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Population dynamics and energy budgets of *T. pulvinata* Uvarov and *P. infumata* Brunn (Orthoptera: Acrididae)

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Abstract. The population dynamics and energy budgets of two grasshopper species *Tristria pulvinata* Uvarov and *Phlaeoba infumata* Brunn were studied in a grassland at Kurukshetra. Males outnumber females. The aboveground net primary production was more in stand I as compared to that in stand II. Mean secondary production was 753.88 mg m^{-2}. Field population of the grasshopper species consumed 308.57 K cal m^{-2} during the study period.

Keywords. *T. pulvinata; P. infumata;* secondary production; energy budgets.

1. Introduction

Secondary producers interact within the ecosystem as consumers, utilizing and recycling the products of net secondary production. Numerically, arthropods generally dominate the animal populations of natural ecosystems. Only recently have ecologists begun to consider the functional role of the arthropod community within the terrestrial ecosystems. Considerable work on related fields has been done in various other grassland ecosystems (Smalley 1960; Odum *et al* 1962; Gyllenberg 1969; Nakamura *et al* 1971; Bhatnagar and Pfadt 1973; Delvi and Pandian 1979; Vats and Kaushal 1981). To clarify the role of consumers of *Desmostachya bipinnata* dominated grassland, the population density and productivity of two grasshopper species were estimated for 2 yrs from June 1976 to May 1978 in the present investigation.

2. Material and methods

2.1 *The study area*

The study site is situated at the university campus at Kurukshetra (29° 58′ N and 76° 51′ E). The climate of Kurukshetra is monsoonic, with an average rainfall of 800 mm. During the study period, the mean maximum temperature varied from 21.3°C (January) to 37.8°C (June) while the mean minimum temperature ranged from 6°C (December) to 24.6°C (June). There are three wet months of rainy season (July to September) and nine dry months. The dry period is further divisible into a cool dry period from October to February (winter season) and a hot dry period from March to June (summer season). The seasonal data on temperature and rainfall of the study site are presented elsewhere (Vats and Kaushal 1981).

2.2 *Vegetation*

Two types of vegetation were recognized. An area with mixed-grasses was designated as stand I, whereas an area dominated by the perennial grass *Desmostachya bipinnata* was referred to as stand II.

2.3 *Estimation of population density, biomass, secondary productivity and energy budget*

Population density was studied using removal-trapping method since the insects once trapped had the least chance to escape. For this purpose, a trap of 1.75 m^2 with a small entrance (82×85 cm) on one side, 40 cm above the ground level was constructed. Wire gauge of 5 meshes per cm was fixed on the sides and top of the trap. It was carried from one sampling spot to another with handles fixed on the opposite sides. The trap was lowered randomly to the ground at ten different spots, five per stand. While moving the trap, the tip of the grassblades was not disturbed. The insects thus entrapped were collected, oven-dried at 60°C, and weighed in a single pan electric balance (accuracy up to 0.1 mg).

Secondary production was calculated by using sampling data to compute the mean biomass present during a sampling period. Production was calculated as:

$$P = S + \sum_{i=2}^{n} \tfrac{1}{2}(N_i + N_{i-1}) \cdot (W_i - W_{i-1})$$

where N_i = the number of grasshoppers present at time i; W_i = the mean weight per grasshopper at i; i = the sample time; S = the standing crop at time i = 1. It was assumed that $N_i \leq N_{i-1}$ and $W_i \geq W_{i-1}$. When W_i was less than W_{i-1}, the production was considered as zero. This expression was also used by others (Wiegert 1965; van Hook 1971 and Riegert and Varley 1973).

The energy content of grasshoppers, plant material and faecal matter was determined by using an adiabatic bomb calorimeter (Phillipson 1964). All the materials were dried in an oven at 60°C, ground to a fine powder by an electric grinder and made into pellets.

For studies on feeding, grasshoppers brought from the field and confined to small cages were fed for 24 hr with fresh plant material of *Desmostachya bipinnata* kept in small tubes containing water. At the end of the experiment, the grasshoppers were weighed; unconsumed plants and egesta were collected and oven-dried at 80°C till a constant weight was obtained. The dry weight equivalents of grasshoppers and plant material were obtained by oven-drying of these materials. Food consumption was calculated as the difference between initial weight of the food provided and the unconsumed material at the end of the experiment after correcting for the weight loss in the food material due to respiration and transpiration. Approximate digestibility (AD) was calculated using the expression:

$$AD = \text{Assimilation/consumption} \times 100$$

Seasonal mean biomass for the estimation of annual consumption was determined by using Petrusewicz and Macfadyen (1970) expression.

$$B = 1/K \sum_{i=1}^{i=k} B_i$$

where, B_i is the successive standing crop estimated and K is the number of sampling times.

