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Comparative Bioenergetics of Insects from Young & Old Plant Ecosystems

Joyce Wright
Western Kentucky University

Wright,

Joyce Carroll

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COMPARATIVE BIOENERGETICS OF INSECTS FROM YOUNG AND OLD PLANT ECOSYSTEMS

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COMPARATIVE BIOENERGETICS OF INSECTS

FROM YOUNG AND OLD PLANT ECOSYSTEMS

Recommended 20 July 1976
(Date)

Joe E. Winstead
Director of Thesis

H.E. Shadowen

Kenneth A. Nicely

Approved July 26, 1976
(Date)

Elmer Gray
Dean of the Graduate College

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COMPARATIVE BIOENERGETICS OF INSECTS FROM

YOUNG AND OLD PLANT ECOSYSTEMS

Joyce C. Wright July, 1976 31 pages

Directed by: J. E. Winstead, K. A. Nicely, and H. E. Shadowen

Department of Biology Western Kentucky University

Caloric values of insects and arachnids from two woods and two meadow ecosystems were compared. No significant difference was found between the orders Diptera, Homoptera, Orthoptera, Hemiptera, Hymenoptera, or Coleoptera. Caloric values of the class Arachnida were significantly higher in the woods ecosystem at the .05 level of significance. The order Lepidoptera differed at the .01 level of significance and was also higher in the woods samples. For all orders combined the caloric values of the woods samples were higher than the meadow samples at the .001 level of significance.

No consistent pattern was found in seasonal variation in caloric values but fluctuations occurred differently in each order. No significant difference was found in caloric values between animals collected in the spring and those collected in the fall.

Members of the orders Neuroptera and Odonata were lowest in energy content in both woods and meadow ecosystems. Hemopterans were among the highest in caloric value in both systems. All other orders were intermediate. The greatest differences in caloric values existed between the woods and meadow lepidopterans. All caloric values in this study were found to be lower than those reported by other workers.

Seasonal distribution of insects within an ecosystem were considered. The numbers within each order varied independently according to season, stage of life cycle, and feeding habits of the various genera within the order.

Although the area from which the samples were taken was not the same for woods and meadow, habitat preference is still obvious in certain orders. Dipterans were more dense in the woods as compared to other orders, while orthopterans accounted for the majority of specimens from the meadows. Arachnids exhibited preference for a wooded habitat.

INTRODUCTION

The concept of community energetics was brought to the attention of biologists primarily through the work of Lindeman (1942). Since that time emphasis has been placed on the transfer of energy between populations and the transfer of energy within communities. Organisms in nature may be looked upon as systems that accumulate energy, with the accumulation of energy by living organisms defined as production.

All consumer organisms depend upon the transfer of energy from the primary producers. As defined by Wiegert (1965), the functional energy dynamics of a community can be measured by the efficiency with which energy is transferred from one trophic level to the next. Attempts have been made to measure, both directly and indirectly, the flow of energy within systems and to find similarities between population processes of energy use. The unit of measurement is the gram calorie and measurements have been undertaken at different levels of ecological organization. The ranges of measurement have encompassed the individual, populations, and entire ecosystems.

The understanding of energy dynamics has been hampered, however, by incomplete knowledge of the energy content of most plants and animals. Also, for many years the attention of community energetics remained focused upon marine and freshwater habitats. This emphasis upon aquatic systems corresponded with investigations of fish production. Until recently there have been few data available on the population dynamics of terrestrial species. This is particularily true in the case of terrestrial primary consumers.

Among the first determinations of caloric values of animals were the efforts of Smalley (1960) on marsh grasshoppers, Golley (1961) on meadow voles, Odum, Connell, and Davenport (1962) on field mice and Wiegert (1964) on the meadow spittlebug. A massive compilation of caloric values has been organized by Cummins and Wuycheck (1971) which is a survey of energy values determined for both plants and animals. Currently that reference serves as a guide for comparisons of studies accomplished by other workers.

Insects have proven to be good research tools in analysis of energy values. They are of workable size and are abundant and relatively available. The distribution of insects encompasses many different habitats so that comparisons between habitats or ecosystems may be made using insects, in many instances, as a common denominator. Even though some variables do exist and must be taken into consideration, organisms that complete a life cycle within one year present some excellent advantages for the study of population energy flow in nature. The amount of body fat, which contains a high energy value, varies with age and season. This may require collection of different age groups at each season for a complete populational analysis. Other factors which may affect caloric values are sex, reproductive state, and nutritional history. Engelmann (1961) has noted that food habits may be of prime importance in determining ecological efficiency. Variation may exist within or between orders or species. For example, homopterans feed upon xylem sap which has its highest concentration early in the spring. These insects would be expected to display a life cycle and caloric values consistent with food availability.

