

Technical Report No. 148  
GRASSHOPPER POPULATION NUMBERS AND BIOMASS  
DYNAMICS ON THE PAWNEE SITE  
FROM FALL OF 1968 THROUGH 1970

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## ABSTRACT

Quantitative samples of orthopteroid insects, especially grasshoppers, have been accumulated from October 1968 through December 1970 on three pasture types of the Pawnee Site. The sampling was done, mainly using a mobile cage and a string frame, each device enclosing a  $2 \text{ m}^2$  area.

Insects of 43 species have been identified using the above and other methods. Common grasshoppers (family Acrididae) comprise 34 of these species of which 11 are important contributors to the population density and biomass of the pastures sampled. There appeared to be some tendency for a few species to be restricted to lowlands where the plant community is different from that of upland sites.

Population density of adults was greatest in late summer (August) or early fall (September and October) and was comprised mainly of four to six species of grasshoppers. Peak densities of adult grasshopper populations for the three years were: 1968 (October),  $19.4/10 \text{ m}^2$ ; 1969 (September),  $7.8/10 \text{ m}^2$ ; and 1970 (August-September),  $5.1/10 \text{ m}^2$ .

There is also a group of four species whose eggs hatch during the summer and over winter as late instar nymphs. These nymphs may be active consumers during warm, calm winter days. Adults of these species appear in late April and early May and remain until approximately the end of June, thus constituting an early summer adult population composed of a much lower density (and biomass) than the fall population.

Ovendry weight data have been accumulated for both sexes of all nymphal instars and adults for most of the abundant and common species. These have been used to calculate biomass for the grasshopper fauna on the

Pawnee Site. In 1970 total biomass during the spring was approximately  $80 \text{ mg}/10 \text{ m}^2$  and climbed to a peak of approximately  $320 \text{ mg}/10 \text{ m}^2$  during September, then fell precipitously to about  $100 \text{ mg}/10 \text{ m}^2$  as the adults died off at the end of the year (composed of the late instar nymphs mentioned above). Annual species biomass curves resemble the general form of the total biomass curve with the six important fall species showing their peaks of biomass at the same time (September) as the total curve while the four early summer species show peak biomass during May. Thus, while the total population density may be greatest in midsummer due to the presence of a large nymphal component, the increase in biomass of the grasshopper population is much more a function of the appearance of adults during the late summer and early fall.

Both peak adult population densities and peak biomass varied from 1968 through 1970. In 1968 the peak biomass was  $1.37 \text{ g}/10 \text{ m}^2$  but only  $0.55 \text{ g}/10 \text{ m}^2$  in 1969 and  $0.33 \text{ g}/10 \text{ m}^2$  in 1970.

An analysis of Central Plains Experimental Range precipitation and temperature data for 1968 and 1969 lends support to the hypothesis that hot, dry weather in June (as in 1968) encourages the emergence and survival of first instar nymphs which results in a larger adult population in the fall, whereas cold, wet weather in June (1969) increases egg and/or early nymph mortality, thus depressing the resultant adult population density and its biomass.

## INTRODUCTION

Grasshoppers are a very conspicuous primary consumer component of most temperate grassland ecosystems. Since they are so conspicuous, . . . . . throughout the year, and (iii) the dynamics of both individual species and total grasshopper biomass on an annual basis. There are other data important to energy flow estimation that have not as yet been collected. These include feeding and defecation rates, egg density and biomass, and respiratory rates. Data for these parameters are available in the literature, but I think it may be questionable as to how accurately they pertain to the orthopteran populations on the Pawnee Site.

Although the major sampling efforts were concentrated on grasshoppers, which in this study were all acridids, i.e., short-horned grasshoppers belonging to the family Acrididae, we also collected all other orthopteroid insects including walkingsticks, mantids, crickets, and long-horned grasshoppers. Some of the species of these other groups are diurnal like the

short-horned grasshoppers, but others are nocturnal. Also, some are cryptozoic. No attempt was made to measure the populations of either the nocturnal or the cryptozoic species.

## METHODS

### Description of Area

All of the quantitative sampling reported here was done on the Pawnee Site which is a short name for the Intensive Site location of the IBP Grassland Biome project. This site lies within the Pawnee National Grasslands, Weld County, Colorado. A more detailed description of the site is contained in Technical Report No. 1 (Jameson 1969) of this series.

Except for some samples taken in the "go back" portion of Section 26, all samples were collected in three areas of Sections 22 and 23, T10N; R66W. The eastern half of Section 22 is located partly on a lowland flood-plain of Little Owl Creek and has a different vegetation from the two upland sites described subsequently. The vegetation in this lowland site has a generous proportion of sedges as well as the two dominant grass species, blue grama and buffalo grass. It is a winter heavy-grazed pasture. During the summers we collected, the vegetation was not noticeably cropped and more closely resembled the physiognomy of the vegetation in Section 23W than in 23E. This collecting site in the eastern half of Section 22 will henceforth be referred to as 22E.

Section 23 is mainly an upland site, and the eastern and western halves are separated by fence. Grazing in both halves is limited to summer, but the intensity differs; the eastern half is heavily grazed, and the western

half is lightly grazed resulting in a physiognomy that is quite different. The vegetation in the eastern half is very low, and bare areas of soil are quite conspicuous. The dominant vegetation on both halves appears to be very similar and composed mainly of blue grama and buffalo grass. Henceforth, the eastern half of this section will be referred to as 23E and the western half as 23W. The exact locations of these sites are shown on Fig. 1, and their grazing and elevation relation are conveniently summarized below:

<u>Collecting Site</u>	<u>Elevation</u>	<u>Grazing Intensity</u>
22E	Lowland	Winter, heavy
23E	Upland	Summer, heavy
23W	Upland	Summer, light
26N	Upland	Summer, light

#### Sampling Techniques

Throughout this study three sampling techniques have been employed to gather quantitative data. During the late spring, summer, and fall, we used a lightweight drop cage (hereafter referred to as "cage") constructed of aluminum and screening for most of the sampling. This cage is open at the bottom, is square with each side measuring 1.414 m, thus enclosing a 2 m<sup>2</sup> sample when lowered to the ground. A strip of sponge rubber was added to the bottom before use in 1970 which improved the closure of the bottom of the cage when placed on more irregular ground. The terrain sampled was generally flat enough to ensure an almost perfect closure at the bottom on most samples. The cage is approximately 1.5 m high and has a small latched door for admittance to collect the sample.

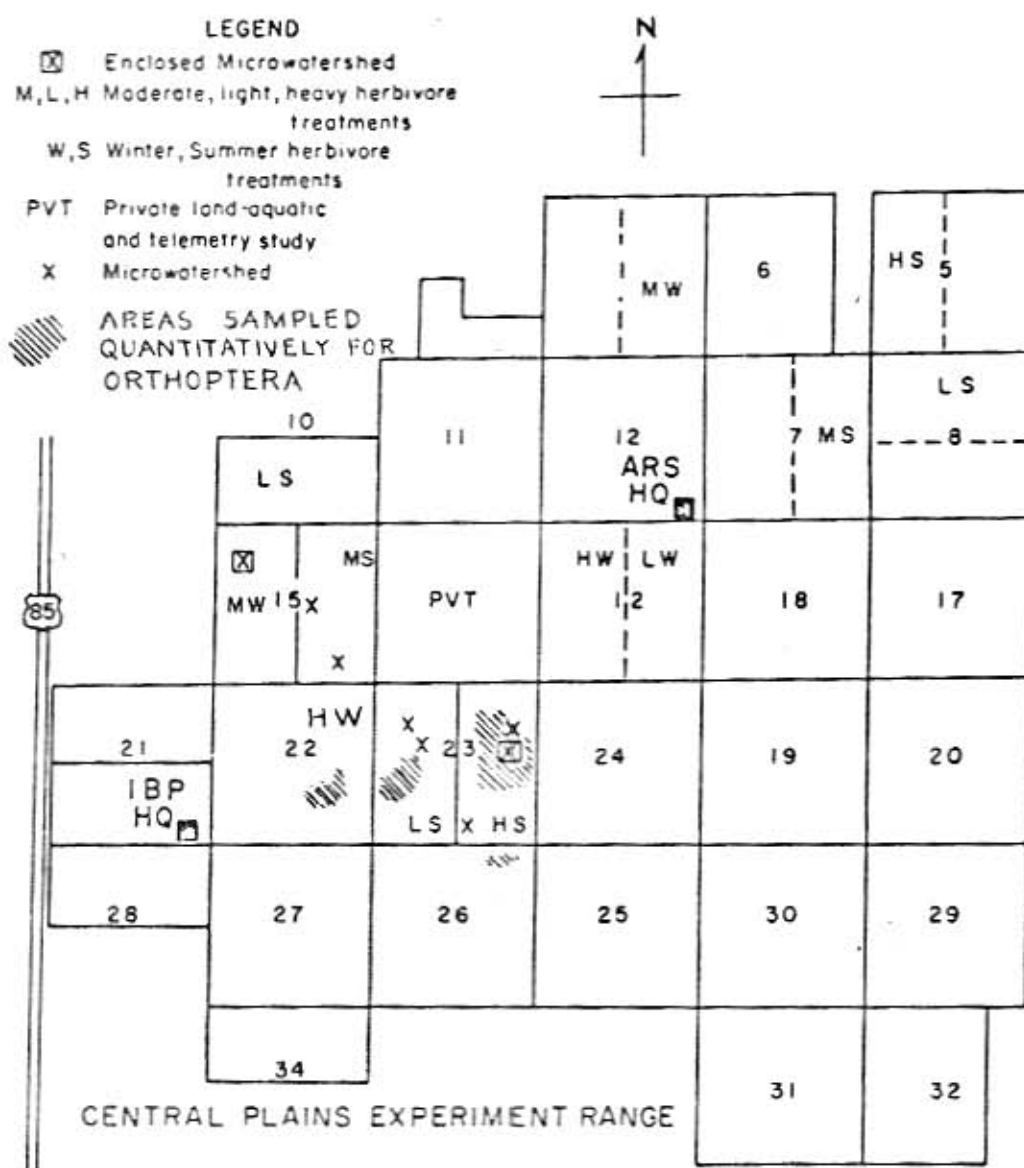


Fig. 1. Map of Pawnee Site with Orthoptera sampling areas.