3. Results

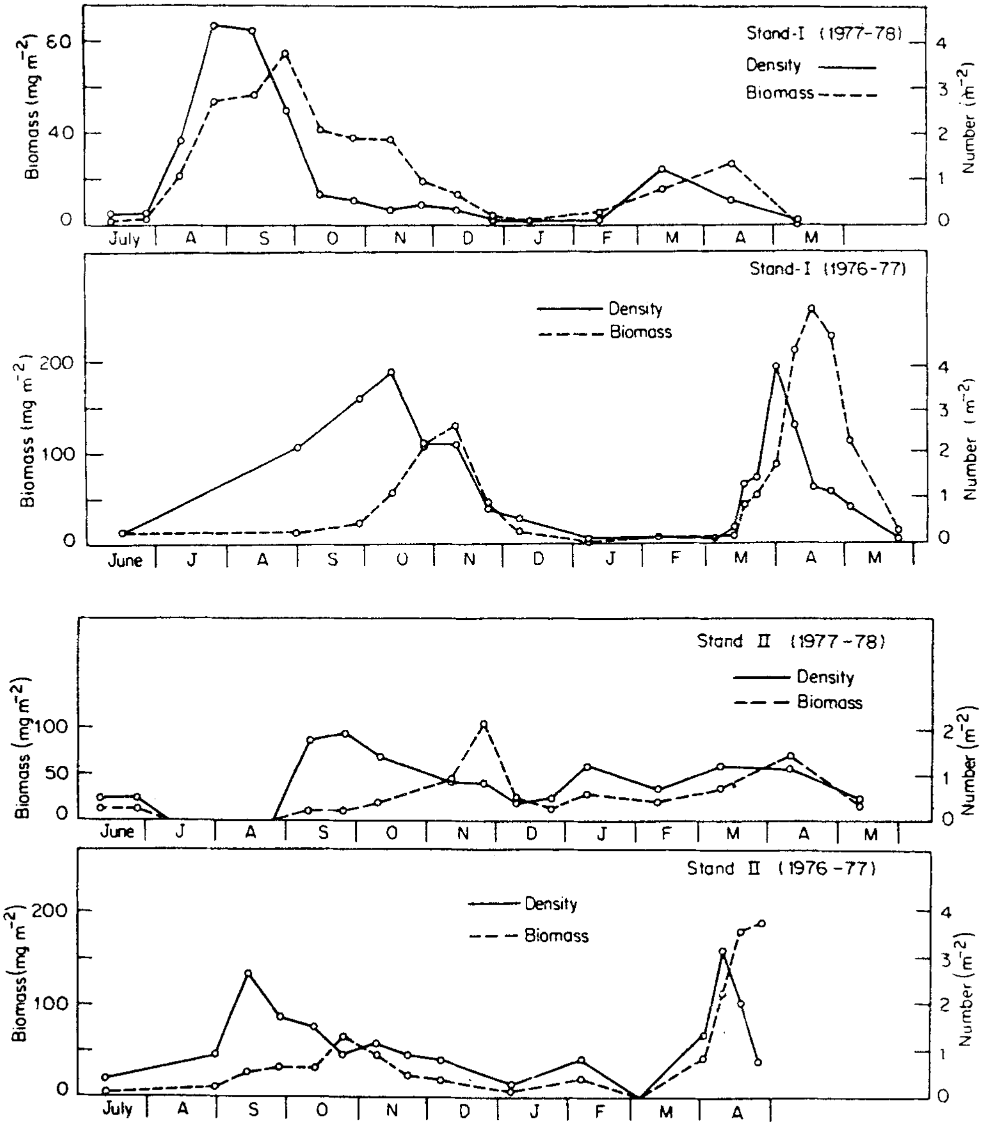
3.1 *Producers*

Eighty-eight plant species were observed in both the stands. Of these, 22 were confined to stand I and 9 to stand II; the remaining were common to both the stands. The maximum number of species was recorded in rainy season (69 in stand I and 58 in stand II) and the minimum in hot dry months of summer (17 in stand I and 13 in stand II). In winter, there were 35 and 30 species in stands I and II, respectively. The live-shoot biomass varied from 1.7±1 (January) to 1487.8±4.8 g m^{-2} (September) in stand I and from 7.8±3.6 (January) to 737.6±2.5 g m^{-2} (October) in stand II. The total live shoot biomass in rainy, winter and summer seasons was 2351.1, 428.8 and 835.5 g m^{-2} in stand I and 986.8, 1013.1 and 502.7 g m^{-2} in stand II, respectively. Aboveground net primary production was 2307 g m^{-2} yr^{-1} on stand I and 1208.4 g m^{-2} yr^{-1} on stand II.