The same is true of orthopterans which are phytophagous. Their biomass is expected to increase throughout the season as the amount of plant material increases. In fact, insects can be catagorized according to food habits. Omnivores include hymenopterans, coleopterans, hemipterans and certain orthopterans of the families Gryllidae and Tettigoniidae. Homopterans, lepidopterans and the orthopteran family Acrididae are herbivorous. The order Odonata, certain hymenopterans, and some members of the class Arachnida are carnivores. But as Price (1975) has pointed out, 85% of all insects are holometabolous with different life cycle stages having different food habits. Thus, the life cycle stage of insects must be understood in many studies of energy values.

Feeding strategies exist among groups of insects. In general, as insects increase in size, the trend is from herbivory to carnivory, to omnivory, and back to herbivory. Carnivores tend to be larger than the herbivores they consume, but as they get larger their food intake requirements increase.

Caloric values for living organisms should fall within a definite range, the lower limit of this range being set by the caloric value of glucose with 3740 calories per gram. Cellulose contains 4180 calories per gram, and the upper limit of organic matter reaches 9370 calories per gram for fats and oils. Since all organisms contain a mixture of the major organic compounds, the energy content would not be expected to be toward the upper limit. Cummins and Wuycheck (1971) predict that most organisms will average 5700 calories per gram with a range from the average of 500 to 1000 calories.

In recent years a general ecological theory has developed that young ecosystems are more productive than older and more stable ecosystems (Odum, 1971). The question arises as to whether organisms living in a younger system would then reflect a higher energy content in terms of calories per gram of biomass than the organisms inhabiting older systems. Preliminary work at Western Kentucky University by J. E. Winstead (unpublished) has indicated that such a potential exists. In student laboratory exercises various comparisons of arthropods from young and old ecosystems in relation to energy content indicated higher caloric values present in the organisms collected from younger ecosystems (Table 1). Although the results of such student work are subject to question, the results indicated a pattern that merited more indepth examination.

This study was designed to test the hypothesis that greater caloric values would be found in arthropods from meadow or young ecosystems when compared to older more mature ecosystems in South Central Kentucky.

Table 1. Summary of caloric data taken from laboratory work in general ecology classes at Western Kentucky University over a three year period (1973, 1974, and 1975).

Arthropods sampled from Meadow and Woods in 1973, 1974, and 1975 (August of each year) in Dekalb County, Tennessee.

Meadow - Average of 25 samples - 5522 calories per gram dry weight

Woods - Average of 13 samples - 5061 calories per gram dry weight

Means differed at the .001 significance level.

Members of the order Diptera sampled from Meadow and Woods in 1973, 1974, and 1975 in Warren County, Kentucky and in Dekalb County, Tennessee.

Meadow - Average of 3 samples - 5590 calories per gram dry weight

Woods - Average of 4 samples - 5113 calories per gram dry weight

Means differed at the .001 significance level.

Orthopterans collected in Warren County, Kentucky.

Meadow - Average of 5 samples - 5483 calories per gram dry weight

Woods - Average of 4 samples - 5202 calories per gram dry weight

Means differed at the .10 significance level.

MATERIALS AND METHODS

The principal collection sites consist of two adjoining woods and meadows in Butler County, Kentucky. These sites are located on land owned by Paul Smith and R. E. Massey and shall be referred to as the Smith woods and meadow or the Massey woods and meadow.

The Smith collection site is located 3 kilometers south of Woodbury, Kentucky off Highway 263 on the Barren River Road. The meadow comprises 4 hectares and the vegetation consisted primarily of redtop (*Triodia* sp.), fescue (*Festuca* sp.), and creeping bush clover (*Lespedeza* sp.). It was grazed continually throughout all collecting periods and therefore grasses were maintained at an approximate height of 2 to 3 inches. Of the 4 sites, this is the youngest system.

The Smith woods is made up of 34 hectares and is an oak-hickory type forest. According to the owner, no timber has been cut since the 1940's and at that time only a few large white oaks were removed. It is not known how long before then that timber was removed. The trees are large and the canopy very dense. Sunlight to the forest floor is limited and it is practically bare of undergrowth. This is the oldest system of the four sampling sites.