The sampling procedure with the cage normally involved two operators who carried the cage between two 5 m long aluminum booms (see Fig. 2) holding the arms over the head so that the booms elevated the bottom of the cage to more than a full meter from the ground. In this manner the cage was transported from one sampling spot to another. The distance from one site to another varied from approximately 30 to 40 m. The cage was not set down if grasshopper hopping or flying activity was noted. On a few occasions the setting down of the cage would excite an observed hop or flight of a grasshopper. If the origin was estimated to be definitely within the sample area, then an effort (generally successful) was made to capture the escaped individual. If not captured, it was not counted in the sample.

After the cage was lowered into place the booms were pulled out, and one or two collectors went into the cage and carefully examined the ground and sides of the cage. All specimens regardless of age, sex, or species of orthopteroid insects were collected either by hand or by a modified small auto vacuum (run on an automobile battery and, later, using a motorcycle battery).

During 1968 and 1969, 15 samples were collected in each pasture thus sampling  $30 \text{ m}^2$  for that pasture on that day. During 1970 the number of samples was increased to 30 thus obtaining  $60 \text{ m}^2$  of total area in each pasture. It generally required 60 to 70 minutes to collect 15 samples under favorable weather conditions when orthopteran populations were moderately high. The greatest amount of time was consumed combing the area carefully for early instar nymphs.

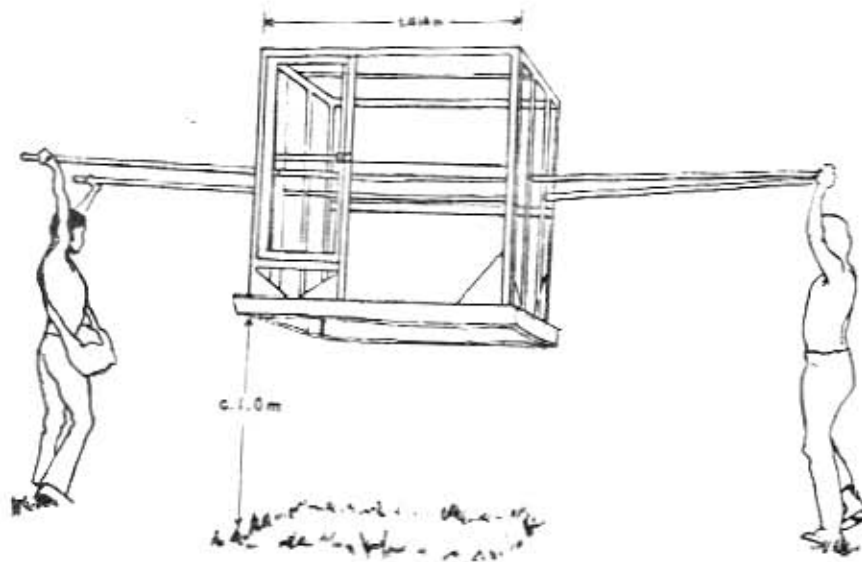


Fig. 2. Two m<sup>2</sup> sampling cage in use.

Beginning in June 1970 we kept records of the total number of adults and the total number of juvenile individual specimens taken in each  $2 \text{ m}^2$  cage sample. These data have been transferred to special data sheets and sent to the IBP programming coordinator at the Natural Resource Ecology Laboratory, Colorado State University, for an analysis of variance.

In winter months when only juveniles were present, we used a simple sampling frame constructed of long nails and string (henceforth, referred to as "string frame"). This device also inclosed a square area of  $1.414 \text{ m}$  on a side. It was moved simply and fairly randomly from spot to spot with the nails driven into the ground by the weight of the operators. A minimum of two people was required to operate the string frame successfully. Care was taken at each sample spot to make the frame close to a square conformation. Variable numbers of samples in each pasture were gathered on each sampling date, but it never was less than 15 and never exceeded 30.

The third sampling method was limited to estimating numbers of three species of band-winged grasshoppers (Oedipodinae) that are characterized by being easily flushed and are very active fliers that display diagnostic wing coloration when they fly. During late April, May, and June populations of *Arphia conspersa* Scudder and *Xanthippus corallipes* Haldeman are large, common adults. The former species has reddish-orange wings at the Pawnee Site, while the latter has yellow wings and is even larger. Hence, the two are easily distinguished. In late summer (August and September) and fall (October) another species of *Arphia* becomes adult, *Arphia pseudonietana* (Scudder), and is very conspicuous in flight with its dark body and bright red wings.

Our walk-flushing technique was limited to counting these three species as adults. Each count consisted of pacing for 100 m in a constant direction and counting the number of adults of these species that flew up from within a 1 m span on either side of the line of walk. Thus each count sampled a  $200\text{ m}^2$  transect. Depending on time available, each worker made 5, 10, or 15 "walks" on a given pasture, and the data for each walk was entered separately on the field data sheet. This technique is henceforth referred to as "walk".

There are two major reasons for collecting data using this method. It is (i) a quick and easy method and (ii) allowed a check or comparison with the cage method in estimating species that are strong, easily flushed fliers that could possibly be underestimated due to their ability to escape while the cage was being lowered into position.

All specimens were generally killed immediately in cyanide jars and then transferred to plastic jars and frozen within a few hours of the initial collection. Identification of sex, age, and species as well as counting was done later in a laboratory using an optivisor or binocular dissecting microscope when necessary. All identified specimens were then stored in vials labeled as to exact location, date, species, sex, and age. These vials were grouped together by collection date and location and returned to the freezer, or, in some cases oven-dried for weighing.

Weather data were recorded at the beginning and end of each sampling period in each pasture. Air temperature at 1 m above the surface, soil temperature at 10 cm below surface, wind direction and velocity, type of clouds, and the time of day (Mountain Standard Time) were recorded on field data sheets.

Insects, especially grasshoppers, are very sensitive to weather conditions. We often were unable to make collections according to schedule due to suboptimal weather conditions. It soon became necessary to establish criteria for judging conditions to be near enough to optimum to assure that samples would be taken under similar and optimal conditions from one sampling time to the next.

Field observations revealed that the most optimal conditions were those of warm temperatures (above 30°C during the summer and above 5°C in winter) combined with bright sun and no wind or precipitation. Lower temperatures, decreased sunlight, more wind and precipitation, or any combination of these resulted, within minutes, in the lowered activity and then disappearance of adults and juveniles and would thus seriously bias any sampling. We established sampling under as close to optimum conditions as possible in order to measure the maximum density during periods of greatest diurnal activity. Thus, no sampling was done when the wind velocity was in excess of 20 mph, during any periods of precipitation, or on very cloudy, cool or cold days. Wind velocity proved to be the most frequently encountered suboptimal condition.

We have calculated biomass estimates by multiplying the mean oven-dry weight of specimens of a given age and sex of a species times the number of specimens of that age, sex, and species in a given pasture or pastures on a given date. All specimens that were used in biomass measurements were first isolated into groups of the same species, sex, age or instar (first instar nymphs were not separated as to sex), and date of collection, then were oven-dried at 110°C for 12 hours. Individual

insects were then weighed to 0.0001 g. Wherever possible, 30 individuals of each category were weighed and entered on a single data sheet. The mean ( $\bar{x}$ ), standard deviation ( $\sigma$ ), and variance ( $\sigma^2$ ) of each sample were then computed. Technical Report No. 19 (Van Horn 1969) has a more detailed account of these procedures for four species. More biomass data for those species as well as data for other abundant or common species is now available.

## RESULTS

### Taxonomic Checklist

Since the inception of this study in 1968, 43 species of Orthoptera (*sensu latu*) in six families have been collected on the Pawnee Site. New species have been added each year. These taxa are recorded on Table 1.

