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

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.

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

Approved:

James M. Pickett
Head, Major Department

N. L. Anderson
Chairman, Examining Committee

Henry L. Parsons
Graduate Dean

MONTANA STATE UNIVERSITY
Bozeman, Montana

December, 1973

ACKNOWLEDGMENT

I am sincerely grateful to my major professor, Dr. Norman L. Anderson, for his interest, encouragement, and constructive discussions during the course of this study. He kindled in me a philosophy that expanded my horizons.

I am indebted to Drs. N. Anderson, S. Visscher, and S. Chapman for their assistance during this study and for the critical reading of this manuscript. I wish to thank Dr. R. Moore for his cooperation.

I wish to acknowledge Dr. J. H. Pepper and Professor E. Hastings for their stimulating discussions and encouragement.

I also wish to thank my fellow students, G. Mussgnug, and Dr. M. Wessel for their assistance and encouragement.

I appreciate the assistance and facilities made available to me by the Civil Engineering Department, Montana State University, and by Dr. T. Lang and Dr. R. Brown.

I wish to acknowledge Mrs. White for typing the manuscript and Mr. Brooks for assistance in obtaining needed materials and tools.

My wife, Gail, deserves special acknowledgment for her patience, understanding, and encouragement and for the artwork in this manuscript.

This investigation was supported by a Title IV NDEA Fellowship, a NSF Fellowship, a teaching assistantship from the Department of

Zoology and Entomology, Montana State University, and a research assistantship from the Montana State Agricultural Experiment Station.

TABLE OF CONTENTS

	Page
VITA	ii
ACKNOWLEDGMENT	iii
LIST OF TABLES	vii
LIST OF FIGURES	x
ABSTRACT	xii
INTRODUCTION	1
Literature Review	5
MATERIALS AND METHODS	12
Tilt Table	17
Wind Tunnel	20
Alternative Humidity Chamber	20
Hatch Sampler	21
INVESTIGATIONS	24
I. Hatching Experiments	24
Discussion	39
II. Humidity Experiments	42
Discussion	49
III. Olfactory Experiments	54
Discussion	79
IV. Photic, Visual, and Thermal Responses	84
Discussion	106
V. Acoustic Emissions	120
Discussion	152
VI. Behavioral Patterns and Individuals Interactions	158
Discussion	196

TABLE OF CONTENTS
(Continued)

	Page
SUMMARY AND CONCLUSIONS	202
APPENDIX A	208
LITERATURE CITED	210

LIST OF TABLES

Table — Page

1. COMPARISON OF MAXIMUM SOLAR RADIATION LEVELS FOR THE FIELD AND THE GLASS-ROOFED ROOM OF THE INSECTARY, 1972 16
2. COMPARISON OF MAXIMUM SOLAR RADIATION LEVELS FOR THE FIBER GLASS AND THE GLASS-ROOFED ROOMS OF THE INSECTARY, 1972 17
3. ECLOSION OF NYMPHS FROM PODS INCUBATED IN LOOSE SAND UNDER A NATURAL PHOTOPERIOD 28
4. ECLOSION OF NYMPHS FROM PODS INCUBATED IN COMPACTED SAND UNDER A NATURAL PHOTOPERIOD 28
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) 31
6. ECLOSION OF NYMPHS FROM EGGS INCUBATED UNDER CONDITIONS OF CONSTANT TEMPERATURE (25°C) AND FLUCTUATING LIGHT . . . 33
7. ECLOSION OF NYMPHS FROM EGGS INCUBATED UNDER FLUCTUATING CONDITIONS OF TEMPERATURE AND LIGHT IN THE INSECTARY 34
8. ECLOSION OF NYMPHS FROM EGGS INCUBATED UNDER CONDITIONS OF CONSTANT TEMPERATURE (25°C) AND FLUCTUATING LIGHT . . . 36
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) 38
10. DISTRIBUTION OF FIRST INSTAR NYMPHS IN THE ALTERNATIVE HUMIDITY CHAMBER 45
11. DISTRIBUTION OF MID-STADIUM, FIRST INSTAR NYMPHS IN THE ALTERNATIVE HUMIDITY CHAMBER 46

LIST OF TABLES
(Continued)

Table Page

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) 47

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 48

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 62

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 66

16. OLFACTORY REACTION OF NYMPHS AND ADULTS OF *A. ELLIOTTI* TO A VARIETY OF SUBSTANCES 68

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. 71

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* 77

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 CONSECUTIVE MORNINGS ARE SUMMARIZED 88

