GRASSHOPPER SPECIES COMPLEXES OF FORAGE CROPS IN THE PIEDMONT REGION OF VIRGINIA

by

John Taylor Lewis Williams

Thesis submitted to the Faculty of the
Virginia Polytechnic Institute and State University
in partial fulfillment of the requirements for the degree of
MASTER OF SCIENCE
in
Entomology

APPROVED:

J.E. Roberts, Sr., Chairman

R.L. Pienkowski

P.J. Semtner

F.W. Ravlin

May, 1984
Blacksburg, Virginia

ACKNOWLEDGEMENTS

My heartfelt gratitude is extended to Dr. Jim Roberts for his exraordinary patience and encouragement throughout the time taken to complete this thesis. I am equally indebted to Dr. Bill Ravlin for his personal interest in me and in my work, and for his timely and creative direction, without which this study could not have been completed. I am also deeply indebted to Dr. Bob Pienkowski and Dr. Paul Semtner for their critical review of this manuscript and for their much welcome advice while the research was being conducted.

Special thanks are due Sharon Meyers for the enormous amount of time and expertise as well as friendship she extended me as I consulted her on the treatment of my data. The entire Statistical Consulting Service at V. P. I. is recognized for the courteous and efficient help I received from them.

Dr. David Nickle at the USDA Insect Systematics Laboratory identified voucher specimens for me and is due my recognition, as is Aubrey Neese for his help in plant identification.

Linda Joyner and Glenell Carson were most gracious in typing several sections of this manuscript without pay. This extremely kind act is deeply appreciated.

The entomology graduate students have been a source of ecouragement and are deeply appreciated. In particular Bob Bellinger and Dr. Boris Kondratieff helped this research and were inspiring examples of the excellence attainable by students in this field.

TO MY WONDERFUL PARENTS, WITH GRATITUDE AND LOVE.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Chapter I

SWEEPNETTING VERSUS UNIT AREA SAMPLING GRASSHOPPER POPULATIONS

1.1 INTRODUCTION

Accurate and precise estimation of insect population densities is essential in both economic and ecological studies, but is made difficult by population heterogeneity and dispersion patterns, and by spatial and temporal variation in the habitat. The problem is compounded when not one species, but a complex, is studied. In order to sample all species in a complex, it is desirable to use two or more collection methods simultaneously in a study (Southwood 1978).

Sweepnetting has been condemned by Southwood (1978) for any synecological work, yet it continues to be used as the sole collection method in many important grasshopper population studies (Daniels and Chedester 1973, Hardman and Smoliak 1980, Holmes et al. 1979, Wilbur and Fritz 1940). Sweepnetting has also been used along with unit area sampling, which measures population density directly. In such cases, the results from both measurements are related. Sweepnet counts are then converted to absolute density estimates, and the measurements from both collection methods are pooled (Smalley 1960).

The data presented here were collected in an extensive ecological study to determine the presence and relative abundance of the different grasshopper species in forage crops. Two sampling methods, one measuring absolute density, and the other (sweepnetting) measuring relative abundances in populations, were used. The question of immediate concern is to determine if the two methods sample proportionately different segments of the grasshopper complex.

1.2 MATERIALS AND METHODS

1.2.1 Sites and Dates of Sampling

The data used in the following analyses were taken from the 1980 season only. This portion of the data was selected because vegetational characteristics, which might affect the efficiency of the sweepnet, were measured along with the two insect collection methods.

Of the ten sites included in this study, five were permanent pastures and five were orchardgrass/redclover mixed hayfields. Sampling dates fell between July 1 and September 12, 1980. Two of the sites were sampled twice, two others three times, and the rest once, making a total of seventeen site-date combinations. The location, altitude, management and size of field are recorded in Table 2. The seventeen date/site combinations are listed in Table 1 below.

TABLE 1

Collection Dates and Sites used in Contingency Tables

TABLE 2

Site Locations and Descriptions and Collection Dates

		Location				Field		Dates and Methods of Collection			
								1979		1980	
Name	County	State Roads	Long.	Lat.	Alt(1)	Type	Size(2)	Drop Trap	Sweepnet	Drop Trap	Sweepnet
Barker	Halifax	607 & 816	78 47'	36 51'	165	hay(3)	3	7/19	7/19 8/09	----	----
Barnes	Lunenberg	613 & 138	78 06'	36 53'	130	hay	1	7/25	7/25	----	----
Bowman	Nottoway	601 & 626	78 05'	37 04'	125	hay	16	7/26	7/26	----	----
Brunk	Albemarle	708 & US29	78 37'	37 58'	185	alfa(4)	8	----	8/03	----	----
Cobb	Charlotte	659 & 671	78 37'	37 09'	175	hay	1	----	----	7/4 7/26	7/4
Gibson	Campbell	646 & 606	78 57'	37 17'	245	hay	2	7/31	7/11 7/31	6/27 7/18 9/2 9/8	6/27 7/18 9/2 9/8
Gmeiner	Albemarle	6 & US250	78 48'	38 02'	275	past(5)	2	7/10 8/03	7/10 8/03	6/24 7/12 8/28	5/3 5/24 6/24 7/12 8/28 10/3
Hines	Pr. Edward	602 & 617	78 15'	37 15'	165	hay	3	7/24	7/24	----	----
Hughes	Nelson	651 & 718	78 53'	37 45'	230	hay	2	8/02	8/02	----	----
Hunter	Campbell	722 & 643	78 56'	37 11'	190	past	1	7/31	7/31	6/26 9/8	5/2 5/23 6/26 9/8
Johnson	Pittsylvania	683 & US40	79 13'	36 56'	180	hay	2	----	----	6/21 7/7 8/19	6/21 8/19
McClenny	Appomattox	601 & 627	78 39'	37 17'	185	hay	3	8/01	7/11 8/01	6/28 7/16	5/2 6/7 6/28 7/16
Oates	Halifax	679 & 671	79 01'	36 43'	130	past	5	7/19 8/09	7/19 8/09	6/17 7/8 8/15	4/12 4/25 5/10 6/17 7/8
Park	Mecklenberg	697 & 793	78 42'	36 42'	130	falw(6)	1	7/20 8/10	7/20 8/10	----	----
Robertson	Nottoway	601 & 601	78 03'	37 03'	105	past	.5	7/26	7/26	----	----
Spencer	Henry	695 & 698	80 01'	36 38'	275	airf(7)	2	8/08	8/08	7/1 7/15 8/26	4/25 5/30 5/9 7/1 7/15 8/26
Stevens	Nelson	US29 & 653	78 55'	37 43'	220	hay	4	8/02	8/02	6/24 7/11 8/22 9/12	4/19 6/24 7/11 8/22 9/12 10/4
Upton	Mecklenberg	678 & 615	78 19'	36 38'	75	past	3	7/20 8/10	7/20 8/10	7/3 8/14	4/12 5/9 5/30 7/3 8/14
Wilkerson	Lunenberg	617 & 138	78 04'	36 53'	125	alfa	2	7/25	7/25	----	----
Winn	Henry	610 & 620	79 42'	36 39'	305	hay	2	7/18	7/18 8/08	----	----

1) Altitude in meters above sea level.
2) Field size in hectares.
3) Orchardgrass/ red clover mixed hayfield.
4) Alfalfa.
5) Fescue/ bluegrass pasture.
6) Fallow.
7) Airfield.

1.2.2 Data Collection

The absolute density collection, hereafter referred to as the 'drop trap', used an apparatus as shown in Figure 1 A dome-shaped wire cage was constructed of 9 ga. clothes-line wire. Poultry wire was stretched over it for added strength. Organdy or similar material was used to cover the dome, which enclosed an area of 0.5 m^2. At the top of the dome a 3 m long bamboo rod was fastened.

In the field the cage was dropped forceably over a point selected according to a stratified random sampling scheme. The full extent of the rod was used, so that the area sampled was roughly 3 meters from the collector. The actively moving grasshoppers could easily be seen through the material and were caught by hand through a sleeve attatched to the dome. The captured insects were placed in 95% ethanol. It was found that the grasshoppers tended to perch on the inner wall of the dome and could be easily knocked into the collection jar. After two or three minutes, when the initially active grasshoppers had been caught, the drop trap was left in place while other data (plant measurements and sweepnetting) were recorded in the immediate vicinity. When I returned to the trap after several minutes, I often found more grasshoppers settled on the inner walls of the dome or otherwise exposed to view. Finally, the cage was lifted while

Figure 1: Drop Trap

I carefully examined the ground and vegetation that had been enclosed Only rarely were insects observed to escape. These were recorded if sight identification could be made.

It is assumed that the above technique measures absolute densities of all species and all life stages.

The second sampling method made use of a 36 cm. diameter round sweepnet with a 92 cm. aluminum handle. Each sample included twelve 180° sweeps through the vegetation.

A brisk walk was maintained while sweeping, the pace being adjusted to minimize loss from flushing the grasshoppers. The sweeping was done in a semi-circular path around the site of the drop trap. The catch was anesthetized by pouring ethyl acetate on the muslin sweeping bag, and was then put in a jar of ethanol.

Plant data was taken using a 183 cm. folding ruler. The ruler was dropped onto the vegetation next to the drop trap. The species (if known) and length transected of each plant touching the ruler were recorded. The erect height of the tallest and shortest plants (excluding seedlings) was also measured.

In the sampling procedure, each field was divided into four plots of approximately equal size. Within each plot four randomly selected points were chosen where one drop trap, one sweepnet and one plant measurement were taken.

This produced a maximum of sixteen observations per field for each measurement. Sampling was completed in 8-10 hours and performed in the morning and afternoon of one day, or the afternoon of one and the morning of the next.

1.2.3 Data Analysis

To compare the two insect collecting methods three dimensional contingency tables were constructed from the original insect counts. The three dimensions of the table were:

1. Collecting method (drop trap or sweepnet)
2. Species (or other insect category)
3. Sampling date-location combination (of which there were 17)

These tables were analyzed using the log-linear model for cross- classified data described by Fienberg (1977).

Four tables were constructed, each differing from the others by altering the grouping of the insect counts in variable 2 above to test separate hypotheses.

1.3 RESULTS

1.3.1 Species Bias in Sweepnetting

Under the assumption that both methods sample the grasshopper complex without bias, it is expected that the proportion of the total catch for a given species will be equal under both sets of data (drop trap counts and sweepnet). For the reasons already presented, a deviation from this expected equality is interpreted as the failure of sweepnetting to reliably measure species or groups of species proportionate to their densities.

Table 3 shows the grasshopper diet group, number of individuals, and percentage of the total count for each species of the two families collected by both methods. The diet group is an assignment to one of three broad feeding categories: mixed-forb feeders choose among the available grasses and forbs with preference for the latter. Grass feeders consume chiefly grasses. Head feeders rely on the flowering and fruiting parts of tall plants and are opportunistically predaceous.

On first inspection, Table 3 reveals few obvious differences between the composition of the two trap collections. The relative rank of species abundance is approximately the same in each case. However, for the two species best represented in the sample, *M. f. femurrubrum* appears to be under-represented in the sweepnet catch, in which Conocephalus sp. nymphs is disproportionately large.

In order to test these apparent differences a three dimensional (trap x species x sampling date-location) cross-classified contingency table was constructed.

It would be desirable to allot nineteen categories to the species dimension in this analysis, according to the number of species found. The relative rarity of most of the species in these collections, however, requires that either the most numerous species alone be included, or that the species be grouped in some reasonable fashion. In this way, there will be sufficiently large numbers in the cells of the table to permit analysis by the contingency table method. The total number of grasshoppers must be roughly ten times the number of cells for the assumption that G^2 approaches a chi-square distribution.