3.2 *Population density and biomass*

Variations in the population densities and biomass of grasshoppers in relation to the seasons are shown in figures 1-4. Two peaks of population density (adult + nymphs) were obtained on both the stands; one during rainy season (first emergence) and another at the beginning of the summer season (second emergence). Hence two generations of both the species were recorded in a year. Population density in the first year reached its maximum value towards the end of rainy season *i.e.* in October on stand I and in September on stand II. Thereafter, it declined with the approach of winter season till February. Again emergence of nymphs occurred, hence second peak was obtained on both the stands during the beginning of summer season *i.e.* March and April. Density declined thereafter because of extreme summer on both the stands. In the two grasshopper species, the average value of adults was 6.3% with 22.8% biomass and nymphs 93.7% with 77.2% biomass.

Grasshoppers entering the population in early summer (March and April) and early rainy season consisted of small nymphs, resulting in sharp decrease in the biomass. Two peaks of biomass were obtained on both the stands, *i.e.* one towards the end of April and another in the beginning of winter period as nymphs of latter stages and adults were present. Biomass values decreased considerably towards extreme summer and winter seasons because of low population density.



Figures 1-4. Variation in population density and biomass of grasshoppers.

3.3 *Secondary production*

Data on seasonal changes in the mean dry weight per individual and secondary production on both the stands are given in tables 1 and 2. However, growth rates are generally not constant because of the presence of different instars of both the species of grasshoppers which hatch at different intervals. The production estimates do not include exoskeleton material moulted by the growing nymphs as it was not possible to identify it in the field and also because of the presence of other insect fauna. The initial standing crop (mg m^{-2}) was used as a minimal estimate of production up to the time, sampling was started.

Table 1. Mean weight per individual and secondary production of grasshoppers on stand I during June 1976 to May 1978.

Date		Mean weight (m^{-2})	Secondary production* ($mg\ m^{-2}$)
1976	15/6	41.18	(9.06)
			Total 9.06
	31/8	6.20	(12.71)
	28/9	7.25	2.74
	12/10	14.71	2.59
	26/10	49.53	103.07
	9/11	59.72	22.06
	23/11	57.58	0.00
	7/12	24.43	0.00
1977	7/1	9.27	0.00
	7/2	38.36	3.20
			Total 146.42
	4/3	54.27	(5.97)
	12/3	27.45	0.00
	17/3	40.51	11.17
	22/3	44.34	5.46
	31/3	22.83	0.00
	8/4	84.20	196.38
	16/4	206.30	229.55
	24/4	202.28	0.00
	2/5	140.96	0.00
	27/5	125.64	0.00
			Total 448.53
	11/7	6.32	(1.39)
	27/7	9.87	0.80
	11/8	11.71	1.89
	26/8	12.64	2.86
	11/9	13.49	3.64
	26/9	33.46	64.70
	11/10	60.26	39.53
	26/10	67.95	4.81
	11/11	109.74	18.81
	26/11	41.53	0.00
	11/12	39.59	0.00
	26/12	24.55	0.00
1978	11/1	23.91	0.00
	11/2	55.45	3.47
			Total 141.90
	11/3	13.18	(16.47)
	11/4	67.49	47.88
	11/5	2.18	0.00
			Total 64.35

*New cohort for secondary production considered during March (first emergence) and July (second emergence) when eggs hatch.

Table 2. Mean weight per individual and secondary production of grasshoppers on stand II during June 1976 to May 1978.

