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THE FOOD-HABITS AND BIOLOGY OF ACRIDIDAE IN AN OLD-FIELD COMMUNITY IN SOUTHEASTERN MICHIGAN[1]

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Inasmuch as the earth supports a wide variety of terrestrial communities differing in size and species composition, and because no two of these communities are identical in terms of foods and feeders, a correspondingly great complexity of feeding relationships is to be expected. Consequently, food-habit studies must take cognizance of dynamic interplay among many factors which vary with place and time, including that between food availability and the food preferences of consumers. Although ecologists have developed some sophisticated models of the various feeding interactions (*e.g.*, Holling, 1963, 1964, 1966), the number of species whose food-habits and preferences have been carefully studied is small. Further knowledge is needed, particularly of the feeding biology of organisms in specific, limited communities and ecosystems.

The present report recognizes and is developed in accordance with these considerations. It deals with feeding in a particular group of insects, the Acrididae, that live in a particular community, Evans Old Field, E. S. George Reserve, Michigan. The Acrididae were chosen for study because they are comparatively large-bodied, readily visible insects with feeding habits that lend themselves to observation; they present, in southeastern Michigan, suitable numbers of species and individuals; they are important within many local ecosystems; and they have long been among the authors' main research interests (Gangwere, 1961). The Old Field was selected as the study site because it is biologically well-known (Evans, 1975); it is typical of abandoned fields in the region; and it is frequented by many Acrididae, insects that are characteristically associated with pastures, fields, and similar open situations. The field studies reported herein were carried out during the growing seasons of 1963, 1964, and 1965, and the laboratory studies since then.

The data reported herein were amassed during the tenure of Basic Research Grant GB-1065 awarded to Wayne State University by the National Science Foundation during the years 1963-1965. As stated, the research was carried out at the E. S. George Reserve of the University of Michigan, and Wayne State University provided other facilities and services essential to the project. In addition, many individuals kindly assisted in one way or another. Included are L. G. Alder, W. A. Kaleva, M. Yacos, C. S. Chang, and G. E. Bence, all formerly of the Department of Biology, Wayne State University, who served as research assistants. Others include M. Bartell, W. J. Graham, P. Kennedy, R. Krauss, A. Lomnicki, W. Maclarney, L. H. Metzgar, W. W. Murdoch, J. Parrish, D. Webb, and G. Zug, formerly of the Department of Zoology, University of Michigan, and R. Ford, L. Gerhardstein, D. J. Malosh, and J. Rice, formerly of the Department of Biology, Wayne State University, who assisted in the capture-recapture experiments. Dr. H. C. Chen, Department of Pediatrics, School of Medicine, and Michael Tyrkus, Department of Biology, Wayne State University, offered advice and assistance during preparation of certain tables of this report. Anthony Dajnowicz of Wayne's Department of Biology helped in the arrangement and cataloging of preserved materials. Holly Mahoney of the Department of Zoology, University of Michigan, Jura Kaupas and Margaret Jordan of the Department of Biology, Wayne State University, typed various manuscript drafts. Costs of

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THE STUDY AREA

The Edwin S. George Reserve is a 514 ha (1,268 acre), fenced wildlife preserve and research area of the University of Michigan. It is located in Livingston County, Michigan, near the village of Pinckney, about 40 km northwest of Ann Arbor and 125 km west-northwest of Detroit. It lies in the Miami-Kewaunee soil area (USDA Yearbook, 1938), and its soils are chiefly loams, mucks, and peats (Cantrall, 1943). Cantrall (*op. cit.*) described its climate as humid, with low thermal efficiency and adequate rainfall during all seasons. Evans and Dahl (1955) gave additional meteorological data.

Approximately 15 percent of the Reserve's area consists of wetlands below the 900-foot contour (Rogers, 1942). These lower expanses are, for the most part, shrub-sedge, grass-sedge-fern, or tamarack (*Larix laricina*) marshes, but some are hardwood swamps or sphagnum-leatherleaf (*Chamaedaphne calyculata*) bogs. In contrast, the uplands above 915 feet are dry. They cover approximately three-fourths of the Reserve, and are about one-third oak-hickory woodland and two-thirds grasslands (Cantrall, *op. cit.*). The latter consists largely of fields cleared by settlers in the last century and then abandoned at about the time (1928) when the lands were presented to the university.

The specific study site, Evans Old Field, has been under investigation since 1948. It is a rectangular plot approximately 330 m × 200 m, bordered on much of its periphery by oak-hickory woods. It possesses a gently rolling land surface interrupted by a series of shallow depressions or swales, and by a loose network of vehicle tracks or roadways. The soil is a gray-brown podzolic sandy loam of the Fox Series, except for the swales which contain accumulations of silt loam apparently developed during the period of cultivation. Ninety-three percent of the plot is dry upland dominated by the grasses *Poa compressa* and *Aristida purpurascens* interspersed with a number of forbs (*cf.* Table V), often with a clumped distribution. The swales, with their luxuriant vegetation of *Poa pratensis* and other mesophilic species, offer a sharply contrasting plant community and habitat. Similarly, the roadways provide an open, sandy environment that supports a number of characteristic, adventive grasses and forbs. Although comparatively slight in extent, the swales and the roadways, occupying three and four percent of the total area respectively, contribute significantly to habitat diversity in the Old Field.

THE ACRIDIDAE

We recorded a total of 23 species of Acrididae[3] from the Old Field. They are listed below with notations as to their usual occurrence in southeastern Michigan (F = field, W = woods, M = marsh) and their local occurrence in the field (ec = ecotone, r = roadway and other bare habitats, sw = moist swale, du = dry upland):

GOMPHOCERINAE (Slant-Faced Grasshoppers)
Ageneotettix deorum deorum (Scudder) Fdu
Chloealtis conspersa Harris Wec
Chorthippus curtipennis curtipennis (Harris) Msw
Orphulella speciosa (Scudder) Fdu
Pseudopomala brachyptera (Scudder) MF
Syrbula admirabilis (Uhler) Fdu

OEDIPODINAE (Band-Winged Grasshoppers)
Arphia pseudonietana pseudonietana (Thomas) Fdu
Arphia sulphurea (Fabricius) Fdu

[3]The subspecific names listed herein will be ignored in the text that follows in favor of the respective specific names. This convenience is not to be construed as a denial of current nomenclatural practice.

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Arphia xanthoptera (Burmeister) Fdu
Chortophaga viridifasciata (DeGeer) Fsw
Dissosteira carolina (Linnaeus) Fr
Encoptolophus sordidus sordidus (Burmeister) Fdu
Pardalophora apiculata (Harris) Fdu
Pardalophora haldemanii (Scudder) Fdu
Spharagemon bolli bolli (Scudder) Fec
Spharagemon collare (Scudder) Fr
Trachyrhachys kiowa fuscifrons (Stal) Fdu

CATANTOPINAE (Spine-Breasted Grasshoppers)
Melanoplus bivittatus (Say) Mec & sw
Melanoplus confusus Scudder Fdu
Melanoplus femur-rubrum femur-rubrum (DeGeer) FM
Melanoplus keeleri luridus (Dodge) Fdu
Melanoplus sanguinipes sanguinipes (Fabricius) Fdu

CYRTACANTHACRIDINAE
Schistocerca emarginata (Scudder) Fdu

Of these species, the 20 marked with an *F* are typically found in upland herbaceous associations in southeastern Michigan. In contrast, *Chorthippus curtipennis* and *Melanoplus bivittatus* are characteristic of marshland, from which they often spread into neighboring communities late in the season. Their occurrence in the Old Field is likely the result of that kind of movement. They are best considered erratics rather than true inhabitants (*sensu* Cantrall, 1943). *Chloealtis conspersa* is generally found in woodland. It too is probably an erratic in the Old Field.

Other uncommon-to-scarce species include *Ageneotettix deorum, Arphia xanthoptera, Pardalophora haldemanii,* and *Trachyrhachys kiowa*, of which only a few specimens of each were recorded. *Pardalophora haldemanii* was once more common on the George Reserve than *P. apiculata* (Cantrall, 1943). Its present scarcity probably constitutes a local faunistic loss attributable to changing habitat conditions involving abandoned land succession. *Ageneotettix deorum, A. xanthoptera, T. kiowa,* and the now-common *Syrbula admirabilis,* on the other hand, appear to be recent arrivals on the George Reserve. They were not recorded during Cantrall's thorough survey of the Orthoptera of the area (1943), which suggests that they are in the process of extending their range.

The majority of the acridids are associated with the dry upland habitat. However, *Chortophaga viridifasciata,* an early maturing species, is found chiefly in the swales, whose limited extent probably accounts for the scarcity of this grasshopper. *Dissosteira carolina* and *Spharagemon collare* are encountered mainly in the sandy roadways and other barren sites that also compose but a small part of the total field area.

SEASONAL OCCURRENCE. We kept records of the presence of Acrididae in the Old Field throughout the spring, summer, and fall of 1963-1965. The occurrence of adults is summarized in Table I. There is evidence of a seasonal progression from *Pardalophora apiculata* and *Arphia sulphurea*, both early-maturing, to *Encoptolophus sordidus* and *Chorthippus curtipennis,* both with adults in late August. Overall, the Old Field Acrididae can be grouped as follows with respect to seasonal occurrence:

SPECIES WITH ADULTS LARGELY CONFINED TO SINGLE SEASON OF YEAR
Spring: *Pardalophora apiculata*
Summer: *Pseudopomala brachyptera*
Fall: *Chorthippus curtipennis*

SPECIES WITH ADULTS PERSISTENT THROUGH TWO SEASONS OF YEAR

Spring-summer: *Arphia sulphurea, Melanoplus confusus*
Summer-fall: *Arphia pseudonietana, Dissosteira carolina, Encoptolophus sordidus,*

Table I. Seasonal occurrence of adults of selected Acrididae, based on all available records, Evans Old Field.

	Weeks of Occurrence																										
	Apr. 20-26	27-3	May 4-10	11-17	18-24	25-31	June 1-7	8-14	15-21	22-28	29-5	July 6-12	13-19	20-26	27-2	Aug. 3-9	10-16	17-23	24-30	31-6	Sept. 7-13	14-20	21-27	28-4	Oct. 5-11	12-18	19-25
Week No.	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
Species	Spring									Summer													Fall				
Pardalophora apiculata	x		x	x	x	x	x	x		x	x																
Arphia sulphurea		x	x	x	x	x	x	x	x	x	x	x	x	x	x												
Melanoplus confusus							x	x	x	x	x	x	x	x	x	x	x	x	x	x	x		x				
Orphulella speciosa										x		x	x	x	x	x	x	x	x	x	x	x	x	x	x		
Pseudopomala brachyptera											x		x		x	x	x										
Melanoplus sanguinipes												x	x	x	x	x	x	x	x	x	x	x	x	x	x		
Dissosteira carolina												x	x	x	x	x	x	x	x	x		x		x	x		
Spharagemon bolli													x		x	x	x	x	x	x	x	x					
Spharagemon collare														x	x	x	x		x	x		x				x	
Melanoplus keeleri														x	x	x	x	x	x	x	x	x	x	x		x	
Arphia pseudonietana														x	x	x	x	x	x	x	x	x	x	x	x	x	x
Schistocerca emarginata															x	x	x	x	x	x	x	x	x	x	x	x	x
Syrbula admirabilis																x	x	x	x	x	x	x	x	x	x	x	x
Melanoplus femur-rubrum																	x	x	x	x	x	x	x	x		x	
Encoptolophus sordidus																		x	x		x	x	x	x	x	x	x
Chorthippus curtipennis																	x				x	x	x	x			

Melanoplus femur-rubrum, Melanoplus keeleri, Melanoplus sanguinipes, Orphullela speciosa, Schistocerca emarginata, Spharagemon bolli, Spharagemon collare, Syrbula admirabilis

The seasonal progression of the Old Field Acrididae correlates with the development of the community's foliage, flowers, and fruits. Hence, the progressive appearance of grasshoppers can be interpreted as a response to the successive appearance of food resources and as a partitioning of those resources among the users, which thereby lessens competition.

RELATIVE DOMINANCE. We made sample collections at intervals of all acridids encountered during the fall of 1964 and throughout the spring, summer, and fall of 1965. The samples ranged in size from 65 to 564 specimens each. They were obtained by traversing transect lines of varying lengths and capturing all adult grasshoppers within net distance of the line. The results are presented in Table II. Seven of the species achieved relative seasonal dominance in the community, as judged arbitrarily by their contribution of 25 percent or more to the total acridid fauna at a given time. These dominants, together with their respective months of dominance, were:

May-June:	*Arphia sulphurea, Pardalophora apiculata*
June-July:	*Melanoplus confusus*
July-Aug.:	*Orphulella speciosa*
Aug.-Sept.:	*Melanoplus keeleri*
September:	*Melanoplus femur-rubrum, Schistocerca emarginata*

Thus, at any given time during the course of the growing season, numerical dominance was achieved by only one or sometimes two species. Dominance by two species was observed near the beginning and end of the season but not in mid-summer. The dominance shared in September by the closely-related *Melanoplus femur-rubrum* and *M. keeleri* presents a particularly interesting situation for further study, on which examination of food-habits might throw light.

RELATIVE DENSITY. The sample collections recorded in Table II were not standardized to involve a uniform amount of collection effort over similar areas. Therefore, to compare the numbers of individuals of a given species from one sample to the next, we have converted the data to numbers collected per 100 square yards of transect per 10 person-hours of collecting. These results are also presented in Table II. The figures given serve as an index of "response to collecting effort" on the part of each species. Such response is likely to be influenced by differences in weather conditions and by physiological changes in the individual animals, making them more or less amenable to capture. Also, because of species' differences in response, the composition of the fauna to be sampled at any given time influences the results. Despite these limitations in the use of such standardized collection data, they are the best indication of relative density that our material can provide. If used with care, they furnish a rough approximation of population change.

For most species, the figures show a trend that rises to the highest value near the middle of the sampling sequence and declines steadily thereafter. Apparent exceptions involve the early-maturing species, such as *Pardalophora apiculata*, for which the highest index occurs at or near the beginning of the sample sequence, and the late-maturing species such as *Melanoplus femur-rubrum, M.* keeleri, for which the index rises steadily to the end of the sampling record. However, comparison of the dates of these high values with the periods of occurrence shown in Table I indicates that, in these cases, sampling was begun after the first appearance of adults, as with *P. apiculata*, or was terminated shortly before the adult population might be expected to peak, as with *M. femur-rubrum* and *M. keeleri*. These seemingly exceptional cases, then, can be considered truncated records. If due allowance is made, they show trends like those of the other species.