I expected tettigoniids to sample at different efficiences from acridids because of their different behavior and habitat requirements. As shown in Table 3, all of the tettigoniid species studied are head feeders. Also, they lay their eggs in the stems of herbaceous plants. Therefore, they frequent the upper strata of the habitat and are more susceptible to sweepnet capture. The acridids are grass and forb feeders and oviposit in the ground or at the base of

TABLE 3

Count Data Summary Collapsed Across Collections

Species	Diet Group	Drop Trap Number of Individuals	Drop Trap %	Sweepnet Number of Individuals	Sweepnet %
ACRIDIDAE					
Melanoplus f. femurrubrum (De Geer)	m-f (a)	824	86.5	3560	89.7
Chortaphaga viridifasciata (De Geer)	g	35	3.7	75	1.9
Dichromorpha viridis (Scudder)	g	29	3.0	81	2.0
Melanoplus d. differentialis (Thomas)	m-f	18	2.0	76	1.9
Syrbula admirabilis (Uhler)	g	19	1.9	94	2.4
Melanoplus s. scudderi (Uhler)	m-f	9	0.9	29	0.7
Encoptolophus s. sordidus (Burmeister)	g	9	0.9	25	0.6
Hippiscus rugosus (Scudder)	g	6	0.6	13	0.3
Melanoplus sanguinipes (F.)	m-f	4	0.4	10	0.2
Arphia xanthoptera (Burmeister)	g	0	0	2	0.1
Orphulella pelidna (Burmeister)	g	0	0	2	0.1
Dissosteira carolina (L.)	g	0	0	1	0.0
		953		3968	
TETTIGONIIDAE					
Conocephalus sp.	h	536	85.9	3692	93.4
Conocephalus strictus (Scudder)	h	73	11.7	192	4.9
Neoconocephalus ensiger (Scudder)	h	10	1.6	16	0.4
Conocephalus f. fasciatus (De Geer)	h	2	0.3	15	0.4
Conocephalus brevipennis (Scudder)	h	1	0.2	10	0.3
Orchelimum agile (De Geer)	h	1	0.2	21	0.5
Scudderia sp.	h	1	0.2	3	0.1
		624		3949	

a) m-f= Mixed-forbivorous, g= Grass, and h= Head Feeding.

plants. The tettigoniids as a group are largely nocturnal whereas acridids tend to be diurnal. Had the sampling taken place at night we would probably observe results opposite to those found here.

The species in Table 4 were grouped by family to produce two categories: Acrididae and Tettigoniidae. The results of this contingency table are read in the following manner, following the notation of Fienberg (1977). Each model is described by its component factors, enclosed in brackets. One digit in a bracket represents a main effect, for example the probability of being a tettigoniid versus an acridid. The first model, abbreviated {1} {2} {3}, contains the main effects of trap, family, and sampling date/location. It assumes independence of the main effects. The second model contains an interaction factor represented by two digits in brackets, the interaction between family and sampling date/location {23}. Since this term is included in the model, it is understood that the main effects of family, {2}, and date/location, {3} are also included, since interaction terms represent deviations from the main effects and would otherwise have no meaning.

The next two columns contain the degrees of freedom (df) and the goodness of fit statistic (G^2). G^2 estimates the lack of fit of the model, the larger the value, the poorer

TABLE 4

Models for Contingency Table of Grasshoppers Grouped by Family

	All Collections (a)		Restricted Collections	
Model (b)	DF (c)	G^2	DF	G^2
1 2 3	49	4568.76* (d)	22	3361.77*
1 23	33	237.72*	15	105.79*
13 2	33	4380.47*	15	3281.33*
12 3	48	4512.33*	21	3331.67*
12 23	32	181.29*	14	75.68*
12 13	32	4324.04*	14	3251.23*
13 23	17	49.43*	8	25.35*
12 13 23	16	19.92	7	9.38

a) 'All collections' signifies that all seventeen location/date combinations were used in the table, 'Restricted' includes only those where sixteen drop and sweep samples were taken.

b) Model factor symbols: 1=method (two categories), 2=family (two categories), and 3=collection (seventeen categories).

c) DF, Degrees of freedom.

d) *, Asterix follows models with inadequate ($p<.05$) fits.

the fit. G^2 follows a Chi-square distribution with the degrees of freedom given. An asterix follows the G^2 value for models that provide an inadequate ($p<.05$) fit. The model containing all first order interactions thus provides an adequate fit to the data.

Having arrived at a model that is adequately fitted to the data, I was able to partition the G^2 values among the factors and inspect those of interest. I was specifically concerned with the interaction between the trapping technique and species of grasshopper, {12}. Another interaction, {13}, measuring the change in efficiency of trapping technique between different sites or sampling dates, is also noteworthy. These G^2 values are listed in Table 5.

Of the other factors, none of the main effects concern us. Factor {1}, for instance, represents the difference in total grasshoppers collected in the sweepnet versus the drop trap, a difference we already know to be large from Table 3. In the totals of the count columns, only 953 individuals of the acridids were collected as compared with 3,968 for sweepnet.

At taxonomic levels higher than species, sweepnetting has a strong family bias. Table 4 shows no adequate fit in any model which does not include all first order interactions. In Table 5, we see that the trap X family interaction is

TABLE 5

G^2 Values for Tests of Family Bias

	Family (a)				M.f. vs Family (b)			
	All (3)		Restr		All		Restr	
Model	DF	G¬2	DF	G¬2	DF	G¬2	DF	G¬2
12	1	29.51	1	15.97	1	4.39	1	6.08
13	16	161.37	7	66.30	16	91.92	7	53.87

a) Species were grouped by family to test the bias of sweepnet between families.

b) Acrididae were placed in two groups (*M. f. femurrubrum* and other) to test whether family were a natural grouping with respect to sweepnetting.

c) 'All' designates that the test was performed for all location/dates. 'Restr' was the test using only those samples having 16 replications.

significant ($G^2=29.51$, df=1, p <.001), with tettigoniids being more readily caught by sweepnetting than acridids (Table 6).

Other factors than family grouping affect the trapping efficiency, as shown by the highly significant ($G^2=161.37$, df=16, p<.001) value for trap X sampling date/location interacion. This effect, {13}, is unfortunately a composite of many variables including site characteristic (ie. vegetation type and structure), season, age of insect population and species composition at each site.

_M_. _femurrubrum_ differed from the other Acrididae in sweepnet efficiency (Table 7) suggesting that the broad heading of 'family' is not a natural grouping for response to trap. The {12} was significant at the .05 level ($G^2=4.39$, p<.05) (not significant at .01), (Table 5) with Table 8 gives the log factor values used in computing the expected values for the contingency table based on family grouping. _M_. _femurrubrum_ better represented in sweep catches than the other acridids (Table 8).

Grasshoppers arranged by diet preference show these patterns: Grasshoppers within diet groupings, or 'guilds' (ie. 'head feeders', 'grass feeders' and 'mixed-forb feeders', respond differently to capture by sweepnet from those in other guilds (Table 9). The {12} factor is significant (Ta-

TABLE 6

Log Values for {12} Factor for Acrididae vs Tettigoniidae

	Acrididae	Tettigoniidae
Droptrap	0.10	- 0.10
Sweepnet	- 0.10	0.10

TABLE 7

Models for Grasshopper Counts, M. femurrubrum vs Acrididae

	All Collections (a)		Restricted Collections	
Model (b)	DF (c)	G^2	DF	G^2
1 2 3	49	629.19* (b)	22	451.06*
1 23	33	122.37*	15	69.96*
13 2	33	533.68*	15	396.32*
12 3	48	621.21*	21	444.11*
12 23	32	114.40*	14	63.01*
12 13	32	525.71*	14	389.37*
13 23	17	26.87*	8	15.22*
12 13 23	16	22.48	7	9.14

a) 'All collections' signifies that all seventeen location/date combinations were used in the table, 'Restricted' includes only those where sixteen drop and sweep samples were taken.

b) Model factor symbols: 1=method (two categories), 2=diet group (three categories), and 3=collection (seventeen categories).

c) DF, Degrees of freedom.

d) *, Asterix follows models with inadequate ($p<.05$) fits.

TABLE 8

Values for {12} Factor for *M. femurrubrum* vs Acrididae

	M. femurrubrum	Acrididae
Droptrap	- 0.06	0.06
Sweepnet	0.06	- 0.06

ble 10, $p<.001$). Table 11 gives the log factor values used in computing the expected values for the contingency table based on diet preference. Head feeders are the most easily caught in the sweepnet (Table 11), followed by mixed-forb feeders. Grass feeders are the most under-represented group in the sweepnet catch.

M. femurrubrum did not differ measurably in its susceptibility to sweepnet capture compared with the other mixed-forb feeders (Table 12). The {12} factor is not significant (Table 10, $G^2=.26$, $p>.10$). This does not mean that the exact species within the diet grouping is irrelevant with respect to trapping method. On the other hand, for the grasshoppers found in this guild we were unable to find differences between these species in the present study.

1.4 DISCUSSION

Many factors work to make one species more susceptible to capture by a given method than to another owing to the distinct attributes of their biologies which will determine the physical position of a grasshopper in the habitat. Among these attributes are escape strategies and efficiencies, diurnal and climatic effect on activity, and feeding preferences. This last factor is especially helpful in explaining the biases in capture rates experienced in the present study, as explained below.

TABLE 9

Models for Contingency Tables of Grasshopper Counts Arranged by Diet

	All Collections (a)		Restricted Collections	
Model (b)	DF (c)	G^2	DF	G^2
1 2 3	82	5007.57* (d)	37	3644.94*
1 23	50	262.02*	23	118.45*
13 2	66	4819.28*	30	3564.61*
12 3	80	4940.32*	35	3605.33*
12 23	48	194.77*	21	78.84*
12 13	64	4752.04*	28	3525.00*
13 23	34	73.73*	16	38.12*
12 13 23	32	39.75	14	14.29

a) 'All collections' signifies that all seventeen location/date combinations were used in the table, 'Restricted' includes only those where sixteen drop and sweep samples were taken.

b) Model factor symbols: 1=method (two categories), 2=diet

TABLE 10

G^2 Values for Tests of Feeding Guild Bias

	Diet (a)				M.f. vs Diet			
	All (c)		Restr		All		Restr	
Model	DF	G¬2	DF	G¬2	DF	G¬2	DF	G¬2
12	2	33.98	2	23.83	1	0.26(ns)	1	0.26(ns)
13	16	155.02	7	64.55	16	88.66	7	47.22

a) Species were grouped by diet grouping to test the bias of sweepnet between guilds.

b) Mixed-forb feeders were placed in two groups (M. f. femurrubrum and other) to test whether guild were a natural grouping with respect to sweepnetting.

c) 'All' designates that the test was performed for all location/dates. 'Restr' was the test using only those samples having 16 replications.

ns) ns, Not significant.

TABLE 11

Log Proportion Values for the {12} Factor for Diet Groups

	Mixed - forb	Head	Grass
Droptrap	- 0.01	- 0.19	0.20
Sweepnet	0.01	0.19	- 0.20

TABLE 12

Models for Contingency Table of *M. femurrubrum* vs. Mixed-Forb Feeders

	All Collections		Restricted Collections	
Model[1]	D.F.	G^2	D.F.	G^2
1 2 3	48	279.67*	22	214.38*
1 23	32	100.16*	15	52.68*
13 2	32	191.23*	15	167.34*
12 3	47	279.63*	21	214.30*
12 23	31	100.13*	14	52.60*
12 13	31	191.19*	14	167.26*
13 23	16	11.73	8	5.64
12 13 23	15	11.47	7	5.38

[1] Model factor symbols: 1=method (two categories), 2=species (two categories), and 3=collection (seventeen categories).

Where the grasshoppers are found in the habitat is to a large degree determined by their diets. This is to some extent mitigated by the extent to which they engage in non-feeding activities (Uvarov 1977). However, it is probable that head feeding species are to be found higher in the vegetation than the other two guilds. The grass feeders, on the other hand, should be located nearer the ground where the leaves are concentrated in the grass species encountered on the study sites (predominantly orchardgrass, Kentucky bluegrass, and fescues). Mixed-forb feeders could be expected to occupy a stratum between these two extremes, since many forb species form leaves above ground level, and mixed-forb feeders also tend to include inflorescences in their diets as well. Given these hypotheses concerning the microhabitat preferences of the guilds, we would expect sweep-netting to be biased in the order of head feeders, mixed-forb feeders, and grass feeders, in as much as sweepnetting efficiency increases as the insects to be sampled ascend the vegetation. This prediction is in fact shown in the data (Table 11).

These considerations of the location in the habitat also explain why _M. femurrubrum_ (a mixed-forb feeder) is captured more efficiently than the other Acrididae (Table 8) but not measurably different from the other members of its guild

(Table 7). Finally, the Tettigoniidae found in this study are height seeking species (esp. the Conocephalinae, Cantrall 1943), and their rate of capture by sweepnetting is, predictably, greater than that for the Acrididae.

Whatever the shortcomings of sweepnetting, the problems are reduced when the insect to be sampled are restricted to species with taxonomic and ecological similarities, as is the case with grasshoppers It is true that total arthropod surveys with sweepnet have failed to produce data consistent over time or to produce a true reflection of the relative abundances of species (Beall 1935, Turnbull and Nicholls 1966). On the other hand, a recent study in Kansas by Evans et al. (1983) found that the acridid species they studied differed slightly in their rate of capture by sweepnet in early summer but not significantly in late summer as the grasshoppers approached maturity. They concluded that sweepnetting "provides a fairly accurate potrayal" of the grasshopper composition in tallgrass prairies.