The Massey collection site is located 2 kilometers east of Morgantown, Kentucky on Highway 231. The meadow comprises 6.4 hectares and is dominated by tall fescue (*Festuca* sp.) with some creeping bush clover (*Lespedeza* sp.) and scattered broom sedge (*Andropogon* sp.). While not farmed or grazed for the past 15 years, it is usually mowed twice a year.

The Massey woods is approximately 14 hectares of oak-hickory forest. Timber was cut extensively 15 years ago and the woods, at the time of this study, had much undergrowth and many understory trees.

The Massey woods and meadow are intermediate in age as ecosystems compared to the Smith sites. All four sites are located on rolling, well-drained land.

In addition to the four principal collecting sites, some small samples were taken from other areas in South Central Kentucky. A composite sample of all orders of insects was collected in the Drakes Creek area of Warren County. A collection of mayflies (Ephemeroptera) was taken from a low region in Morgantown, Kentucky within two kilometers of Green River. A sample of aphids was collected in Woodbury, Kentucky and a collection of orthopterans of the family Gryllidae was taken within the city limits of Bowling Green, Kentucky. The two latter collections were from grassy areas which would be classified as young ecosystems.

Attempts were made to collect insects during specific seasons. Five collecting periods of three weeks each were conducted. These were during the late fall of 1974 and during early spring, early and late summer, and fall of 1975. Comparisons were made between caloric values of different seasons as well as population comparisons between orders of insects.

Within the collection sites random samples of insects were made using standard sized sweep nets. All insects were killed in the field using potassium cyanide. Within two to three hours after collection, all insects were frozen and stored frozen until ready for analysis.

After thawing, insects were classified to the order level and in some cases to the family level. Upon classification and counting the samples were dried for a minimum of 48 hours at 80 C. Dried insect material was ground in a Wiley Mill or, if a particular collection was small, a mortar and pestle was used for grinding.

Ground samples were packed into preweighed gelatin capsules. Encapsulated samples were then burned in a Parr Oxygen Bomb Calorimeter to determine a sample's energy value. The standard procedure for determining energy values is discussed in the Parr Manual (1960). Corrections were made for energy content of the gelatin capsules. Corrections for the formation of acids during combustion were made by titrating washings from the bomb with 0.0725 normal solution of Na_2CO_3. Corrections were also made for exothermic heat produced by the fuse wire.

Statistical analysis followed Student's t test procedures as outlined by Steel and Torrie (1960).

RESULTS

It was hypothesized that younger ecosystems were more productive than older ecosystems and that caloric values of organisms living in these systems would reflect these energy values. Therefore, the ideal results of this investigation would have been that of highest energy values from the Smith meadow, obviously the youngest system of the four sites, followed in order of increasing age and decreasing energy content by the Massey meadow, Massey woods, and Smith woods.

The actual results were, in fact, quite different. The Smith woods was by far the most productive according to caloric values of the insects collected there with an overall mean value of 5081 calories per gram for all orders of insects combined. This was followed by the Massey meadow with 4579 calories per gram and the Massey woods with 4469 calories per gram. Finally, the Smith meadow, which had been thought to be the youngest and most productive of all systems considered, had the lowest energy value of all sites with 4438 calories per gram of biomass.

Comparisons were made between each order of insects collected from woods and from meadow. In all orders except Diptera and Orthoptera, the caloric values of woods insects were higher than were those of the same order collected from the meadow. The difference was slightly greater in the order Orthoptera than in the order Diptera (Table 2). The class Arachnida was also considered. However, there were significant differences only between the arachnids and the order Lepidoptera. The woods arachnids were higher in caloric value than those from the meadow

Table 2. Comparison of mean caloric values of woods to meadow insects ranked in order of increasing difference between means.

Order	Woods	Meadow	t Value	degrees of freedom	Significance Level
Diptera	4563	4584	0.094	9	n.s.
Homoptera	4689	4668	0.097	7	n.s.
Orthoptera	4521	4551	0.29	9	n.s.
Mixed Insects	4688	4513	1.34	9	n.s.
Hemiptera	4990	4745	1.59	9	n.s.
Hymenoptera	4657	4387	1.84	9	n.s.
Coleoptera	4931	4650	1.94	9	n.s.
Arachnida	4953	4496	3.23	9	.05*
Lepidoptera	5107	4266	3.49	7	.01**
Overall	4775	4509	4.12	175	.001***

n.s. No significant difference
* Significant difference
** Highly significant difference
*** Very highly significant difference

at the .05 level of significance, while the lepidopterans differed at the .01 level and were also higher. On an overall basis the woods insects were significantly higher in caloric value than meadow insects at the .001 level of significance.

