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**1974 PROGRESS REPORT
[FINAL]**

**THE FUNCTIONAL RELATIONSHIPS AMONG THE ORGANISMS
COMPRISING DETRITUS-BASED FOODCHAINS AT THE
ROCK VALLEY SITE**

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ABSTRACT

This report describes an incomplete study of the production ecology of detritus-based food chains in the northern Mohave Desert. Under laboratory conditions, the tenebrionid beetle *Eleodes armata* continued to reproduce as long as physical factors were held favorable, although the rate of egg-laying decreased with time. It was also found that hatch success was negatively correlated with egg-laying rate. Data are also presented on the growth rate and metabolism of larvae. The approach used to study the trophic relationships of soil microarthropods proved unsuccessful and the project was terminated before new approaches could be tried. Considerable data were collected on the availability of detritus within the system and these data are included.

INTRODUCTION AND OBJECTIVES

The work reported here was accomplished between late March 1974 and early September 1974. Because the work had been planned for a two-year period, or longer, the results are obviously incomplete. The objectives were to 1) delineate the trophic relationships of the invertebrate detritivores in Rock Valley, 2) estimate the amount and rate of movement of material passing through that foodweb, 3) formulate hypotheses relative to the "critical pathways" of the foodweb and 4) begin small-scale manipulations to test those hypotheses. Relative to objectives 1 and 2, work was begun on analysis of microarthropod foodwebs via microcosm experiments, assessment of detrital pools and the productivity of tenebrionid beetles.

METHODS AND RESULTS

Adult *Eleodes armata* (Coleoptera:Tenebrionidae) were collected in Rock Valley and used in laboratory experiments in Los Angeles. Four females were placed with one male in glass chambers having a 2-cm-deep layer of sterile sand in the bottom. The insects were kept in growth chambers in which there was a 14-hr light:10-hr dark photoperiod and in which temperature was varied with illumination (29 C days and 21 C nights). The sand was sifted and eggs were collected at two- to three-day intervals for two months. Egg production was highly irregular (Table 1) but followed a roughly exponential decline from a maximum rate of 27 eggs/female per day at the beginning of the experiment to a minimum of 3.3 eggs/female per day 56 days later.

Eggs were transferred to filter paper in petri dishes and examined at regular intervals for hatched larvae. Those laid earliest in the experiment took the longest time to hatch. Of the first egg batch, 39% had hatched by the end of one week and another 35% hatched during the second week. The remainder failed to hatch. By the end of the third week of egg collections, hatching was being accomplished within seven days, although the hatch success rate remained at near 75%. As the experiment progressed and total egg production decreased, hatch success increased and there was a significant negative correlation between egg production and hatching success ($r = -0.517$; $P < 0.01$).

Once larvae were hatched, survivorship was highly dependent upon our laboratory skills and no conclusions can be made that are relevant to field conditions. Growth rate, however, is a function of both temperature and food

availability. Larvae were reared with an excess of food and at a constant 23 C. Consequently, our data represent maximum growth rates which can easily be adjusted to field conditions (Table 2).

The growth curve, plotted as increasing live weight versus time, was sigmoid. The experiment terminated at 46 days, but projections indicate the curve would reach an asymptote at about 70 days and this time is taken as the predicted onset of pupation. Further feeding produces no further growth and the larval stage is completed. A regression equation of the form:

$$Y = ae^{bX}$$

Table 1. Laboratory egg-laying and hatching rates for *Eleodes armata* (Coleoptera:Tenebrionidae)

Date	Eggs Layed	Eggs per female-day	Number hatched			% hatched
			7 days	14 days	total	
7-5	541	27.0	210	401	401	74
7-8	422	14.1	100	231	231	55
7-10	262	13.1	190	216	216	82
7-12	177	8.8	136	149	149	84
7-15	249	8.3	144	159	159	64
7-17	258	12.9	*	*	*	*
7-19	278	13.9	145	145	145	52
7-22	122	4.1	95	104	104	85
7-24	298	14.9	218	218	218	73
7-26	300	15.0	270	270	270	90
7-29	148	4.9	119	120	120	81
7-31	125	6.2	113	113	113	90
8-2	307	15.4	263	263	263	86
8-5	206	6.9	120	120	120	58
8-7	154	7.7	91	92	92	60
8-9	136	6.8	114	114	114	84
8-12	133	4.4	107	107	107	80
8-14	84	4.2	79	79	79	94
8-16	143	8.9	108	108	108	76
8-19	158	6.6	*	*	*	*
8-21	76	4.8	72	72	72	95
8-23	141	8.8	111	111	111	79
8-26	79	3.3	77	77	77	97
8-28	88	5.5	88	88	88	100

* eggs removed for separate experiment

where Y is live weight (mg) and X is time in days, yielded the following results: $a = 0.180$, $b = 0.070$ and $r^2 = 0.929$ ($P < 0.01$).