From a qualitative standpoint, sweepnetting is excellent for detecting the presence of a species. Fenton and Howell (1957) found it to sample the most species in their comparison of five sampling techniques in alfalfa. Sweepnetting is thus valuable in faunal studies, but its reliability in determining relative abundances of species is limited. For grasshopper complexes, attention to the ecological position of the individual species, especially to their location in the habitat, may help to correct this problem and increase the quantitative validity of sweepnet data.

Chapter II

GRASSHOPPER SPECIES SURVEY IN FORAGE CROPS IN THE PIEDMONT REGION OF VIRGINIA

2.1 INTRODUCTION

Fox (1917) surveyed the Orthoptera of Virginia. His early studies were not confined to agricultural sites since his purpose was to evaluate species complexes and habitats in the three physiographic provinces (Appalachia, Coastal Plain, and Piedmont) of the state.

Uvarov (1977) has summarized the literature on the grasshopper species complexes from the life zones on all continents including North America. More recent studies on this continent include those of Banfill and Brusven (1973) and Scoggan and Brusven (1973) (Idaho), Bland and Swayze (1973) (Michigan), Bechtel et al (1981) (Nevada), Campbell et al. (1974) (Kansas), Daniels and Chedester (1973) (Texas), Hardmon and Smoliak (1980), LaRochelle (1980) (Quebec), and Otte (1976) (North and South American deserts).

The purpose of this study is to identify and quantify the species components of grasshopper complexes in hayfield and pasture agroecosysystems in Virginia. The data was taken in two seasons from the Piedmont physiographic province. This survey data, which is lacking for this economically important group in this area, is intended as a preliminary assessment of the grasshopper complex. The ecology of these insects will be examined more closely in a following section.

2.2 MATERIALS AND METHODS

The sites and dates of collection are summarized in Table 2.

The study area was located in the Piedmont province, which coincides with the Upper Austral life zone (described by Rehn and Hebard 1916) in Virginia.

Grasshoppers were collected by the two methods (drop trap and sweepnet) described in Chapter 1 Section 2. Both adults and nymphs were collected. In July and August of 1979, fields were divided into four quadrants and four dropnet samples (a total of 16 per site) were taken per quadrant.

the insects from the four replications per quadrant were combined into a single jar. Fifty 180° sweeps of the sweepnet were also taken in each quadrant for a total of four separate samples. No detailed plant data was taken in 1979.

In 1980, sixteen sweepnet samples were taken per field at randomly selected points (four per quadrant). Samples were placed in separate alcohol containers in separate muslin bags within a large alcohol jar. Sweepnet data only was taken from April to mid-June. Dropnet and plant data were taken with sweepnet beginning June 21. A 183 cm. folding ruler was laid down on the ground at each randomly selected point. Each plant species transecting the ruler was noted and the length of transection measured. The height of the tallest plant transecting the ruler was recorded. A summary of the plant data is found in table 13. Grasshoppers were taken to the lab and identified to species, instar, and sex if adult.

2.3 RESULTS

The species and numbers of grasshoppers collected in both years by both sample methods for all sites are presented in Table 14 . Only acridids were collected in 1979. tettigoniids (six species) and tetrigids (two species) were also collected in 1980.

Melanoplus f. femurrubrum (De Geer) was the dominant acridid both in terms of numbers and sites occupied. *M. differentialis differentialis* (Thomas) was widespread, and was second to *M. femurrubrum* in numbers of individuals of Acrididae collected. Both findings are contrast with Fox (1917) who identified *M. sanguinipes* (F.) as the dominant species in the Piedmont, and found no *M. differentialis*. The latter species is probably an adventive in eastern North Am-

TABLE 13

Summary of Plant Data Recorded in 1980 from Study Sites

Site	Date	Crop (1)	Plant Height (cm)	Grass/Forb Ratio (2)	Ground Cover (%)	Dominant Plant Species					
						1	%	2	%	3	%
Cobb	7/04	h	51	2.9	83	D. g.	45	P. l.	30	T. p.	11
Cobb	7/26	h	54	0.35	80	P. l.	36	D. g.	18	P. m.	17
Gibson	6/27	h	52	0.95	84	D. g.	39	P. l.	36	T. p.	21
Gibson	7/18	h	42	1.9	77	D. g.	50	P. l.	31	T. p.	12
Gibson	9/02	h	29	6.1	45	D. g.	68	P. l.	19	UF	4
Johnson	7/07	h	36	0.54	70	T. p.	50	AG	18	D. g.	10
Johnson	8/19	h	36	4.4	57	AG	51	UF	12	D. g.	10
McClenny	6/28	h	39	2.0	85	T. p.	41	F.sp.	23	D. g.	18
McClenny	7/16	h	42	3.1	83	T. p.	27	F.sp.	22	D. g.	18
Stevens	6/24	h	34	3.7	84	D. g.	50	T. p.	26	F.sp.	12
Stevens	7/11	h	35	2.4	82	D. g.	58	T. p.	19	P. l.	6
Stevens	8/22	h	65	2.5	89	D. g.	50	S. c.	14	UF	13
Stevens	9/12	h	25	5.0	59	D. g.	58	AG	11	UF	10
Gmeiner	6/24	p	29	9.7	94	F.sp.	52	D. g.	29	T. r.	6
Gmeiner	7/12	p	28	12.5	94	P. p.	57	D. g.	20	F.sp.	7
Gmeiner	8/28	p	46	7.4	98	P. p.	41	D. g.	25	T. r.	15
Hunter	6/26	p	97	5.9	93	F.sp.	49	P. p.	17	T. p.	14
Hunter	9/08	p	59	14.7	94	F.sp.	49	AG	25	P. p.	14
Oates	7/08	p	100	21.3	96	F.sp.	71	P. p.	18	S. c.	4
Oates	8/15	p	93	15.1	95	F.sp.	59	P. p.	22	AG	8
Spencer	7/01	p (3)	102	24.6	97	F.sp.	48	A.sp.	38	T. r.	5
Spencer	7/15	p	102	29.3	97	A.sp.	47	F.sp.	41	P. p.	4
Spencer	8/26	p	88	35.9	97	A.sp.	59	F.sp.	25	P. p.	3
Upton	7/03	p	31	1.5	89	F.sp.	40	T. r.	20	L. b.	18
Upton	8/14	p	32	4.9	68	F.sp.	40	L. b.	32	P. p.	9

1) h= orchardgrass/red clover hayfield, p= pasture.

2) The ratio of amount of monocots to dicots measured. Range of possible values from 36 for pure grass to 0.031 for pure forb stand.

3) The Spencer site was an airfield. The vegetational structure and composition resembeled the pas tures more closely than the hayfield.

4) AG= Annual grasses, A. sp.= *Andropogon* sp., D. g.= *Dactylis glomerata* L., F. sp.= *Festuca* sp., L. b.= *Lespedeza bicolor* Turcz., P. l.= *Plantago lanceolata* L., P. m.= *Plantago major* L., P. p.= *Poa pratensis* L., S. c.= *Solanum carolinense* L., T. p.= *Trifolium pratense* L., T. r.= *Trifolium repens* L. UF= Unknown forb.

TABLE 14

Counts of Grasshoppers Collected in Virginia's Piedmont

Family and Species	1979 Insect Count	1979 Frequency(1)	1980 Insect Count	1980 Frequency
Acrididae				
Melanoplus f. femurrubrum (De Geer)	3810	18	7123	10
M. differentialis (Thomas)	240	18	396	10
Dichromorpha viridis (Scudder)	261	14	180	10
Chortophaga viridifasciata (De Geer)	209	17	176	10
Hippiscus rugosus (Scudder)	184	12	40	10
Syrbula admirabilis (Uhler)	105	13	109	10
Melanoplus scudderi (Uhler)	84	10	62	8
Encoptolophus sordidus (Burmeister)	50	8	68	8
Melanoplus sanguinipes vulturnus (Gurney and Brooks)	37	9	36	8
Orphulella pelidna (Burmeister)	15	4	2	2
Arphia xanthoptera (Burmeister)	8	3	2	2
Schistocerca damnifica (Saussure)	8	2	0	0
Dissosteira carolina (L.)	1	1	1	1
Leptysma marginicollis (Serville)	2	1	0	0
Melanoplus bivittatus (Say)	2	2	0	0
TOTAL	5016		8195	
Tetrigidae (2)				
Tettigidea lateralis (Say)			46	5
Tetrix ornata (Say)			8	3
TOTAL			54	
Tettigoniidae (2)				
Conocephalinae nymphs (3)			6992	10
Conocephalus strictus (Scudder) (adults)			401	8
C. fasciatus (De Geer) "			31	9
Orchelimum agile (De Geer) "			22	2
Conocephalus brevipennis (Scudder) "			11	1
Neoconocephalus sp. (4)			55	8
Scudderia sp. (5)			16	6
TOTAL			7528	

---

1) Number of sites at which species was collected (any sampling date).

2) Collected in 1980 only.

3) Nymphs of *Conocephalus* sp. and *Orchelimum* sp. could not be distinguished, and are included together in this category.

4) One adult male *Neoconocephalus retusus* (Scudder) was found in 1980 and *Neoconocephalus robustus* (Scudder) in 1979. It is not known which of the nine North American species of Neoconocephalus this category contains since all but two individuals collected were nymphs.

5) One adult male *Scudderia texensis* Saussure-Pictet was found on a study site in 1980. This category may represent this species, or perhaps *S. furcata* Brunner.

erica since it was not reported in this region before Rehn (1900) noted its establishment in Philadelphia. Morse (1904) lists its range as "Austral zones, almost exclusively west of the Appalachians." He found it at Chattanooga, Tennessee "in considerable numbers in the rank vegetation of the bottomland along a creek." In addition to the eastern studies previously mentioned, _M. differentialis_ is absent from early faunal lists in New Jersey (Rhen 1904) and North Carolina (Sherman and Brimely 1911). Fox (1914) noted its establishment eight years later in the Delaware River basin. By 1940, _M. differentialis_ was reported from Virginia (Roberts 1942).

The Tettigoniidae were also abundant (Table 15). The nymphs of Conocephalinae were found at all sites and rivalled _M. femurrubrum_ as a dominant component of the fauna at five of the sites . Although the nymphs of the various species could not be separated, most were probably _Conocephalus strictus_ (Scudder), which occurs in xeric situations. and frequents mixed grass-forb sites (Cantrall 1968). Most of the late instar nymphs were easily recognizable as _C. strictus_ but were not recorded as such as the remaining nymphs of the subfamily Conocephalinae were difficult to identify. Only adult Tettigoniidae were identified to species. Nymphs were identified to subfamily.

TABLE 15

Grasshoppers Collected in Virginia Forage Crops

	1979				1980			
	Hay		Pasture		Hay		Pasture	
Family and Species	Insect Count	Frequency	Insect Count	Frequency	Insect Count	Frequency	Insect Count	Frequency
Acrididae								
M. f. femurrubrum	1623	8	1807	8	4765	5	2290	5
M. d. differentialis	127	8	106	8	267	5	127	5
D. viridis	66	7	195	7	48	5	132	5
C. viridifasciata	61	8	142	7	40	5	135	5
H. rugosos	89	6	94	5	16	5	23	5
S. admirabilis	57	6	44	7	89	5	20	5
M. scudderi	34	5	27	4	38	5	24	3
E. sordidus	45	5	5	3	62	5	6	3
M. sanguinipes	20	6	17	3	22	5	14	3
O. pelidna	5	2	10	2	1	1	1	1
A. xanthoptera	2	2	6	1	1	1	1	1
S. damnifica	0	0	7	1	0	0	0	0
D. carolina	1	1	0	0	0	0	1	1
L. marginicollis	0	0	2	1	0	0	0	0
M. bivittatus	0	0	2	2	0	0	0	0
TOTAL	2130		2464		5349		2774	
Tetrigidae					8	2	38	
Tettigidea lateralis					5	2	3	
Tetrix ornata					13		41	
TOTAL								
Tettigoniidae								
Conocephalinae nymphs					2100	5	4867	5
C. strictus (adults)					50	3	257	5
C. fasciatus "					14	4	13	5
O. agile "					13	1	9	1
C. brevipennis "					11	1	0	0
Neoconocephalus sp.					38	5	17	3
Scudderia sp.					11	4	5	2
TOTAL					2237		5168	

When the collections between hayfields and pastures are compared, the similarities are more notable than the differences. The same species of grasshoppers were found in both hayfields and pastures. The dominance rank for the acridid species was similar for both habitats.

The greatest difference between the hayfields and the pastures was the ratio of tettigoniids to acridids, which was less than one in the hayfields and greater than one in the pastures. This was due to the increase of Conocephalus in the pastures. These insects are phytophilous, rarely descending from the grasses on which they perch "within two to twelve inches of the tops... " (Cantrall 1943). The hayfields were harvested, and two of the pastures were clipped in 1980 by the growers, eliminating the preferred habitat of these insects. Factors responsible for the abundance of Tettigoniidae in pastures will be examined in Chapter 3.