High index values were achieved by *Melanoplus femur-rubrum* and *M. keeleri* (Table II), which support our impression that these two are the most abundant acridids in the Old Field. *Melanoplus confusus* also reached a high value, which suggests it is an abundant species of early summer. Moderately high values between 1 and 2 were

Table II. Relative abundance of Acrididae, Evans Old Field, 1964 & 1965.

Collection Date	14-V	21-V	4-VI	11-VI	25-VI	2-VII	16-VII	6-VIII	3-IX	20-IX	24-IX	27-IX	12-IX	17-IX	26-IX	29-IX
Sample Size	64	144	87	126	109	106	132	71	167	253	203	271	411	223	355	564
Species							1965							1964		
Pardalophora	87.7*	49.3	40.2	17.5	0.9											
apiculata	1.88	0.65	0.70	0.36	0.02											
Arphia	12.3	50.7	59.8	19.8	11.0	3.8	0.8									
sulphurea	0.26	0.67	1.04	0.41	0.27	0.14	0.01									
Melanoplus				62.7	88.1	88.7	53.8	4.2	1.2				0.5		0.3	
confusus				1.31	2.12	3.35	1.01	0.08	0.03				0.02		0.01	
Pseudopomala						7.5	5.3	2.8								
brachyptera						0.29	0.10	0.06								
Orphulella							32.6	60.6	9.0	5.1	1.5	1.8	4.4	4.5	2.8	1.6
speciosa							0.61	1.19	0.25	0.29	0.08	0.15	0.14	0.17	0.12	0.08
Melanoplus							3.0	7.0	3.6	2.8	0.5	1.2	4.1	6.3	3.7	4.4
sanguinipes							0.06	0.14	0.10	0.16	0.03	0.09	0.13	0.24	0.15	0.23
Spharagemon							3.0	4.2	1.2	0.4			0.5	0.4		
bolli							0.06	0.08	0.03	0.02			0.02	0.02		
Dissosteira							0.8	2.8	1.8							
carolina							0.01	0.06	0.05							
Chloealtis							0.8									
conspersa							0.01									
Melanoplus								7.0	35.9	34.4	33.0	34.3	32.6	26.9	34.6	29.8
keeleri								0.14	0.99	1.92	1.83	2.76	1.04	1.01	1.42	1.56
Schistocerca								4.2	26.3	14.2	3.4	1.5	3.9	3.1	3.1	2.7
emarginata								0.08	0.73	0.80	0.19	0.12	0.12	0.12	0.13	0.14

Arphia								4.2	4.2	1.2	1.0	1.5	6.3	4.9	4.2	5.1
pseudonietana								0.08	0.12	0.07	0.05	0.12	0.20	0.19	0.17	0.27
Melanoplus								1.4								
bivittatus								0.03								
Spharagemon								1.4		0.8						
collare								0.03		0.04						
Melanoplus									13.2	33.6	52.7	56.1	38.0	46.2	44.8	49.5
femur-rubrum									0.36	1.88	2.91	4.52	1.21	1.73	1.84	2.58
Syrbula									3.0	6.3	5.4	1.8	5.4	6.3	3.4	3.7
admirabilis									0.08	0.35	0.30	0.15	0.17	0.24	0.14	0.19
Chortophaga									0.6							
viridifasciata									0.02							
Encoptolophus										1.2	2.0	1.8	3.9	0.4	1.7	2.5
sordidus										0.07	0.11	0.15	0.12	0.02	0.07	0.13
Chorthippus											0.5		0.5	0.9	1.1	0.7
curtipennis											0.03		0.02	0.03	0.05	0.04
Arphia															0.3	
xanthoptera															0.01	
Total Species	2	2	2	3	3	3	8	11	11	10	9	8	11	10	11	9

*Upper part of each couplet indicates abundance in terms of percent of total adults collected; lower part indicates density in terms of numbers collected per 100 yards covered by 10 man-hours of collecting.

recorded for *Arphia sulphurea, Orphulella speciosa,* and *Pardalophora apiculata.* These grasshoppers should probably be ranked as exhibiting second-order abundance. Low values were achieved for the remainder of the species, all of which have relatively small adult populations.

ESTIMATION OF POPULATION SIZE. In 1964 and 1965, we net-captured, marked with paint, and recaptured samples of the Old Field's Acrididae so as to estimate population size. Five or more persons participated on each occasion, spending an average of 15.3 person-hours per sampling. Most of the species we encountered exhibited varying degrees of aggregation in their spatial distribution, as well as considerable ability to elude capture by hiding in the vegetation or by taking flight. In consequence, it was difficult to obtain samples of satisfactory size. A summary of the more successful efforts is presented in Table III.

As can be seen, the number of recaptures proved disappointingly small. It is likely, as has been documented elsewhere (*e.g.,* by Edwards, 1961, and Baldwin, Riordan, and Smith, 1958), that the marked specimens did not move far from the point of release, and therefore did not spread appropriately throughout the unmarked population. Finally, transformation from nymph to adult generally requires several weeks with some lack of synchrony between the sexes, so that additions to the various adult populations may well have occurred during the interval between marking and recapturing. Consequently, some of the assumptions underlying the capture-recapture method of estimating population size were not met.

Nevertheless, we found it useful to apply the Lincoln or Peterson Index formula, as modified by Bailey (1951), to the most suitable data. The resulting estimates of population size, standard deviation, and percent deviation, given separately for the two sexes, are shown in Table IV. While little statistical confidence can be placed in them, we believe they provide an indication of the order of magnitude of the populations of Acrididae in the Old Field. We determined that the relatively abundant species, such as *Melanoplus femur-rubrum* and *M. keeleri,* were likely represented by several thousand individuals each; the less common species, such as *Arphia sulphurea* and *Pardalophora apiculata,* by hundreds of individuals; and the rarer species, such as *Chortophaga viridifasciata,* by probably less than one-hundred individuals.

ENERGY DYNAMICS. In the Old Field, the Acrididae constitute a major group of primary consumers. Their energy dynamics was investigated in the seasons of 1959 and 1960 by R. G. Wiegert (1965), who found them greatly outnumbering the partly carnivorous Tettigoniidae during both years. In Wiegert's collection, the single acridid genus *Melanoplus* comprised 68 percent of the grasshoppers taken in the Old Field in 1959 and 63 percent of those samples in 1960. Wiegert calculated that the grasshopper population in 1959 ingested 4.8 kcal/m^2/year, which is less than 0.5 percent of the net annual primary production. This resulted in an addition of 123 mg of grasshopper tissue per square meter to the animal biomass production of that year. Application of this value to the entire area of Evans Old Field yields an estimate of 8,118 g of grasshoppers produced there in 1959. The year 1960 was much less productive of grasshoppers; 72 mg of tissue per square meter were added that season, for a field total of 4,752 g.

Feeding studies involving *Melanoplus femur-rubrum* and the host plant *Lespedeza cuneata* were carried out in 1963 in South Carolina (Wiegert, *op. cit.*). They indicate that this acridid assimilated approximately 35 percent of the food energy ingested. This assimilation efficiency may be compared with the 27.4 percent reported by Smalley (1960) for the salt marsh katydid *Orchelimum fidicinum* and the 60 percent by Connell (1959) for the locust *Schistocerca americana.*

A study of energy flow through a population of *Chorthippus parallelus* on a meadow in Finland led Gyllenberg (1969) to estimate that the insect consumes 1.4-2.7 percent of the net production of above-ground vegetation, assimilates 0.4-0.8 percent, and removes but does not use an amount of plant material 70 percent greater than the matter consumed. He concluded that this population is not a factor in the regulation of the community's annual net primary production.

Table III. Capture-recapture experiments with Acrididae, Evans Old Field, 1964 & 1965.

Males					Females				
Marking Sample		Recapture Sample			Marking Sample		Recapture Sample		
Date	No. Marked	Date	Total Capt.	No. Prev. Marked	Date	No. Marked	Date	Total Capt.	No. Prev. Marked
1965					*Pardalophora apiculata*				
14-V	53	21-V	62	2	14-V	4	21-V	9	0
21-V	62	4-VI	28	3	21-V	9	4-VI	7	1
4-VI	28	11-VI	18	4	4-VI	7	11-VI	4	1
1965					*Arphia sulphurea*				
21-V	36	4-VI	36	1	21-V	37	4-VI	16	4
4-VI	36	25-VI	12	1	4-VI	16	25-VI	0	0
1965					*Melanoplus confusus*				
11-VI	43	25-VI	58	0	11-VI	36	25-VI	38	0
25-VI	58	2-VII	61	1	25-VI	38	2-VII	33	1
2-VII	61	16-VII	55	2	2-VII	33	16-VII	16	1
1965					*Orphulella speciosa*				
16-VII	27	6-VIII	24	0	16-VII	16	6-VIII	19	0
1964					*Melanoplus femur-rubrum*				
8-IX	76	12-IX	75	3	8-IX	58	12-IX	81	6
12-IX	75	17-IX	41	3	12-IX	81	17-IX	62	1
17-IX	41	26-IX	76	1	17-IX	62	26-IX	83	3
1965									
3-IX	17	20-IX	45	1	3-IX	5	20-IX	40	0
20-IX	45	24-IX	49	2	20-IX	40	24-IX	58	0
1964					*Melanoplus keeleri*				
8-IX	72	12-IX	65	3	8-IX	90	12-IX	69	3
12-IX	65	17-IX	30	3	12-IX	69	17-IX	30	1
17-IX	30	26-IX	55	4	17-IX	30	26-IX	68	2
1965									
3-IX	35	20-IX	42	1	3-IX	25	20-IX	41	1
20-IX	42	24-IX	19	0	20-IX	41	24-IX	48	1
1965					*Schistocerca emarginata*				
3-IX	32	20-IX	30	1	3-IX	12	20-IX	6	0

THE VEGETATION

The time of abandonment of the Old Field has been fairly accurately dated to 1925 or 1926 (Evans, 1975). Its vegetation was first examined carefully in 1948, by which time two major community types, those of the dry uplands and of the moist swales, were already well established (Evans and Cain, 1952). This early survey listed 92 species of vascular plants, including 24 species of grass, sedge, or rush, 59 species of forbs, and 9

Table IV. Estimated size of populations of Acrididae, Evans Old Field, 1964 & 1965.

Date	Males			Females		
	Estimated Population	Standard Deviation	Percent Deviation	Estimated Population	Standard Deviation	Percent Deviation
			Pardalophora apiculata			
1965–14-V	1095	534	48.8	——	——	——
21-V	450	187	41.6	——	——	——
4-VI	106	37	34.9	——	——	——
			Arphia sulphurea			
1965–21-V	666	375	56.3	126	43	34.1
4–VI	234	125	53.4	——	——	——
			Melanoplus confusus			
1965–25-VI	1798	1020	56.7	646	362	56.0
2-VII	1139	554	48.6	281	152	54.2
			Orphulella speciosa			
1965–16-VII	648	449	69.3	320	221	69.0
			Melanoplus femur-rubrum			
1964–8-IX	1444	629	43.6	679	229	33.7
12-IX	788	335	42.5	2552	1450	56.8
17-IX	1579	896	56.7	1302	568	43.6
1965–20-IX	750	365	48.7	2360	1654	70.1
			Melanoplus keeleri			
1964–8-IX	1188	515	43.4	1575	684	43.4
12-IX	504	210	41.7	1070	597	55.8
17-IX	336	143	42.6	690	337	48.8
1965–20-IX	798	549	68.8	1005	568	56.5

species of woody plants, and noted their markedly clumped distribution, which gave the vegetation a mosaic or patchwork appearance. More detailed studies in 1953 led to the recognition of 11 vegetation types of lesser magnitude, based on microhabitat differences in soil texture, soil moisture, and light penetration (Evans and Dahl, 1955). At that time, secondary succession appeared to be progressing slowly, impeded perhaps by the general sterility of the soil and by the presence of a herd of white-tailed deer (*Odocoileus virginianus*). However, by 1963 when the grasshopper studies reported herein were initiated, the Old Field's flora had been enriched by the invasion of 38 additional species, including 2 grasses, 28 forbs, and 8 woody plants (Evans, 1975). Although the character of the vegetation was still clearly that of a grassland, the amount of bare soil exposed had decreased considerably, perennial forbs were gradually assuming dominance (Wiegert and Evans, 1964), and the distinctions between minor plant communities were becoming obscured. Although a few forbs found in 1948-1953, such as *Sisyrinchium albidum, Arabis hirsuta,* and *Vernonia altissima*, were no longer present by 1963, the total flora had increased to 122 species (25 graminoids, 81 forbs, and 16 woody plants), and the new arrivals had added distinctly to the diversity of food materials available to the grasshoppers and other herbivorous animals. Plant species occurring on the Old Field in 1963-1965 have been listed elsewhere (Evans, 1975).

FLORISTIC COMPOSITION. As noted earlier, the upland vegetation which included 21 graminoids, 71 forbs, and 12 woody plants, was dominated by two grasses: Poa *compressa*, flowering in June, and *Aristida purpurascens*, which matures in August. Several other grasses, including *Panicum oligosanthes, P. depauperatum, Danthonia spicata*, and *Leptoloma cognatum*, were also prominent. Interspersed with them were a number of conspicuous composites, notably of the genera *Solidago, Antennaria, Hieracium*, and *Liatris*, legumes (*Lespedeza, Desmodium*), and rosaceous plants (*Potentilla, Fragaria, Rubus*), and a diversity of less abundant taxa, such as *Oxalis, Euphorbia, Asclepias, Monarda*, and *Hypericum*. Shrubs of *Juniperus* and *Crataegus* and small saplings of *Carya* and *Quercus* were also well-distributed over the Old Field, often showing the effects of heavy browsing by deer.

The swale vegetation included 6 grasses, 22 forbs, and 6 woody plants, and was grass-dominated, throughout by *Poa pratensis* and often at the margins by *Setaria glauca*. Although less diverse than the upland flora, the species composition was distinct. Few if any specimens of such common upland taxa as *Solidago, Lespedeza*, and *Hieracium* were encountered in the swales, whose most conspicuous forbs included *Asclepias syriaca, Cirsium vulgare*, and *Urtica dioica*, along with the semi-woody *Rubus flagellaris*. By 1963 the woody plants *Cornus stolonifera, Spiraea alba*, and *Ceanothus americanus* had succeeded in establishing one or two individuals each in or close to the swales. The greatest control over the swale habitat was clearly exerted by *Poa pratensis*; its dense mat probably prevented the successful establishment of many upland species and created a more mesic microenvironment favorable to other swale plants.