Of this total number of species three are long-horned grasshoppers (Tettigoniidae), and 34 are short-horned grasshoppers (Acrididae), thus comprising a total of 37 species commonly referred to as grasshoppers. Ten of these 37 species have been found to be common or abundant enough to comprise almost the total (95 to 99%) diurnal population density and biomass of the pastures sampled at the Pawnee Site. These "important species" are: *Psolessa texana*, *Eritettix simplex*, *Opeia obscura*, *Phlibostroma quadrimaculatum*, *Cordillacris cremulata*, *Xanthippus corallipes*, *Arphia conspersa*, *Arphia pseudonietana*, *Trachyrhachis* sp., and *Melanoplus gladstoni*.

Species of crickets and gryllacridids that are nocturnal or cryptozoic were not quantitatively sampled and comprise an unknown density and biomass. The one mantid, *Litaneutria minor*, was collected in cage samples quite regularly and thus comprises a common orthopteroid insect on the

Table 1. Taxonomic list of orthopteroid insects on Pawnee Site.

Taxon	Peak Biomass (Ad. & Juv.) (mg)	Date of Peak	Abundance Status	Aspect	Restriction
Family Mantidae					
<i>Litaneutria minor</i> (Scudder)			Common	Late	
Family Phasmidae					
<i>Parabacillus coloradus</i> (Scudder)			Rare	Mid-late	
**Family Gryllacrididae					
** <i>Ceuthophilus pallidus</i> Thomas			Common?	Mid	Nocturnal
Family Gryllidae					
<i>Acheta assimilis</i> (Fabricius)			Common?	Mid-late	Nocturnal
<i>Oecanthus nigricornis</i> Walker			Rare	Late	Lowland
** <i>Nemobius fasciatus</i> DeGeer			Common?	Mid	Nocturnal
Family Tettigoniidae					
<i>Conocephalus fasciatus</i> (DeGeer)			Rare	Mid	Lowland?
<i>Conocephalus saltans</i> (Scudder)			Rare	Mid	Lowland
<i>Pediodectes nigromarginata</i> (Caudell)			Rare	Late	
Family Acrididae					
Subfamily Acridinae					
<i>Psolessa texana</i> Scudder	58	7 May	Abundant	Early	
<i>Eritettix simplex</i> (Scudder)	29	9 May	Abundant	Early	
<i>Opeia obscura</i> (Thomas)	119	30 Aug.	Abundant	Late	
<i>Philbostroma quadrimaculatum</i> (Thomas)	86	30 Aug.	Abundant	Late	
<i>Mermiria maculipennis</i> Bruner			Common?	Mid	
<i>Cordillacris crenulata</i> (Bruner)	19	19 July	Common	Mid	
* <i>Cordillacris occipitalis</i> (Thomas)			Rare	Mid	
<i>Ageneotettix deorum</i> (Scudder)			Rare	Mid	
<i>Amphitornis coloradus</i> (Thomas)			Rare	Mid	
Subfamily Oedipodinae					
<i>Xanthippus corallipes</i> Haldeman	18	20 Sept.	Common	Early	
<i>Arphia conspersa</i> Scudder	69	3 May	Common	Early	
<i>Arphia pseudonietana</i> (Scudder)	34	30 Aug.	Common	Late	Upland
<i>Trachyrhachis kiowa</i> (Thomas)	62	5 Sept.	Common	Late	
<i>Trachyrhachis aspera</i> (Scudder)			Rare	Late	
<i>Trimerotropis campestris</i> McNeill			Rare?	Late	Playa?
<i>Tropidolophus formosus</i> (Say)			Rare	Late	
<i>Encoptolophus sordidus</i> (Burmeister)			Common	Late	Lowland
<i>Spharagemon equale</i> (Say)			Rare	Late	
+ <i>Spharagemon collare</i> (Scudder)			Rare	Late?	
<i>Dissosteira carolina</i> (Linnaeus)			Rare	Late?	
<i>Derotnema haydenii</i> (Thomas)			Rare	Late?	
<i>Paropomala wyomingensis</i> (Thomas)			Rare	Late?	
* <i>Chortophaga viridifasciata</i> (DeGeer)			Rare	Early	
+ <i>Heliaula rufa</i> (Scudder)			Rare	Early	
Subfamily Cyrtacanthacridinae					
<i>Melanoplus gladstoni</i> Scudder	276	19 Sept.	Abundant	Late	
<i>Melanoplus infantilis</i> Scudder			Common	Late	
<i>Melanoplus sanguinipes</i> (Fabricius)			Common?	Late	
<i>Melanoplus bivittatus</i> (Say)			Rare (adult)	Late	
<i>Melanoplus femur-rubrum</i> (DeGeer)			Rare	Mid	
<i>Melanoplus packardii</i> Scudder			Common	Late	
<i>Hesperotettix viridis</i> (Thomas)			Rare	Late	Lowland?
* <i>Hesperotettix speciosus</i> (Scudder)			Rare	Mid	
<i>Aeoloplides turbulli</i> (Thomas)			Rare	Mid?	
<i>Phoetaliotes nebrascensis</i> (Thomas)			Rare	Late	

\* New taxa taken by Van Horn during 1970.

\*\* New taxa taken by R. T. Bell during 1970 in pit traps (personal communication).

+ Taxa recorded by Lavigne (1968, personal communication).

Pawnee Site, but at a higher (carnivore or secondary consumer) trophic level than the grasshoppers, all of which are mainly primary consumers. For this reason *Litaneutria* has not been added into biomass calculations for the orthopteran component of the primary consumer trophic level.

The total 43 species are arranged into three categories of abundance: abundant, common, and rare. These categories reflect three ranges of population density as determined at their peak of abundance whether the population is composed of nymphs, adults, or a mixture of both:

Abundant =  $>1$  individual/10 m<sup>2</sup>

Common = 0.10 to 1.00 individual/10 m<sup>2</sup>

Rare =  $<0.10$  individual/10 m<sup>2</sup>

Of these species 5 are listed as abundant, 13 as common, and 25 as rare.

All of the abundant species are important in biomass estimation, and some of the common species as, for example, *Xanthippus corallipes*, which though not abundant, are very big, heavy-bodied species with a large biomass. None of the rare species have been used in biomass calculations.

#### Phenology

During all three years of our field work two definite patterns of emergence of nymphs and adults have been detected. This pattern involves grasshoppers with life cycles of two types which can be labeled as "early" and "late".

The "early" season species overwinters in later (3 through 5) nymphal instars and metamorphoses into the adult stage during April and May at the Pawnee Site. By the end of June they have oviposited and have largely disappeared. But the eggs soon hatch and first instar nymphs (1) appear by midsummer. This type of life cycle is depicted graphically in Fig. 3.



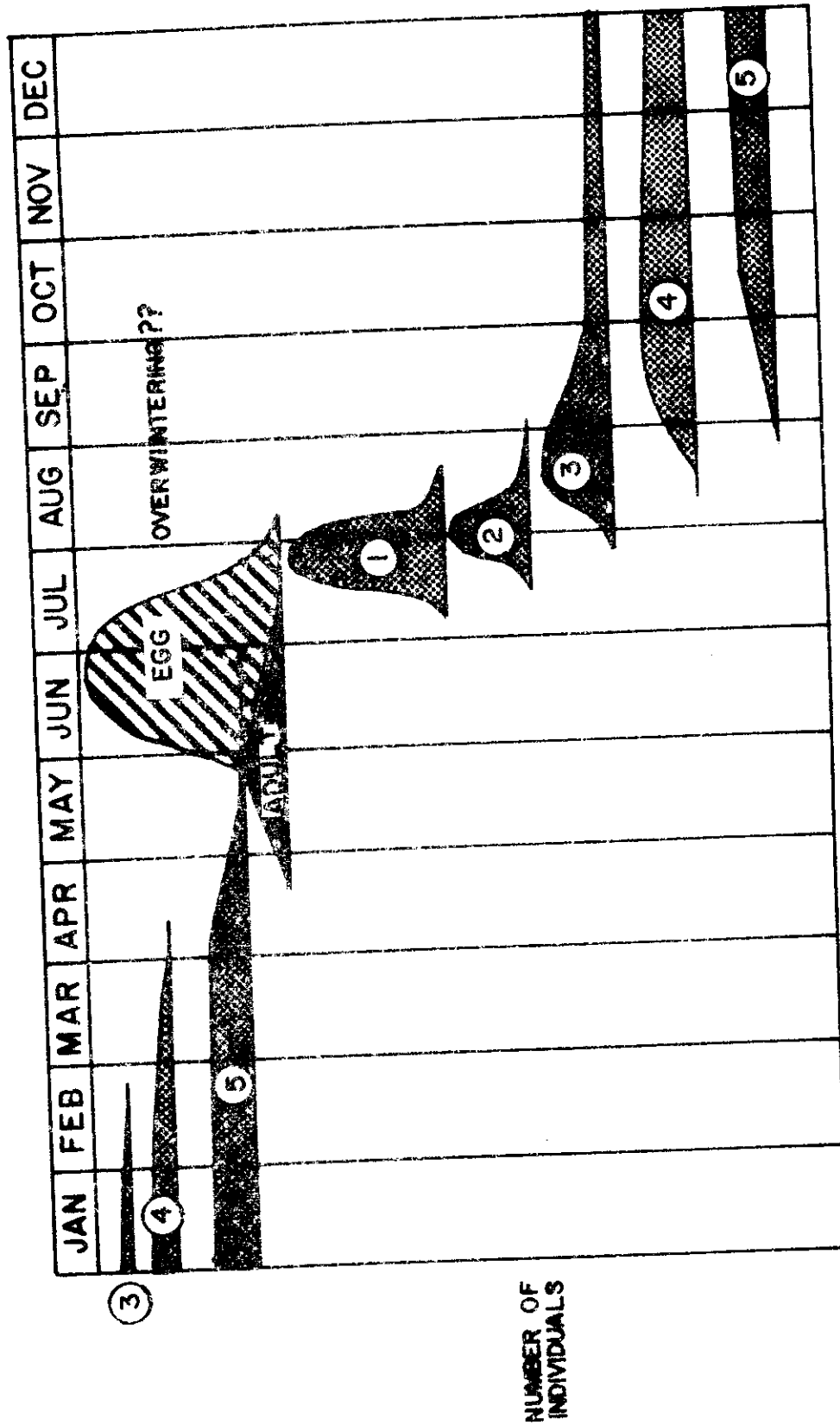


Fig. 3. Life cycle of 'early' season grasshopper species.