Comparisons were made between individual orders and between all orders combined of insects collected in the spring and those collected in the fall to determine if a seasonal variation in caloric values existed (Table 3). In no instance was there a significant difference. Since the orthopterans had higher values in the meadow samples, this comparison was also done omitting this order. Still no significant difference was found.

Table 4 illustrates the differences between the orders of woods and meadow insects and the class Arachnida when the mean caloric values are ranked in order of increasing energy content. In both cases, neuropterans were lowest in caloric value and were followed by the order Odonata. Hemipterans were among the highest in energy content in both woods and meadow. The greatest differences existed between the woods and meadow lepidopterans.

Insects were not compared to the generic level because of lack of enough material to constitute samples for burning. However, some observations were made during the classification to orders and it was noticable that while members of the orders Neuroptera and Odonata from woods and meadow were similar and may well have belonged to a few like genera, this was not true of the order Lepidoptera. Lepidopterans from the woods consisted almost entirely of small moths that were found on the leaf litter and moved about near the surface. Lepidopterans collected from the meadow were practically all large butterflies. This obvious

Table 3. Comparison of caloric values of insects between spring and fall collections.

I. Comparison of caloric values of spring woods collections to fall woods collections for all orders.

Ia. Comparison of caloric values of spring woods collections to fall woods collections for all orders except Orthoptera.

II. Comparison of caloric values of spring meadow collections to fall meadow collections for all orders.

IIa. Comparison of caloric values of spring meadow collections to fall meadow collections for all orders except Orthoptera.

III. Comparison of all spring collections, woods and meadow, to all fall collections for all orders.

IIIa. Comparison of all spring collections, woods and meadow, to all fall collections for all orders except Orthoptera.

	Degrees of Freedom	t Value	Significance Level
I.	36	0.28	n.s.
Ia.	32	0.11	n.s.
II.	38	0.82	n.s.
IIa.	34	1.00	n.s.
III.	76	0.45	n.s.
IIIa.	68	0.82	n.s.

n.s. - no significant difference

Table 4. Mean caloric values of orders of insects ranked in order of increasing energy content. (The class Arachnida is included).

Woods		Meadow	
Neuroptera	4341	Neuroptera	2744
Odonata	4477	Odonata	3390
Ortnoptera	4521	Lepidoptera	4266
Diptera	4563	Hymenoptera	4387
Hymenoptera	4657	Arachnida	4496
Mixed Insects	4688	Mixed Insects	4513
Homoptera	4689	Orthoptera	4551
Coleoptera	4931	Diptera	4584
Arachnida	4953	Coleoptera	4650
Hemiptera	4990	Homoptera	4668
Lepidoptera	5107	Hemiptera	4745

difference between genera, rather than a mixture of genera, may account for the difference in caloric values between woods and meadow insects of this order. The same principle may be applied to a lesser degree among the other orders. In all cases, mobility of certain genera of insects as well as habitat preference must be taken into consideration when looking at woods versus meadow comparisons.

A few small collections were made in addition to those from the four principal sites (Table 5). One was a composite of all orders from the Drakes Creek area. Again, as in Dr. Winstead's work, the meadow samples were higher in energy content with 4344 calories per gram than were the woods samples with 4052 calories per gram. This contrasts with those collected from the Butler County sites in which the overall value of woods insects was higher than that of meadow insects.

A separate collection of aphids was taken from a weedy area, which would be classified as a young ecosystem, in Butler County (Table 5). Their value of 4072 calories per gram is lower than the combined value for meadow homopterans of 4668 calories per gram. This again illustrates that caloric values of different genera within orders vary widely.

A collection of orthopterans of the family Gryllidae taken from a young ecosystem in Warren County had a caloric value of 5118 calories per gram (Table 5). This value is higher than the value for orthopterans in general taken from the Smith and Massey meadows with a value of 4551 calories per gram. It is also higher than any value found for the family Gryllidae collected from any of the Butler County sites (Table 7).

A collection of mayflies (Ephemoroptera) was taken as they emerged and were laying eggs. They were separated from the eggs and values were

Table 5. Caloric values for collections of insects in addition to those from the four principal collecting sites.

Drakes Creek, Warren County, Kentucky. Mixed insects collected 4/24/75.

Meadow - 4344 cal/gm dry weight
Woods - 4052 cal/gm dry weight

Woodbury, Kentucky. Order Homoptera, Family Aphididae collected 5/13/75.

Young System - 4072 cal/gm dry weight

Bowling Green, Kentucky. Order Orthoptera, Family Gryllidae collected 8/23/75.