Because of its relatively small area and its specialized substrate conditions (*e.g.*, compacted soil surface, development of small clay lenses), the roadway also supported a less diverse flora (18 species of graminoids, 40 species of forbs, and 2 species of woody plants) than did the dry uplands, but it included a number of species largely restricted to this habitat. Such characteristic roadway plants were the grasses *Eragrostis spectabilis* and *Festuca* (*Vulpia*) *octoflora* and the forbs *Chenopodium album, Lepidium virginicum, Potentilla norvegica, Plantago lanceolata, P. rugelii*, and *Taraxacum officinale*. Many are recognized as weedy plants typical of roadsides and similar barren sites, and most of the species which established themselves on the Old Field after 1948 belonged to this category. As studies on the Old Field have expanded, use of the roadways has increased, thereby enlarging the extent of this habitat type and increasing the probability of accidental transport and establishment of opportunistic species.

PLANT FREQUENCY. In 1964 we recorded the frequency of occurrence of all vascular plants encountered in a series of square-yard quadrats randomly selected over the Old Field as a whole. We surveyed 200 such quadrats, five of which were located in or at the edge of swales. Forty-five species were ubiquitous enough to be recorded in five or more quadrats, and their frequencies are presented in Table V. Among the species found relatively frequently (those with an F percent of 10 or more) were 7 grasses, 13 forbs, and 1 woody plant. These data suggest that the Old Field vegetation is composed of a few widespread, common species and a larger number of rare ones. Assuming that most of them are potential sources of food for grasshoppers, we conclude that there is a wide range of food plants for the resident Acrididae whose availability could have considerable influence on the latter's local distribution and food-habits.

A special frequency survey was made in the roadway habitat, which is important to such Acrididae as *Dissosteira carolina, Spharagemon collare*, and *Arphia pseudonietana*. These grasshoppers can be referred to as "bare ground Acrididae" because of their predilection for places with exposed soil and scant vegetation. Not only do they customarily inhabit these arid situations, but when flushed they usually alight there instead of seeking shelter in nearby vegetation. Such acridids might be expected to select their food from this roadside habitat and thus to draw upon a different plant assemblage from that available to the upland and swale grasshoppers.

The roadway survey involved 50 square-yard quadrats taken at 10-yard intervals along the mid-line of the road. Each quadrat overlapped bare ground at both sides. The results are given in Table V. Many of the species that occurred with high frequencies in the field also ranked high in the roadways, but the latter also includes as prominent taxa quite a few that were of low frequency in the overall survey, such as *Eragrostis spectabilis*,

Table V. Frequency of vascular plants in selected square-yard quadrats, Evans Old Field, 1964.

Species	Overall Field* F (%)	Overall Field* Rank	Roadway** F (%)	Roadway** Rank
		Graminoids		
Aristida purpurascens	88.5	1	84.0	2
Poa compressa	83.5	2	92.0	1
Leptoloma cognatum	28.5	13	48.0	10
Panicum oligosanthes	19.5	14	60.0	7
Panicum depauperatum	16.5	15	34.0	13
Danthonia spicata	15.0	17	18.0	18
Poa pratensis	14.0	18	4.0	23
Cyperus filiculmis	8.5	22	20.0	17
Panicum lanuginosum	5.0	27	—	—
Eragrostis spectabilis	4.5	28	70.0	5
Juncus tenuis	4.0	29	34.0	13
		Forbs		
Rumex acetosella	80.5	3	74.0	4
Solidago nemoralis	75.5	4	78.0	3
Antennaria neglecta	73.5	5	60.0	7
Lespedeza capitata	73.5	5	44.0	11
Liatris aspera	61.0	6	62.0	6
Hieracium longipilum	47.5	7	24.0	16
Solidago rigida	41.5	8	14.0	19
Hieracium gronovii	41.0	9	8.0	22
Solidago juncea	40.5	10	18.0	18
Antennaria fallax	35.0	11	36.0	12
Lespedeza virginica	31.5	12	48.0	10
Oxalis stricta	16.0	16	54.0	8
Desmodium sessilifolium	10.0	19	—	—
Tragopogon pratensis	9.5	20	—	—
Calium pilosum	9.0	21	—	—
Euphorbia corollata	8.5	22	—	—
Anemone cylindrica	7.5	23	4.0	23
Lactuca spp.	7.5	23	—	—
Physalis heterophylla	6.5	24	—	—
Erigeron strigosus	6.0	25	—	—
Fragaria virginiana	6.0	25	4.0	23
Lechea villosa	5.5	26	8.0	22
Houstonia longifolia	5.5	26	4.0	23
Asclepias syriaca	4.5	28	—	—
Monarda fistulosa	4.5	28	—	—
Polygala polygama	4.0	29	—	—
Hypericum perforatum	3.0	31	10.0	21
Plantago rugelii	2.5	32	30.0	15
Potentilla argentea	2.5	32	18.0	18
Potentilla intermedia	2.5	32	10.0	21
Potentilla norvegica	2.5	32	50.0	9

Table V: Continued.

Species	Overall Field* F (%)	Overall Field* Rank	Roadway** F (%)	Roadway** Rank
		Woody Plants		
Carya ovalis	16.5	15	—	—
Rubus flagellaris	9.5	20	10.0	21
Quercus velutina	3.5	30	—	—

*Based on 200 randomly selected quadrats. Twenty-eight species, with frequency values of 2.0% or less, are not tabulated above.

**Based on 50 quadrats taken at 10-yard intervals. Sixteen species, occurring in 1 or 2 quadrats only, are not tabulated above. Species missing from the Overall Field Survey but of higher frequency in the Roadway Survey include: *Sporobolus vaginiflorus,* F(%) 50, Rank 9; *Polygonum aviculare,* F(%) 32, Rank 14; *Ambrosia artemisiifolia,* F(%) 18, Rank 18; *Hieracium aurantiacum,* F(%) 12, Rank 20; *Plantago aristata,* F(%) 12, Rank 20; *Hedeoma hispida,* F(%) 4, Rank 23.

Sporobolus vaginiflorus, Potentilla norvegica, Polygonum aviculare, and *Plantago* spp. The data are consistent with the conclusion that the roadways supported a distinct assemblage of plants, thus adding to the diversity of the Old Field as a habitat and food source for the local Acrididae.

PLANT DENSITY. Density, the actual number of individuals per unit area of the community under study, is a more realistic index of abundance than frequency. Unfortunately, it is more laborious to measure, so it was impractical to obtain data for all 135 plant species known from the Old Field. However, we were able in 1965 to determine density values for 28 species that ranked high in the food preference tests to be described below. Using the same locations employed in the 1964 frequency survey, we counted numbers of individual plants, or flowering stems in the case of rhizomatous forms, of each of these high-ranking species in every second quadrat in the order of random draw. In one quadrat only six of the species were counted, so that N = 100 in these cases, vs. N = 99 in the others. The resulting mean densities and accompanying frequency values for the 28 species are given in Table VI. In general, plants with high frequency values had high densities, and species of low frequency were low in density. Notable exceptions were *Panicum oligosanthes, Desmodium sessilifolium,* and *Carya ovalis*, characterized by fairly high frequency values of 11-33 percent, but by densities of less than one or two per square yard. These populations consisted of widely scattered individuals rather than of clumps, and were responsible for a rather different distributional pattern as potential grasshopper food from that of the more abundant species.

PLANT BIOMASS. Based on the 1959 and 1960 samples of the standing crop of grasses and forbs taken in the Old Field, the net production of plant shoots was estimated as 1,328-1,392 kcal/m^2 on the upland areas and 4,102-4,629 kcal/m^2 on the swales (Wiegert and Evans, 1964). In 1960, the standing crop in mid-April contained slightly more than 70 percent grass, which decreased to less than 50 percent in midsummer and less than 30 percent by late fall. In 1965 we amassed additional biomass data in conjunction with the density studies reported above. For each of the 28 plant species ranking high in the food preference tests, 50 to 100 individuals were collected, transferred to a deep-freeze unit, and subsequently processed. Each plant was clipped of parts not suitable for grasshopper feeding, and the remaining parts were immediately weighed, oven dried at 100 degrees Centigrade until weight loss ceased, placed in an

Table VI. Density and frequency of vascular plants in randomly selected square-yard quadrats, Evans Old Field, 1965.

Species	Total No. in 99 Quadrats	Mean Density Per Sq. Yard	Freq. (%)
	Graminoids		
Aristida purpurascens	1625*	147.7	89.9
Leptoloma cognatum	1592*	16.1	41.4
Poa pratensis	1539*	15.5	20.2
Poa compressa	1014*	92.2	80.8
Panicum oligosanthes	189	1.9	33.3
Eragrostis spectabilis	121	1.2	6.0
Cyperus filiculmis	70	0.71	15.2
Juncus tenuis	35	0.35	4.0
Carex bicknellii	10	0.10	1.0
Setaria glauca	2	0.02	1.0
	Dicots		
Rumex acetosella	4846*	48.9	87.9
Solidago juncea	1069	10.8	48.5
Hieracium spp.	281	2.8	71.7
Rubus flagellaris	71	0.72	11.1
Monarda fistulosa	71	0.72	3.0
Desmodium sessilifolium	28	0.28	11.1
Euphorbia corollata	23	0.23	8.1
Plantago rugelii	15	0.15	2.0
Erigeron strigosus	7	0.07	5.1
Chrysanthemum leucanthemum	0	0.00	0.0
Plantago aristata	0	0.00	0.0
Rudbeckia hirta	0	0.00	0.0
	Total No. in 100 Quadrats		
	Dicots		
Solidago nemoralis	1628	16.28	89
Lespedeza capitata	431	4.31	62
Solidago rigida	372	3.72	41
Liatris aspera	354	3.54	66
Lespedeza virginica	248	2.48	27
Carya ovalis	22	0.22	14

*The individual of this species were so numerous that their count had to be based on a square-foot sample. Allowance is made for this variable in the calculations of density per square yard.

airtight container with a desiccating agent for at least 24 hours, and weighed again to ascertain the final dehydrated weight. The resulting weights were applied to the density values to obtain dry weight biomass per square yard. These data are presented in Table VII. The grasses *Aristida purpurascens* and *Poa compressa* and the forbs *Liatris aspera, Lespedeza capitata*, and three species of *Solidago* each contributed in excess of 5 grams per square yard to the total dry weight biomass. Water content ranged from 13 percent per plant in *Lespedeza capitata* to 79 percent in *Rumex acetosella*, and may affect the grasshoppers' food selection.

Table VII. Biomass of selected plant parts suitable for feeding by Acrididae, Evans Old Field, 1965.

Species	Sample size	Water Per Plant (%)	Dry Wt. Per Plant (gm)	Density Per Sq. Yard	Biomass Per Sq. Yard (gm) (Dry Wt. × Density)
			Graminoids		
Aristida purpurascens	200	43	0.089	147.7	13.15
Poa compressa	100	41	0.128	92.2	11.80
Poa pratensis	100	59	0.112	15.5	1.74
Leptoloma cognatum	100	18	0.094	16.1	1.51
Panicum oligosanthes	100	37	0.269	1.9	0.51
Eragrostis spectabilis	100	25	0.254	1.2	0.30
Cyperus filiculmis	94	22	0.063	0.7	0.04
Juncus tenuis	100	24	0.036	0.4	0.01
Setaria spp.	100	14	0.215	0.02	0.004
			Forbs		
Solidago nemoralis	100	57	1.281	16.3	20.88
Solidago rigida	50	54	4.824	3.7	17.85
Solidago juncea	100	57	1.155	10.8	12.47
Lespedeza capitata	50	13	1.742	4.3	7.49
Liatris aspera	50	51	1.560	3.5	5.46
Lespedeza virginica	50	20	1.507	2.5	3.77
Rumex acetosella	200	79	0.076	48.9	3.72
Hieracium spp.	100	61	0.690	2.8	1.93
Monarda fistulosa	100	65	0.352	0.7	0.25
Desmodium sessilifolium	100	56	0.638	0.3	0.19
Plantago rugelii	100	66	0.833	0.2	0.17
Plantago aristata	100	40	0.290	0.00	0.00
			Woody Plants		
Carya ovalis	10	45	0.054	0.2	1.81
Rubus flagellaris	100	49	1.074	0.7	0.75

METHODS OF STUDY

EXAMINATION OF MOUTHPARTS. Variations in mandibular morphology and armature in grasshoppers are broadly correlated with food-habits (Isely, 1944, Gangwere, 1961, 1965, Gangwere and Morales, 1974). In the acridids, the mandibles are adapted for feeding primarily on grasses, on forbs, or for taking intermediate types of diet. Consequently, we examined the mouthparts of the grasshoppers that were collected for crop content analysis so as to ascertain their form, degree of wear, and principal structural features. For each species collected, a detailed drawing of the right mandible was made, for we contend this is the diagnostic member of the pair. The data appear in Table VIII.

Table VIII. Classification and distribution of structural adaptations of mandibles in Acridadae, Evans Old Field, 1963-1965.

Groups & Species* / ADAPTATION	Graminivorous-Type	Herbivorous-Type	Forbivorous-Type	Sample Size
GOMPHOCERINAE				
Pseudopomala brachyptera	X			26
Syrbula admirabilis	X			22
Chorthippus curtipennis	X			3
Chloealtis conspersa	X			3
Orphulella speciosa	X			37
OEDIPODINAE				
Arphia sulphurea	X			12
Encoptolophus sordidus	X			3
Arphia pseudonietana	X ⟶			23
Dissosteira carolina	X ⟶			14
Spharagemon collare		⟵ X		14
Pardalophora apiculata		⟵ X		3
Pardalophora haldemanii		⟵ X		3
Spharagemon bolli		⟵ X		40
Chortophaga viridifasciata		X		3
CYRTACANTHACRIDINAE				
Schistocerca emarginata			⟵ X	16
CATANTOPINAE				
Melanoplus sanguinipes			⟵ X	30
Melanoplus bivittatus			X	3
Melanoplus confusus			X	40
Melanoplus keeleri			X	15
Melanoplus femur-rubrum			X	8

*Arranged according to type and strength of adaptation starting with the most graminivorous type, extending through the herbivorous types to the forbivorous types, and ending with the most forbivorous type. Arrows indicate at least a degree of intermediate tendency and the direction of that tendency.

Grass-feeding or graminivorous-type mandibles feature incisor and molar surfaces composed of parallel ridges, sometimes worn into a continuous cutting edge. Broad-leaved herb or forbivorous-type mandibles have sharp, irregular dentes and a right molar area that consists of a central concavity surrounded by sharp dentes. Herbivorous-type mandibles are a structural compromise between the two kinds just listed. The incisor dentes are tooth-like rather than ridge-like, so the mandibles resemble the forbivorous-type. However, they are recognizable by the molar surface of the right mandible, which consists of transversely excavated parallel ridges.