The more typical grasshopper life cycle is the "late" type in which eggs hatch in early summer and adults appear in the late summer or early fall (Fig. 4). Some species appear as adults by midsummer (mid-July) and may be labeled "mid". The aspection status of each species for which there is available information is shown on Table 1 in the Aspect column.

Thus far our data have not suggested that upland sites differ in species composition or in population density regardless of grazing intensity. Thus, the populations in 23E and 23W are very similar. However, there is some tendency for certain species to be limited to the lowland site (22E) which has a different vegetation composition (especially a greater proportion of sedges). One species, *Trimerotropis campestris*, was very abundant during 1969 on the dry, cracked, bare earth bed of Lynn Lake, a playa in Section 23 which was inundated in June 1969 and was subsequently devoid of vegetation during the remainder of the 1969 growing season. In 1970 this playa had a vegetation cover, and the numbers of *Trimerotropis* were far below those of 1969. This suggests the possibility of a special habitat for expression of the maximum biotic potential of this species and thus a habitat restriction, at least from a reproductive point of view.

At least three species on the list are cryptozoic and mainly nocturnal in activity. We found the common field cricket, *Acheta assimilis*, fairly often in our sampling hiding under dung or debris. However, we made no sustained efforts to sample such cryptozoic species so that the density of this species has not been very exactly determined, but it probably is a common species by the definition given above. Two other cricket-like species were taken by Ross Bell in pit traps during the summer of 1970 (*Ceuthophilus*

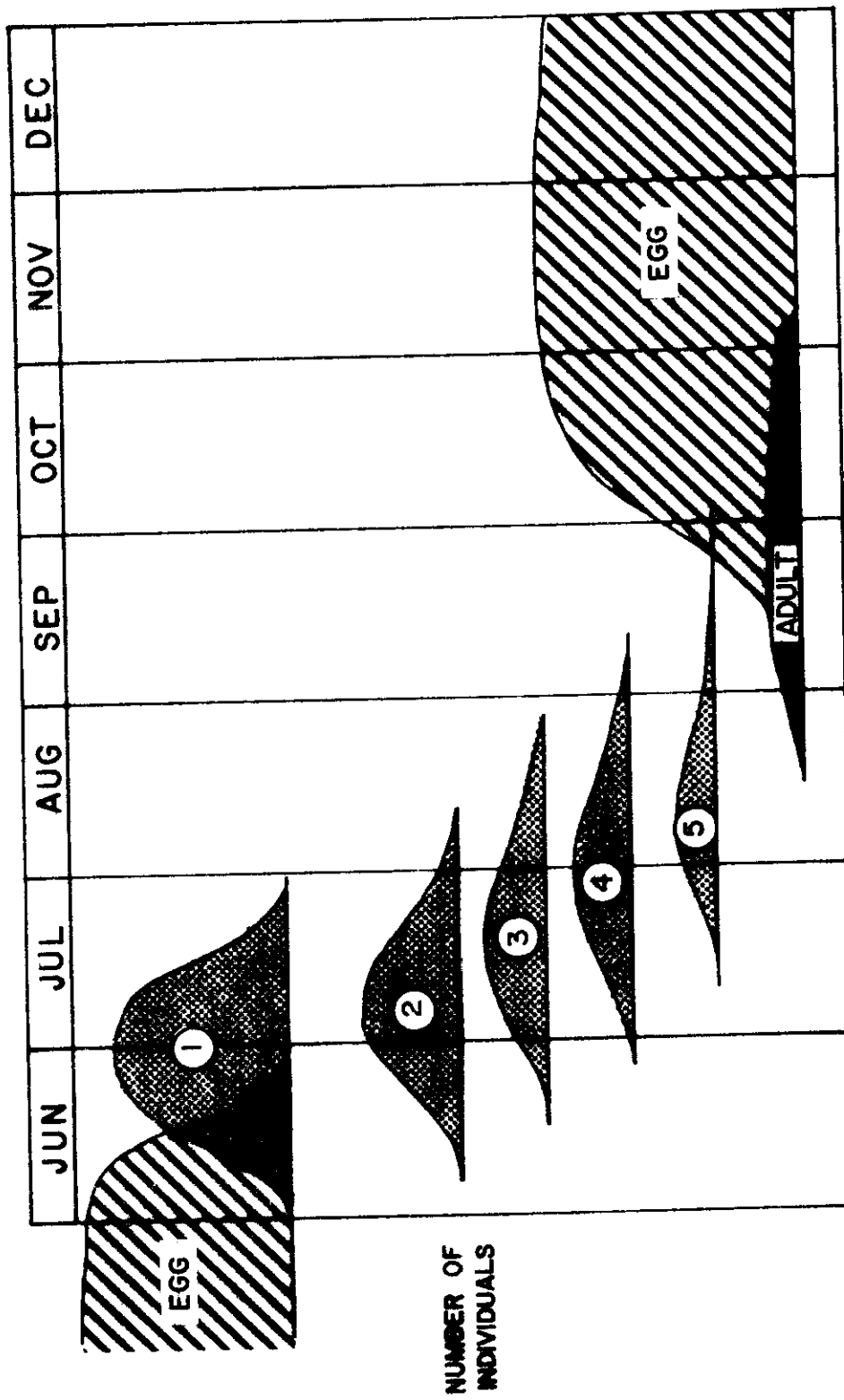


Fig. 4. Life cycle of "late" season grasshopper species.

*pallidus* and *Nemobius fasciatus*). Both of these species are nocturnal and were not taken in any of our sampling. These three species contribute to the primary consumer level, and though it is probably small, we have not quantitatively measured the extent in density or biomass.

The species mentioned above are entered on the checklist and their restriction, either by habitat or time of activity, is appropriately entered in the Restriction column. All other species with no remark in this column may be considered as diurnal and found in both upland and lowland areas.

#### Population Density

All of the raw data from string frame, cage, and walk-flush samples have been converted to numbers of individuals per  $10 \text{ m}^2$  and are summarized in Tables 2 through 7 and Fig. 5 (1970). Appendix I gives population density curves for the most abundant species through 1969 and 1970.

The raw data strongly suggest that no more than a dozen species of grasshoppers (all in Acrididae) comprise at least 95% of the total number of individuals on the three pastures sampled. These species with their peak juvenile and adult population densities are given (Table 2) for late 1968 when the cage was first put into operation and through 1969 and 1970.

In all cases where juvenile and adult densities of a species have comparable figures, these have been compared in 1969 and 1970 (extreme right-hand columns, Table 2). These figures suggest that the juvenile population density was anywhere from 1.7 to 72.0 times that of the adult population and that some species may have much higher mortality rates than others.

Table 2. Peak population densities of more abundant grasshopper species in late 1968 through 1970.

Species	No. Individuals/10 m <sup>2</sup>						No. of Times Juvenile Population Exceeds Adult Population	
	1968 (late)		1969		1970			
	Juvenile	Adult	Juvenile	Adult	Juvenile	Adult	1969	1970
<i>Pseolesea texana</i> - Early	1.85	---	5.7	1.7	8.8	1.3	---	4.4 <u>a/</u>
<i>Eritettix simplex</i> - Early	---	---	4.0 <u>a/</u>	0.2	3.2	0.7	---	5.7 <u>a/</u>
<i>Opeia obscura</i> - Late	---	6.7	13.8	6.7	9.7	3.5	2.0	2.8
<i>Phibostroma quadrimaculatum</i> - Late	---	0.6	2.8	1.7	5.2	1.3	1.7	4.0
<i>Condillacris</i> sp. - Late	---	---	0.7	0.3	5.0	1.3	2.3	3.8
<i>Xanthippus corallipes</i> - Early	1.4	---	7.2	---	0.5	0.1	---	72.0 <u>a/</u>
<i>Arphia conspersa</i> - Early	1.25	---	2.2	0.6	1.2	0.5	2.8	4.4 <u>a/</u>
<i>Arphia pseudonietana</i> - Late	0.75	0.75	2.8	0.1	2.7	0.3	28.0	9.0
<i>Trachyrhachis</i> sp. - Late	---	1.0	1.4	0.7	2.5	0.5	2.0	5.0
<i>Enoptolophus sordidus</i> - Late lowland	---	5.3	19.7	---	---	0.5	---	---
<i>Melanoplus gladstoni</i> - Late	---	7.7	20.5	3.4	8.0	2.4	6.0	3.3
<i>Hesperotettix viridis</i> - Late lowland	---	---	18.7	---	3.0	---	---	---

a/ Adults of 1970 compared to juveniles of 1969, and adults of 1969 compared to juveniles of 1968.