Date	Mean weight (mg insect^{-1})	Secondary production* (mg m^{-2})
1976		
12/7	9.68	(3.29)
30/8	10.46	0.49
13/9	9.87	0.00
27/9	17.81	17.23
11/10	20.74	4.69
25/10	72.46	62.06
8/11	39.41	0.00
22/11	25.36	0.00
6/12	23.02	0.00
1977		
6/1	28.13	2.62
6/2	29.01	0.45
		Total 90.83
1/4	28.39	(38.89)
9/4	34.82	14.66
17/4	87.42	137.81
25/4	241.20	218.37
10/6	22.93	0.00
26/6	23.20	0.12
		Total 409.85
10/9	4.22	(7.17)
25/9	4.90	1.20
10/10	12.64	12.27
10/11	53.64	44.08
25/11	131.73	62.08
10/12	70.82	0.00
25/12	24.61	0.00
1978		
10/1	24.77	0.13
10/2	26.73	0.46
		Total 127.39
10/3	30.82	(34.83)
10/4	61.58	34.61
10/5	35.98	0.00
		Total 69.44

*New cohort for secondary production considered during March (first emergence) and July (second emergence) when eggs hatch.

3.4 *Energy content*

Table 3 comprises energy values of different biological materials. The energy value for grasshoppers > faeces > plant material (see also Bailey and Riegert 1973; Campbell *et al* 1976).

3.5 *Assimilation rates*

The relationship between food consumption and egesta is presented in table 4. When calculated against duration of a stage per day, the adult females consumed more than the males of both species. The female also consumes more than male in *Parapleurus alliaceous* (Matsumoto 1971); in *Paprides nitidus*, *Siagus australis* and *Brachaspis nivalis* (White and Watson 1972); in *Poecilocerus pictus* (Delvi and Pandian 1979) and in *Parahieroglyphus bilineatus* (Vats and Kaushal 1981). The rate of egestion is higher in females than in males of both the species. Similar results were obtained by Matsumoto (1971) and Vats and Kaushal (1981).

Males were more efficient in assimilating the consumed food than females. Similar observations were obtained by White (1978); Vats and Kaushal (1981); but in *B. nivalis*, females have higher AD than males (White 1978).

Table 3. Energy values of biological materials.

Material	Energy value ($J\ mg^{-1}$ dry wt.)	
T. pulvinata (all stages)	21.62	Mean 21.445
P. infumata (all stages)	21.27	
Faeces (mixed)	20.4	
Plant material	19.56	

All values on oven dry weights.

Table 4. Relationship between food consumption and egestion for the two grasshopper species fed on *Desmostachya bipinnata*.

Stage		Initial biomass ($J\ insect^{-1}$)	Consumption ($J\ insect^{-1}\ day^{-1}$)	Egesta ($J\ insect^{-1}\ day^{-1}$)	AD (%)
T. pulvinata					
Fifth instar	M	1189.25	287.12 (34.74)	179.91 (15.59)	37.34
	F	4108.35	1000.82 (51.66)	752.53 (60.11)	24.81
Adult	M	1599.98	278.35 (28.09)	188.89 (20.15)	32.14
	F	5081.46	942.97 (44.02)	759.21 (44.14)	19.49
				Mean	28.45
P. infumata					
Fifth instar	M	723.22	227.1 (21.28)	154.07 (12.29)	32.16
	F	610.68	762.77 (52.12)	592.68 (56.35)	22.29
Adult	M	1063.6	187.97 (18.43)	131.59 (13.12)	29.99
	F	3786.41	676.07 (35.62)	555.23 (49.16)	17.87
				Mean	25.58

Standard error given in parentheses.

Table 5. Consumption by the field population of *T. pulvinata* and *P. infumata* during June 1976 to May 1978.

Season	No. of days	*Mean biomass ($mg\ m^{-2}$)	Consumption ($cal\ m^{-2}$)
		Stand I	
Summer (March-June)	244 ×	76.629×5.131**×0.935***	89700.86
Rainy (July-Sept.)	184 ×	12.617×5.131×0.935	11137.49
Winter (Oct.-Feb.)	302 ×	45.105×5.131×0.935	65349.95
			Total 166.19 $kcal.m^{-2}$
		Stand II	
Summer	244 ×	62.927×5.131×0.935	73661.49
Rainy	184 ×	9.49 ×5.131×0.935	8377.17
Winter	302 ×	41.648×5.131×0.935	60341.31
			Total 142.38 $kcal\ m^{-2}$

*Mean biomass from tables 1 and 2; **Energy content; ***Weight specific consumption

3.6 *Effect of field population on the vegetation*

On the basis of weight-specific consumption, determined under laboratory conditions and the time series biomass determined in the field, the effect of field population on vegetation can be determined. The total annual consumption has been obtained by totalling the consumption for all seasons calculated as under:

$$C_S = B \times N \times C_W$$

where C_S is the seasonal consumption, B is the mean seasonal biomass, N is the number of days in a season during which the hoppers were available and C_W is the weight-specific consumption. Average weight-specific consumption for adults of both the species comes to 0.935 $cal\ mg^{-1}\ day^{-1}$ (tables 3 and 4).