ANALYSES OF CROP CONTENTS. The contents of grasshopper crops, like those of vertebrate stomachs, often yield materials that are of diagnostic value in the study of food habits (Isely and Alexander, 1949, Gangwere, 1961, Gangwere and Morales, 1974). Therefore, once each week during the summers of 1963 and 1964 we collected by aerial insect net a total of five or more specimens of each common Old Field acridid. These animals were killed and stored in 80 percent alcohol for subsequent dissection and examination of crop contents. In the laboratory we removed the crops, slit them open, emptied the contents onto microscope slides, and made them into permanent preparations using CMC-10 mounting medium. The resulting data are presented in Table IX.

The precision of analysis was improved over the ordinary through an additional procedure adopted. We collected 87 species of the Old Field vascular plants, which total includes all but the rare and seasonal plants that cannot be significant in acridid food selection. We preserved the plant specimens in alcohol until they could be processed in the manner of Mulkern and Anderson (1959). In the laboratory we chopped the plants to appropriate size using the micro-assembly unit of a Waring blender, and with CMC-10 mounting medium made them into permanent microscope slide preparations. In this way we obtained a reference collection of known plant materials that approximate those found naturally within the crops of Acrididae. From these slides, we developed a key for the specific determination of the Old Field unknown plant materials (Nelson and Gangwere, in preparation) which we used in the analyses.

OBSERVATIONS OF FEEDING IN NATURE. Isely and Alexander (1949) argued that feeding records under natural conditions are both difficult to amass and unreliable to use as indices to the food-habits of Orthoptera. Others, including Anderson and Wright (1952), Gangwere (1961), and Gangwere and Morales (1974), have used feeding records extensively, and find the method accurate and productive. Feeding observations are most successfully obtained with phytophilous, nocturnally active species having a preference for relatively high vegetation, which not only exposes them to view but also provides shelter to hide the observer. Unfortunately, these conditions were not met in the present study. The Old Field's Acrididae are diurnally active, and the habitat consists of open land with low, dense vegetation. Therefore, we were rarely able to obtain satisfactory observations of feeding under natural circumstances, and had to rely mainly on experimental feeding tests conducted in the field in cages exposed to ambient meteorological conditions. These tests were of two types: (1) to test the grasshoppers' degree of acceptance of each plant species offered exclusively as food, and (2) to ascertain their preferences among selected plant species presented simultaneously. These are described below as Food Latitude Tests and Differential Feeding Tests, respectively.

FOOD LATITUDE TESTS. Because acridids sometimes starve rather than accept certain plants as food, we wished to determine the response of the Old Field grasshoppers to the principal plant species of their habitat offered exclusively. Individuals of 11 species of Acrididae were each denied food for 24 hours and then placed separately in cages containing a given kind of plant. Records were made after an exposure of 24 hours of each individual's acceptance or rejection of that plant as food. Evidence of plant tissue consumption, such as fresh damage to a leaf blade or of production of fecal pellets, was interpreted as an indication of acceptance.

DIFFERENTIAL FEEDING TESTS. As with the preceding, these tests were conducted in a screened insectary adjacent to the Old Field. For a given test, approximately 20 individuals of a selected species of grasshopper were placed in a cylindrical screen

Table IX. Crop contents of Acridadae, Evans Old Field, 1963-1964.*

Groups & Species	Sample Size	Percentage Total Crop Contents			Determinable Material
		Graminoid	Dicot	Insect	Ranking*
GOMPHOCERINAE					
Chloealtis conspersa	4	85	15	0	
Chorthippus curtipennis	4	100	0	0	
Orphulella speciosa	48	> 99	<1	0	1) *Aristida-Poa* 2) *Poa* spp. 3) Grass spp. 4) *D. spicata* 5) Trace: *P. oligosanthes*, *A. purpurascens*
Pseudopomala brachyptera	21	100	0	0	1) *Aristida-Poa* 2) *D. spicata* 3) *Poa* spp. 4) Trace: Grass spp., *A. purpurascens*
Syrbula admirabilis	18	100	0	0	1) *Aristida-Poa* 2) *D. spicata* 3) *A. purpurascens* 4) Trace: *P. oligosanthes*
OEDIPODINAE					
Arphia pseudonietana	16	>99	<1	0	1) *Poa* spp. 2) *Aristida-Poa* 3) Grass spp. 4) Trace: *D. spicata*, *Lespedeza* spp., *S. nemoralis*
Arphia sulphurea	10	100	0	0	1) *Poa* spp. 2) Grass spp. 3) *Aristida-Poa*, *D. spicata*

Chortophaga viridifasciata	6	73	27	0	1) *Poa* spp., Dicot spp.
Dissosteira carolina	7	68	15	17	1) *Poa* spp. 2) Insect spp. 3) Trace: *T. pratensis*, Dicot spp.
Encoptolophus sordidus	5	85	0	15	
Pardalophora apiculata	6	75	25	0	1) *P. oligosanthes* 2) *P. aristata, S. nemoralis*
Spharagemon bolli	20	22	76	2	1) *P. heterophylla* 2) Dicot spp. 3) *D. illinoense* 4) *Aristida-Poa* 5) *Lespedeza* spp. 6) Trace: Grass spp., *Poa* spp., *R. acetosella, Lactuca* spp., *S. rigida*, Insect spp.
Spharagemon collare	6	66	29	5	1) *Aristida-Poa, Poa* spp. 2) *P. aristata, L. virginicum* 3) Trace: Insect spp.
CATANTOPINAE					
Melanoplus bivittatus	5	52	40	8	1) *R. flagellaris*, Insect spp. 2) Grass spp.
Melanoplus confusus	41	12	82	6	1) *S. nemoralis* 2) Dicot spp. 3) *Lespedeza* spp. 4) Insect spp. 5) Trace: *Aristida-Poa, P. oligosanthes*, Grass spp., *D. spicata, S. juncea, Solidago* spp., *D. illinoense, D. carota, E. strigosus, Lactuca* spp., *A. minus, H. perforatum, T. pratensis, O. stricta, A. millefolium, H. canadense, R. flagellaris*, Insect spp.

Table IX: Continued.

Groups & Species	Sample Size	Percentage Total Crop Contents			Determinable Material
		Graminoid	Dicot	Insect	Ranking*
Melanoplus femur-rubrum	8	46	54	0	1) *Poa* spp. 2) *Lespedeza* spp. 3) *L. aspera*
Melanoplus keeleri	22	19	>80	<1	1) *Lespedeza* spp. 2) *S. rigida* 3) Grass spp., *L. villosa* 4) Trace: *Poa* spp., *Aristida-Poa, R. flagellaris, R. acetosella, L. aspera, Solidago* spp., *S. nemoralis, H. canadense, A. neglecta,* Dicot spp., Insect spp.
Melanoplus sanguinipes	10	21	75	4	1) *S. nemoralis* 2) *Lespedeza* spp. 3) Grass spp. 4) Trace: *Poa* spp., *S. rigida, S. juncea, P. heterophylla, H. gronovii, Quercus* spp., *P. aristata, L. aspera, H. canadense, T. pratensis,* Insect spp.
CYRTACANTHACRIDINAE					
Schistocerca emarginata	17	<1	>99	0	1) *Lespedeza* spp. 2) *R. flagellaris* 3) Trace: Grass spp., Dicot spp.

*A listing of the percentage composition of the crop content belonging to graminoid, dicot, and insect food categories, and of the rank, in decreasing order of importance, of determined foods. The several species of *Lespedeza,* which are difficult to separate, are given as *Lespedeza* spp. In most cases a content of this type can be presumed to be the abundant *L. capitata.* The two species of *Poa,* which are also difficult to determine, are listed as *Poa* spp. This content is predominated by the abundant *P. compressa,* except for swale specimens. Finally, *Poa* spp. and *Aristida purpurascens,* being separable on the basis of trichome or stomatal size, may be difficult to determine. If a content of this type is not clearly distinguishable, it is listed as *Aristida-Poa.* In this event the composition can often be surmised owing the plants' seasonal occurrence, a spring content being *Poa* spp. and a fall one *A. purpurascens.*

cage, where they were given an assortment of potential food plants and water. Records were made of acceptance or rejection within 24 hours of exposure. The resulting data were analyzed in the manner of Gangwere (1961) and the "preference value" of each plant offered as food expressed by the ratio of the number of times that plant was accepted to the number of times it was nibbled or rejected; *e.g.*, the preference value of the grass *Eragrostis spectabilis* with respect to the grasshopper *Arphia pseudonietana* was 9:2, indicating that in 11 tests this plant was accepted nine times and nibbled or rejected twice. A synopsis of all tests conducted appears in Appendix I.

RESULTS

EXAMINATION OF MOUTHPARTS. We analyzed the mandibles of 8 to 40 individuals each of 13 common species of Acrididae of the Old Field, as well as those of three individuals each of several other species that are uncommon or seasonal in the field. The mandibles of most were referable to one or the other of the two major adaptive categories, graminivorous-type or forbivorous-type, while those of the remaining species were referable to the herbivorous or mixed-feeding type. However, the situation is more complicated than that would indicate. Mandibles are subject to greater or lesser variation, both from individual to individual and from species to species. Almost half of the 20 species of Acrididae investigated exhibited some degree of intermediate tendency, either belonging outright to the herbivorous-type adaptation or belonging to the graminivorous or forbivorous-type but being variably modified toward the herbivorous-type. The Gomphocerinae proved to be exclusively graminivorous-type in adaptation; the Catantopinae forbivorous-type, sometimes with a tendency toward the herbivorous-type; and the Oedipodinae either graminivorous-type or herbivorous-type, usually subject to modification. This pronounced variability made it possible to arrange the species according to type and strength of mandibular adaptation (Table VIII), ranging from the most graminivorous (*Pseudopomala brachyptera*) to the most forbivorous (*Melanoplus femur-rubrum*).

Viewing the acridid mandibular adaptations in light of their possessors' food-habits, we find that the graminivorous-type jaws are restricted to grass-feeding species, which represent about half of the grasshoppers investigated. The herbivorous or the forbivorous-type jaws are characteristic of the remaining species, of which all with the former adaptation and some with the latter eat grass as well as dicots. Thus, possession of forbivorous-type mandibles does not preclude grass-feeding, so the adaptation is not as restrictive as that of graminivores.

The mandibles of males and females of the same species proved to be similar except in size, those of the female sex being appreciably larger. There did not seem to be any significant disparity in the mandibles of different instars, at least in the later stages that we saw.

ANALYSES OF CROP CONTENTS. The crop materials of 6 to 48 specimens each of 15 species of Acrididae of the Old Field were analyzed in detail, and those of another five species were subjected to gross analysis only (Table IX). The analyzed content was overwhelmingly graminoid in the Gomphocerinae and in the oedipodine genus *Arphia*. The determinable food plants in these two groups included *Poa* spp., *Aristida purpurascens*, and lesser amounts of *Danthonia spicata* and *Panicum oligosanthes*. At the opposite extreme is the cyrtacanthacridine *Schistocerca emarginata*. Its content was overwhelmingly dicot, consisting of *Lespedeza* spp., lesser amounts of *Rubus flagellaris*, and traces of other plants. The Oedipodinae, exclusive of *Arphia* and the ecotonal *Spharagemon bolli*, had a content dominated by grass, chiefly *Poa* spp. and *Aristida purpurascens*, but including a variety of dicots. The Catantopinae had a content that in three Melanopli was predominantly dicot, consisting of *Solidago* spp., *Lespedeza* spp., and other forbs, and in two other Melanopli was composed almost equally of grass and dicots. Both the catantopines and the oedipodines had, in some instances, up to 17 percent insect remains in the crop material.

Table X. Food latitude tests on individual grasshoppers offered exclusive plants following day's starvation, Evans Old Field, 1964 & 1964.

GROUPS & SPECIES	GRAMINOIDS		WOODY PLANTS		FORBS		LOWER PLANTS		ALL PLANTS		ALL PLANTS percentage accepted
	Acc.	Rej.	Acc.	Rej.	Acc.	Rej.	Acc.	Rej.	Acc.	Rej.	
GOMPHOCERINAE											
Orphulella speciosa	7*	3	0	2	2	18	0	1	9	24	27
Syrbula admirabilis	3	3	—	—	1	11	—	—	4	14	22
OEDIPODINAE											
Arphia pseudonietana	8	4	0	2	1	34	—	—	9	40	18
Dissosteira carolina	7	2	2	1	5	19	—	—	14	22	39
Spharagemon bolli	2	9	0	2	11	11	—	—	13	22	37
Spharagemon collare	7	4	2	2	6	22	0	1	15	29	34
CATANTOPINAE											
Melanoplus confusus	10	4	5	5	26	19	1	0	42	28	60
Melanoplus femur-rubrum	6	3	1	1	15	7	—	—	22	11	67
Melanoplus keeleri	7	1	1	0	15	3	—	—	23	4	85
Melanoplus sanguinipes	11	1	2	3	26	9	1	0	40	13	75
CYRTACANTHACRIDINAE											
Schistocerca emarginata	7	2	3	0	8	14	—	—	18	16	53

*The digits indicate the number of plant species accepted for feeding (Acc.) or rejected (Rej.).

Surprisingly few plants, a total of 27 taxa, appear in the determined crop material. Most are present on an occasional or trace basis only, but some are more common. This supports our contention that, overall, the rare and seasonal plants of the Old Field are not significant factors in the feeding of the local Acrididae. The most important food plants found, arranged in decreasing order, are: *Lespedeza* spp., *Aristida purpurascens, Danthonia spicata, Solidago nemoralis, Rubus flagellaris, Panicum oligosanthes,* and *Physalis heterophylla.* All are abundant in the field, except *P. heterophylla* whose unexpected importance is explicable on the basis of its attractiveness to one species, *Spharagemon bolli,* and its occurrence with that grasshopper in the field-wood ectone.

FOOD LATITUDE TESTS. We subjected 11 species of Acrididae of the Old Field to food latitude tests, recording their response after starvation to an average of 39 plant species offered exclusively during one to three trials each. A summary of the data appears in Table X. The two species of Gomphocerinae tested accepted most grass species offered them but practically none of the dicots. The several Oedipodinae accepted most of the grass but comparatively few of the dicots, except for the ecotonal *Spharagemon bolli,* which disdained most grass. The several Cantantopinae accepted most of the grass, most of the forbs, and half of the woody plants given. The single representative of the Cyrtacanthacridinae, *Schistocerca emarginata,* accepted most of the grass, all of the woody plants, and a third of the forbs. This result is consistent with the insects' behavior in the field. Overall food latitude for the various groups was; Gomphocerinae, 15 percent of all plants offered accepted; Oedipodinae, 32 percent; Cyrtacanthacridinae, 53 percent; and Catantopinae, 72 percent. Based on evidence gained elsewhere during this project, the above percentage values appear to be reliable indices to the latitude of feeding in the respective groups.