Table 3. Total grasshopper population density on the Pawnee Site, 1969.

Date	Cage: No./30 m <sup>2</sup> String: No./20 m <sup>2</sup>										No./10 m <sup>2</sup> Upland			
	Total Adult					Total Juvenile					Adult	Juvenile	Total (all ages)	
	23E		22E		Total Adult	23E		22E		Total Juvenile				
	23E	23W	22E	22W		23E	23W	22E	22W					
February 22													6.3	6.3
March 21													4.7	4.7
April 11											0.8		2.1	2.9
June 21					12								1.5	1.5
June 22		5	4			47		42			1.7		15.7	17.4
July 4	1				70						0.3			
July 5		1	0			153		200			0.3	37.2 <sup>a/</sup>	37.5	
July 9	8			3	29				110		1.0	36.6	37.6	
July 10														
July 19	9	2	2		49	92		175	11	141	1.8	23.5	25.3	
July 26	1	1			54	75			2	129	0.3	21.5	21.8	
July 27			0			104								
August 9	14				20						4.7	6.7	11.4	
August 10		9				59					3.0	19.7	22.7	
August 30	25				9						3.0	8.3	11.3	
September 12	14	23	35		18	11		11	37	29	6.2	4.8	11.0	
September 27	9		0		13			13						
October 25	16	7	9		19	14		10	23	33	3.8	5.5	9.3	
November 22	0	0	1		16	14		15	0	30	0	5.0	5.0	

<sup>a/</sup> Treating 4 and 5 July as same day.

Table 4. Total grasshopper population density on the Pawnee Site, 1970..

Date	Cage: No./60 (or 30) m <sup>2</sup>								No./10 m <sup>2</sup> Upland		
	Total Adult			Total Juvenile			Total Adult	Total Juvenile	Adult	Juvenile	Total (all ages)
	23E	23W	22E	23E	23W	22E	23E + 23W	23E + 23W			
May 3	4	8		9	2		12	11	2.0	1.8	3.8
May 17	5	10	6	2	0	0	15	2	2.5	0.4	2.9
June 5	11	13	4	21	29	4	24	50	2.0	4.2	6.2
June 6			10			7					
June 7	6	16		27	15		22	42	1.8	3.5	5.3
June 9			4			128					
June 13	1	5	6	13	30	11	6	43	0.5	3.6	4.1
June 16			4			12					
June 17	3	9		50	48		12	98	1.0	8.2	9.2
June 18	3			25							
June 23	8			60							
June 24	1	3	0	82	80	64	4	162	0.4	13.5	13.9
June 25		7			90				1.2	15.0	16.2
June 26			1			64					
July 8	9	4	3	43	90	113	13	133	1.1	11.1	12.2
July 9	10			36					1.7	6.0	7.7
July 10			3			94					
July 11		6			93				1.0	15.5	16.5
July 13	4	10		57	247		14	304	1.2	25.3	26.5
July 14	1	5	2	73	69	89	6	142	0.5	11.8	12.3
July 27			0			42					
July 28	6	16		155	125		22	380	1.8	31.7	33.5
July 29		9	1		52	69			1.5	8.6	10.1
July 30	8			51					1.3	8.5	9.8
August 6	10			44					1.7	7.3	9.0
August 11			13			88					
August 19	19			77					3.2	12.8	16.0
August 20		25	20		59	82			4.2	9.8	14.0
August 30			35			42					
August 31	25	36		45	71		61	116	5.1	9.7	14.8
September 5	16			46					2.7	7.7	10.4
September 6		19	15		47	20			3.2	7.8	11.0
September 20	10	24		50	52		34	102	2.8	8.5	11.3
December 5	0	0	0	13	22	8	0	35	0.0	2.9	2.9

Table 5. Comparison of cage samples taken on the same day in 23E and 23W, 1970.

Date	More in 23E		More in 23W		Approx. Same in Both	
	Adult	Juvenile	Adult	Juvenile	Adult	Juvenile
May 3		X	X			
May 17			X			X
June 5				X	X	
June 7		X	X			
June 13			X	X		
June 17			X			X
June 24					X	X
July 8	X			X		
July 13			X	X		
July 14			X			X
July 28			X			X
August 31			X	X		
September 20			X			X
December 5				X	X	
Total (14 dates)	1	2	10	6	3	6
TOTAL (ad. + juv.)		3		16		9



Table 6. Comparison of maximum juvenile and adult population densities and mortality rates on upland sites from late 1968 (October) through 1970.

Population Component	Probable Time of Density	1968		1969		1970	
		Maximum Total Density	Mortality (%)	Maximum Total Density	Mortality (%)	Maximum Total Density	Mortality (%)
Early juvenile	Late July and August (of previous year)	---	---	10.3 <u>a/</u>	83.5	5.0 <u>b/</u>	50.0 <u>c/</u>
Early adult	Late April to early June	---	---	1.7 <u>d/</u>	---	2.5	---
Late juvenile	Late June to early July	---	---	37.2	77.7	31.7	84.0
Late adult	Late August to mid-October	13.7	---	8.3	---	5.1	---

a/ From 11 October 1968 and probably too late to represent the maximum juvenile population density.

b/ From 12 and 27 September which are highest densities recorded, but are very late and thus probably grossly underestimate the juvenile peak.

c/ Probably a gross underestimate due to underestimate of peak juvenile density.

d/ From 22 June which is late and probably lower than true maximum density.

Table 7. Comparison of cage data with walk-flush data for adult grasshopper population densities (no./10 m<sup>2</sup>) of three grasshopper species.

Date	Section	<i>Xanthippus corallipes</i>		<i>Arphia conspersa</i>		<i>Arphia pseudonietana</i>	
		Cage	Walk	Cage	Walk	Cage	Walk
June 13	23E	0.	0.	0.	0.		
	23W	0.17	0.0008	0.	0.0010		
	22E	0.	0.0013	0.	0.0015		
June 16	22E	0.	0.0008	0.	0.0012		
June 17	23E	0.	0.0015	0.	0.0010		
	23W	0.	0.0004	0.	0.0023		
June 18	23W	--	0.0006	--	0.0003		
June 23	23E	0.	0.0002	0.	0.0001		
	23W	--	0.0006	--	0.0006		
June 24	23E	0.	0.0005	0.	0.0002		
	22E	0.	0.0002	0.	0.0002		
June 25	23W	0.	0.0003	0.	0.0005		
June 26	22E	--	0.0002	--	0.0002		
August 30	22E					0.033	0.0062
August 31	23E					0.017	0.0030
	23W					0.	0.0010
September 5	23E					0.	0.0023
September 6	23W					0.	0.0023