Total consumption by grasshoppers on both the stands was 308.57 $kcal\ m^{-2}$ during June 1976 to May 1978. Consumption was higher on stand I (166.19 $kcal\ m^{-2}$) than on stand II (142.38 $kcal\ m^{-2}$) because of higher population density (table 5).

4. Discussion

A maximum density of 4.34 m^{-2} on stand I and 3.19 m^{-2} on stand II as observed presently appear to be rather low because of our trapping technique as compared to the densities in other grassland communities (20 m^{-2} in terrestrial ecosystem Parker 1952; 31.5 m^{-2} of *Chorthippus parallelus* in *Agrotis tenuis* grassland Gyllenberg 1969; 8.5 m^{-2} in *Andropogon virginicus* van Hook 1971; 4.4 m^{-2} in Natural grassland Riergert *et al* 1974 and 3.76 m^{-2} in short-grass prairie van Horn 1972).

Thus different species are dominant in different communities depending upon the vegetation and climatic conditions of the regions concerned.

Maximum biomass values were 257.87mg m^{-2} on stand I and 190.55 mg m^{-2} on stand II. Biomass values vary with the type of vegetation (817.4 mg m^{-2} in the old field and alfalfa field Wiegert 1965; 1150.32 mg m^{-2} in the oldfield ecosystem at Tennessee van Hook 1971; 189 mg m^{-2} in the mixed-grass forbs at Georgia Menhinick 1967 and 83.72 mg m^{-2} in natural grassland Riegert *et al* 1974).

Maximum values of population density which normally occur in the beginning of rainy season, were recorded in October on stand I and in September on stand II in the first year of study period. This was due to temporary water-logging of the area under investigation. Emergence occurred in the rainy season on both the stands in the second year when both temperature and moisture were favourable.

Criddle (1917) reported that abundance of grasshoppers is negatively correlated to rainfall. Pradhan and Peswani (1961) stated that high and low temperature adversely affected the population density of *Hieroglyphus nigrorepletus*.

Minimum values of population density were obtained during extreme summer (May-June) and winter seasons (December-February) when productivity was low, rainfall scanty and temperature high in summer and low in winter. These factors are also known to affect the population density of grasshoppers (Andrewartha and Birch 1954; Clark *et al* 1967; Bhatnagar and Pfadt 1972; Dempster 1975).

Net secondary production of 810.26 mg m^{-2} on stand I and 697.51 mg m^{-2} on stand II in the present study appears to be higher as compared to the secondary production in other grasslands. Net secondary production of grasshoppers in an oldfield ecosystem at Michigan was 122 mg m^{-2} in 1959; 71.7 mg m^{-2} in 1960 and 878.9 mg m^{-2} in alfalfa field in 1960 (Wiegert 1965). Riegert and Varley (1973) on the basis of collective biomass data obtained the values of 45.97, 24.51 and 47.29 mg m^{-2} in the unstressed, burned and grazed plots respectively. The relatively high values reported in the present study were probably due to higher primary productivity or by greater accuracy of the equation used here.

Assimilation efficiency in the present study falls within 27-80% as reported by Odum and Smalley (1959), Wiegert and Evans (1967); Delvi and Pandian (1979) and White (1978).

Field population of grasshoppers ingested 0.9% of the net primary production indicating that they had little impact on the primary production. Wiegert (1965) also reported that total ingestion by grasshoppers was less than 0.5% in the oldfield and 2.5% on the alfalfa field.

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References

Andrewartha H G and Birch L C 1954 *The distribution and abundance of animals*; (Chicago: University of Chicago) p.782

Bailey C G and Riegert P W 1973 An energy budget of *Encoptolophus sordidus costalis* (Scudder) (Orthoptera: Acrididae) in a grassland ecosystem; *Can. J. Zool.* **51** 91-100

Bhatnagar K N and Pfadt R E 1973 *Growth, density and biomass of grasshoppers in the short-grass and mixed-grass associations*; *Tech. Report U.S. IBP Grassland Biome No.* 225; Colorado. State University: Fort-Collins p.120

Campbell A, Singh N B and Sinha R N 1976 Bioenergetics of granary weevil; *Sitophilus granarius* (L.) (Coleoptera: Curculionidae); *Can. J. Zool.* **54** 786-798