DIFFERENTIAL FEEDING TESTS. Each of 14 species of Acrididae of the Old Field was subjected to 6 to 42 differential feeding tests, involving an average of 34 plant species per acridid. The results are summarized in Tables XII and XIII and in Appendix I. The Gomphocerinae tested accepted 88 percent of the grass species offered and only 2 percent of the dicots; the Oedipodinae 89 percent of the grass, 41 percent of the forbs, and 45 percent of the woody plants; the Catantopinae 58 percent of the grass, 78 percent of the forbs, and 63 percent of the woody plants; and the single representative of the Cyrtacanthacridinae 61 percent of the grass, 56 percent of the forbs, and 100 percent of the woody plants (Table XIII). On this basis, and in light of the data of Appendix I, the four subfamilies are diagnosed respectively as graminivorous, graminivorous or herbivorous, forbivorous or forbivorous-herbivorous, and herbivorous-dendrophagous. The species range from the most graminivorous (*Pseudopomala brachyptera*) to the most forbivorous (*Melanoplus keeleri*) to the most dendrophagous (*Schistocerca emarginata*).

SUMMARIES OF FOOD-HABITS IN OLD FIELD ACRIDIDAE

There is an extensive literature dealing with feeding in the North American Acrididae upon which we have drawn. We have used this material together with the results of our own observations and experiments to characterize the food-habits of the Old Field's acridids in the following section.

GOMPHOCERINAE

Chloealtis conspersa. The scarcity of this species on the Old Field precluded extensive study of its food-habits. The few crop contents we were able to analyze (Table IX) consisted mostly of grass together with some dicotyledonous fragments. The mandibular adaptation is of the graminivorous type. These data support previously published findings that *conspersa* is a graminivore that occasionally varies its diet with dicot material. On the Old Field it appears to take, in decreasing order of selection, the following foods: *Poa* spp., *Juncus tenuis, Danthonia spicata,* other graminoids, and occasional forbs.

Chorthippus curtipennis. On the Old Field this species is localized in the swales, so its

Table XI. Comparative acceptance of vascular plants by Acrididae during food latitude tests, Evans Old Field, 1964 & 1965.

PLANT SPECIES*	RANK	NO. GRASSHOPPER SPP. ACCEPTING	NO. GRASSHOPPER SPP. REJECTING
Poa compressa	1	11	0
Plantago aristata	2	9	2
Panicum depauperatum	3	8	2
Quercus rubra	3	4	1
Leptoloma cognatum	4	8	3
Aristida purpurascens	5	6	3
Rubus flagellaris	5	6	3
Danthonia spicata	6	7	4
Monarda fistulosa	6	7	4
Cyperus filiculmis	7	6	4
Hieracium longipilum	7	6	4
Setaria glauca	7	6	4
Plantago rugelii	7	3	2
Panicum oligosanthes	8	7	5
Ambrosia artemisiifolia	9	6	5
Rumex acetosella	9	6	5
Carya ovalis	10	5	5
Erigeron strigosus	10	5	5
Poa pratensis	10	5	5
Lespedeza capitata	11	5	6
Potentilla intermedia	11	5	6
Solidago juncea	11	5	6
Lactuca sp.	12	4	6
Liatris aspera	12	4	6
Solidago nemoralis	12	4	6
Euphorbia corollata	13	3	5
Lechea villosa	13	3	5
Asclepias syriaca	14	2	5
Solidago rigida	15	3	8
Tragopogon pratensis	15	3	8
Oxalis stricta	16	2	7
Achillea millefolium	17	1	4
Physalis heterophylla	18	1	7
Antennaria neglecta	19	1	8
Hypericum perforatum	19	1	8
Gnaphalium obtusifolium	20	0	9

*Only plants tested against five or more species of Acrididae are listed.

diet is influenced by the restricted nature of the local vegetation. Only a few individuals were available for study. Their crop contents (Table IX) proved entirely grass and their mandibular adaptation is of the graminivorous type. Reports in the literature indicate that *curtipennis* is a grass-feeder. We conclude that in the Old Field swales it takes *Poa pratensis,* lesser amounts of *Setaria glauca,* and other graminoids, but not dicots.

Orphulella speciosa. This campestral slant-face, a dominant species in the Old Field during July and August, perches chiefly on short vegetation. Although crop content analyses (Table IX) indicate that it makes occasional use of dicotyledonous foods, its mandibles are of the graminivorous type. Its strong reliance on grass is shown by its acceptance of 92 percent of the graminoids, but only 5 percent of the forbs offered in the differential feeding tests (Table XIII) in which the former were taken at a preference level of 3.8 and the latter at a level of 0.5 (Table XII). During the food latitude tests only two of 20 forb species offered were accepted (Table X). On the basis of these preferences, *speciosa* can be characterized as a more or less strict grass-feeder in the Old Field, where its diet consists largely of *Poa compressa* and *Aristida purpurascens.*

Pseudopomala brachyptera. Formerly restricted on the Reserve to marshes and other wetlands (Cantrall, 1943), this species proved surprisingly common on the Old Field during mid-summer. Its mandibles are graminivorous in adaptation, and its crop contents were composed entirely of grass. During the differential feeding tests it accepted 85 percent of the graminoids offered (Table XIII), taking them at a preference level of 3.8 (Table XII), but none of the dicotyledonous plants. We conclude that in the Old Field, *brachyptera* restricts its feeding to grass, especially favoring *Poa compressa.*

Syrbula admirabilis. This grasshopper, like *Pseudopomala brachyptera,* has a strongly slanted face, and it perches principally in grass clumps. Its mandibular adaptation is of the graminivorous type, and its crop contents included grass only (Table IX). It rejected all of the forb species offered in the food latitude tests (Table X), except on one occasion under starvation pressure when it tried the forb *Hieracium gronovii.* Similarly, in the differential feeding tests it refused most of the dicots offered. The preference level for those few taken averaged only 0.4, versus a level of 3.1 for the graminoids, of which 86 percent of those offered were accepted (Table XII). Indeed, *admirabilis* appears selective even with respect to graminoids. For example, *Poa compressa* ranked high in its differential feeding tests, whereas *P. pratensis* ranked low and was rejected as an exclusive food offered after starvation. We conclude that on the Old Field, *admirabilis* is strongly graminivorous, and selects *Poa compressa* and *Aristida purpurascens* over other grasses.

OEDIPODINAE

Arphia pseudonietana. On the Old Field in late summer and early fall, this grasshopper occurs frequently on the roadways and other exposed surfaces throughout the uplands. Although Isely (1944) studied its mandibular morphology and classified it as mixed-feeding or herbivorous, we interpret its mouthparts to be graminivorous in type. Its crop contents were almost entirely grass (Table IX). During the differential feeding tests it accepted 93 percent of the graminoids, as against 24 percent of the forbs offered, taking them at a preference level of 3.7, versus one of 1.2 for the forbs (Tables XII, XIII). We regard *pseudonietana* as a graminivorous species that even following starvation is reluctant to accept dicotyledonous plants. In the roadways as well as on the uplands it eats *Poa compressa,* lesser amounts of *Aristida purpurascens,* and some other grasses. Interestingly, it is highly attracted to certain grasses, particularly *Poa pratensis,* that are sparsely represented in its preferred Old Field habitat.

Arphia sulphurea. In contrast to its congener on the Old Field, this species appears early in the season and is dominant in May and June. Previous study of its food-habits in the nearby Southwest Field (Gangwere 1965a) had characterized it as a grass-eater, and this was confirmed by the present investigations. We found its crop contents from the Old Field to be 100 percent grass (Table IX) and its mandibular adaptation is clearly of the graminivorous type. In the differential feeding tests it accepted all of the grass but only 10 percent of the forbs offered, taking them at a preference level of 3.8, versus 0.6 for the forbs (Tables XII, XIII). Thus, *sulphurea* appears to be a strict graminivore whose common local food is *Poa compressa.*

Chortophaga viridifasciata. This species is not well-established on the Old Field. The few individuals that were encountered were largely limited to the swales. The crop contents were composed chiefly of grass, but a little dicot material was also present (Table IX). The mandibular adaptation appears to be herbivorous in type. We were unable to carry out any experimental studies on this grasshopper, but in a series of differential feeding tests run in June, 1971, by Wayne State University entomology students with specimens from Lower Huron Metropolitan Park, Wayne Co., Michigan, it

TABLE XII. Differential feeding tests of Acrididae on various plants, positional index based on maximal feeding 5.0 and minimal 0.0, Evans Old Field, 1963-1965.

PLANT GROUPS AND SPECIES	GOMPHO-CERINAE			OEDIPODINAE					CATANTOPINAE					CYRTACANTHA-CRIDINAE	
ACRIDIDAE	*Orphulella speciosa*	*Pseudopomala brachyptera*	*Syrbula admirabilis*	*Arphia pseudonietana*	*Arphia sulphurea*	*Dissosteira carolina*	*Spharagemon bolli*	*Spharagemon collare*	*Melanoplus bivittatus*	*Melanoplus confusus*	*Melanoplus femur-rubrum*	*Melanoplus keeleri*	*Melanoplus sanguinipes*	*Schistocerca emarginata*	Average Acceptance of Plants by All Acridids
GRAMINEAE															
Aristida purpurascens	4.1	–	4.4	3.8	–	2.6	1.7	3.1	0.7	0.9	0.9	0.1	0.7	1.2	2.0
Eragrostis spectabilis	3.5	–	2.7	3.0	–	3.5	2.5	3.4	–	2.2	1.0	2.0	1.5	1.5	2.4
Leptoloma cognatum	4.0	–	2.6	3.7	–	3.4	2.9	2.9	–	–	0.6	0.8	0.6	1.5	2.3
Panicum oligosanthes	3.7	4.2	3.1	3.6	4.2	3.8	4.0	4.0	2.4	1.7	2.0	0.6	2.0	2.1	3.0
Poa compressa	4.9	4.8	4.9	4.9	5.0	5.0	3.9	4.9	2.1	1.9	3.5	2.1	2.9	3.1	3.9
Poa pratensis	2.9	3.4	1.8	5.0	3.0	0.5	1.9	0.1	4.3	2.8	4.6	1.9	4.7	1.5	2.7
Setaria sp.	4.0	–	3.4	4.0	–	–	4.7	–	–	4.5	2.4	3.3	3.9	3.2	3.7
CYPERACEAE															
Carex bicknellii	3.5	–	–	–	–	–	3.0	–	–	1.0	–	–	2.6	–	2.5
Cyperus filiculmis	–	–	–	3.3	–	4.2	3.8	3.7	–	–	–	–	–	–	3.8
JUNCACEAE															
Juncus tenuis	3.8	2.8	2.0	2.2	2.8	2.8	2.3	2.4	–	2.4	1.0	0.6	2.6	1.0	2.2
Av. Acceptance Graminoids/Acridid	3.8	3.8	3.1	3.7	3.8	3.2	3.1	3.1	2.4	2.2	2.0	1.4	2.4	1.9	2.9*
JUGLANDACEAE															
Carya ovalis	0.2	–	0.0	–	0.0	–	3.1	–	–	1.6	1.0	0.3	2.3	3.0	1.3
FAGACEAE															
Quercus rubra	1.4	–	–	–	0.2	–	0.9	–	–	0.1	1.0	2.0	1.6	3.5	1.4
ROSACEAE															
Rubus flagellaris	0.0	–	0.0	0.0	–	0.4	3.5	2.2	2.6	2.1	1.9	1.9	3.6	4.9	1.9
Av. Acceptance Woody Plants/Acridid	0.6	–	0.0	0.0	0.1	0.4	2.5	2.2	2.6	1.3	1.3	1.4	2.5	3.8	1.4*

POLYGONACEAE															
Rumex acetosella	2.5	–	2.0	1.2	1.7	4.0	4.7	4.0	4.1	3.2	4.0	5.0	4.8	4.7	3.5
LEGUMINOSAE															
Desmodium sessilifolium	–	–	–	–	1.2	–	4.5	–	–	1.5	–	–	5.0	3.5	3.1
Lespedeza capitata	0.5	0.0	0.0	0.4	0.6	2.6	3.7	2.5	1.1	1.4	1.7	1.6	1.9	4.6	1.6
Lespedeza hirta	0.4	–	–	–	–	–	2.2	–	–	1.2	–	–	1.0	–	1.2
Lespedeza virginica	1.0	0.0	1.2	–	1.0	–	2.8	–	–	1.9	0.3	0.6	1.9	3.3	1.4
CISTACEAE															
Lechea villosa	0.0	–	0.0	0.6	–	1.4	1.2	0.7	–	0.2	–	–	0.2	–	0.5
EUPHORBIACEAE															
Euphorbia corollata	0.3	–	–	–	–	–	3.6	–	–	2.0	–	–	3.2	–	2.3
ASCLEPIADACEAE															
Asclepias syriaca	0.3	0.0	–	–	–	–	2.8	–	–	3.7	3.3	5.0	3.9	0.3	2.4
LABIATAE															
Monarda fistulosa	0.8	0.0	–	–	0.5	–	3.0	–	–	4.5	3.8	3.3	4.2	0.3	2.3
PLANTAGINACEAE															
Plantago aristata	0.8	–	–	2.9	–	3.2	4.1	3.5	–	3.8	–	–	4.0	–	3.2
Plantago rugelii	0.0	–	0.0	1.9	–	3.7	3.8	2.8	–	4.0	–	–	5.0	–	2.7
COMPOSITAE															
Antennaria neglecta	0.0	–	0.5	1.5	0.3	2.4	2.8	1.6	2.3	1.6	4.0	2.8	2.2	3.0	1.9
Chrysanthemum leucanthemum	0.0	0.0	0.0	–	–	–	3.0	–	–	5.0	–	–	4.8	–	2.1
Erigeron strigosus	0.8	0.4	0.0	3.0	–	2.0	3.2	1.4	4.2	4.5	–	–	4.2	2.0	2.3
Gnaphalium obtusifolium	0.0	–	–	–	–	–	0.0	–	–	1.3	1.0	2.0	1.0	2.0	1.0
Hieracium longipilum	0.0	–	0.0	1.0	0.2	4.1	2.3	2.7	4.6	2.8	4.3	3.0	3.9	2.4	2.4
Liatris aspera	0.9	–	0.0	0.8	–	1.8	2.3	2.1	1.0	3.1	2.5	4.5	1.4	0.7	1.8
Rudbeckia serotina	0.6	0.0	–	–	–	–	4.0	–	–	4.2	4.0	4.5	3.6	4.0	3.1
Solidago juncea	0.6	0.0	–	–	–	3.0	1.4	–	–	4.0	4.5	3.8	3.5	1.4	2.5
Solidago nemoralis	0.5	0.0	–	0.0	0.2	0.3	2.1	1.6	3.3	3.5	4.1	4.3	2.9	1.3	1.9
Solidago rigida	0.0	0.0	0.1	0.1	0.0	0.6	0.5	0.1	2.4	1.9	3.1	4.3	1.6	1.1	1.1
Av. Acceptance Forbs/Acridid	0.5	0.0	0.4	1.2	0.6	2.4	2.8	2.1	2.9	2.8	3.1	3.4	3.1	2.3	2.0*

*Grand average acceptance.