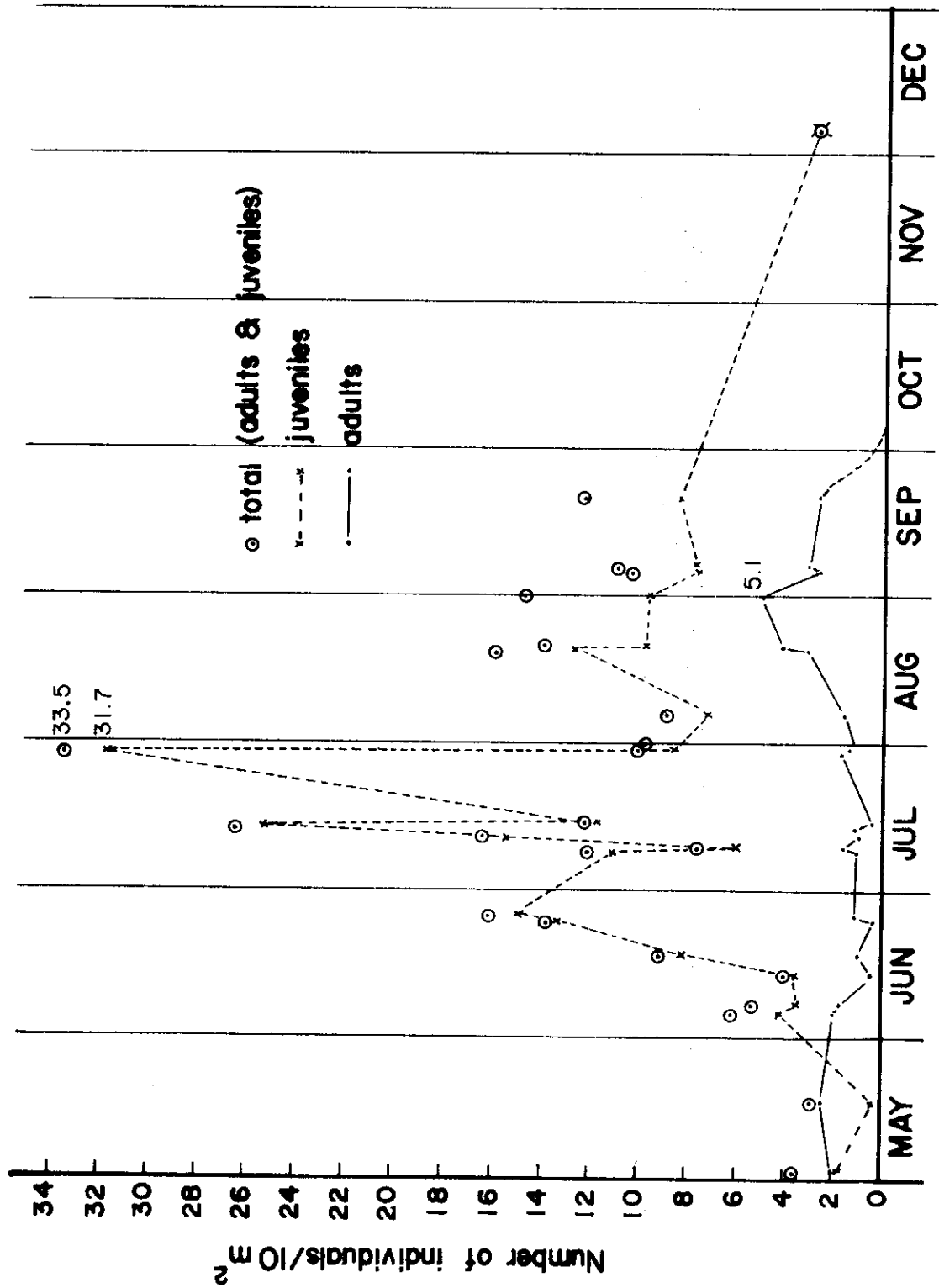


Fig. 5. Total upland grasshopper population density dynamics, 1970.

Total grasshopper population densities for the grasshopper fauna as a whole are shown on Tables 3 and 4 for 1969 and 1970, respectively. Total juvenile numbers are entered separately from adults. On several dates 23E and 23W were both sampled permitting the addition of the two sampling areas (divided by two to gain an average between heavy-grazed and light-grazed pastures) for upland summer-grazed pastures.

Table 5 compares the samples from 23E and 23W during 1970. This analysis shows clearly that the populations of adults in 23W, the light-grazed pasture, were higher; the same holds true to a lesser degree for juveniles.

From Tables 3 and 4 are extracted the peak juvenile and adult densities for both years, adding data from October of 1968. (From Table 3 I averaged the juvenile cage samples of July 4 and 5 to give what may be a more realistic, and certainly a more conservative, maximum peak density even though they were not taken on the same day.) From these extracted maxima can be calculated estimates of mortality from hatching of eggs through the five nymphal instar stadia. To calculate the mortality of the early season fauna, the maximum juvenile abundance from July or August of the previous year is divided into the maximum adult population density for the year being considered. For the late fauna mortality the juvenile peak is divided into the peak adult density of the same year.

The data from our 'walk' sampling are summarized in Table 6 and are compared to data for these species from the cage samples. Although all three of these species are conspicuous, they are also of rather low adult population density as the data indicate. So low is their density that they are rarely taken in the cage samples, but by covering a much larger area

on the "walks" (3000 to 6000 m<sup>2</sup>) all three were regularly flushed. Data for July are lacking from Table 6 because we assumed the complete absence of any adults of these three species for July and most of August and thus did not sample with this method during that interval.

The species population density curves included in Appendix I for 1969 include so few dates that the individual curves for age groups have too few points to generate a line in which one could place much confidence. However, in 1969 there are enough collecting dates to generate lines for the individual age groups of the most abundant species to show the staggered appearance and buildup of successive instars and the larger population densities of earlier age groups. Thus these groups of curves, based on real data, show some resemblance to the theoretical curves of Fig. 3 and 4.

#### Biomass

Ovendy weight data for all ages and sexes of 12 of the more abundant grasshopper species on the Pawnee Site (containing more than 2200 specimens) are summarized in Table 8. Both species of *Trachyrhachis* are combined here because of our inability to distinguish the nymphs as to species.

In all species the adult female weighed more than the male, often by a factor of two or more. However, this tendency becomes progressively less apparent in earlier age classes. Thus, in most cases the sexes from first through third nymphal individuals do not differ in weight.

Table 8. Biomass data (ovendry weights) for more abundant species of Pawnee grasshoppers.

Species	Age	Sex	Wt.(mg)	N	Species	Age	Sex	Wt.(mg)	N
<i>Peolessea texana</i>	Adult	♂	26	53	<i>Mermiria maculipennis</i>	Adult	♂	19	6
	Adult	♀	60	60		Adult	♀	38	7
	5	♂	18	39		5	♂	15	4
		♀	24	28			♀	29	2
	4	♂	9	29		4	♂	10	3
		♀	15	33			♀	12	1
	3	♂	6	26		3	♂	4	1
		♀	7	21			♀	8	1
	2	♂	4	21		2	♂	5	1
		♀	3	43			♀	3	2
	1	♂	2	69		1	♂	2	5
		♀					♀		
<i>Eritettix simplex</i>	Adult	♂	28	7	<i>Cordillacris crenulata</i>	Adult	♂	12	17
	Adult	♀	72	25		Adult	♀	24	12
	5	♂	26	8		5	♂	13	14
		♀	26	4			♀	15	12
	4	♂	20	15		4	♂	3	15
		♀	17	7			♀	5	9
	3	♂	8	10		3	♂	5	4
		♀	10	18			♀	6	6
	2	♂	4	8		2	♂	3	6
		♀	4	11			♀	3	3
	1	♂	2	20		1	♂	2	16
		♀					♀		
<i>Opeia obscura</i>	Adult	♂	18	37	<i>Xanthippus corallipes</i>	Adult	♂	190	6
	Adult	♀	56	23		Adult	♀	578	9
	5	♂	12	26		5	♂	132	43
		♀	21	13			♀	209	23
	4	♂	7	64		4	♂	74	39
		♀					♀	112	36
	3	♂	7	17		3	♂	42	6
		♀	7				♀	49	13
	2	♂	3	38		2	♂	21	5
		♀	3	60			♀	24	13
	1	♂	2	150		1	♂	7	23
		♀					♀		
<i>Phlibostroma quadrimaculatum</i>	Adult	♂	29	34	<i>Arphia conspersa</i>	Adult	♂	83	16
	Adult	♀	79	44		Adult	♀	165	16
	5	♂	16	9		5	♂	61	5
		♀	29	10			♀	61	3
	4	♂	10	10		4	♂	32	1
		♀	18	10			♀	13	7
	3	♂	8	6		3	♂	17	10
		♀	10	10			♀	16	6
	2	♂	3	6		2	♂	8	5
		♀	4	12			♀	10	5
	1	♂	2	12		1	♂	4	14
		♀					♀		
<i>Arphia pseudonietana</i>	Adult	♂	102	29	<i>Trachyrhachis sp.</i>	Adult	♂	30	2
	Adult	♀	207	19		Adult	♀	83	11
	5	♂	70	7		5	♂	23	12
		♀	65	7			♀	51	4
	4	♂	32	5		4	♂	22	7
		♀	50	5			♀	19	3
	3	♂	9	3		3	♂	8	9
		♀	22	6			♀	7	12
	2	♂	8	9		2	♂	6	4
		♀	5	4			♀	4	4
	1	♂	4	16		1	♂	3	18
		♀					♀		
<i>Encoptolophus sordidus</i>	Adult	♂	48	7	<i>Melanoplus gladstoni</i>	Adult	♂	88	25
	Adult	♀	133	4		Adult	♀	118	23
	5	♂				5	♂	35	10
		♀					♀	59	10
	4	♂	10	7		4	♂	26	30
		♀	13	6			♀	20	20
	3	♂	8	8		3	♂	10	30
		♀	9	6			♀	10	30
	2	♂	5	10		2	♂	8	30
		♀	6	13			♀	6	30
	1	♂				1	♂	1.49	60
		♀					♀		

Utilizing the weight data from Table 8, Table 9 is generated which gives the total biomass dynamics for each species and for the grasshopper fauna as a whole through 1970. Each number in the body of the table represents the number of milligrams of dry-weight biomass of all the specimens caught in the sample of that day, taking into account both age and sex of each specimen. The totals for the whole fauna are shown graphically as Fig. 6.