Of the Acrididae collected, proportionately more Chortaphaga viridifasciata (De Geer), and Dichromorpha viridis (Scudder) were represented in pastures than in hayfields. These two graminivorous species were present in all sites but one.

Encoptolophus sordidus (Burmeister) is a sun-loving Oedipodine (Blatchely 1920) that was found in greater abundance in hayfields where the percent ground cover was generally lower than in the pastures.

All species collected were found as nymphs, often first instars, on the study sites. These species are considered to be normal components of hayfield and pasture communities (eg. Cantrall 1943, Uvarov 1977). For example, *M. femurrubrum* requires food within 48 hours of hatching This fact, along with its extremely strong negative geotaxis (which compels hatchlings to ascend vegetation) makes it unlikely that these grasshoppers were hatched from areas far from the grassland on which they were found (Bland 1981). No record of post-hatching marching behavior of the sort demonstrated by the lubber grasshopper (Watson 1942) exists for the species listed.

In addition to those listed, the following species were also taken by qualitative collecting at the study sites:

Field margins:

Melanoplus keeleri (Thomas)

Orchelimum vulgare (Harris)

Borders of streams (through pastures)

Metalepta brevicornis (Johannson)

Paroxya clavuliger (Serville)

Bare areas:

Pardalophora phoenicoptera (Burmeister)

Disscsteria carolina (L.)

General:

Schistocerca americana (Drury)

Neoconocephalus robustus (Scudder)

2.4 DISCUSSION

As compared with western North American grasshopper faunas, the complexes in the hayfields and pastures studied here are species-poor and dominated by one or two common species. This is a reflection of the difference between rangeland modified from prairie and that imposed on cleard forest land. Forest habitat, whose orthopteran fauna contrasts starkly with adjacent grassland (Cantrall and Young 1954) provide few species which can colonize meadows. The disruptions of the clearing and the cultural activity necessary to maintain these sites create habitats under constant change which can be exploited only by those few species that have loose habitat requirements. Abundance is a property of such grasshoppers (Gause 1930). It follows that a widely distributed, polyphagous species like *M. f. femurrubrum* should dominate the species-poor grasshopper communities in ths study. Uvarov (1977), reviewing the Russian literature, reports Rubtzov's and Berezkov's findings that derelict grasslands and fallows contained high numbers of a few 'pest' species, whereas natural meadow grasshopper complexes were species rich, but low in numbers of individuals.

M. femurrubrum was not the most numerous species in 1914 according to Fox (1917). He reported no *M. differentialis*, which was found at all sites in 1979 and 1980. Moreover, bivoltine *M. sanguinipes*, collected in small numbers in the present study was reported by Fox (1917) to have been the dominate species. Though it is possible that the present finding is an aberration of the two-year period in which the study was conducted, it is not likely. The two years were vastly different climatologically. For the five month period between May and September 1979 there was a cumulative surplus of 16.9 cm. of rainfall (U. S. Weather Service 1979) in the western piedmont region of Virginia. For the same period in 1980 there was a deficit of 16.7 cm. (U. S. Weather Service 1980).

Bland and Swayze (1973), studying four species of *Melanoplus* in Michigan, showed some apparent seasonal separation among the four. The possibility exists that the introduction of *M. differentialis*, which overlaps the first generation of *M. sanguinipes* in diet and seasonal occurence, may have exerted enough competetive pressure on the first generation to allow the late season *M. femurrubrum* to establish dominance. However, the three species occurred together in the Indiana field studied by Cantrall and Young (1954). Their data suggest that all three coexist together as dominant components with *M. femurrubrum* only slightly more numerous than the other two. In any case, the potential competition between these insects would be an interesting area of study.

Chapter III

SHIFTS IN GRASSHOPPER FEEDING GUILDS WITH VEGETATION CHANGES

3.1 INTRODUCTION

In dealing with a large number of species, it is useful to group them according to their resource use patterns. Such grouping is not artificial, since it has been shown by May (1972) from theoretical considerations that natural communities are more stable when arranged in "blocks" of species, where species within a block interact strongly in competition for a resource, but only weakly with those outside the block. Therefore, it is expected that a stable community will contain groups of similarly functioning species, rather than an arrangement of individualists with no discernible organization in resource pattern. The team 'guild' (Root 1973) denotes "a group ("block") of species that exploits the same resource in a similar way." Guild structure has been found among natural communities of grasshoppers for diet and microhabitat use (Joern and Lawler 1981). Guild membership can be determined using cluster analysis of measured overlap in resource use of, for example, grasshopper species by crop content, or by *a priori* considerations of known resource patterns (Inger and Colwell 1976).

By examining community structure in this way, important management concerns may be addressed. For example, based on diet patterns, which grasshopper species are potentially harmful to the valuable plant species? Also, do certain cultural practices alter the grasshopper populations so that their impact on the crop is changed?

The objectives of this study were:

1. To identify the feeding guilds of grasshopper complexes in forage crops in the piedmont region of Virginia.
2. To relate proportion of each guild in the total grasshopper population of a site to vegetational parameters.

3.2 MATERIALS AND METHODS

Grasshoppers from the families Tettigoniidae and Acrididae were collected by the two techniques (drop trap and sweepnetting) described in Chapter 1. Plant sampling procedures have also been detailed there.

Ten sites were each sampled once within the period between June 26 and July 18, 1980 (Table 16). This coincided with the early to mid (ca 3rd) instars of the most abundant grasshoppers present and when populations were at their peak in terms of numbers of individuals (see Appendix 2). This also followed the first harvest of hayfields by several weeks, so that populations could stabilize following this perturbation. The restriction of collections within this short period insured that natural progression of community structure with the advancing season (eg. migrations of adults) did not obscure comparisons between sites.

Numbers of individuals, as opposed to insect biomass, are the unit of measure of the relative size of each guild. It would perhaps have been more meaningful to have used biomass to measure guild size, but the most common species have similar developmental histories, and reach maturity at approximately the same time (see appendix). Discrepancies due to age differences were probably minimal. One notable exception is *Chortophaga viridifasciata* (De Geer), a grass feeding species which overwinters as a late instar nymph or adult, and probably reaches a peak in numbers in early fall. This species was the principal component of the grass feeding guild and probably it (and its guild) was under-represented in the sampling. This, however, does not invalidate comparisons between different sites, but means that the grass feeding component was under-represented everywhere.

The data used used here include counts of individual grasshopper species, plant height, % ground cover and ratio of grasses to forbs (grass/forb ratio). Pierson product-moment correlation coefficients were computed.

TABLE 16

Sites and Dates of Sampling

Farm Name	Date	Number of Drop Samples	Number of Sweep Samples
Cobb	VII-4	16	7
Gibson	VII-18	16	14
Gmeiner	VII-12	16	16
Hunter	VI-26	16	-
Johnson	VII-7	16	-
McClenny	VII-16	16	16
Oates	VII-8	16	8
Spencer	VII-1	14	12
Stevens	VII-11	16	16
Upton	VII-3	16	16

I have chosen to use published records of diet patterns for the grasshopper species found to determine the guilds present in the forage crops. No data was taken concerning grasshopper diet in this study. However, extensive information for each of the species collected can be found in the literature and are summarized in Tables 17, 18 and 19.

3.3 RESULTS

3.3.1 Factors Determining Guild Membership

In order to approach the subject of grasshopper feeding guilds, it is necessary to understand the relationship of feeding to microhabitat preferences, behavicr and morphology. Very early in the study of acridology (ie. Morse 1904) it was noted that certain species frequented the ground stratum, while others lived mainly on vegetation, hence the terms 'geophilous' (ground loving) and 'phytophilous' (plant loving). Uvarov (1977) redefined and extended these concepts to arrange grasshopper species into five categories or 'life-forms'. The pertinent ones here are 'terricole' (ground dwelling), 'herbicole' (forb dwelling), and 'graminicole' (grass dwelling). Grasshopper species have mcrphological adaptations consistent with the life-form category to which they belong: terricoles have a dorso- ventrally compressed thorax and short body, resulting in a rather robust appearance. The tarsal arolia and prosternal process, both used in climbing, are absent or reduced and the face is verticle or only slightly oblique. Coloration is modified to match the ground stratum. Herbicoles have a generalized, "normal" body shape; the face is slightly oblique, and the prosternal process and tarsal arolia are prominent. Graminicoles, to varying degrees, have elongated, laterally compressed bodies, oblique faces, large tarsal arolia, and in some species long hind femora.

The foregoing classification system pertains only to acridid grasshoppers, but some of the same principles apply to the Tettigoniidae. It should be appreciated that taxonomy, in as much as it follows morphology and behavior, will determine species membership in the guilds.

3.3.2 Literature Records of Feeding

The feeding records from the literature are summarized in Tables 17, 18 and 19. In order to simplify and condense the information pertinent to this study, the records have been generalized. The species of flora eaten is grouped under the broader category of "grass" or "forb". Also, the part of the plant (leaf, flower or seed) is included when available. This allows a general delineation of diet pattern, such as "grass flower feeder" or "forb leaf feeder". No inference may be made from the literature on the specific choice of food for the sites in this study since the plant spectra available for food differ from those in the Texas, Kansas, Michigan and North Dakota sites in the published studies.

The techniques used to determine grasshopper feeding are mandibular morphology, laboratory differential feeding tests, field observations, and crop and/or fecal analysis. Details of conducting these techniques can be found in the references given, and in Mulkern and Anderson (1959) and Mulkern (1967).

Mandibular morphology involves a study of the structure of the mandibles (and other mouth parts), which can be categorized by adaptation for graminivory, forbivory, dendrophagy, etc. Therefore, this method can be used only to determine general food habits. Gangwere (1961) considered this information too imprecise and misleading for his purposes, but in this present application it is properly used to confirm species placement within guilds.

Laboratory differential feeding tests involve the use of cuttings of one or more plant species offered simultaneously to caged grasshoppers. Each plant species is ranked according to desirability, determined by the amount of plant material removed from the cuttings. Its limitations are typi-

TABLE 17

Feeding Records of Mixed-forb Feeding Grasshoppers from Literature Sources (1)

Species	Mandib. Type	Forb Leaf	Forb Inflores.	Grass Leaf	Grass Inflores.	Insect Parts
Conocephalus brevipennis	F-S-C	O* C***	O** C*	O*	O***	O** C*
C. fasciatus	F-S-C	C***	O*** C**	L**	L*** O** C**	C**
C. strictus	C-S (2)	O* C**	O*** C*		O** C*	O* C**
Orchelimum vulgare (2)	F-S-C	C**	C***		O*** C***	C*
Neoconocephalus (3) *ensiger*	S		O**		L*** O*** C***	C*
Scudderia texensis	FF (4)	L** (4) O***	L*** O*** C***			

C=crop and/or fecal analysis, C-S=carnivorous-seminivorous, F-S-C=forbivorous-seminivorous-carnivorous, L=laboratory preference, O=field observation, S=seminivorous, *=rare, **=common, ***=preferred

1)Data Compiled from Gangwere 1961 unles otherwise noted.
2)Not often encountered. *O. agile* was well represented, but no record of its diet exists. *O. agile* probable has a diet similar to *O. vulgare*.
3)This species was not encountered in this study. No literature exists on its congener, *N. retusus*, which was found. *N. ensiger* is included to indicate the probable diet of *N. retusus*.
4)Isely, 1944.