Table XIII. Relative acceptance of plants belonging to graminoid, forb, & woody food categories by Acrididae, based on differential feeding tests, Evans Old Field, 1963-1965.

GROUPS & SPECIES OF FEEDER	GRAMINOIDS		FORBS		WOODY PLANTS	
	N	% Acc.	N	% Acc.	N	% Acc.
GOMPHOCERINAE						
Orphulella speciosa	117*	92*	180	5	25	0
Pseudopomala brachyptera	47	85	78	0	0	–
Syrbula admirabilis	84	86	99	0	15	0
OEDIPODINAE						
Arphia pseudonietana	80	93	105	24	6	0
Arphia sulphurea	24	100	48	10	11	0
Dissosteira carolina	84	87	105	52	6	83
Spharagemon bolli	162	81	248	63	34	74
Spharagemon collare	87	86	126	56	9	67
CATANTOPINAE						
Melanoplus bivittatus	35	54	54	74	9	89
Melanoplus confusus	142	58	264	75	30	53
Melanoplus femur-rubrum	54	70	63	79	14	43
Melanoplus keeleri	70	34	87	83	19	37
Melanoplus sanguinipes	167	74	262	81	32	94
CYRTACANTHACRIDINAE						
Schistocerca emarginata	85	61	95	56	24	100

*The digits indicate the number of trials (N) and the percentage of acceptance (% Acc.) per food category per insect.

exhibited the following decreasing order of food preference: (1) *Plantago major*, (2) *Bromus tectorum*, (3) *Poa pratensis*, (4) *Capsella bursa-pastoris* (nibbled), (5) *Taraxacum officinale* (nibbled), and (6) *Ulmus americana* (untouched). We conclude that *viridifasciata* should be classed as an herbivore rather than as a graminivore. In its Old Field swale habitat it probably consumes *Poa pratensis*, *Cirsium* sp., and *Monarda fistulosa*, along with other grasses and forbs.

Dissosteira carolina. The "Carolina grasshopper" is the most characteristic "bare ground acridid" found in the Old Field. Its mouthparts are graminivorous in type, but its crop contents included grasses, forbs, and insect remains (Table IX). In the differential feeding tests, it accepted 87 percent of the graminoids offered, as well as 52 percent of the forbs and 83 percent of the woody plants, taking them at preference levels of 3.2, 2.4, and 0.4 respectively (Tables XII, XIII). Considerable latitude in feeding was also indicated by its acceptance following starvation of seven of nine graminoids and five of 24 forbs (Table X). Preferred species, ranked in decreasing order of food selection, include: (1) *Poa compressa*, (2) *Rumex acetosella*, *Eragrostis spectabilis*, *Panicum* spp., *Leptoloma cognatum*, and *Plantago rugelii*, and (3) various other grasses and forbs. This listing includes only vascular plants, but *carolina* also feeds on lichens, moss, dry plant debris, and even dead insect remains (Gangwere, 1961, and this study).

Encoptolophus sordidus. This geophilic species was not common in 1963-1965 on the Old Field, where it is found mainly on the uplands. Its mandibles are graminivorous in type, but its crop contents consisted of grass together with some dicot and insect fragments (Table IX). Earlier authors (Mulkern *et al.*, 1969, Lambley, Campbell, and Knutson, 1972) having found *sordidus* to select its food in proportion to availability, its diet in the Old Field can be presumed similar to that given in Gangwere (1961). *Poa compressa* is likely the common food plant, with other grasses secondary. *Poa pratensis,* a grass taken frequently by *sordidus* in North Dakota (Mulkern, Toczek, and Brusven, 1964) and Kansas (Campbell *et al.*, 1974), is probably not an important food source on the Old Field because of its restriction there to swale environments not frequented by this grasshopper.

Pardalophora apiculata. This species shared spring dominance on the Old Field with *Arphia sulphurea,* and was already in reduced numbers by the time we began our field studies each year. The specimens we examined had herbivorous-type mandibles, and their crops contained grass and lesser amounts of dicotyledonous material (Table IX). No experimental feeding tests were carried out on *apiculata,* but the available data (Gangwere, 1961) suggest that this species takes *Poa compressa*, lesser amounts of other grass, and occasional dicots.

Spharagemon bolli. On the Old Field, *bolli* occurs principally in the field-wood margin and along the adjacent roadway and sparsely vegetated surfaces. Its mandibular adaptation is of the herbivorous type, and its crop contents were mostly dicot material but included some graminoids. In the food latitude tests, *bolli* accepted few of the grasses but many of the dicots offered (Table X). On the other hand, in the differential feeding tests it accepted 81 percent of the graminoids offered, compared with 63 percent of the forbs and 75 percent of the woody plants, taking these categories at preference levels of 3.1, 2.8, and 2.5 respectively. A few natural feeding records were taken, two on *Poa compressa* and one on a sapling of *Quercus* sp. It seems best to classify *bolli* as an herbivore that selects widely from available foods. On the Old Field, its probable food plants in decreasing order of selection are: (1) *Poa compressa,* (2) *Rumex acetosella* and *Lespedeza* spp., (3) *Carya* sp., and (4) other plants.

Spharagemon collare. This geophilic species is found on the Old Field especially in the roadways. Like its congener, it has mandibles of the herbivorous type. It accepted 86 percent of the grasses, 56 percent of the forbs, and 67 percent of the woody plants offered in the differential feeding tests, taking them at preference levels of 3.1, 2.1, and 2.2 respectively. The crop contents indicate that it prefers grass to forbs (Table IX), and in the food latitude tests it accepted the majority of the graminoids offered but rejected 22 of 28 species of forb (Table X). *Spharagemon collare's* food plants on the Old Field are probably as follows, listed in decreasing order of selection: (1) *Poa compressa,* (2) *Panicum* spp., *Rumex acetosella, Aristida purpurascens, Eragrostis spectabilis, Leptoloma cognatum,* and *Lespedeza* spp., and (3) *Cyperus filiculmis, Plantago aristata, P. rugelii,* and *Hieracium longipilum.*

CATANTOPINAE

Melanoplus bivittatus. On the Old Field, this erratic from marsh habitats was rarely encountered always in patches of tall vegetation, chiefly in the swales. Its mandibular adaptation is of the forbivorous type. Its crop contents proved to be composed largely of grass and dicots, together with a few insect remains (Table IX). In the differential feeding experiments, it accepted 54 percent of the graminoids, 74 percent of the forbs, and 89 percent of the woody plants offered, taking them at preference levels of 2.4, 2.9, and 2.6 respectively (Tables XII, XIII). The available data suggest that on the Old Field the common food plants of *bivittatus* include *Poa pratensis, Rumex acetosella, Hieracium longipilum, Rubus flagellaris,* and *Solidago nemoralis.*

Melanoplus confusus. This is a dominant species in the Old Field from June through July. Like *M. bivittatus,* its mandibles are forbivorous in type, and its crop contents were mostly dicotyledonous material with only a little grass (Table IX). It accepted 58 percent of the grasses, 75 percent of the forbs, and 53 percent of the woody plant species offered in the differential feeding tests, taking them at preference levels of 2.2, 2.8, and 1.3 respectively (Tables XII, XIII). We conclude that the local diet of *confusus* consists of the following, listed in descending order of selection: (1) *Solidago* spp., (2) *Liatris aspera, Rumex acetosella,* and *Poa* spp., (3) other forbs, and (4) other grass.

Melanoplus femur-rubrum. This grasshopper was both ubiquitous and abundant in the Old Field during its late summer-fall period of maturity, occurring commonly in the swales and roadways as well as on the uplands. Its mandibular adaptation is, like that of the other Old Field Melanopli, forbivorous in type, but in the differential feeding tests it accepted 70 percent of the graminoids, 79 percent of the forbs, and 43 percent of the woody plants offered, taking them at preference levels of 2.0, 3.1, and 1.3 respectively (Tables XII, XIII). The crop analyses indicated a content almost equally divided between graminoid and dicot material (Table IX). Our data suggest that on the Old Field, *femur-rubrum's* foods include, in decreasing order of selection: (1) *Solidago* spp. and *Poa* spp., (2) *Hieracium longipilum, Liatris aspera, Rumex acetosella,* and *Lespedeza* spp., (3) other forbs, and (4) other grasses. In the swales, several upland food plants, notably *Solidago* spp., *L. aspera*, and *Lespedeza* spp., disappear and are replaced by more mesic species such as *Asclepias syriaca* and *Monarda fistulosa,* which probably become more important food items for this grasshopper.

Some previously unreported differential feeding tests run by Wayne State University entomology students on laboratory-reared *M. femur-rubrum* in June, 1973, are of interest even though they involve a different assemblage of plants from those present in the Old Field. These tests indicate the following sequence of food preferences: (1) *Taraxacum officinale,* (2) *Poa* sp. and *Arctium* sp., (3) *Setaria* sp., (4) *Plantago major* and *P. lanceolata*, and (5) *Labiatae* sp. (nibbled).

Melanoplus keeleri. This species shares dominance on the Old Field with *M. femur-rubrum* in late August and September, but is somewhat more restricted to the upland areas. Its mandibles exhibit the forbivorous-type adaptation; its crop contents were predominantly dicotyledonous material (Table IX); and in the differential feeding tests it accepted 34 percent of the grasses, 83 percent of the forbs, and 37 percent of the woody plants offered, taking them at preference levels of 1.4, 3.4, and 1.4 respectively. Under starvation conditions it accepted 85 percent of all plant species offered, more than any other grasshopper tested (Table X). It is notable for its feeding on goldenrods (*Solidago* spp.), especially *S. rigida,* a large, rough-textured forb ignored by most other acridids. On the Old Field, *keeleri's* foods include, in decreasing order of selection: (1) *Solidago* spp., (2) *Lespedeza* spp., *Liatris aspera,* and *Rumex acetosella*, (3) *Hieracium* spp., (4) other forbs, and (5) grasses.

Melanoplus sanguinipes. Although often confused with *M. femur-rubrum,* this species appears earlier in the season and seems to lack the other's latitude of habitat occupancy. It is most common on the upland parts of the Old Field. Its mandibular adaptation is forbivorous in type, and its crop contents consisted largely of forbs, with only a little grass (Table IX). It accepted 74 percent of the graminoids, 81 percent of the forbs, and 94 percent of the woody plants offered in the differential feeding tests, taking them at preference levels of 2.4, 3.1, and 2.5 respectively (Tables XII, XIII). On the Old Field, its decreasing order of food selection seems to be: (1) *Solidago* spp., (2) *Poa* spp., *Rumex acetosella, Lespedeza* spp., and *Hieracium* spp., and (3) other grasses and forbs.

CYRTACANTHACRIDINAE

Schistocerca emarginata. This grasshopper is conspicuous on the Old Field in September. In its behavior it differs markedly from the other local acridids, being more like that of its close relatives the true "locusts" of other parts of the world. Although frequently encountered on sparsely vegetated ground, it is most often perched on stout plants, particularly shrubs of *Rubus* and saplings of *Carya* and *Quercus*. When flushed, it commonly flies to the lower branches of a nearby tree. Its mandibles are forbivorous in type, and its crop contents consisted entirely of dicotyledonous material, mostly *Lespedeza* spp. (Table IX). In the differential feeding tests it accepted 100 percent of the woody plants offered and 56 percent of the forbs, taking these plants at preference levels of 3.8 and 2.3 respectively (Tables XII, XIII). Though 61 percent of the grasses offered were accepted, they were taken at relatively low preference levels. Under starvation conditions however, seven of nine graminoid species offered were taken. We conclude that the local diet of *emarginata* includes, in decreasing order of selection: (1) *Lespedeza* spp., (2) *Rumex acetosella, Poa compressa, Carya ovalis, Rubus flagellaris,* and probably *Quercus velutina,* (3) other dicots, and (4) other grasses.

DISCUSSION

FOOD SELECTION AND MANDIBULAR ADAPTATION. A positive correlation between grasshoppers' mandibular structure and food-habits is well-established. The relationship was pointed out by Isely (1944) who investigated certain Texan species, and later by Gangwere (1965) who dealt with the southeastern Michigan fauna. Their research, and that of others since then, describes and gives illustrations of sufficient numbers of species to establish overall group variability.

Until recently the heavily sclerotized mandibles of orthopteroids were considered permanent and invariable. This misconception was corrected by Chapman and Gangwere who, working independently of one another, established that mandibles are subject to wear. Chapman (1964) offered experimental proof that certain South African grasshoppers given abrasive food undergo mandibular alteration. A few months later, Gangwere (1965a) showed that the mandibles of newly molted *Arphia sulphurea* exhibit the graminivorous-herbivorous-type adaptation, while older individuals of that species have mandibles of graminivorous-type derived from the former by wear. From the present study it now appears that many acridids start with a given jaw adaptation, usually of a more intermediate type, and then with wear convert to the definitive type of their species. The phenomenon of wear with age and use is apparently more prevalent than thought heretofore.

The factors of senescence and wear are not the only potential sources of mandibular variation. There are at least two other possibilities, nymphal polymorphism and sexual dimorphism. In the present study we did not consider nymphal variation, for it is a specialized subject treated in a recent contribution from Wayne State University (Sastry, 1975), in which it was shown that first-stage nymphs of *Melanoplus femur-rubrum* have sharp, serrate dentes adapted for parenchymo-phytophagous feeding, while older nymphs and adults of that species have conventional forbivorous-type mandibles.

We did investigate the possibility of sexual dimorphism. The desirability of doing so was suggested by the fact that mature female acridids are commonly larger, sometimes twice as large, as mature males of the same species, and often have somewhat different habits that could be reflected in mandibular structure. As noted earlier, the only sex-related disparity we found was in the larger size of the female mandible.

FOOD SELECTION, ADAPTATION, AND BEHAVIOR. The five species of Gomphocerinae whose food-habits were studied in the Old Field are diurnally active, phytophilous grasshoppers that perch either on short grassy vegetation or in clumps of tall grass. Their mandibular adaptation is invariably of the graminivorous-type, and is most strongly developed in *Pseudopomala brachyptera, Syrbula admirabilis,* and *Chorthippus curtipennis*. These three are the species that most strongly display the habit of perching on tall grass, and they have the most pronounced graminivory. The first two of them also exhibit the most characteristic gomphocerine body form and slant face. The remaining species, *Chloealtis conspersa* and *Orphulella speciosa*, are likewise predominantly grass-feeders, but they have the potential of varying their diet with limited amounts of forb material. Thus there is good correlation between the degree of restriction to graminoid food plants and the feeding morphology and behavior of the Old Field Gomphocerinae.