By the same process the biomass dynamics for 1969 and the total biomass for late (October 10) 1968 have been calculated and compared with the dynamics of 1970 in Fig. 7. The curves have been smoothed and the dotted portions portray probable trends, but without actual winter sample data to support them. The most significant comparisons that can be made are the late summer maxima which decline greatly from 1968 to 1970 (from 1.37 g/10 m<sup>2</sup> in 1968 to 0.56 g in 1969 and to 0.33 g in 1970).

These data, especially the more extensive data collected during 1970, indicate that the annual increase in biomass throughout the summer is a function of growth of individual organisms despite the loss of numbers through nymphal mortality. A large number of early instar grasshoppers in the early summer weigh very little, but a much lower adult population in late summer and fall weigh much more per unit area because of the much greater biomass per individual adult.

Judging from the more complete 1970 data, there appears to be no discernible hump in the biomass curve for the early adult population even though the largest, heaviest species, *Xanthippus corallipes*, was in its adult stage at this time. An explanation is that the total early adult

Table 9. Total biomass dynamics for abundant grasshopper species 1970.

Species	April			May			June												July				
	10	3	17	5	6	7	8	9	13	15	16	17	18	23	24	25	26	8	9	11	12	13	14
Early																							
<i>Peotlessa texana</i>	65	30	38	48	45	58			18	14	4	30	12	62	14	35	4	9	15	28	3	13	5
<i>Eritettix simplex</i>	9	3		13	17			29	10	24	17				3					5		8	
<i>Xanthippus corallipes</i>		6		8					9		7	9	3	4	3	3	2	5					
<i>Arphia conspersa</i>	3	69	27			14			2	2	2								3			4	
Mid																							
<i>Trachyrhachis</i> sp.							4						4	5	3			1	21	4	3	9	
<i>Cordillacris</i> sp.				1	5	5	4				12			10	10	2		15	14	8	16		
Late																							
<i>Opeia obscura</i>				2	2	1	30	6	40	1	3	7	3	10	16	12	13	28	9	29	50	27	
<i>Melanoplus gladstoni</i>				3	2	1		6	2	1	3	1	3	1	17	7	4	3	6	14	26	10	
<i>Phliostrota quadrimaculatum</i>								10			1	1		2	1			1	4	1	20	9	
<i>Arphia pseudonietana</i>								1							1						9	7	
TOTALS	77	78	65	75	47	95	39	90	46	14	42	78	26	93	67	61	24	62	69	92	3	145	71

Species	July			August												September			October			December		
	27	28	29	30	6	10	11	12	13	19	20	30	31	5	6	7	19	20	2	3	4	17	7	
Early																								
<i>Peotlessa texana</i>		11	6	1	3	10	13		39	12	11	20		22	10	13	11	31	41		44	22		
<i>Eritettix simplex</i>					5	4	5	4	4	2	3	3			13		7	2	7		10	9		
<i>Xanthippus corallipes</i>					1	1	12	8	3			1		3	5		1	18	1		10	49		
<i>Arphia conspersa</i>	12	4			2	22	10	3	13	27				2	21		6		7		14	17		
Mid																								
<i>Trachyrhachis</i> sp.	5	17	13		10	18	19	37	43	26	8	36		62	4		14		21		10			
<i>Cordillacris</i> sp.	12	19	15		6		10		4	5	10													
Late																								
<i>Opeia obscura</i>	13	99	31	58	45	69	76	42	56	87	119	106		44	75		13	60	61	43	10	12		
<i>Melanoplus gladstoni</i>	10	68	14	7	2	65	56		63	49	115			62			276	22	106	20		23		
<i>Phliostrota quadrimaculatum</i>	11	7	16	5	6	14	21	21	37	21	86	24		44			10	22	26	26	12			
<i>Arphia pseudonietana</i>		6	13	7	11	3	8	13	2	22	34	17		2	2		4				4			
TOTALS	63	212	112	93	91	26	195	222	138	221	238	308	332	179	192	13	318	179	167	166	36	139	97	



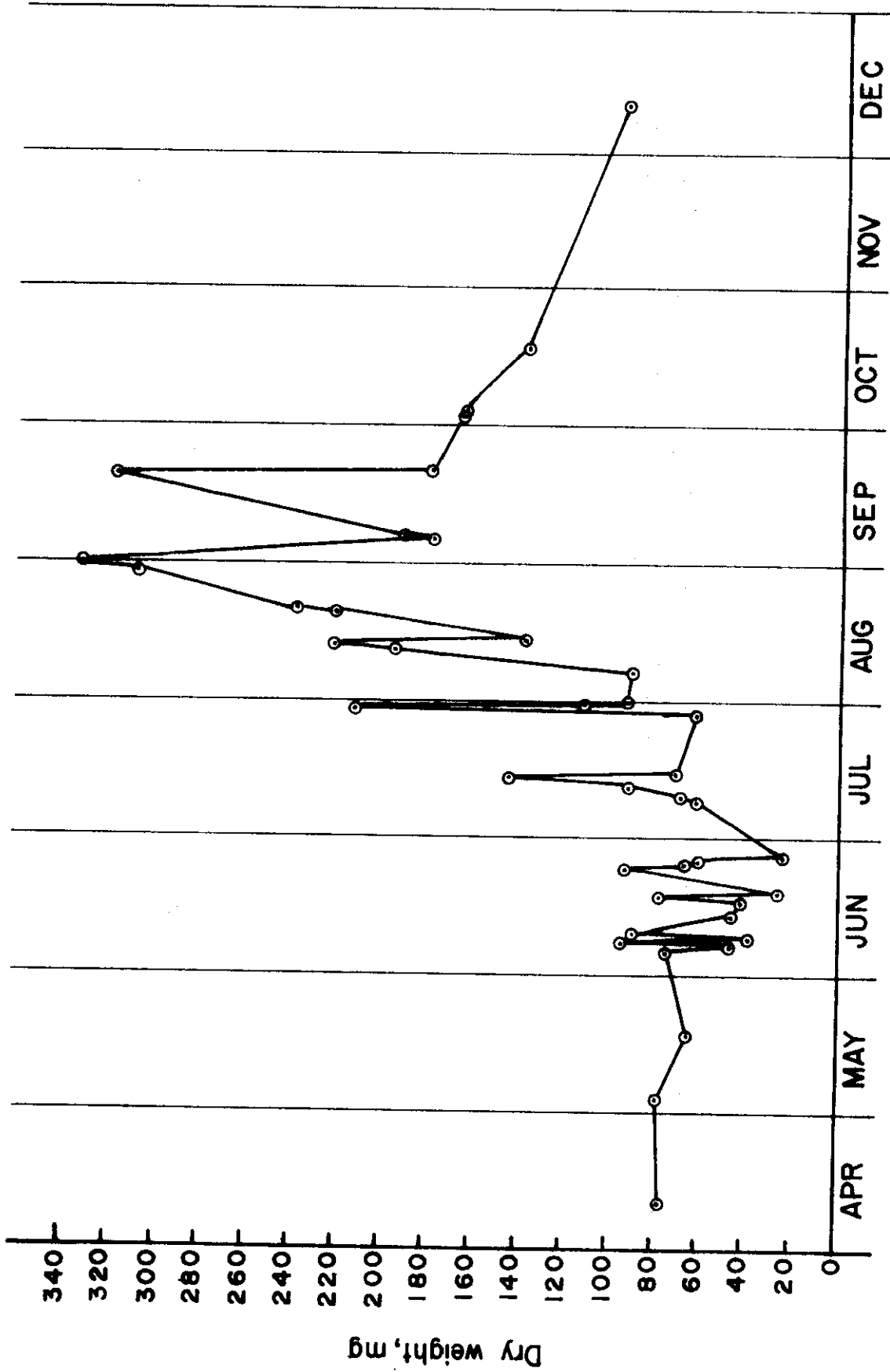


Fig. 6. Total grasshopper biomass dynamics, 1970.

