Ph.D. Thesis. University of London.

Hunter, S. J. and P. W. Classen. 1914. Grasshopper control in the southern division of Kansas. J. Econ. Ent. 7: 73-82.

Jacobs, W. 1953. Verhaltensbiologische studien an feldheuschreck Ztschr. f. Teirpsychol. Beiheft I: 1-228.

Jander, R. 1963. Insect orientation. Ann. Rev. Entomol. 8: 95-114.

Kalmus, H. 1942. Anemotaxis in *Drosophila*. Nature, Lond. 150: 405.

Kaufmann, T. 1965. Observations on aggregation, migration, and feeding habits on *Zonocerus variegatus* in Ghana. Ann. Entomol. Soc. Am. 58: 426-436.

Kennedy, J. S. 1937. The humidity reactions of the African Migratory Locust, *Locusta migratoria migratorioides* R. & F., gregarious phase. J. Exp. Biol., Cambridge 14: 187-197.

_____. 1939. The behaviour of the Desert Locust *Schistocerca gregaria* (Forsk.) (Orthopt.) in an outbreak centre. Trans. Ent. Soc. Lond. 89: 385-542.

_____. 1945. Observations on the mass migration of Desert Locust hoppers. Trans. R. Ent. Soc. Lond. 95: 247-262.

_____. 1951. The migration of the Desert Locust *(Schistocerca gregaria* Forsk.). I. The behaviour of swarms. II. A theory of long-range migrations. Phil. Trans., Lond.(B) 235: 163-290.

_____., and J. E. Moorehouse. 1969. Laboratory observations on locust responses to wind-borne grass odour. Ent. Exp. & Appl. 12: 487-503.

Kerfoot, W. B. 1967. Dorsal light receptors. Nature 215: 305-306.

_____. 1968. Orientometer for study of insect behavior. Science. 162: 477.

King, J. A. 1967. Behavioral modification of the gene pool, p. 22-43. In Jerry Hirsch (Ed.). Behavior-genetic analysis. McGraw-Hill, New York. 522 p.

Klopfer, P. H. and J. J. Hatch. 1968. Experimental considerations, p. 31-43. In T. A. Sebeok (Ed.). Animal Communication, Indiana University Press, Bloomington. 686 p.

Lépiney, J. De. 1930. Sur le comportement des larves de *Schistocerca gregaria* Forsk. Concentration et dissémination des individus, voyages des bandes larvaires, nutrition. C. R. Soc. Biol., Paris. 104: 265-265.

Loher, W. 1971. Acoustical behavior and information. Unpublished. Termination report of the cooperative regional research project W-92.

_____., and M. K. Chandrashekaran. 1970. Acoustical and sexual behaviour in the grasshopper *Chimarocophala pacifica pacifica* (Oedipodinae). Ent. Exp. & Appl. 13: 71-84.

Manning, A. 1963. Selection for mating speed in *Drosophila melanogaster* based on the behaviour of one sex. Anim. Behav. 11: 116-120.

_____. 1967. Genes and the evolution of insect behavior, p. 44-60. In Jerry Hirsch (Ed.), Behavior-genetic analysis. McGraw-Hill, New York. 522 p.

Mayr, E. 1958. Behavior and systematics, p. 341-362. In A. Roe and G. G. Simpson (Eds.), Behavior and Evolution. Yale University Press, New Haven, Conn.

_____. 1970. Populations, Species, and Evolution. Harvard University Press, Cambridge, Mass. 453 p.

Médioni, J. 1961. Le probleme de l'existence d'un sens dermatoptique chez les insectes. L'etat actuel de la question. Psychol. Franc. 6: 11-20.

Merrel, D. J. 1949. Selective mating in *D. melanogaster*. Genetics. 34: 370-389.

Moorehouse, J. E. 1971. Experimental analysis of the locomotor behaviour of *Schistocerca gregaria* induced by odour. J. Insect Physiol. 17: 913-920.

Moriarty, F. 1959. The 24-hr Rhythm of emergence of *Ephestia kühniella* Zell. from the pupa. J. Insect Physiol. 3: 357-366.

Morris, G. K. 1971. Aggression in male Conocephaline grasshoppers (Tettigoniidae). Anim. Behav. 19: 132-137.

Morris, R. F. 1959. Single factor analysis in population dynamics. Ecology 40: 580-588.

Mulkern, G. B. 1969. Behavioral influences on food selection in grasshoppers (Orthoptera: Acrididae). Ent. Exp. & Appl. 12: 509-523.