TABLE 18

Feeding Records of Grass Feeding Grasshoppers from Literature Sources (1)

Species	Mandib. Type	Forb Leaf	Forb Inflores.	Grass Leaf	Grass Inflores.	Insect Parts
Arphia xanthoptera	G (2)			C*** (3)		
Chortophaga viridifasciata	M (G)(2)	L** C** (4)	L* O**	L*** O*** C***	L*** C*	
Dichromorpha viridis	G (2)			C*** (5,6)		
Dissosteira carolina	G	L** O*** C**	L*	L*** O*** C***	L**	
Encoptolophus sordidus	G	L* C*		L*** O*** C***	L* C*	C*
Hippiscus rugosus	G (2)	L* (7) C* (5,8)		L*** (7) O*** (9) C*** (3,5,8)		
Orphulella pelidna	G (2)					
Syrbula admirabilis	G	L*		L*** O*** C***	L*	

C=crop and/or fecal analysis, C-S=carnivorous-seminivorous, F-S-C=forbivorous-seminivorous-carnivorous, L=laboratory preference, O=field observation, S=seminivorous, *=rare, **=common, ***=preferred

1)Data Compiled from Gangwere 1961 unles otherwise noted.
2)Isely, 1944
3)Mulkern, et. al., 1969
4)Gangwere, 1976
5)Lambley, et. al., 1972
6)Isely, 1946
7)Isely, 1938
8)Mulkern, 1964
9)Anderson and Wright, 1952

TABLE 19

Feeding Records of Head Feeding Grasshoppers from Literature Sources (1)

Species	Mandib. Type	Forb Leaf	Forb Inflores.	Grass Leaf	Grass Inflores.	Insect Parts
Melanoplus differentialis	M (2)	L*** (3,4,5) O*** (3) C*** (6)		L*** (3,4,5) O*** (3) C*** (6)		
M. femurrubrum	F	L** O*** C***	L*** O*** C*	L*** O* C**	L* O*	
M. sanguinipes	M-F	L** O*** C***	L** O* C**	L*** O** C***	L***	
M. scudderi	M-F	L*** O* C***	L*** O*** C***	L* C*	L*	

C=crop and/or fecal analysis, C-S=carnivorous-seminivorous, F-S-C=forbivorous-seminivorous-carnivorous, L=laboratory preference, O=field observation, S=seminivorous, *=rare, **=common, ***=preferred

1)Data Compiled from Gangwere 1961 unles otherwise noted.
2)Isely, 1944
3)Isely, 1938
4)Barnes, 1963
5)Caplan, 1966
6)Mulkern, et. al., 1969

cal of laboratory derived data: behavioral alterations in an unnatural setting cause unpredictable biases in the results. Furthermore, the necessity of offering each plant species in equal availability removes the factor of the host finding ability of the grasshopper. Thus rare plants are selected in the laboratory in larger amounts than would be possible under field conditions. Also, grasshoppers may be offered plants or plant parts which would be inaccessible to them in nature. In this present study, only secondary emphasis will be placed on this method.

Analysis of grasshopper crop content involves dissection of the crop and measuring the plant fragments found. Gangwere (1961) placed less confidence in this method than in either his cage tests or his field observations. He apparently could identify little more than the general type of plant consumed (ie. grass blade, pollen grain etc.). Subsequent improvements in the identification of crop fragments (Mulkern and Anderson 1959) made possible identification to species using 'type' slides of plant fragments. Uvarov (1977) noted the superiority of this ammended technigue to all others in evaluating grasshopper diets. Analysis of fecal material, accomplished by collecting and examining the feces of live field collected grasshoppers, enables data to be amassed quickly. Unfortunately, this method suffers perhaps even more acutely from imprecision than the unimproved crop technique.

Gangwere (1961) performed his field observations by collecting both plant and insect when he noticed a grasshopper feeding. The extent of his records silence the objections raised by Uvarov (1977) that "casual records of the plants eaten can be worthless ...". Gangwere himself placed great confidence in this method.

The information most useful for our purpose of grouping the species according to feeding is that derived from field observation and the crop and fecal analyses. The objection of imprecision concerning the latter two have no bearing in this case since specific content of the diet is not claimed. Laboratory preference and mandibular morphology, because of the limitations mentioned above, are provided as supplemental information. Where discrepancies exist, mandibular morphology and laboratory feeding tests help determine guild membership.

3.3.3 Guilds

The guilds and their members are listed in Table 20 below. Two general comments must be made about the guilds themselves: First, although they are based on diet, microhabitat requirements are highly correlated with diet. In a sense this is regrettable, since microhabitat factors confounds the conclusions based on diet. On the other hand, this is a realistic reflection of grasshopper feeding habits for the reasons just outlined above. The second observation is that guild placement follows taxonomic division at the subfamily level. The guild concept was developed partly to avoid grouping based on taxonomy, but in this case phylogeny seems to be a factor in guild membership, as Joern and Lawlor (1981) also found.

3.3.3.1 Head Feeders

This guild contains the three tettigoniid subfamilies represented in this study. These insects are plant dwelling in habit, spending most of their time near the tops of tall plants. With few exceptions, they lay their eggs in plant stems rather than in the soil. Cantrall (1943) reports that:

> All of the Conocephalinae are agile and wary insects. During the day individuals of both sexes of all eight species are usually perched within two to twelve inches of the tops of the sedges, grasses, and shrubs in their favorite haunts. Here they cling, sometimes head up, sometimes head down... All of the Conocephalinae are primarily diurnal and are most active in the heat of the day.

When available, reproductive plant parts are chosen over vegetative ones. Species differ in the relative acceptability of forbs and grasses. Opportunistic predation is exhi-

TABLE 20

Guild Membership of Forage Crop Grasshoppers

Part I. Head Feeders
Conocephalus brevipennis (Scudder)
C. fasciatus (De Geer)
C. strictus (Scudder)
Neoconocephalus retusus (Scudder)
Orchelimum agile (De Geer)
O. vulgare Harris
Scudderia texensis Saussure-Pictet
Part II. Mixed Forb Feeders
Melanoplus d. differentialis (Thomas)
M. f. femurrubrum (De Geer)
M. sanguinipes vulturnus (F.)
M. scudderi (Uhler)
Part III. Grass Feeders
Arphia xanthoptera (Burmeister)
Chortaphaga viridifasciata (De Geer)
Dichromorpha viridis (Scudder)
Dissosteira carolina (L.)
Ecoptolophus sordidus (Burmeister)
Hippiscus rugosus (Scudder)
Orphulella pelidna (Burmeister)
Syrbula admirabilis (Uhler)

bited in all but the Phaneropterinae (Isely 1941). *Conocephalus strictus* the most numerous species found, is apparently the most carnivorous as shown by the amount of insect parts found in its crop and fecal records.

Gangwere's (1961) study showed from crop and fecal analyses of the Conocephalinae that flowering parts were not found in greater amounts than other foods, and in some cases less than forb leaves or insect parts. Isely and Alexander (1949) reported that the feeding in the conocephalines they studied was restricted mainly to the reproductive parts of both monocots and dicots, and to insects. They concluded that leaves were an unimportant component in their diets. Flower parts are perhaps more quickly broken up in the grasshopper crop than are leaves, leaving only pollen grains to record flower feeding. That flowers are in fact most extensively fed upon is evident from Gangwere's (1961) field observations, taken at all hours of the day.

3.3.3.2 Mixed Forb Feeders

This guild has members with wide food preferences and is not restricted to forbs. Their latitude in diet makes them likely candidates for crop pests, and it is in this guild that we find three important noxious species: *M. d. differentialis*, *M. f. femurrubrum*, and *M. sangunipes vulturnus*.

A discussion of *M. f. femurrubrum*, the most numerous species found here and one whose diet has been extensively studied, will serve as an illustration of the feeding habits of this guild. Gangwere et al. (1976), in outdoor cage feeding tests, observed *M. f. femurrubrum* to accept 70% of the graminoids, 79% of the forbs, and 43% of the woody plants offered to it. Crop analysis data from a study of native tallgrass prairies in Kansas (Campbell et al. 1974) recorded eight of 29 grasses, one of three grass-like plants, 27 of 56 forbs, and one of six woody plants present ingested by *M. femurrubrum*. Forbs are more heavily ingested than grasses: Grass-forb indexes (ranging from 100 for pure forbivory to -100 for graminivory) normally fall in the 0 to 50 range, indicating mixed-forbivorous feeding. This can vary widely, however. Lambley et al. (1972) in Kansas found a range for the grass-forb index from -63 to 75 in six different planted pastures, "generally in proportion to availability of forbs or grasses". Several grass species seem to be particularly acceptable, especially *Poa pratensis* L. (Kentucky bluegrass), *Dactylis glomerata* L. (orchardgrass), *Phleum pratense* L. (timothy),and *Bromus inermis* Leyss. (bromegrass) (Bailey and Mukerji 1976. These authors, however, found that orchardgrass did not support development to the adult stage when offered to caged grasshoppers as the sole food.

B. inermis supported complete complete development with 33% mortality, and *P. pratense* and *P. pratensis* were not studied).

The Melanoplinae in general tend to be a phytophilous group: Nymphs of *M. femurrubrum* exhibit strong phototaxis (Bland 1981), and orientation to vertical (plant-like) lines (Mulkern 1969). These habits could explain the significant inclusion of reproductive parts in this and the other mixed-forb feeders.

It is concluded that this guild has a broad range of feeding habits but tends toward forbs. Both vegetative and reproductive parts are fed upon with no indication that either is preferred over the other.

3.3.3.3 Grass Feeders

In contrast to head and forb feeders, grass feeding grasshoppers tend to be more restricted in their feeding, relying on grasses for the bulk of their diets. Two exceptions occur: *Dissoteira carolina* L. and *Chortaphaga viridifasciata* (De Geer) are commonly reported as mixed feeders with preference for grasses. The studies in Michigan by Gangwere (1961) and Gangwere et al. (1976) confirm that, though forbs are consumed in significant amounts, both species consume mostly monocots in nature and are more likely to choose grasses in cage studies.

The other species in this guild are decidedly graminivorous based on the evidence available. Bailey and Riegert (1971), while finding that some forbs were consumed by *Encoptolophus sordidus* (Burmeister) after a period of starvation, nevertheless found only 1% of the field collected individuals contained forbs in their crop contents, the rest being insect matter (never more than 1% of a crop's content) or grasses. The diet of *Orphulella pelidna* (Burmeister) has not been studied, but that of *O. speciosa* (Scudder) is consistently reported as a strict grass feeder.

3.3.4 Guild Structure in Relation to Vegetation

Having defined the guilds and determined their constituency, it is possible to examine the changes in the proportion of each guild with changes in measurable vegetational characteristics. Specifically, what is the relationship between plant height, % ground cover, and grass/forb ratio with the proportion of each feeding guild?

Correlation matrices are presented in Tables 21 and 22. Plant height appears to affect the community structure more directly than either % ground cover or grass/forb ratio. Head feeders are more numerous in tall vegetation (corr coeff.= .972, $p<.0001$) whereas mixed-forb feeders dominate in short (corr. coeff.= -.96083). The nonsignificant correlations (Table 21) with % ground cover are probably explained by their own highly significant correlation with plant height. The same may be true of head and mixed-forb feeders' correlations with grass/forb ratio. These results are duplicated with sweepnet data, showing that they are not artifacts of collection method.

The relationship between guild population size and plant height is presented in Figures 2, 3, 4, and 5. Predictably, head feeder populations tend to increase with an increase in plant height. Mixed-forb feeders seem to respond in the opposite fashion, though less perfectly so. It is important that actual population figures be examined as well as the proportions of each guild so that it can be determined which guild in fact responds to the environmental factor in question. In this case, it appears that both head and mixed-forb feeders respond, though the relationship for the latter is not significant ($p > .05$). Increased sample size might reveal a statistically significant trend.

Grass feeders show no relationship to any of the three environmental factors measured. The low population levels of these species made reliable sampling difficult, perhaps obscuring relationships. The size in number and heterogeneity of these species is large and it is quite possible that this diversity allows maintenance of small but stable population levels under widely disparate environmental conditions.