Young System - 5118 cal/gm dry weight

Morgantown, Kentucky. Order Ephemeroptera collected 7/9/75.

Aquatic situation
Mayflies - 4858 cal/gm dry weight
Mayfly eggs - 5135 cal/gm dry weight

obtained for insects and eggs separately (Table 5). These differed by a value of 4858 calories per gram for the mayflies to 5135 calories per gram for the eggs.

Values obtained in this study were compared to those obtained by other workers. The most complete study thus far was done by Cummins and Wuycheck (1971). A summary of their results and those of other workers is given in Table 6, as well as a list of differences between the highest and lowest values. Most researchers do not indicate the age of the ecosystem from which their specimens were obtained. Wiegert (1965) and Van Hook (1971) worked with insects from a meadow and a grasslands, respectively. Lawton (1971) was concerned with an aquatic situation and Smalley's (1960) collection was from a salt marsh. Cummins and Wuycheck (1971) list a wide range of values for many orders of plants and animals but do not indicate where these were collected.

Several collections from the Smith and Massey sites contained enough material that the insects could be classified to the family level and caloric values obtained for them (Table 7). For the most part, these insects show a trend toward increasing energy content at the time of egg laying followed by a decrease in the late fall. However, in several instances, the families Acrididae and Tettigoniidae show a high value in the spring with a decrease in late summer and another increase in the fall before the final decrease again in late fall. No spring values were available because insects were too immature to allow classification to the family level and still provide enough material for burning.

A total of 38,160 insects and arachnids were collected from the Smith and Massey sites and classified to the order level (Table 8). Of this number, 15,265 were collected from the woods and 22,895 from the

Table 6. Energy content in calories per gram for insects and arachnids from research by other workers and from the present study. The last column lists the greatest difference between those values.

	Cummins & Wuycheck	Other researchers*	Present study	Differences
AQUATIC				
INSECTA	4823			
EPHEMEROPTERA	5469		4858	611
ODONATA	5117	5283	3934	1349
DIPTERA	4276			
COLEOPTERA	5371			
TERRESTRIAL				
ARACHNIDA	4825	5734	4725	1009
INSECTA	5454			
HEMIPTERA	5638		4868	770
HYMENOPTERA	4629		4522	293
COLEOPTERA	5556		4791	765
DIPTERA	5783		4574	1209
ORTHOPTERA	5300		4536	764
Acrididae	5077	5363	4786	581
		5367		
		5203		
Tettigoniidae	5449	5431	4674	1029
		5703		
Gryllidae		5634	4446	1188
Blattidae				4720
HOMOPTERA		5808	4679	1129
Cicadellidae			4753	
Aphididae			4072	
NEUROPTERA			3543	
LEPIDOPTERA			4687	
MIXED INSECTS	5280		4601	679

*Values from Golley, 1961; Lawton, 1971; Smalley, 1960; Van Hook, 1971; and Wiegert, 1964.

Table 7. Seasonal variation in caloric values of several families of orthopterans and homopterans from the Smith-Massey collection sites.

	Summer	Late Summer	Fall	Late Fall
MASSEY MEADOW				
ORTHOPTERA				
Acrididae	4673	4650	5079	4418
Tettigoniidae	4708	4544	4819	4638
Gryllidae		4722	4822	4541
HOMOPTERA				
Cicadellidae				4632
SMITH MEADOW				
ORTHOPTERA				
Acrididae	4714	4765	5600	4685
Tettigoniidae	5100	4732	4664	4346
Gryllidae			4204	
HOMOPTERA				
Cicadellidae				5115
MASSEY WOODS				
ORTHOPTERA				
Acrididae		4324		4950
Tettigoniidae		4616	4901	4185
Gryllidae			4642	4756
Blattidae				4720
SMITH WOODS				
ORTHOPTERA				
Acrididae				
Tettigoniidae	4742	4629	4808	
Gryllidae			3437	
HOMOPTERA				
Cicadellidae				4513
Averages	4787	4622	4697	4629

Table 8. Numbers and distribution of insects and arachnids.