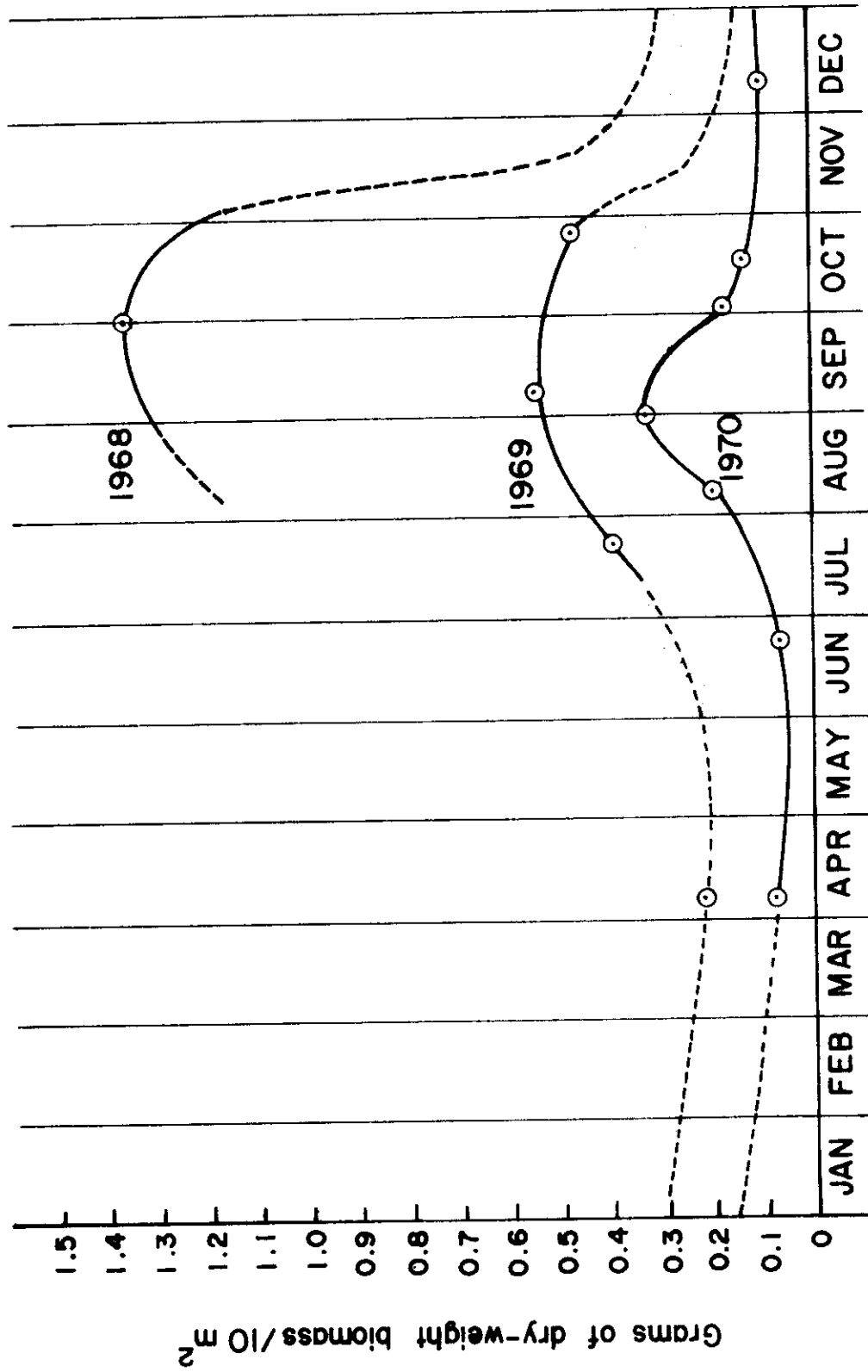


Fig. 7. Total grasshopper biomass dynamics, 1968-1970.

population was very low and that only *Psolessa texana*, a very small-sized species had a population density large enough ( $1.3 \text{ adults}/10 \text{ m}^2$ ) to appear consistently in cage samples during May and June.

Fig. 8 provides dynamics of generalized annual grasshopper density and biomass.

## DISCUSSION

### Status of Taxonomic Survey

All of our sampling occurred within a one mile radius in Sections 22, 23, and 26 where the upland plant community is dominated by blue grama and buffalo grass and the lowland site by the above plants plus sedges and forbs in greater relative abundance. Thus we sampled not more than two subtypes of the total grassland community of the Pawnee Site. Lavigne (1969), however, reported a list of orthopterans from several other vegetation subtypes on the Pawnee Site, and he listed two species, *Spharagemon collare* (Scudder) and *Heliaula rufa* (Scudder), that we did not take. R. T. Bell utilized pit traps during the summer of 1970 and collected two nocturnal species, *Ceuthophilus pallidus* Thomas and *Nemobius fasciatus* DeGeer, which entirely escaped our diurnal sampling. Thus, I suspect that between these two efforts most of the Pawnee grasshopper species are recorded, and while it is probable that a few more species may be found, it is unlikely that a common or abundant species has been overlooked. Of course, there may very well be an invasion by other species from some adjacent area in the future.

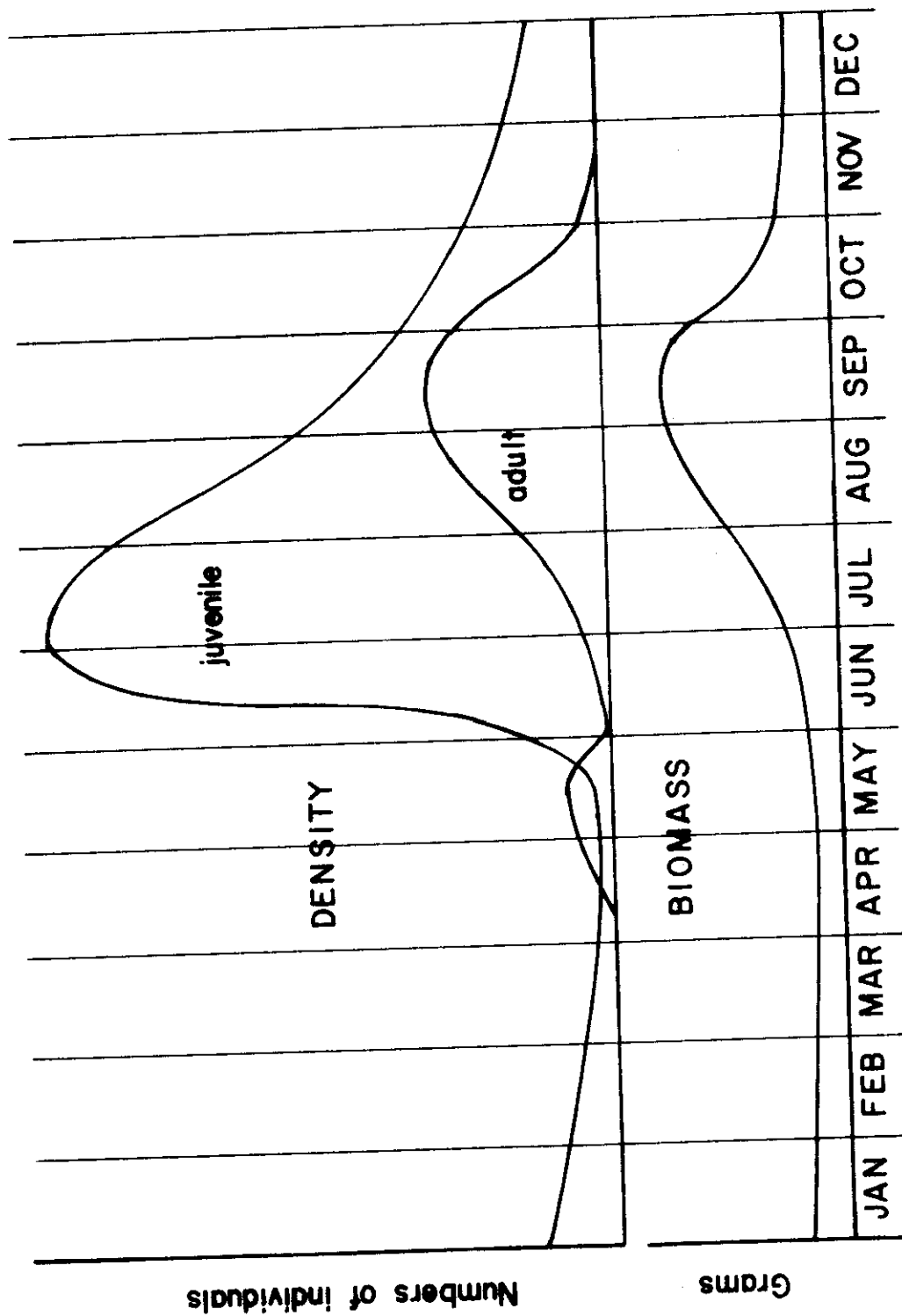


Fig. 8. Generalized annual grasshopper density and biomass dynamics.

### Critique of Sampling Methods

The string frame technique seems quite adequate for sampling during the winter and early spring when there are no flying forms. It is quick, easy, and requires only two people to operate a  $2 \text{ m}^2$  frame.

Our three year experience with the  $2 \text{ m}^2$  cage leaves the following impressions. It is of sufficient size and weight that two young men usually become quite fatigued before taking 30 individual samples. The presence of a third person is highly desirable to (i) relieve one of the operators during the sampling and (ii) be an added check against losing specimens from the sample area through unavoidable spaces between the bottom of the cage and a rough surface.

Although large, and thus somewhat heavy and unwieldy, the size of the sample ( $2 \text{ m}^2$ ) is probably just adequate for sampling grasshoppers. A comparison should be made between the population density data that this study accumulated with that gathered by the  $0.5 \text{ m}^2$  quick trap employed during 1970 for all aboveground invertebrates (including grasshoppers). I suspect that the quick trap data will show a much lower estimate partly because too many specimens escape when the trap is dropped. Our cage also underestimates the population density due to escape of specimens as the cage is lowered, but the loss is probably much less than with the quick trap.

It seems logical to me that our data represent minimum density (and biomass) figures. A better estimate would be obtained if the cage could have been lowered faster (or dropped) to the ground, but its design, construction, and materials (primarily aluminum) did not permit such rugged