TABLE 21

Correlation Matrix for Drop Trap Collection Proportions(a)

	Head Feeders	Mixed-Forb Feeders	Grass Feeders	Plant Height	% Ground Cover	Grass/Forb Ratio
Head Feeders		-0.99661 0.0001	-0.39609 0.2572	0.97204 0.0001	0.54607 0.1025	0.65996 0.0378
Mixed-Forb Feeders			0.31917 0.3687	-0.96083 0.0001	-0.53852 0.1083	-0.64833 0.0426
Grass Feeders				-0.47331 0.1671	-0.27980 0.4336	-0.36614 0.2981
Plant Height					0.62988 0.0510	0.72152 0.0185
% Ground Cover						0.75937 0.0108
Grass/Forb Ratio						

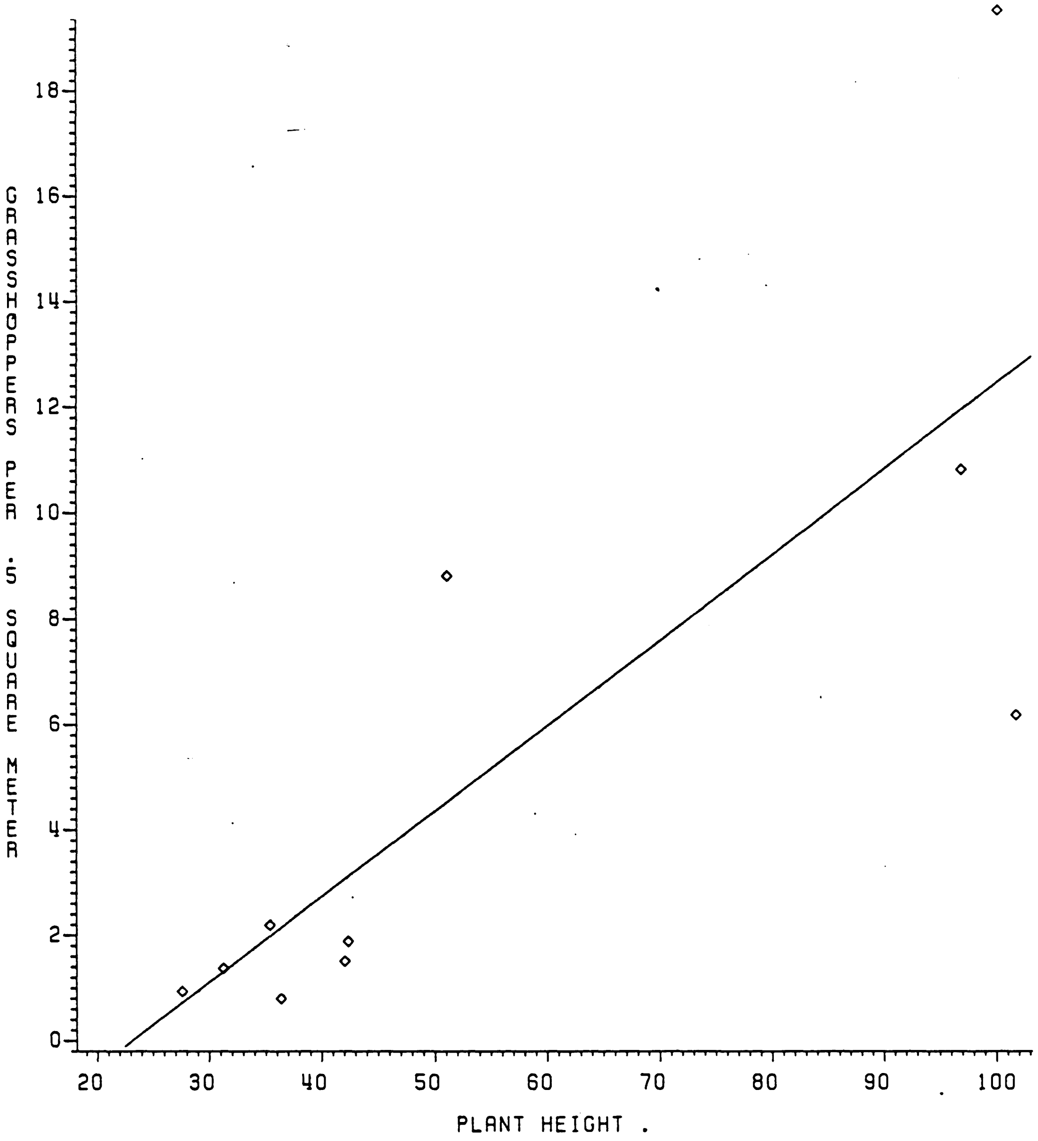
a) Pairs of numbers are Pearson product-moment correlations above and their probability values beneath.

TABLE 22

Correlation Matrix for Sweepnet Collection Proportions

	Head Feeders	Mixed-Forb Feeders	Grass Feeders	Plant Height	% Ground Cover	Grass/Forb Ratio
Head Feeders		-0.99595 0.0001	-0.12542 0.7478	0.96718 0.0001	0.52386 0.1477	0.65668 0.0547
Mixed-Forb Feeders			0.03569 0.9274	-0.95111 0.0001	-0.50316 0.1673	-0.62990 0.0690
Grass Feeders				-0.25524 0.5074	-0.27064 0.4812	-0.34842 0.3581
Plant Height					0.62988 0.0510	0.72152 0.0185
% Ground Cover						0.75937 0.0108
Grass/Forb Ratio						

a) Pairs of numbers are Pearson product-moment correlations above and their probability values beneath.