Order	Total	Massey Woods	Smith Woods	Woods Totals	Massey Meadow	Smith Meadow	Meadow Total
ODONATA	28	3	12	15	12	1	13
NEUROPTERA	43	13	17	30	11	2	13
COLEOPTERA	2235	979	380	1359	593	283	876
LEPIDOPTERA	2356	830	1304	2134	94	128	222
HYMENOPTERA	3107	729	1126	1855	572	680	1252
HOMOPTERA	3118	486	490	976	1038	1104	2142
HEMIPTERA	6516	1373	329	1702	4194	620	4814
DIPTERA	7482	2153	2751	4904	1061	1517	2578
ORTHOPTERA	10600	255	126	381	6968	3251	10219
MIXED INSECTS	231	78	35	113	45	73	118
ARACHNIDS	2444	1111	685	1796	416	232	648
TOTALS	38160	8010	7255	15265	15004	7891	22895

meadows. The larger number from the meadow was due almost entirely to members of the orders Hemiptera and Orthoptera. Dipterans accounted for the majority of insects from the woods. Since no attempt was made to take an equal number of sweeps when collecting, these numbers cannot be used to determine and compare densities between woods and meadow habitats. The number of insects of a particular order can be compared to the number of insects of other orders within a given ecosystem. Fluctuations within an ecosystem and between ecosystems can also be compared.

Seasonal differences and habitat preferences were very evident among the orders. Overall, members of the orders Homoptera, Hemiptera, and Orthoptera were more numerous in the meadows. Comparatively, all other orders were found in higher numbers in the woods. The numbers of those insects belonging to the orders Odonata, Neuroptera, and Hymenoptera differed only slightly while two to three times as many coleopterans, lepidopterans, dipterans, and arachnids were found in the wooded areas.

Seasonal fluctuations within orders are indicated in Table 9. Collections are designated late fall (September 28 to October 13, 1974), spring (May 27 to June 14, 1975), summer (June 29 to July 19, 1975), late summer (August 6 to August 23, 1975) and fall (September 8 to September 20, 1975). Numbers of insects may be compared between orders within a season or between seasons.

Members of the orders Odonata and Neuroptera were low in number throughout all collecting periods but were lower in the late summer and fall. Their numbers were highest during the spring.

Coleopterans were found in higher numbers in the woods during the late summer and fall; however, during the spring and summer they were more abundant in the meadow collections.

Table 9. Seasonal variation in numbers and distribution of insects and arachnids.

Order	Late Fall Sept. 28-Oct. 13 1974		Spring May 27-June 14 1975		Summer June 29-July 19 1975		Late Summer Aug. 6-Aug. 23 1975		Fall Sept. 8-Sept. 20 1975	
	Woods	Meadow	Woods	Meadow	Woods	Meadow	Woods	Meadow	Woods	Meadow
ODONATA	0	1	10	1	4	3	1	7	0	1
NEUROPTERA	4	6	9	6	13	0	2	1	2	0
COLEOPTERA	66	158	528	256	613	182	127	234	25	46
LEPIDOPTERA	46	39	818	62	611	14	541	95	118	12
HYMENOPTERA	263	587	563	360	502	148	415	103	112	54
HOMOPTERA	127	513	172	610	266	358	348	585	63	76
HEMIPTERA	158	47	142	3968	593	454	671	314	138	31
DIPTERA	924	588	2271	1257	977	330	628	365	104	38
ORTHOPTERA	29	541	101	4093	165	3049	59	2379	27	157
PSOCOPTERA	13	3	2	0	0	0	0	0	0	0
ARACHNIDS	251	126	333	99	569	114	486	270	157	39
TOTALS	1881	2609	4949	10712	4313	4652	3278	4353	746	454

Lepidopterans and dipterans were consistently higher in number in the woods collections and reached their highest numbers during the spring and summer when these orders accounted for almost half the total number of insects collected from wooded areas.

The number of hymenopterans in woods compared to meadow fluctuated greatly throughout the seasons. Overall they were found in higher numbers in the woods collections, but in the late fall a larger number was found in the meadow.

Homopterans were consistently more abundant in meadow collections throughout all collecting periods, and their numbers did not fluctuate with the seasons. Hemipterans, on the other hand, were found in higher numbers in the woods in all summer and fall collections but increased to such proportions in the meadows during the spring that they accounted for more than one third of the entire spring meadow collection.

Orthopterans were highest in number of all insects throughout all meadow collections except in late fall when they were slightly surpassed by dipterans and hymenopterans.

A very few insects belonging to the order Psocoptera were found in the late fall and spring collections. Since there were not enough to constitute a sample for burning, they were included with the mixed insects. Of a total of 18 psocopterans, 15 were collected from wooded areas.

Members of the class Arachnida were higher in number in all woods collections, reaching their peak in the summer collecting period and declining again in the late summer and fall.

DISCUSSION

The results of this investigation differed both from expected results and from the findings of other researchers. Although the reasons for this difference are not clear, there do exist several possibilities ranging from the methods employed to the regions involved.