Mussgnug, G. L. 1972. The structure and performance of an adult population of *Aulocara elliotti* (Thomas) (Orthoptera, Acrididae) near Billings, Montana. Master's Thesis, Montana State University.

Nerney, N. J. 1954. Range grasshopper investigations in Arizona -1953. U.S.D.A., Agr. Res. Service Special Report Z-120.

Norris, M. J. 1968. Laboratory experiments on oviposition responses of the desert locust, *Schistocerca gregaria* (Forskäl). Anti-Locust Bull. 43: 1-47.

O'Brien, F. E. M. 1946. The control of humidity by saturated salt solutions; a compilation of data. Rep. Brit. Elect. Res. Ass. London. No. 166.

Otte, D. 1970. A comparative study of communicative behavior in grasshoppers. Misc. Publ., Museum of Zoology, Univ. Mich. No. 141. 168 p.

_____. 1972. Simple versus elaborate behavior in grasshoppers. An analysis of communication in the genus *Syrbula*. Behaviour. 42: 291-322.

Otto, E. 1951. Untersuchungen zur Frage der geruchlichen Orientierung bei Insekten. Zool. Fahrb. Abt. Allg. Zoologie Physiology. 62: 65-92.

Parker, J. R. 1933. Factors largely responsible for years of grasshopper abundance. Proc. World's Grain Exhibition and Conference, Canada. 2: 472-473.

_____. 1937. Losses caused by grasshoppers and the expenditure occurred in their control during the period 1925-34. 4th Int. Conf. Anti-Locust Res. I.L.C. No. 25, Appendix 2.

Pepper, J. H. and E. Hastings. 1952. The effects of solar radiation on grasshopper temperatures and activities. Ecology 33(1): 96-103.

Perdeck, A. C. 1958. The isolating value of specific song patterns in two sibling species of grasshoppers *(Chorthippus brunneus* Thunb. and *C. biguttulus* L.*)*. Behaviour. 12: 1-75.

Pfadt, R. E. 1949. Food-plants, distribution and abundance of the big-headed grasshopper, *Aulocara elliotti* (Thos.). Jour. Kans. Entomol. Soc. 22(2): 69-74.

Phipps, J. 1963. Laboratory observations on the activity of Acridoidea. J. Insect Physiol. 9: 531-543.

Pielou, D. P. 1948. Observations on the behaviour of the red locust *Nomadacris septemfasciata*. Proc. Roy. Entomol. Soc., London (A) 23:

Pittendrigh, C. S. and V. G. Bruce. 1959. Photoperiodism and related phenomena in plants and animals. American Association for the Advancement of Science. 475-505.

Pringle, J. W. S. 1956. Insect Song. Endeavour 15: 68-72.

Riegert, P. W. 1958. Humidity reactions of *Melanoplus bivittatus* (Say), and *Camnula pellucida* (Scudd.) (Orthoptera: Acrididae): Reactions of starved and moulting grasshoppers. Can. Entomol. 90(11): 680-684.

_____. 1959. Humidity reactions of *Melanoplus bivittatus* (Say) and *Camnulla pellucida* (Scudd.) (Orthoptera, Acrididae): Reactions of normal grasshoppers. Can. Entomol. 91(1): 35-40.

_____. 1960. The humidity reactions of *Melanoplus bivittatus* (Say) (Orthoptera, Acrididae): Antennal sensilla and Hygroreception. Can. Entomol. 92(8): 561-570.

_____. 1967. Some observations on the biology and behaviour of *Camnula pellucida* (Orthoptera: Acrididae). Can. Entomol. 99(9): 952-971.

Roberts, S. 1965. Photoreception and entrainment of cockroach activity rhythms. Science. 148: 958-959.

Roemhild, G. R. 1961. Studies on the eggs of the grasshopper species *Aulocara elliotti*, Thos. Ph.D. Thesis, Montana State University. 94 p.

_____. 1965. Cyclical temperature effects on diapause termination of eggs of *Aulocara elliotti* (Thomas). J. Insect Physiol., 11: 1633-1639.

Scott, W. N. 1936. An experimental analysis of the factors governing the hour of emergence of adult insects from their pupae. Trans. Roy. Ent. Soc., London. 85: 303-330.

Shotwell, R. L. 1941. The species and distribution of grasshoppers in the 1939 outbreak. U.S.D.A., B.E.P.Q. Insect Pest Survey Bull. 21: 295.

_____. 1942. Life histories and habits of some grasshoppers of economic importance on the Great Plains. U.S.D.A. Tech. Bull. 774.