The eight species of Oedipodinae that we studied are variably geophilous. Some, such as *Chortophaga viridifasciata*, exhibit a flexible association with the ground that allows them to climb and flush onto vegetation, while others, such as *Dissosteira carolina* and *Encoptolophus sordidus*, are true "bare ground Acrididae" restricted to arid situations with at most sparse vegetation from which they are reluctant to flush. All are strongly diurnal, and their predilection for bright sunshine sometimes immobilizes them for the brief periods on otherwise clear days when the sum is temporarily obscured by clouds. They exhibit two kinds of food-habit that, with the partial exception of *D. carolina*, accord closely with their herbivorous or graminivorous-type mandibular adaptation. One of these food-habits found in *D. carolina, Spharagemon bolli, S. collare,* and others, is herbivory. Insects of this type accept grass only slightly or not at all more readily than they do forbs. The other food-habit is graminivory. It is found in *Arphia pseudonietana* and *A. sulphurea*, which, though not restricted to graminoids, feed upon grass almost exclusively, ignoring most dicots.

An ancillary food-habit, insect scavenging, was found in four species of the Old Field Oedipodinae. It was pronounced in *Encoptolophus sordidus* and *D. carolina,* whose preference for the bare ground and roadway habitat of the Old Field gives them frequent access to crushed insects. Such scavenging has already been documented for the group (Gangwere, 1961, 1973, Lavigne and Pfadt, 1964), especially for species that frequent xeric habitats.

The Catantopinae studied are phytophilous Melanopli that perch on low vegetation or, on occasion, on shrubs or saplings. They are typically diurnal, though some may be active on warm summer nights as well as during the day. Certain genera of the world fauna of Catantopinae are known to be graminivorous, but none of that type is found in Michigan. Our Old Field species are forbivores that may approach herbivory. This is confirmed by the mandibles, which are forbivorous-type, sometimes modified toward the herbivorous-type.

During the course of the differential feeding tests, all five catantopine species investigated accepted forbs more readily than grass and, in turn, grass more readily than woody plants. Therefore, it came as a surprise that during the food latitude tests they took more species of grass than of forbs. This suggests that grass as well as forbs are important items of diet in the local Catantopinae, and that fact was subsequently confirmed by the crop analyses.

As with oedipodines, the Old Field Catantopinae often exhibit scavenging behavior. Insect sclerites were recorded from the crop contents of most of the species, and a *Melanoplus* sp. was observed eating in the field a fresh, dead *Dissosteira carolina.*

The only cyrtacanthacridine found in the Old Field, *Schistocerca emarginata,* is a diurnally active, semi-arbusticolous species of great mobility. In foodhabits it is primarily dendrophagous, but it is also attracted to certain forbs, notably *Lespedeza* spp., the remains of which predominated in the crop contents. It disdains most grass.

LATITUDE OF FEEDING. The Old Field Acrididae differ strongly in terms of feeding latitude, though all take sufficient numbers of food to require a polyphagous classification. Least polyphagous are the Gomphocerinae. They accepted only 25 percent of all plant species offered during the food latitude tests, and virtually all were graminoid. Of the several gomphocerines we investigated, *Syrbula admirabilis* proved to be the most restricted and *Orphulella speciosa* the least restricted.

In contrast, the Catantopinae accepted 72 percent of all plants offered during the food latitude tests, and in these tests, and in the differential feeding tests, took freely of plants belonging to all three of the major food categories, *viz*., grass, forb, and woody plant types. One must conclude that these forbivores-herbivores have unusually great latitude of food selection. Based on all results, *Melanoplus sanguinipes* has the greatest latitude, and *M. femur-rubrum* is next. While *M. keeleri* reached a deceptively high 85 percent acceptance level during the food latitude tests, this grasshopper proved to be more selective under the more natural conditions of the differential feeding tests than either *M. sanguinipes* or *M. femur-rubrum. Melanoplus confusus* is probably the most selective species of the five Melanopli studied.

The only cyrtacanthacridine studied, *Schistocerca emarginata,* selects from among all three major food categories and approaches the Catantopinae in latitude of feeding.

The Oedipodinae, which accepted 32 percent of all plants offered during the food latitude tests, proved to be intermediate in feeding latitude between the Gomphocerinae and the Catantopinae. The oedipodines as already noted, are herbivorous except for the two species of *Arphia,* both of which are graminivorous. One of the latter, *A. pseudonietana*, with an 18 percent level of plant acceptance during the food latitude tests, seems to be among the more selective acridids of the Old Field.

VARIABILITY IN FEEDING. In Appendix I certain frequently tested food plants of the Old Field Acrididae are presented in categories of decreasing preference value. The categories as listed are not fixed and invariable, but are idealized values or trends subject to variation throughout the collecting season. There are many instances in which, in every test of an acridid species, a particular food plant held its preferential rank with respect to all other plants listed in the feeding sequence. However, there are other instances of a minor nature in which this was not the result. The explanation is to be found in part in seasonal variation, both on the part of the food plants and on the part of the insects that eat them. As plants grow, their tissues toughen, their content of steroids, auxins, and other chemical substances becomes altered, and they develop new parts, including flowers and fruits, that may be more attractive than the original vegetative parts. Finally, toward the end of the growing season as the plants dry and brown, they sometimes become unacceptable as food. Accompanying these plant changes are parallel, physiological changes in the feeders themselves as they molt, mature, reproduce, and undergo alteration in their feeding behavior until eventually they become senescent and die.

Variability notwithstanding, the food sequences listed in Appendix I are consistent. During our initial year of study, we completed preliminary differential feeding tests on a number of Acrididae, analyzed the data, and then, for each grasshopper species, arranged the food plants into a tentative preferential sequence. We repeated this process over the next two years. In most instances the approximate preferential rank postulated on the basis of preliminary testing held true during subsequent experimentation, even in instances involving food plants not previously compared with one another.

Differential feeding tests are experiments to determine the comparative preference value of a small number of uniformly available foods. In effect, they cancel out the factor of food availability. However, foods in nature grow in complex vegetational associations, the many plants of which are neither equally abundant nor equally accessible. Therefore, the feeders must make their selection from within a heterogeneous, unequal food context. Were it not so, the Old Field Acrididae would be expected to feed, on the average, exactly as indicated by their preferences as listed in Appendix I. They do not. Instead, they diet in accordance with a somewhat fortuitous compromise between preference and availability. This is demonstrated by the data of Table IX, the crop content analyses, our only direct index of food selection in nature.

Therein would appear to lie the essential difference between the polyphagy of the Old Field Acrididae and the stenophagy of certain other insects. The food selection of acridids, as noted, usually involves a compromise between preference and availability and varies accordingly, both with time and place. The feeding of stenophagous insects, in contrast, seems based more strictly on preference, and tends to be absolute to the extent that they starve in absence of a specific required food. Under the conditions present on the Old Field, it seems most unlikely that any acridid could die for lack of food.

FEEDING AND COMPETITION. Earlier in this study we noted some instances of co-dominance among the Acrididae of the Old Field. Relationships of this type could result in marked interspecific competition among the co-dominants as they seek the limited food resources of their community. Our observations provide some evidence relative to that possibility.

One co-dominant relationship that we noted involves the spring grasshoppers *Arphia sulphurea* and *Pardalophora apiculata.* Though they frequent the same upland environment, the latter's pronounced geophily assures for it a somewhat different habitat selection from that of the former. They share some host plants, notably *Poa compressa.* However, these foods are invariably abundant, ubiquitous plants throughout the uplands, so are not likely to be drawn upon excessively by the feeding insect populations. We conclude that any food competition between *A. sulphurea* and *P. apiculata* is negligible.

Another co-dominant relationship found in the Old Field involves the fall grasshoppers

Melanoplus keeleri, M. femur-rubrum, and *Schistocerca emarginata*. The phytophilous *M. keeleri* and *M. femur-rubrum,* the two most abundant acridids in the Old Field, occur together throughout the uplands, but the latter is also common in the swales. Consequently, there are partial habitat differences between the two. There are also substantial feeding differences. Both are forbivores, but *M. femur-rubrum* has a significant grass intake in addition to its regular forb intake. The two share some host plants, including *Solidago* spp., *Hieracium longipilum,* and *Liatris aspera*, but these foods are abundant forms not readily subject to excessive grasshopper foraging. The differences between the two Melanopli and the strong-flying, semi-arbusticolous *S. emarginata* are even greater. *S. emarginata* has a different habitat selection, and it eats *Lespedeza* spp. and various shrubs different from those taken by the former. Again, we must conclude that food competition is unlikely.

The remaining Acrididae of the Old Field are mostly low density species specialized for occupancy of one or another habitat. They are asynchronous in seasonal occurrence, and they differ in food-habit. Among them they select a wide variety of food plants, but those taken in common are mostly ubiquitous, abundant plants not likely to be damaged by excessive grasshopper foraging.

In light of the polyphagy of most of the tested grasshoppers, which permits them to turn more or less readily from one food to another, these facts suggest that little interspecific competition is to be found among the Old Field Acrididae.

FOOD PLANT ACCEPTABILITY. Our studies provide information on the extent to which the three major food categories (grass, forbs, and woody plants) are acceptable to the Old Field Acrididae. An analysis of the data is instructive. In the differential feeding tests (Table XII), grasses, with an overall preference value of 2.9, proved more acceptable than forbs (preference value 2.0), and the latter more acceptable than woody plants (preference value, 1.5). Such generalizations are deceptive, however, inasmuch as they mask individual species' differences in acceptability. The overall preference value of grass ranged from 3.9 for *Poa compressa,* to 2.0 for *Aristida purpurascens,* which are the dominant graminoids of the Old Field. Likewise, the preference value of forbs varied between 3.5 for *Rumex acetosella,* and 1.0 for *Gnaphalium obtusifolium,* while that of woody plants varied between 1.9 for *Rubus flagellaris,* and 1.3 for *Carya ovalis*. Furthermore, plants that are not acceptable to acridids as a whole may nonetheless be important food sources for particular grasshoppers. Every plant that in our studies had a high level of biomass in the Old Field proved to be a favorite of one or another acridid. Prominent among these plants were *Poa compressa, Aristida purpurascens, Rumex acetosella, Lespedeza* spp., *Liatris aspera,* and *Solidago* spp. In fact, those among them that were especially high in biomass proved to be almost universal foods for certain acridid subfamilies. For example, *Poa compressa* and *Aristida purpurascens* outranked all other plants in acceptance by the Old Field Gomphocerinae, and *Solidago* spp. was foremost in acceptance by the Catantopinae.

With such a diversity of food resources at the disposal of the 23 species of the Old Field Acrididae, one would expect that a few food plants would prove acceptable to most if not all of the grasshoppers, and that a few of the latter would have a wide latitude of food selection. This is precisely the result obtained during our study. One would also expect a tendency toward specific relationships, *i.e.,* some plants to be accepted by only one species of grasshopper and some acridids to be restricted to a single food plant. In fact, there was little indication of such restriction in the Old Field. All of the grasshoppers that we studied proved to be polyphagous as already pointed out, and only two abundant plants, *Antennaria neglecta* and *Hypericum perforatum,* were accepted by only a single species of grasshopper each during the food latitude tests (Table XI). If this apparent scarcity of one-to-one relationships among food plants and the grasshoppers that feed on them is a widespread, not a local phenomenon, it suggests that food-habits have not played as important a role in the speciation of the Acrididae as they have in some other animal groups.

SUMMARY

1. An investigation was carried out during 1963-1965 on food selection in 23 species of Acrididae, or grasshoppers, in a mixed grass-herbaceous field community, Evans Old Field, E. S. George Reserve, southeastern Michigan.

2. *Ageneotettix deorum, Arphia xanthoptera, Syrbula admirabilis,* and *Trachyrhachys kiowa* appear to be recent arrivals on the George Reserve and *Pardalophora haldemanii* to have disappeared, presumably owing to changing habitat conditions.

3. Adults of *Pardalophora apiculata* were found restricted to the spring season, those of *Pseudopomala brachyptera* to the summer, and those of *Chorthippus curtipennis* to the fall. The remaining species proved to be adult over two or more seasons of the year, generally summer-fall.

4. *Arphia sulphurea, Melanoplus confusus, M. femur-rubrum, M. keeleri, Orphulella speciosa, Pardalophora apiculata,* and *Schistocera emarginata* achieved seasonal dominance in the Old Field, as measured arbitrarily by contributions of 25 percent or more to the total acridid fauna at particular periods during 1964-1965.

5. Capture-recapture experiments were carried out and the data analyzed by means of the Lincoln or Peterson Index formula as modified by Bailey (1951). The resulting estimates indicate that the populations of abundant species such as *Melanoplus femur-rubrum* and *M. keeleri* consist of several thousand individuals each, the less common species such as *Arphia sulphurea* and *Pardalphora apiculata* of hundreds of individuals, and the rarer species such as *Chortophaga viridifasciata* of less than one-hundred individuals.

6. The flora of Evans Old Field was found to contain 122 species of vascular plants, including 25 graminoids, certain of which are the dominant species of the field, and interspersed among them, 81 forbs and 16 woody plants. The vegetation proved divisible into upland, roadway, and swale habitat types, and was characterized by many minor plant associations that form a complex mosaic patchwork.

7. Twenty-one plant species proved relatively ubiquitous, as determined arbitrarily by an F value of 10.0 percent or more in the frequency survey of the Old Field as a whole. Five forbs and two grasses were found in over half of the 200 square-yard quadrats examined. A separate frequency survey of the roadways found 31 plant species ubiquitous, and determined the presence of five grasses and six forbs in over half of the 50 "bare ground" quadrats examined.

8. The forbs *Rumex acetosella, Solidago juncea,* and *S. nemoralis* and the grasses *Aristida purpurascens, Poa compressa, P. pratensis,* and *Leptoloma cognatum* proved abundant, as measured arbitrarily by a mean density of 10 or more individual plants per square yard.

9. The grasses *Aristida purpurascens* and *Poa compressa* and the forbs *Lespedeza capitata, Liatris aspera,* and *Solidago* spp., each with values of 5 gm per square yard or greater, reached especially high biomass levels.

10. The mandibles of 20 species of Acrididae of the Old Field were analyzed to determine the adaptation. The possibility of a mandibular sexual dimorphism was investigated with a negative result; the mandibles of males and females of the same species differed only in size.