It was hypothesized that there would be higher energy content in the younger, more productive meadow ecosystems compared to the more mature wooded areas. This was not found to be true in the Butler County collecting sites. Except for the order Lepidoptera and the class Arachnida there was no signifivant difference between the energy values of animals collected from the woods and meadow sites, and in these two cases the organisms collected from the woods had the higher energy content. For all orders combined the caloric values of the woods samples were higher than the meadow samples at the .001 level of significance.

As previously pointed out, the genera of lepidopterans from these two systems were quite different. No attempt was made to distinguish between the genera of archnida; however, it might be assumed that since these animals are without the more rapid means of locomotion provided by flight the genera adapted to a woods or to a meadow habitat would be found in that habitat. In no other order of insects was there a noticable distinction between genera but rather a combination of many genera. Therefore the possibility exists that insects, due to their mobility, may have moved quite freely between the two habitats. Some attempt was made to prevent the removal of animals from the ecotone by maintaining a distance of 10 meters from the border between woods and meadow while collecting. If there was an intermingling of insects then the hypothesis is not necessarily proven false but rather the ecosystems chosen are not distinct enough. However, this does not explain the fact that differences in caloric values did exist, though they were not significant in most orders; these values were higher in the woods samples than in those from the meadow.

Another discrepancy exists between the caloric values of insects from this investigation and those values obtained by other workers. In all cases, values determined in this study were lower than those of other researchers. The mean caloric value of all insects reported by Cummins and Wuycheck (1971) is 5203 calories per gram. From this study the mean caloric value for all orders from woods and meadow systems combined is 4664 calories per gram. Table 6 compares some of these values directly and illustrates their differences, which range from 293 to 1349 calories per gram. In most cases values obtained by other researchers are fairly close. However, only four comparisons can be made and one of these four, the class Arachnida, differs by as much as 909 calories per gram. This seems to indicate that if more data from other sources were available, more variation might exist between their values as well as between those from the present study.

Lawton (1971), Smalley (1960), Van Hook (1971), and Wiegert (1964) further break down their research into seasonal studies of the insects with which they worked (Table 10). In almost all cases the energy content increased throughout the season to egg laying time, and then decreased slightly after the eggs were layed. The researchers do not indicate whether this difference in values between seasons is at a

Table 10. Seasonal variation in calories per gram of insects.

Lawton, 1971. Order Odonata. Genus Pyrrhosoma.

Life Cycle State	Calories Per Gram
Newly hatched	5125
Post-October final instar	5271
Stage 2 final instar	5446
Stage 3 final instar	5292

Smalley, 1960. Order Orthoptera. Family Tettigoniidae. Orchelimum fidicinium.

Life Cycle Stage	Calories Per Gram
5-10 mm	5033
10-15 mm	5302
15-20 mm	5798
adults	5590

Van Hook, 1971. Order Orthoptera. Families Gryllidae, Acrididae, and Tettigoniidae. Class Arachnida, genus Lycosa.

Season	Gryllidae	Acrididae	Tettigoniidae	Lycosa
Spring	5223	4821	5185	5379
Summer	5850	5547	6129	5964
Fall	5753	5736	5796	5859

Wiegert, 1964. Order Homoptera. Philaenus spumarius.

Life Cycle Stage	Calories Per Gram
Eggs	6307
Nymphs	5336
Adult males	5740
Adult females	5875
Adult (mean)	5808

significant level. The results of the present study show an increase in the fall and a decrease in the late fall, and agree with the values found by other workers in this instance. However, there is in most cases a high value in the spring or summer followed by a drop in the late summer before the fall increase (Table 7).

Storage of insects over a period of time might alter their caloric values by oxidation of the organic matter and subsequent change in chemical composition. Paine (1971) states that because of this oxidation not more than 30 days should elapse between sampling. However, Van Hook (1971) pooled weekly samples into monthly samples to provide enough material for burning. Wiegert (1965) oven dried samples and stored them for several months. Both of these workers still obtained higher values than those determined in this study.

The ecosystems from which the insects were collected might be responsible for the lower caloric values. Golley (1961) points out that caloric values vary with light intensity, length of day, amount of nutrients, and type of soil, and records show significant differences in caloric values between vegetation collected from different ecological communities. The collection sites in Butler County lie with a region of South Central Kentucky that has a nutrient poor soil. Plants, the primary producers, are dependent upon soil nutrients, as well as sunlight and moisture, for growth. If there is a relationship between poor soil nutrient content and caloric values of vegetation, the animals which consume these plants might also reflect the lower energy content and account for the overall lower caloric values obtained in this study.