LIST OF TABLES
(Continued)

Table		Page
20.	DAILY ACTIVITY PATTERNS OF ADULT *A. ELLIOTTI* AND ASSOCIATED AIR TEMPERATURES	90
21.	RESPONSES OF NYMPHS AND ADULTS OF *A. ELLIOTTI* TO DIFFERENT LIGHT SOURCES	96
22.	COMPARATIVE SONG CHARACTERS OF MALE AND FEMALE EMISSIONS OF *A. ELLIOTTI*	132

LIST OF FIGURES

Figure		Page
1.	Tilt Table	18
2.	Hatch Sampler	22
3.	Hatching of eggs of *A. elliotti* in the insectary	26
4.	Movements of an adult female of *A. elliotti* in the Y-tube olfactometer	56
5.	Responses of Unfed Hatchlings to Four Speeds of Wind	63
6.	Illumination of the glass-roofed room of the insectary by sunlight	87
7.	Choice chamber for testing the responses of *A. elliotti* to different colors and intensities of light.	95
8.	Responses of sighted and blinded adults of *A. elliotti* to a 30 W. ultraviolet light	99
9.	Diagram of pathways taken by adults of *A. elliotti* when presented with a choice of figures (shapes) painted on black on white cards	105
10.	Oscillograms of a female responding song	124
11.	Oscillograms of male calling songs	133
12.	Oscillograms of male songs showing an entire sequence of chirps	134
13.	Charts of the rate of repetition of chirps of calling and responding songs	135
14.	Male reflex cry and male disturbance songs	143
15.	Charts of the rate of repetiiton of chirps of male disturbance and reflex sounds	144
16.	Feeding and basking positions of *A. elliotti*	161

LIST OF FIGURES
(Continued)

Figure Page

17. Movements of adult *A. elliotti* on an inclined plane . . . 167

18. Typical positions and leg movements of *A. elliotti* . . . 171

19. Oviposition and copulation of *A. elliotti* 181

20. Mating behavior of *A. elliotti* 184

21. Complex courtship of *A. elliotti* performed by a male with a blinded female 190

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.

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*	Maximum Solar Radiation 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.

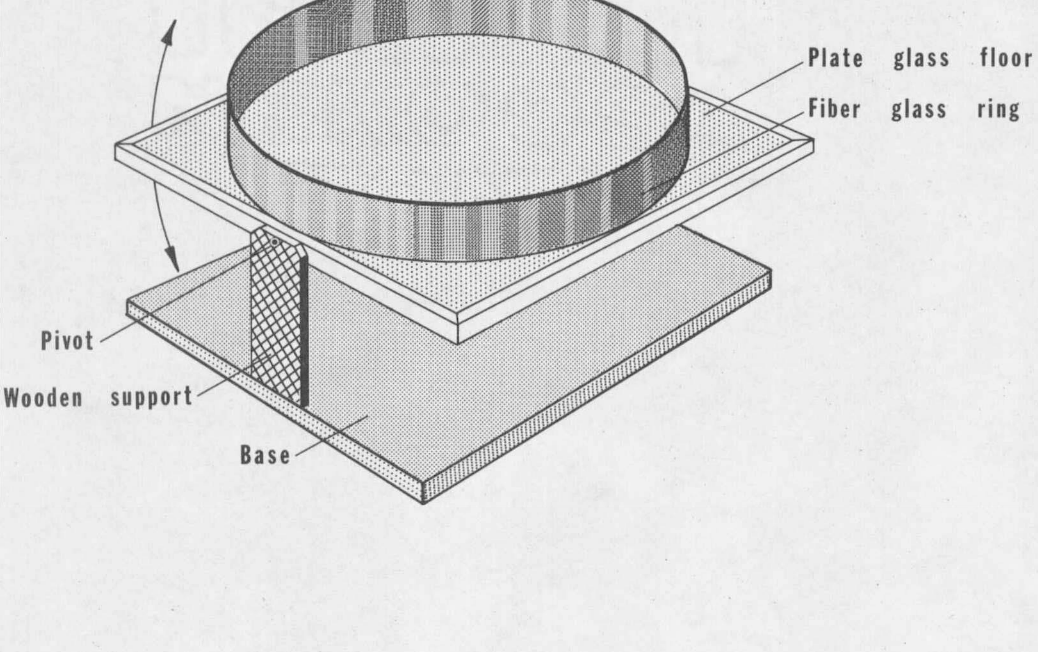

Figure 1. Tilt Table.