Skoog, F. E., F. T. Cowan, and R. V. Connin. 1960. Laboratory tests with insecticides, attractants, and repellants, Bozeman, Montana. U.S.D.A. Agr. Res. Service Special Report Z-109.

Slifer, E. H. 1954. The reaction of a grasshopper to odorous material held near one of its feet (Orthoptera: Acrididae). Proc. Roy. Ent. Soc. London (A) 29: 177-179.

_____. 1955. The detection of odors and water vapor by grasshoppers (Orthoptera, Acrididae) and some new evidence concerning the sense organs which may be involved. J. Exp. Zool. 130(2): 301-318.

_____. 1956. The response of a grasshopper, *Romalea microptera* (Beauvois), to strong odours following amputation of the metathoracic leg at different levels. Proc. Roy. Ent. Soc., London (A) 31(7-9): 95-98.

Solomon, M. E. 1949. The natural control of animal populations. J. Anim. Ecol. 18: 1-35.

Strand, A. L. 1937. Montana insect pests for 1935 and 1936. Mont. Exp. Sta. Bull. 333.

Strelnikov, I. D. 1936. Effect of solar radiation and the microclimate upon the body temperature and the behaviour of the larvae of *Locusta migratoria* L. (In Russian with English summary). Trav. Inst. Zool. Acad. Sci. U.R.S.S. 2: 637-733.

Strohecker, H. F., W. W. Middlekauff, and D. C. Rentz. 1968. The grasshoppers of California (Orthoptera: Acridoidea). Bull. Calif. Insect Survey. 10: 177 p.

Thorpe, W. H. 1963. The ontogeny of behavior, p. 485-518. In J. A. Moore (Ed.). Ideas in Modern Biology; Proceedings XVI International Congress of Zoology. 6: 563 p.

Tinbergen, N. 1951. The study of instinct. Clarendon Press, Oxford.

Uvarov, B. 1966. Grasshoppers and locusts. Vol. 1. Cambridge University Press, London. p. 481.

Van Horn, S. N. 1963. The embryogenesis and embryonic variability of *Aulocara elliotti* Thomas (Acrididae, Orthoptera). Ph.D. Thesis, Montana State College, Bozeman. 172 p.

Viaud, G. 1956. Taxies et tropismes dans le comportement instinctif, p. 5. In Masson (Ed.) L'instinct dans le comportement des animaux et de l'homme, Paris.

Visscher, S. N. 1971. Studies on the embryogenesis of *Aulocara elliotti* (Orthoptera; Acrididae). III. Influence of maternal environment and aging on development of the progeny. Ann. Entomol. Soc. Am. 64(5): 1057-1074.

Volkonsky, M. 1939. Sur la photo-akinèse des acridiens. Arch. Inst. Pasteur Algér. 17: 194-220.

_____. 1942. Observations sur le comportement du Criquet Pelerin *(Schistocerca gregaria* Forsk.*)* dans le Sahara algero-nigérien. Arch. Inst. Pasteur Algér. 20: 236-248.

Wallace, G. K. 1958. Some experiments on form perception in the nymphs of the desert locust, *Schistocerca gregaria* Forskäl. Jour. Exp. Biol. 35(4): 756-775.

_____. 1959. Visual scanning in the desert locust *Schistocerca gregaria* Forskäl. Jour. Exp. Biol. 36(3): 512-525.

Watson, J. R. and H. E. Bratley. 1940. Preliminary report on lubberly locust control. Florida Ent. 23: 7-10.

Weih, A. S. 1951. Untersuchungen uber das Wechselsingen (Anaphonie) und uber das angborene Lautschema einiger Feldheuschrecken, Z. Tierpsychol. 8: 1-41.

Wessel, M. H. 1973. The early embryology of *Aulocara elliotti* (Thomas) (Orthoptera: Acrididae) with studies on the effects of maternal age and environment on the developmental rate of the egg. Ph.D. Thesis. Montana State University.

White, R. M. and P. J. G. Rock. 1945. A contribution to the knowledge of the Acrididae of Alberta. Sci. Agr. 25: 577-596.

Williams, L. H. 1954. The feeding habits and food preferences of Acrididae and the factors which determine them. Trans. Roy. Ent. Soc. London. 105: 423-454.

Wright, S. 1949. Adaptation and selection, p. 365-380. In G. L. Jepsen, E. Mayr, and G. G. Simpson (Eds.). Genetics, Paleontology, and Evolution. Princeton University Press, Princeton, N. J.

Young, A. J. 1971. Studies on the acoustic behaviour of certain Orthoptera. Anim. Behav. 19: 727-743.

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