11. The Acrididae taken for mouthpart analysis were also processed to disclose crop content. The crop materials of 19 species were analyzed.

12. The precision of crop content analysis was enhanced through development of a reference microscope slide collection of the macerated tissues of 87 species of vascular plants from the Old Field. These materials proved sufficiently diagnostic for development of a key for the specific determination of unknown crop contents.

13. Eleven species of Acrididae were subjected to food latitude tests that indicate the response of individual grasshoppers to 35 common plant species given on an exclusive basis, and the result, either feeding or starvation, was noted.

14. Differential feeding tests were undertaken to ascertain the preferences of 14

species of Acrididae among foods presented simultaneously. Each was exposed to an average of 34 plant species.

15. Among others, the Old Field gomphocerines *Orphulella speciosa, Pseudopomala brachyptera,* and *Syrbula admirabilis* proved rigidly graminivorous, the oedipodines *Arphia pseudonietana* and *A. sulphurea* graminivorous but capable of turning to forbs; the oedipodines *Chortophaga viridifasciata, Dissosteira carolina, Spharagemon bolli,* and *S. collare* herbivorous; the catantopines *Melanoplus confusus, M. femur-rubrum, M. keeleri,* and *M. sanguinipes* forbivorous or herbivorous-forbivorous; and the cyrtacanthacridine *Schistocerca emarginata* herbivorous-dendrophagous.

16. All of the Old Field Acrididae were found to be polyphagous, though variably so. The gomphocerines proved highly restricted, the oedipodines somewhat restricted, and the catantopines relatively unrestricted.

17. The polyphagous food selection of the Old Field Acrididae usually involves a compromise between the insects' feeding preferences and the availability of their foods, and varies accordingly. This flexible behavior is different from that of stenophagous insects, which tend to select according to preference alone.

18. Little or no interspecific food competition was noted among the Acrididae of the Old Field. This is presumably a consequence of their overall polyphagy, seasonal asynchrony, and variable habitat selection.

19. Grasses have a higher overall food preference value with respect to the Old Field Acrididae than do forbs, which, in turn, have a higher value than do woody plants. Nevertheless, there is individual variation both from plant to plant and from grasshopper to grasshopper.

20. Every food plant with a high level of biomass proved to be a favorite of one or another acridid, and those foods (such as *Aristida purpurascens, Poa compressa,* and *Solidago* spp.) that reach especially high levels are almost universal foods for given grasshopper subfamilies.

21. There were few if any instances in which individual plant species of the Old Field were acceptable to but one grasshopper species. Likewise, no acridids were determined to be monophagous. This indicates a scarcity of one-to-one feeding relationships between the Acrididae and the plants that they eat, and suggests that food-habits have not played as important a role in grasshopper speciation as they have in some other animal groups.

APPENDIX

Summary of Differential Feeding Tests, Evans Old Field, 1963-1965.*

Orphulella speciosa
(Tested 25 times July-September, 1963, once July, 1964, & five times September, 1965)

Poa compressa 31:0 > *Aristida purpurascens* 14:0 > *Setaria* sp. 6:0 > *Panicum oligosanthes* 24:0 > *Eragrostis spectabilis* 5:1 > *Poa pratensis* 17:7 > *Liatris aspera* 1:15 & *Lespedeza virginica* 1:5 > *Solidago juncea* 2:21 & *Solidago nemoralis* 1:13 & *Lespedeza capitata* 1:22 > *Solidago rigida* 0:20 & *Rubus flagellaris* 0:11 & *Carya ovalis* 0:10 & *Asclepias syriaca* 1:8 > Untouched: *Euphorbia corollata* 0:6 & *Gnaphalium obtusifolium* 0:6 & *Chrysanthemum leucanthemum* 0:7 & *Erigeron strigosus* 0:8 & *Hieracium longipilum* 0:15

Pseudopomala brachyptera
(Tested nine times July, 1963, & five times June, 1964)

Poa compressa 14:0 > *Panicum oligosanthes* 14:0 > *Juncus tenuis* 4:2 > *Poa pratensis* 9:4 > Untouched: *Rudbeckia serotina* 0:4 & *Erigeron strigosus* 0:8

Syrbula admirabilis
(Tested 13 times August-September, 1963, once July, 1964, & five times September, 1965)

Poa compressa 19:0 > *Aristida purpurascens* 9:0 > *Setaria* sp. 8:0 > *Eragrostis spectabilis* 6:0 > *Leptoloma cognatum* 5:0 > *Panicum oligosanthes* 16:1 > *Poa pratensis* 7:7 > *Lespedeza virginica* 0:6 & *Monarda fistulosa* 0:5 > *Solidago nemoralis* 0:13 & *Solidago rigida* 0:18 > Untouched: *Asclepias syriaca* 0:5 & *Carya ovalis* 0:5 & *Erigeron strigosus* 0:5 & *Liatris aspera* 0:6 & *Hieracium longipilum* 0:7 & *Rubus flagellaris* 0:8 & *Solidago juncea* 0:8 & *Lespedeza capitata* 0:13

Arphia pseudonietana
(Tested 12 times July-August, 1964, & five times August, 1965)

Poa pratensis 6:0 > *Poa compressa* 17:0 > *Leptoloma cognatum* 12:0 & *Panicum oligosanthes* 5:0 & *Aristida purpurascens* 6:0 > *Cyperus filiculmis* 11:0 & *Eragrostis spectabilis* 9:2 > *Plantago aristata* 9:2 > *Plantago rugelii* 5:5 & *Juncus tenuis* 7:4 > *Rumex acetosella* 0:5 & *Antennaria neglecta* 3:3 > *Hieracium longipilum* 2:4 > *Lespedeza capitata* 1:15 > *Lechea villosa* 0:11 & *Liatris aspera* 1:12 > *Solidago rigida* 0:16 > Untouched: *Rubus flagellaris* 0:6 & *Solidago nemoralis* 0:6

Arphia sulphurea
(Tested six times June-July, 1965)

Poa compressa 6:0 > *Panicum oligosanthes* 6:0 > *Poa pratensis* 6:0 & *Juncus tenuis* 6:0 > *Rumex acetosella* 3:3 > *Desmodium sessilifolium* 1:5 > *Lespedeza capitata* 0:5 > *Monarda fistulosa* 0:6 & *Antennaria neglecta* 1:5 > *Quercus* sp. 0:6 & *Hieracium longipilum* 0:6 > Untouched: *Carya ovalis* 0:5 & *Solidago juncea* 0:6 & *Solidago rigida* 0:6

Dissosteira carolina
(Tested 13 times August, 1964, & five times July-August, 1965)

Poa compressa 18:0 > *Hieracium longipilum* 6:1 > *Plantago rugelii* 9:2 & *Cyperus filiculmis* 10:0 > *Panicum oligosanthes* 6:0 > *Leptoloma cognatum* 12:0 > *Antennaria neglecta* 5:0 > *Lespedeza capitata* 13:4 & *Eragrostis spectabilis* 11:0 & *Plantago aristata* 9:1 & *Aristida purpurascens* 6:2 & *Juncus tenuis* 8:3 & *Rubus flagellaris* 5:1 > *Liatris aspera* 8:10 > *Lechea villosa* 1:11 > *Solidago nemoralis* 0:6 & *Solidago rigida* 1:16 & *Poa pratensis* 1:6

Spharagemon bolli
(Tested 22 times July-September, 1963, six times July, 1964, & 12 times July-August, 1965)

Poa compressa 36:2 > *Panicum oligosanthes* 27:0 > *Lespedeza capitata* 31:1 > *Carya ovalis* 10:2 & *Rubus flagellaris* 14:1 > *Leptoloma cognatum* 9:1 & *Juncus tenuis* 9:3 & *Antennaria neglecta* 8:3 & *Eragrostis spectabilis* 9:2 & *Erigeron strigosus* 9:2 > *Liatris aspera* 16:5 & *Poa pratensis* 15:4 > *Solidago nemoralis* 7:10 & *Solidago juncea* 7:15 > *Aristida purpurascens* 7:12 > *Solidago rigida* 2:29

Remarks: The preferences of *S. bolli* are not pronounced, but its food plants fall consistently into the above sequence, except for *Asclepias syriaca* (7:3) and *Hieracium longipilum* (12:11). *Asclepias syriaca* belongs somewhere in the middle of the sequence and *H. longipilum* between the middle and bottom.

Spharagemon collare
(Tested 15 times July-August, 1964, & five times July, 1965)

Series I (Upland Vegetation): *Poa compressa* 18:0 > *Rumex acetosella* 8:1 > *Panicum oligosanthes* 8:0 > *Aristida purpurascens* 8:0 > *Lespedeza capitata* 14:4 & *Hieracium longipilum* 6:3 & *Liatris aspera* 8:4 & *Rubus flagellaris* 6:3 > *Antennaria neglecta* 4:3 & *Erigeron strigosus* 3:4 & *Solidago nemoralis* 4:5 > *Lechea villosa* 1:10 > *Solidago rigida* 0:18

Series II (Roadway Vegetation): *Poa compressa* 18:0 > *Cyperus filiculmis* 9:0 > *Plantago aristata* 9:0 & *Eragrostis spectabilis* 9:0 > *Leptoloma cognatum* 7:1 & *Plantago rugelii* 8:1 & *Lespedeza capitata* 14:4 > *Juncus tenuis* 6:2 > *Liatris aspera* 8:4 > *Lechea villosa* 1:10 > *Solidago rigida* 0:18

Melanoplus bivittatus
(Tested nine times July-August, 1964)

Hieracium longipilum 8:0 > *Rumex acetosella* 8:0 & *Erigeron strigosus* 5:0 > *Poa pratensis* 8:1 > *Solidago nemoralis* 7:1 > *Rubus flagellaris* 8:1 > *Panicum oligosanthes* 6:2 & *Solidago rigida* 6:2 & *Antennaria neglecta* 6:3 & *Poa compressa* 5:4 > *Lespedeza capitata* 1:6 > *Aristida purpurascens* 0:8

Melanoplus confusus
(Tested 29 times July-September, 1963, five times July, 1964, & six times June-July, 1965)

Monarda fistulosa 11:0 > *Solidago juncea* 33:0 > *Erigeron strigosus* 11:0 > *Liatris aspera* 15:0 > *Rumex acetosella* 10:2 & *Poa pratensis* 22:6 & *Solidago nemoralis* 15:2 & *Juncus tenuis* 9:2 > *Rubus flagellaris* 8:2 & *Lespedeza virginica* 6:6 & *Poa compressa* 18:19 & *Solidago rigida* 16:13 & *Antennaria neglecta* 8:4 & *Lespedeza capitata* 16:11 & *Panicum oligosanthes* 18:18 > *Quercus rubra* 2:9

Remarks: The preferences of *M. confusus* become less pronounced in the above sequence following *R. acetosella*. The preference value of *Aristida purpurascens* (9:15) is uncertain with respect to this feeder.

Melanoplus femur-rubrum
(Tested six times September, 1963, & five times September, 1965)

Poa pratensis 9:0 > *Hieracium longipilum* 6:0 > *Solidago nemoralis* 11:0 & *Solidago rigida* 8:2 & *Poa compressa* 10:0 > *Setaria* sp. 5:0 & *Liatris aspera* 5:0 > *Rubus flagellaris* 6:1 > *Panicum oligosanthes* 7:3 & *Eragrostis spectabilis* 4:1 & *Lespedeza capitata* 9:3 > *Leptoloma cognatum* 3:3 & *Carya ovalis* 3:3 & *Aristida purpurascens* 3.5

Melanoplus keeleri
(Tested nine times September, 1963, & six times September, 1965)

Asclepias syriaca 5:0 > *Solidago juncea* 5:0 > *Solidago nemoralis* 14:0 & *Solidago rigida* 15:0 > *Liatris aspera* 8:0 > *Hieracium longipilum* 6:1 & *Setaria* sp. 6:0 > *Poa compressa* 8:6 > *Eragrostis spectabilis* 3:3 > *Lespedeza capitata* 6:8 & *Rubus flagellaris* 4:6 & *Poa pratensis* 4:5 > *Leptoloma cognatum* 0:8 & *Panicum oligosanthes* 3:11 & *Lespedeza virginica* 1:4 & *Carya ovalis* 1:5 & *Juncus tenuis* 1:4 & *Aristida purpurascens* 0:9

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Melanoplus sanguinipes
(Tested 28 times July-September, 1963, eight times July, 1964, & six times August, 1965)

Setaria sp. 11:0 >*Rumex acetosella* 10:0 & *Poa pratensis* 29:0 >*Solidago juncea* 26:1 & *Hieracium longipilum* 24:1 & *Asclepias syriaca* 9:3 & *Erigeron strigosus* 13:0 >*Rubus flagellaris* 17:0 >*Poa compressa* 37:5 & *Carya ovalis* 11:1 >*Solidago nemoralis* 24:2 >*Panicum oligosanthes* 22:9 & *Lespedeza capitata* 23:7 & *Lespedeza virginica* 7:4 & *Antennaria neglecta* 8:2 & *Solidago rigida* 20:11 >*Liatris aspera* 13:8 & *Eragrostis spectabilis* 6:5

Remarks: *Asclepias syriaca* & *Hieracium longipilum* proved exceptionally variable phenologically, so may have a somewhat higher optimal preference value than indicated above for *M. sanguinipes*.

Schistocerca emarginata
(Tested six times September, 1963, eight times August, 1964, & five times August, 1965)

Rubus flagellaris 15:0> *Lespedeza capitata* 17:1 >*Poa compressa* 17:2 & *Setaria* sp. 4:1 & *Carya ovalis* 4:1 >*Hieracium longipilum* 10:4 >*Panicum oligosanthes* 9:5 & *Antennaria neglecta* 7:1 & *Leptoloma cognatum* 3:6> *Solidago nemoralis* 6:1 & *Solidago rigida* 5:13 & *Aistida purpurascens* 3:11 & *Poa pratensis* 7:8> *Liatris aspera* 1:11

Remarks: The preference value of *Solidago juncea* (1:4) is uncertain with respect to *S. emarginata*. It falls somewhere near the bottom of the above sequence of food plants.

*The Appendix lists foods according to decreasing preference value separated by the symbol >. Those foods to the left of a particular > are generally preferred over those to the right of that symbol, while those in the same category, joined by the symbol &, are approximately equally preferred. These categories represent average values under a particular set of conditions at a fixed time of year. Listed together with the plant names is an acceptance-rejection ratio, which is a comparison of the frequency of eating as opposed to that of nibbling or complete rejection. For example, a plant with a ratio of 9:2 was eaten nine times and nibbled or rejected twice. The reader may turn to Gangwere (1961) for detailed information concerning formulation of this table.

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