Other variables might be considered. For instance, a single animal may not inhabit a single trophic level and may even change food habits according to seasons. Further, interactions between insects and their plant food and between insects and their predators influence the amount of energy that passes from one trophic level to the next.

There may exist a relationship between assimilation efficiency and energy content. If so, it is possible that insects may have to be compared at the generic level or perhaps even the species level due to differing assimilation efficiencies. According to Paine (1971) all the food consumed by heterotrophs is not assimilated. Up to 90% of the total food intake may pass through the body and out as feces, giving an assimilation of only 10%. At the other extreme, some organisms may have an assimilation efficiency of 75% with carnivores being the most efficient. Because of this, when several genera are combined their differing caloric values might tend to cancel each other giving an appearance of no significant difference.

Even if there should be no direct relationship between assimilation efficiency and caloric value, gut contents at any given time must be taken into consideration. Various plant parts very likely have different caloric values. A genus of insect feeding upon a specific plant part would be expected to reflect that value. Hemipterans feed upon plant sap which is high in caloric content and may explain the high mean caloric value found for this order. This is another reason for comparing insects at the genus level.

The summer and fall collections in particular were taken during a very dry period. The wooded areas, because of the canopy and accumulation of leaf litter on the forest floor, provided a wetter situation than the meadows. This may have encouraged migration of some insects from meadow to woods, either permanently or temporarily, that normally would have been found in the meadow.

Distribution of the insects relative to other orders within an ecosystem was as expected (Table 8). The phytophagous homopterans, hemipterans and orthopterans were found in higher numbers in the meadows. All other orders and the class Arachnida were higher in number in the wooded areas. This latter group consists of animals that are primarily carnivorous or saprophagous rather than herbivorous. The greatest difference exists between numbers of woods and meadow lepidopterans and dipterans. Most dipterans are small and would prefer the more moist situation offered by the woods habitat because of loss of body moisture due to surface to volume ratio. This is also true of the genera of lepidopterans that made up the majority of the lepidopteran collection.

Although this study revealed some interesting points, more could be learned by pursuing it further. It would be impossible to duplicate the study on the same sites because of disturbance of the Smith meadow and the Massey woods since these collections were made. However, other areas in Butler County should be examined using larger meadows and woods; this would provide a greater distance between the ecosystems to reduce the intermingling of woods and meadow species. It could then be determined if the woods insects are significantly higher in caloric value than those from the meadow. If so, the next step would be a vegetational analysis of caloric values to determine if there is a direct relationship.

Studies in areas in which the soil is richer than that found in the region of Kentucky in which Butler County lies might be carried out in order to determine if the original hypothesis is correct or if indeed there is no significant difference between caloric values of all orders of insects from woods and meadow ecosystems. This would also reveal whether the low values were due to the collection area.

The effect of storage on insects needs to be examined to determine if this could account for the overall low values, since all the insects used in the present study were stored for a prolonged period of time.

Perhaps a more significant aspect of the results of this investigation is that the caloric values do vary from data gathered in other studies. As research into the field of community energetics continues, it appears that energy contents of organisms are not limited to a particular value. Currently one can only speculate, but it is interesting to note that Golley (1969) found that leaf litter of tropical wet forests had lower caloric values than the litter of temperate forests in Minnesota and in England. That study would suggest that tropical areas, in terms of caloric values, are energy poor when the values are based on calories per gram of biomass. Earlier Hadley and Bliss (1964) had shown caloric values of alpine plants to be much higher than plants from lower altitudes in the temperate zones. In a comparison of different populations of the same species, Abdulrahman (1973) has published data that indicates more northern populations of *Xanthium strumarium* L. have higher caloric values per unit weight than southern populations within the continental United States. Such variation in energy accumulation of the primary producers and the indication of energy differences from the present study indicates the need for a comprehensive inventory of standing crop energy values in natural systems. At this point in time there is a distinct lack of such information.

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VITA

Joyce Carroll Wright was born in Louisville, Kentucky, on January 18, 1942, the daughter of Mr. and Mrs. Ernie Carroll. She graduated from Butler County High School in 1960, entered Western Kentucky University, Bowling Green, Kentucky, in 1969 and was awarded a Bachelor of Science Degree with a major in Biology in May of 1974. In the fall of 1974, she entered the Graduate Program in Biology at Western Kentucky University.

Permanent home address: Woodbury, Kentucky 42288