Y = -3.75 + .162X
RSQUARE = 0.649

Figure 2: Relationship of Head Feeder Density to Plant Height

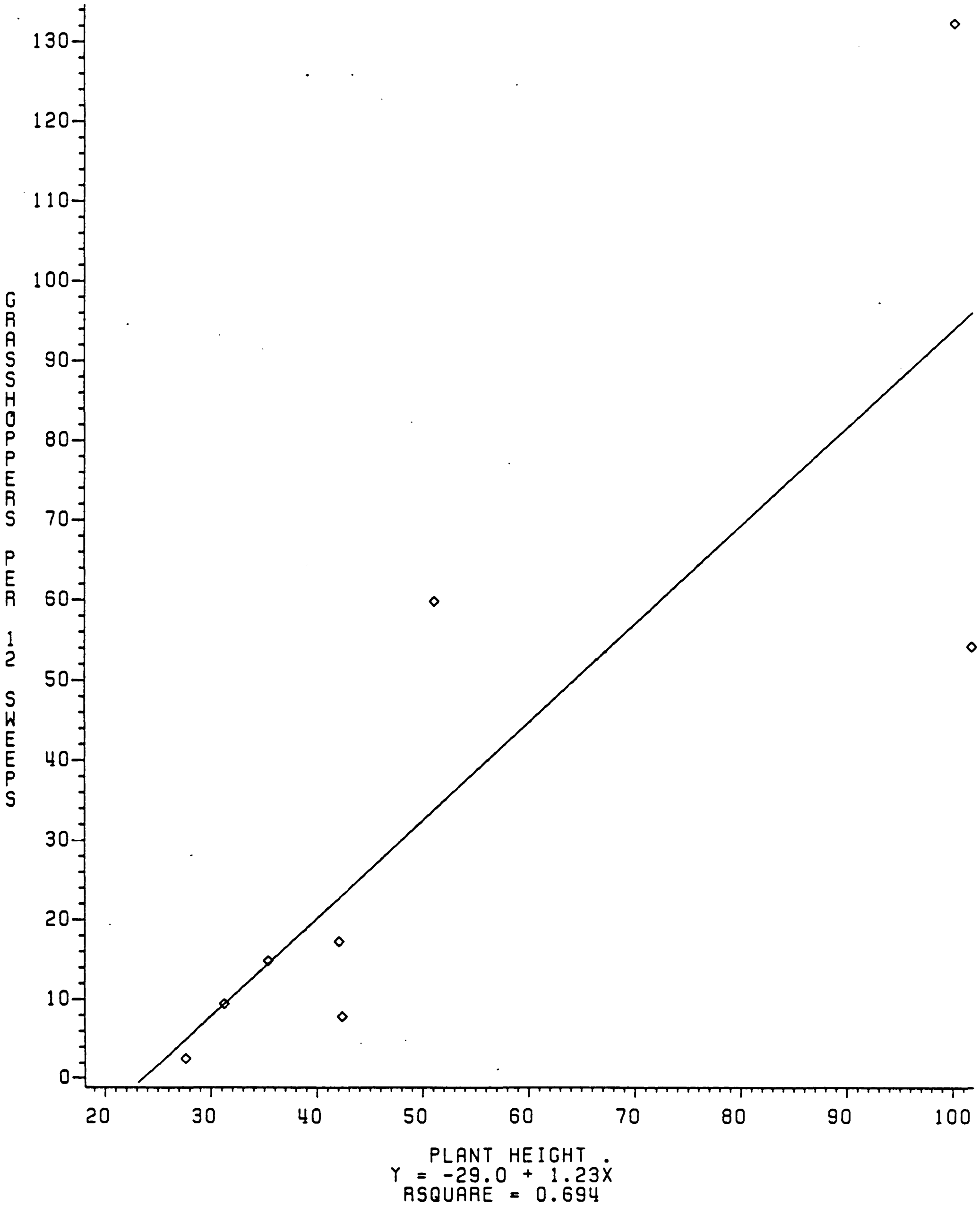


Figure 3: Relationship of Head Feeder Relative Population Size to Plant Height

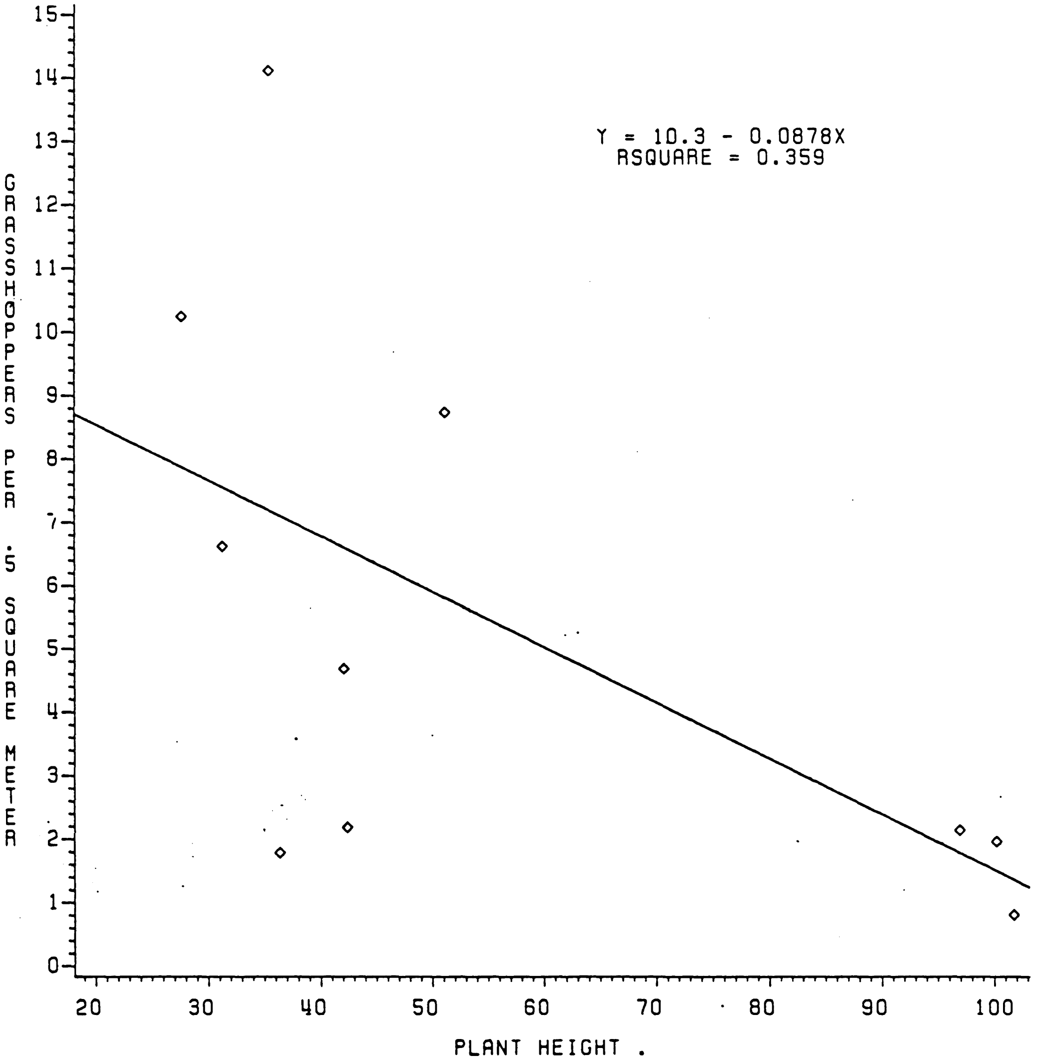


Figure 4: Relationship of Mixed-Forb Feeder Density to Plant Height

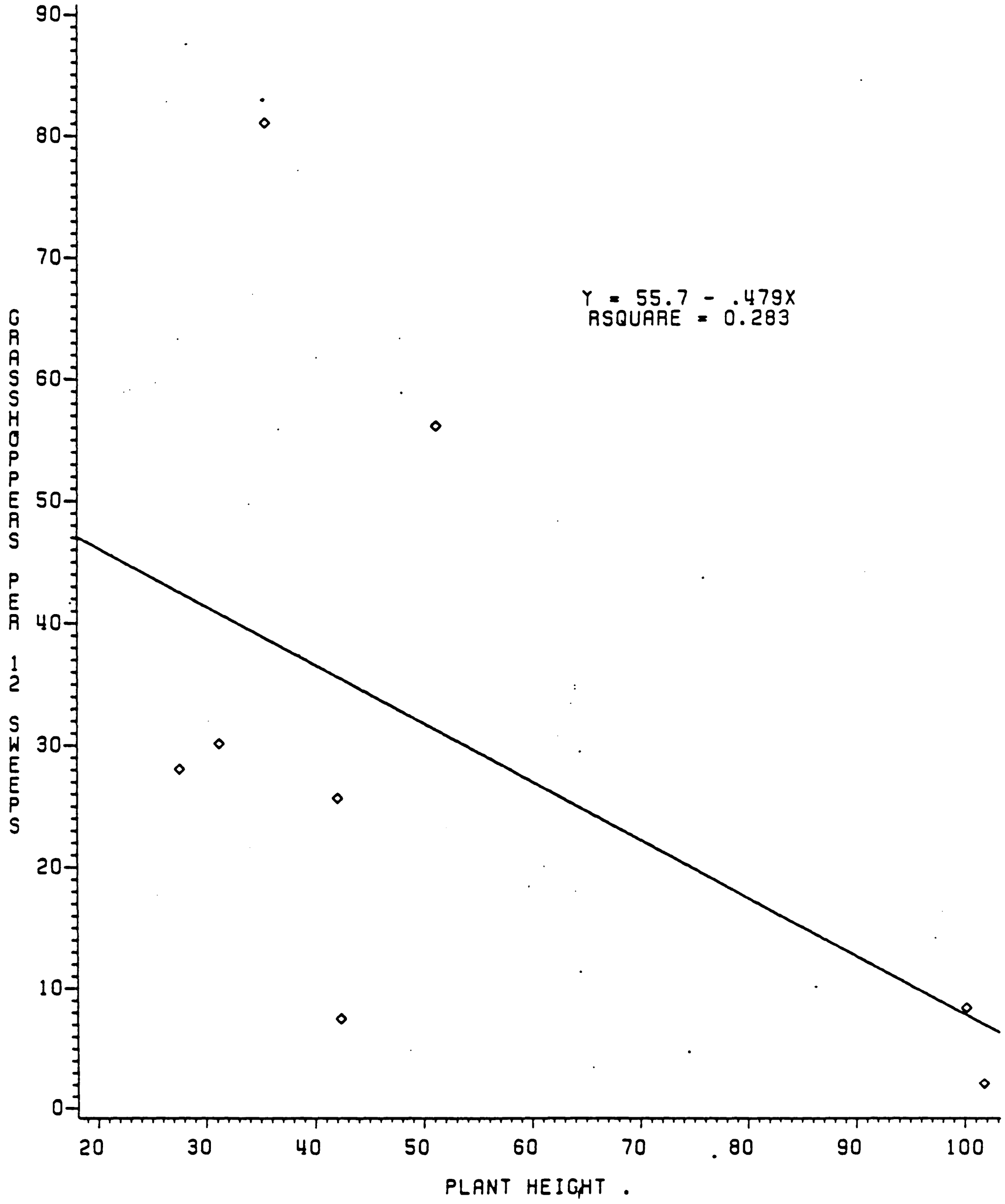


Figure 5: Relationship of Mixed-Forb Feeder Relative Population Size to Plant Height

Mixed-forb feeder density versus plant height presents a problem. In the three tallest vegetation sites, densities were very low (Figures 4 and 5). At lower values, a wider range of densities was found. Two data points in particular stand out apart from the others in the group of observations with densities lower than 50 cm. At both sites, harvesting had occurred prior to sampling, and grasshopper hatching was known (from pre-season surveys) to have already occurred at one site. Based on observations in this study and from reports from growers in this area it is felt that harvest occuring when grasshoppers are in the nymphal or adult stages lowers grasshopper populations, either through forcing emigration or mortality, or perhaps both. The cuttings probably explain the low grasshopper populations at these sites, which were chosen because they were previously known to support populations large enough for study.

3.4 DISCUSSION

Plant height apparently affected organization of the guilds more noticeably than either % ground cover or grass/forb ratio. This was especially true for head feeders, whose population levels were positively correlated with plant height. Anderson (1964) noted a general decrease in density of acridid levels with an increase in plant height. No definite relationship was shown for acridids here. However, if we take into account the two sites where cutting had occurred after egg hatch, it appears that the densities of mixed-forb feeders, composed entirely of shorthorned grasshoppers, were negatively correlated with plant height. (This is in contrast to Capinera and Sechrist 1982, who noted a positive correlation of the acridid subfamily Catantopinae numbers with plant biomass.) These responses for the two guilds resulted in a strong relationship between guild sizes and plant height, as head feeders thrived relative to forb feeders with increasing height.

These guilds having been constructed according to diet, we might conclude that these patterns emerge as a result of food resource changes. The number of inflorescences will increase with increase in plant height, especially in situations where fescue (*Festuca* sp.) and orchardgrass (*D. glomerata*), two of the three most common grasses found, predominate. Conversely, low plant height is maintained to prolong vegetative biomass production at the expense of reproductive growth in well managed hayfields and pastures. The guilds may therefore respond to changes in vegetation as food.

An alternate explanation, however, is provided by a consideration of the affect of plant height on shelter. An increase plant height alters the microhabitat through shading and restriction of airflow. Anderson et al. (1979) found that two shorthorned grasshopper species, *Psoloessa d. delicatula* Scudder and *Eritettix simplex* Scudder, with similar diets (graminivorous) selected different habitats based on plant height. *P. delicatula* chose short grass areas, where it was able to maintain its body temperature above ambient air through solar orientation. *E. simplex*, which did not exhibit these behavioral adaptations, chose tall grass habitats and thus avoided the thermal and hydric stresses associated with short vegetation. Species in the family Tettigoniidae, which in the present study includes all the members of the head feeding guild, characteristically inhabit moist situations and are nocturnally active. The Conocephalinae are primarily diurnal and tolerate drier situations, but may retain the inability to regulate body temperature and moisture. Their need for the stability tall vegetation affords may therefore be greater than that of the Acrididae. Therefore, the dominance of the head feeding guild in tall vegetation may be an artifact of microhabitat influences rather than a response to food resource.

Neither grass/forb ratio nor % ground cover produced correlations that could not be explained by plant height, with which both were highly correlated. Anderson (1964) found graminivorous species more numerous where grasses composed more than 40% of the vegetation. Since grass feeding species comprised so small a percentage of the grasshopper fauna, such a relationship may have been obscured. Anderson (1964) also found that all acridid populations were more likely to be established at densities greater than 1/m² where % ground cover in native grasslands was greater than 40%. The range of foliage cover values in this study was from 70% to 97%, and probably was not wide enough to produce observable differences between habitats.

Evidence for the existence of guilds was shown for grasshopper communities in Texas, and other western, rangeland by Joern and Lawlor (1981). These authors found that ca. 75% of the grasshopper species fit into diet and microhabitat guilds of two or more species based on a conservative clustering technique. Moreover, they found that general, less restricted guilds were present at different sites. A close parallel to the grasshopper communities found here in Virginia was described, remarkably, from the Greater Caucasus of Georgia (Soviet Union) by Stolyarov (1977). He recognised three 'life forms' in his consideration of the orthopteran biomass consumption in subalpine pastures: 'Herbivorous Chortobionts' (= mixed feeding grasshoppers adapted to lving on grasses) inhabiting the upper ('surface') layers of vegetation 'facultative chortobionts' on the lower plant parts and feeding on broad-leaved grasses, and 'chortobionts of the Graminae', strict grass feeders. The first life form corresponds roughly to head feeders, the second to our mixed-forb feeders, and the last to the grass feeders. described in this study. Seasonal shifts in the share of the total insect biomass among the three life forms was observed, along with changes in the flora. There was no mention of the effect of plant height on the dominance of the three groups. The similarity in community organization between the Caucasus meadows and those found in Virginia suggests that these guilds are functional units inherent to grassland habitats, occupied by different Orthopteran species according to the regional biota.

A practical approach to grasshopper economic importance and control can be made using the guilds recognised here. Grass feeders, though competing directly with livestock for forage, were not found in sufficient numbers to warrant control in 1980 in Virginia. If the species are indeed functional equivalents, and the total community share does not fluctuate greatly from year to year for this guild, then little impact on forages could be expected. Graminivorous species are a more serious problem in western rangelands, where the most valuable forage plants are perennial grasses and where these species form a larger portion of the grasshopper complex.

The head feeding guild, which was the dominant component in tall vegetation, presents a complex picture. On the one hand, it might be argued that in tall grass pastures feeding on inflorescences prevents re-seeding of valuable forage plants. Wilbur (1936) found damage to inflorescences of many grasses at high levels when grasshopper populations were normal (non-outbreak) in Kansas pastures. He observed that ca. 50% of the heads of such grasses as wheat grass (*Agropyron smithii* Rybd.) and side oats grama (*Bouteloua gracilis* (Michx.)) were damaged. Natural reseeding of Virginia forage grasses is not considered an important management practice, since such plants as bluegrass, fescue and orchardgrass reproduce vegetatively through tillering. Head feeders may in fact be beneficial to these grasses by consuming the inflorescences of tall annual weeds which depend on re-seeding for survival. However, the members of this guild feed not only on reproductive parts, but also compete with livestock for forage.

The mixed-forb guild, because of its population size and its diet, may present the greatest potential threat to forage crops in the area studied. A wide variety of plants and both leaves and flowering parts are consumed by these grasshoppers. Because of the life histories of these species only the fall hay crop is threatened. The potential for damage to high acre value crops adjoining grasslands and roadsides makes the monitoring of this guild particularly important. Their breadth of diet and capacity for local movement make them a threat to the tobacco, corn, and home garden plots in the piedmont counties studied.

Mangan et al. (1982) investigated the differences in populations of meadow insects in forage plots seeded with different legume species (alfalfa, birdsfoot trefoil, and red clover). Most grasshopper species showed a weak tendency toward unseeded control plots and and those with birdsfoot trefoil, and away from clover. The authors concluded that generalist and grass feeding species like grasshoppers exert a beneficial effect on legume establishment in hayfields.

The practice of clipping may favor the forb feeding guild by maintaining a low, vigorously growing plant cover. Clipping, however, may offer a means of controlling the grasshopper complex if the clipping regime includes an early to mid summer harvest corresponding to the third to the sixth week following egg hatch (approximately June 25 through July 10, see Appendix). During this period, such a perturbation would expose the early instars to adverse microclimatic stresses, predation, and loss of food. As was previously mentioned, this practice drastically reduced the grasshopper fauna on at least one site in 1980.

REFERENCES CITED

Anderson, N. L., 1964. Some relationships between grasshoppers and vegetation. Ann. Entomol. Soc. Am. 57: 736-742.

Anderson, N. L., and J. C. Wright. 1952. Grasshopper investigations on Montana rangelands. Mont. Agric. Exp. Stn. Bull. 486. 46 p.

Anderson, R. V., C. B. Tracy, and Z. Abramsky. 1979. Habitat selection tion in two species of short-horned grasshoppers. Oecologia. 38: 359-374.

Bailey, C. G., and M. K. Mukerji. 1976. Feeding habits and food preferences of *Melanoplus bivittatus* and *M. femurrubrum* (Orthoptera: Acrididae). Can. Entomol. 108: 1207-1211.

Bailey, C. G., and P. W. Riegert. 1971. Food preferences of the dusky grasshopper, *Encoptolophus sordidus costalis* (Scudder) (Orthoptera: Acrididae). Can. J. Zool. 49: 1271-1274.

Banfill, J. C., and M. A. Brusven. 1973. Food habits and ecology of grasshoppers in the Seven Devils Mountains and Salmon River breaks of Idaho. Melanderia 12: 1-21.

Barnes, O.L. 1963. Food plant tests with the differential grasshopper. J. Econ. Entomol. 56: 396-399.

Beall, G. 1935. Study of arthropod populations by the method of sweeping. Ecology 16: 216-225.

Bechtel, R. C., L. M. Hanks, and R.W. Rust. 1981. Orthopteroids of the Sand Mountains and Blow Sand Mountains, Nevada. Entomol. News 92: 125-129.

Bland, R. G. 1981. Survival and food detection by first instar *Melanoplus femurrubrum* (*Orthoptera*: *Acrididae*). Great Lakes Entomol. 14: 197-204.

Bland, R. G., and D.D. Swayze. 1973. Chronological and geographical distribution of orthopteroid populations in an abandoned Michigan field. Environ. Entomol. 2: 737-742.

Campbell, J. B., W. H. Arnett, J. D. Lambley, O. K. Jantz, and H. Knutson. 1974. Grasshoppers (Acrididae) of the Flint Hills native tallgrass prairie in Kansas. Kans. Agric. Exp. Stn. Res. Paper 19. 147 p.

Cantrall, I. J. 1943. The ecology of the Orthoptera and Dermaptera of the George Reserve, Michigan. Misc. Publ. Mus. Zool. Univ. Mich. no. 54. 182 p. bib. Cantrall, I. J. 1968. An annotated list of the Dermaptera, Dictyoptera, Phaneroptera, and Orthoptera of Michigan. Mich. Entomol. 1: 299-346.

Cantrall, I. J. and F. M. Young. 1954. Contrasts in the orthopteran faunas of grassland, forest, and transitional areas in southern Indiana. Proc. Ind. Acad. Sci. 63: 157-162.