Clark L R, Geier P W, Hughes R G and Morris R F 1967 *The ecology of insect populations in theory and practice;* (London: Methuen) p.232

Criddle N 1917 Precipitation in relation to prevalence and distribution; *Can. Entomol.* **49** 77-80

Delvi M R and Pandian T J 1979 Ecological energetics of the grasshopper *Poecilocerus pictus* in Bangalore fields; *Proc. Indian Acad. Sci. (Anim. Sci.)* **B88** 241-256

Dempster J P 1975 *Animal population ecology*; (London: Academic Press) p.155

Gyllenberg G 1969 The energy flow through a *Chorthippus parallelus* (Zett.) (Orthoptera) population in a meadow in Tvarminne, Finland; *Acta Zool. Fennica* **123** 1-74

Matsumoto T 1971 Estimation of population productivity of *Paraplerus alliaceus* Germer (Orthoptera: Acrididae) on a *Miscanthus sinensis* Anders. II Population productivity in terms of dry weight; *Oecologia* **7** 16-25

Menhinick E F 1967 Structure, stability and energy flow in plants and arthropods in a *Sericea lespedeza* stand; *Ecol. Monogr.* **37** 255-272

Nakamura K, Nakamura M, Matsumoto T and Hayakawa K 1971 Estimation of population productivity of *Parapleurus alliaceus* Germer (Orthoptera) in *Miscanthus sinensis* grassland. I: Estimation of population parameters; *Oecologia* **7** 1-15

Odum E P and Smalley A E 1959 Comparison of population energy flow of a herbivorous and deposit feeding invertebrate in a saltmarsh ecosystem; *Proc. Natl. Acad. Sci. Wash.* **45** 617-622

Odum E P, Connel C E and Davenport L B 1962 Population energy flow of three primary consumer components of oldfield ecosystems; *Ecology* **43** 88-96

Parker R E 1952 *Grasshoppers, Insects, the year book of agriculture*, (Washington: USDA) p.595-605

Petrusewicz R C and Macfadyen A 1970 *Productivity of terrestrial animals*: *Principles and methods* (IBP) Handbook 13; (Oxford: Blackwells) p.190

Phillipson J 1964 A miniature bomb calorimeter for small biological samples; *Oikos* **15** 130-139

Pradhan S and Peswani K M 1961 Studies on the ecology and control of *Hieroglyphus nigrorepletus* Bol. (Phadka); *The Indian J. Entomol.* **23** 79-105

Riegert P W and Varley J L 1973 *Aboveground Invertebrates. II. Population dynamics and biomass production of grasshoppers. Tech. Report IBP Grassland Biome, Matador Project No.*16; University of Saskatchewan, Saskatchewan p.134

Riegert P W, Varley J L and Willard J R 1974 *Aboveground Invertebrates. V. A summary of population, biomass and energy flow. Tech. Report IBP Grassland Biome No.*67; University of Saskatchewan, Saskatchewan p.28

Smalley A E 1960 Energy flow of a salt marsh grasshopper population; *Ecology* **41** 672-677

van Hook R I 1971 Energy and nutrient dynamics of spider and Orthopteran populations in a grassland ecosystem; *Ecol. Monogr.* **41** 1-26

van Horn D H 1972 *Grasshopper population numbers and biomass dynamics on the Pawnee site from fall of 1968 through 1970. Tech. Report U.S. IBP Grassland Biome No.*148; Colorado State University, Fort Collins p.70

Vats L K and Kaushal B R 1981 Population dynamics, secondary productivity and energy budget of *Parahieroglyphus bilineatus* Bol. (Orthoptera: Acrididae Catantopinae) *Acta Oecologia/Oecologia Generalis* **2** 355-369

White E G 1978 Energetics and consumption rates of alpine grasshoppers (Orthoptera; Acrididae) in New Zeland; *Oecologia (Berl)* **33** 17-44

White E G and Watson R N 1972 A good consumption study of three New Zealand alpine grasshopper species; *N.Z.J. Agric. Res.* **15** 17-44

Wiegert R G 1965 Energy dynamics of the grasshopper populations in an oldfield and alfalfa ecosystems; *Oikos* **16** 161-176

Wiegert R G and Evans R C 1967 Investigations of secondary productivity in grassland; In secondary productivity in terrestrial ecosystems (Ed. Petrusewicz K.) Warsaw; *Inst. Ecol. Polish Acad. Sci.* pp.499-518