Capinera, J. L., and T. S. Sechrist. 1982. Grasshopper (Acrididae) -host plant associations: Response of grasshopper populations to cattle grazing intensity. Can. Entomol. 114: 1055-1061.

Caplan, E. 1966. Differential feeding and niche relationships among Orthoptera. Ecology 47: 1074-1076.

Clark, E. J. 1948. Studies in the ecology of British grasshoppers. Trans. Roy. Entomol. Soc. London 99: 173-222.

Daniels, N. E., and L. D. Chedester. 1973. Grasshopper collections on three land types. Texas Agr. Exp. Sta. Misc. Publ. 1100. 4 p.

Evans, E. W., R. A. Rogers, and D. J. Opferman. 1983. Sampling grasshoppers (Orthoptera: Acrididae) on burned and unburned tallgrass prairie: Night trapping versus sweeping. Environ. Entomol. 12: 1449-1454.

Fenton, F. A., and D. E. Howell. 1957. A comparison of sampling alfalfa fields for arthropod populations. Ann. Entomol. Soc. Amer. 50: 606-611.

Fienberg, S. E. 1977. The Analysis of Cross-Classified Categorical Data. MIT Press, Cambridge, Mass. 198 pp.

Fox, H. 1914. Data on the ortopteran faunistics of eastern Pennsylvania and southern New Jersey. Proc. Acad. Natur. Sci. Phil. 441-534.

Fox, H. 1917. Field notes on the Virginia Ortoptera. Proc. U. S. Nat. Mus. 52: 199-234.

Gangwere, S. K. 1961. A monograph of food selection in Orthoptera. Trans. Amer. Entomol. Soc. 87: 67-230.

Gangwere, S. K., F.C. Evans, and M. L. Nelson. 1976. The food habits and biology of Acrididae in an old-field community in southeastern Michigan. Great Lakes Entomol. 9: 83-123.

Gause, G. F., 1930. Studies on the ecology of the Orthoptera. Ecology 11: 307-325.

Hardman, J. W. and S. Smoliak. 1980. Potential Economic impact of rangeland grasshoppers in southeast Alberta. Can. Entomol. 112: 277-280.

Hewitt, G. B. 1977. Review of forage losses caused by rangeland grasshoppers. U. S. Dept. Agric. Misc. Publ. 1348. 24p.

Holmes, N. D., D. S. Smith, and A. Johnston. 1979. Effect of grazing by cattle on the abundance of grasshoppers on fescue grassland. J. Range Management 32: 310-311.

Inger, R. F. and R. K. Colwell. 1977. Organization of contiguous communities of amphibians and reptiles in Thailand. Ecol. Monogr. 47: 229-253.

Isely, F. B. 1938. The relation of Texas Acrididae to plants and soils. Ecol. Monogr. 8: 551-604.

Isely, F. B. 1941. Researches concerning Texas Tettigoniidae. Ecol. Monogr. 11: 457-475.

Isely, F. B. 1944. Correlations between mandibular morphology and food specificity in grasshoppers. Ann. Entomol. Soc. Am. 37:47-67.

Isely, F. B. 1946. Differential feeding in relation to local distribution of grasshoppers. Ecology 27: 128-138.

Isely, F. B. and G. Alexader 1949. Analysis of insect food habits by crop examination. Science 109: 115-116.

Joern, A. and L. R. Lawler. 1981. Guild structure in grasshopper assemblages based on food and microhabitat resources. Oikos 37: 93-104.

Lambley, J. D., J. B. Campbell, and H. Knutson. 1972. Food preferences of grasshoppers in six planted pastures in eastern Kansas. J. Kans. Entomol. Soc. 45(1): 59-92.

LaRochelle, A. 1980. Catalogue des orthopteres du Quebec. Cordulia. Suppl. 7, 36 p.

Mangan, R. L., R. A. Byers, A. Wutz, and W. C. Templeton. 1982. Host plant associations of insects collected in swards with and without legumes seeded by minimum tillage. Environ. Entomol. 11: 255-260.

May, R. M. 1972. Will a large complex system be stable? Nature 238: 413-414.

Morse, A. P. 1904. Researches on North American Acrididae. Publ. Carnegie Inst. 68: 56 p.

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

Mulkern, G. B. 1980. Population fluctuations and competitive relationships of grasshopper species (Orthoptera: acrididae) Trans. Am. Entomol. Soc. 106: 1-41.

Mulkern, G. B. and J. F. Anderson. 1959. A technique for studying the food habits and preferences of grasshoppers. J. Econ. Entomol. 52: 342.

Mulkern, G. B., K. P. Pruess, H. Knutson, A. F. Hagen, J. B. Campbell, and J. D. Lambley. 1969. Food habits and preferences of grassland grasshoppers of the North Central Plains. Bull. Agric. Stn. N. Dak. State Univ. 481: 1-32.

Mulkern, G. B., D. R. Toczek, and M. A. Brusven. 1964. Biology and ecology of North Dakota grasshoppers associated with the Sand Hills Prairies. N. Dak. Agric. Exp. Stn. Res. Rep. No. 11, 59 p.

Otte, D. 1976. Species richness patterns of New World desert grasshoppers in relation to plant diversity. J. Biogeography 3: 197-209.

Rehn, J. A. G. 1900. *Melanoplus differentialis* in New Jersey and Pennsylvania. Can. Entomol. 32: 28.

Rehn, J. A. G. and M. Hebard. 1916. Studies in the Dermaptera and Orthoptera of the coastal plain and piedmont region of the southeastern United States. Proc. Acad. Natur. Sci. Phil. 87-314.

Roberts, H. R. 1942. Two subspecies of *Melanoplus differentialis* and related new species form Mexico with discussion of their variations. Trans. Am. Entomol. Soc. 68: 151-166.

Root, R. M. 1973. Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*) Ecol. Monogr. 43: 95-124.

Scoggan, A. C. and M. A. Brusven. 1973. Grasshopper-plant community associations in Idaho in relation to the natural and altered environment. Melandera 12: 22-23.

Sherman, F. and C. S. Brimley. 1911. Orthoptera of North Carolina. Entomol. News, XXII: 387-392.

Smalley, A. E. 1960. Energy flow of a salt marsh grasshopper population. Ecology 41: 672-677.

Southwood, T. R. E. 1978. Ecological methods with particular reference to the study of insect populations. Chapman and Hall. London. 524 p.

Stolyarov, M. V. 1977. Ecological populations of Orthoptera, and the dynamics of their biomass and consumption in the high mountains of the Greater Caucasus in Georgia. Entomol. Obozr. 56: 532-545.

Turnbull, A. L. and C. F. Nicholls. 1966. A "quick trap" for area sampling of arthropods in grassland communities. J. Econ. Entomol. 59: 1100-1104.

U. S. Weather Service. 1979. Climatological Data, Virginia. 89 no. 13: 1-11.

U. S. Weather Service. 1980. Climatological Data, Virginia. 90 no. 13: 1-11.

Uvarov, B. 1977. Grasshopper and locusts. Vol. 2. London Centre Overseas Pest. Res. 613 p.

Watson, J. R. 1941. Migrations and food preferences of the lubberly locust. Fla. Entomol. 24: 40-42.

Wilbur, D. A. 1936. Grasshopper injury to the inflorescence of pasture grasses. J. Kans. Entomol. Soc. 9: 1-12.

Wilbur, D. A. and R. F. Fritz. 1940. Grasshopper populations of typical pastures in the bluestem region of Kansas. J. Kans. Entomol. Soc. 13: 86-100.

Appendix A

SEASONAL OCCURRENCE OF GRASSHOPPERS

TABLE 23

Seasonal Occurrence of Mixed-Forb Feeders

Part I. Mixed-forb Feeders

			April				May				June				July				August				September				October			
Species	Stage	Year	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
Melanoplus d. differentialis	Nymph	1979a														74	41	25	44	5										
		1980b		1		5		21		33	17		38	151	77	25	2	20												
	Adult	'79																	23	17			4							
		'80																			1	4								
M. f. femurrubrum	Nymph	'79														625	712	909	1192	246										
		'80							8	94	2828		51	2267	1272	2280	411	34		92	98	48								
	Adult	'79															1	1	101	23										
		'80																		46	111	45	163	42			32			
M. sanguinipes vulturnus	Nymph	'79														5	3	2	3	3										
		'80				2		4	1	3	3			4			1			1	2		3	1						
	Adult	'79														1	11	4	3	2										
		'80													5		2				1									
M. s. scudderi	Nymph	'79																												
		'80									4		4	12	21		5	11		1		1								
	Adult	'79																	1	2										
		'80																			1	2	1							

TABLE 24

Seasonal Occurrence of Grass Feeders

			April				May				June				July				August				September				October			
Species	Stage	Year	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
Arphia xanthoptera	Nymph	1979a															4	1												
		1980b													2															
	Adult	'79																1		3										
		'80																					1							
Chortophaga viridifasciata	Nymph	'79														3	20	96	45	28										
		'80		3		6							1	13	47	22		2		13	9		23	2			3			
	Adult	'79															1	6		10										
		'80		3	6	4	2	5		1										1	2	2								
Dichromorpha viridis	Nymph	'79														17	65	32	29	16										
		'80								1	1		3	45	77	25	5													
	Adult	'79															8	36	22	36										
		'80														1		1		7	2	5	8							
Encoptolophus sordidus	Nymph	'79														1 4	6	3	33											
		'80							1				3	24	8	24	3	2			1									
	Adult	'79																												
		'80																		1			1							
Hippiscus rugosus	Nymph	'79														4	5	8	33											
		'80								2	1		3	9	15	3	2													
	Adult	'79															2	13	20	22										
		'80																		1	1		3							
Orphulella pelidna	Nymph	'79														7														
		'80													1															
	Adult	'79														4			2	2										
		'80																		1										
Syrbula admirabilis	Nymph	'79														1	13	41	38	3										
		'80											2	8	30	41	12				4	1								
	Adult	'79																2	3	4										
		'80																		1	7	1	1	1						

TABLE 25

Seasonal Distribution of Head Feeders

Part III. Head Feeders, 1980 (1)

		May				June				July				August				September				October	
Species	Stage	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2
Conocephalinae	Nymph (2)		45	71	232	40		431	1487	2925	1005	256	41		125	149	148	30	6				
Conocephalus brevipennis	Adult															6	5						
C. fasciatus	Adult								5	5	4	2			4			6	3			2	
C. strictus	Adult														31	32	66	267	3			2	
Neoconocephalus sp. (3)	Nymph		1	2		1		6	16	9	7	6			1	4	1						
	Adult												1					1					
Orchelimum agile	Adult															13		9					
Scudderia sp.	Nymph		2		2				6	4	2												
	Adult (4)																	1					

1) Head feeders, all Tettigoniidae, were collected in 1980 only.
2) Nymphs of the genera *Conocephalus* and *Orchelimum*.
3) The adults were *Neoconocephalus retusus* (Scudder).
4) The adult was *Scudderia texensis* Saussure-Pictet.

GRASSHOPPER SPECIES COMPLEXES OF FORAGE CROPS IN THE PIEDMONT REGION OF VIRGINIA

by

J. Taylor L. Williams

(ABSTRACT)

Field collections of grasshoppers (Orthopera: Acrididae, Tetrigidae, and Tettigoniidae) from twenty hayfield and pasture sites in twelve counties in Virginia were made in 1979 and 1980. Fifteen Acrididae, two Tetrigidae, and six Tettigoniidae species were found among the 20,793 grasshoppers collected. *Melanoplus femurrubrum femurrubrum* (DeGeer) dominated the acridid fauna in both years, comprising 76.0% and 86.9% in 1979 and 1980, respectively.

Two collection methods, sweepnetting and drop trapping, were used. It was assumed that the drop trap gave an absolute estimate of population densities and that discrepancies between the two collections were due to failure of sweepnet-

ting to reliably sample the complex. Sweepnetting was found to bias against Acrididae in favor of the Tettigoniidae in the complex studied. With species grouped by feeding preferences (guilds), sweepnetting sampled head (inflorescence) feeders above mixed-forb feeders, and mixed-forb feeders above grass feeders. Compared with other Acrididae, *M.f. femurrubrum* was over-represented in sweepnet samples above the composite of the other acridids. Within its guild its representation did not differ from the drop trap samples.

Differences in the composition of the species complex from site to site were examined according to guilds based on diet, and were correlated with measurable properties of the vegetation. The proportion of head feeders was positively correlated with the plant height. Mixed-forb feeders were negatively correlated. Other vegetation properties (grass/forb ratio and per cent of ground cover) were themselves highly correlated with plant height, and yielded no patterns that were as strong as those with plant height.