Metabolic rates of developing larvae are shown in Table 3. The data fit the well-known power function relationship for change in metabolic rate as a function of size. Metabolic rate was found to be equal to live weight to the 0.58 power and the weight-specific metabolic rate was a function of live weight to the -0.42 power ($r^2 = 0.69$; $P < 0.01$).

Table 2. Growth of *Eleodes armata* larvae at 23 C

days post-hatching	mean live weight, mg	N
1	0.43	576
7	2.48	83
8	1.49	182
9	2.16	168
10	4.95	145
11	4.78	26
13	5.94	15
14	7.79	52
15	12.09	20
16	6.84	113
17	13.39	118
18	13.23	13
21	40.32	6
25	77.50	2
29	115.64	1
32	150.21	2
36	202.89	1
42	215.00	1
46	247.00	1

A regression equation of the form $Y = ae^{bX}$, where Y is live weight (mg), and X is time in days, yielded the following results:
 $a = -0.1799$, $b = 0.0703$, $r^2 = 0.9294$

The second part of our work concerned the analysis of soil invertebrate foodwebs and estimates of the productivity of the soil invertebrate populations. Microcosms were established which consisted of 500 ml of Rock Valley soil, sifted to remove larger rocks, and placed into plastic, screw-top jars. The soil was then wetted to bring the moisture content up to 20% of dry weight, approximately the soil moisture in the field during late winter. The invertebrate populations were augmented with the extract of 2 liters of Rock Valley soil to increase the density and provide more animals with which to work. Available food supply was increased by the addition of detritus labeled with cesium-137.

The populations in microcosm exhibited a near exponential increase in density but a severe decline in diversity (Table 4). The population growth was due to an acarid mite. Only one oribatid mite and one prostigmatid mite were present beyond the third week. Acarids are generally considered to be detritivores or fungivores, as are oribatids, and prostigmatids are usually predators. Only the acarids were common enough throughout the experiment to provide realistic radionuclide turnover data which, in the absence of

Table 3. Metabolism of *Eleodes armata* larvae at 24 C

larvae/chamber	live wt. \pm S.D.	$\mu\text{l O}_2 \text{ hr}^{-1} \pm$ S.D.	N
1	158.86 \pm	52.39 \pm 14.54	5
3	66.25 \pm 6.68	28.99 \pm 1.43	5
6	35.45 \pm 2.20	41.19 \pm 7.93	5
5	28.95 \pm 1.74	26.71 \pm 3.35	5
4	21.18 \pm 2.28	20.89 \pm 1.80	5
7	7.83 \pm 1.31	7.99 \pm 0.74	5

A regression of the form $Y = aX^b$, where Y = $\mu\text{l O}_2 \text{ g}^{-1} \text{ hr}^{-1}$ and X = live wt. (mg), yielded the following results:
 $a = 3313$, $b = -0.4247$, $r^2 = .6895$

Table 4. Density (individuals/500 ml), number of species and diversity (α) of soil invertebrates in microcosms

	DAYS IN MICROCOSM											
	2	6	8	10	12	14	16	19	22	25	33	43
DENSITY	47	51	44	47	296	900	644	2601	3067	3000	3000	3000
SPECIES	9	5	5	4	7	3	4	4	3	3	2	3
α	2.08	1.02	1.06	.78	1.05	.29	.46	.38	.25			

$$\alpha = \frac{S - 1}{\log_e N}$$

where S = number of groups (species) and N = number of individuals (Southwood, 1966, after Margalef, 1951)

comparative data, are of little use. In the absence of comparative radionuclide turnover data or specific feeding studies, taxonomic affinities remain our best indicator of community function.

The third part of our study was concerned with the nature of the available food supply. Detritus was arbitrarily divided into two size classes, larger or smaller than 500 μ effective diameter. The larger fractions were collected by Bamberg, analyzed for caloric and nitrogen content by us, with the data being reported by Vollmer et al. (1975). Fractions included stems (both current growth and old stem), roots and particulate detritus.

The smaller fraction represents detritus available to the microfauna and was analyzed according to depth and distance from shrubs to parallel population studies concentrating on those groups (Edney et al. 1974, Freckman et al. 1974). As with microfaunal populations, both carbon (Walkley) and nitrogen (Kjeldahl) generally declined with depth in the soil and with distance from the shrub bases. The pattern was shown most strongly with depth immediately below shrubs and with distance away from shrub bases along the top 10 cm of soil (Tables 5 and 6). There was little effect with depth in areas between shrubs, which indicates that root turnover may be a major component of detritus availability. Over the short time span investigated, no seasonal trends could be shown, although significant differences in distribution did occur.

The collection of soil-carbon data by the Walkley method is quite laborious and we investigated the feasibility of determining carbon content by loss-on-ignition. Results from Walkley and loss-on-ignition differ for a number of

reasons, including additional water losses and loss of CO₂ derived from carbonates during ignition. If techniques are held constant, however, one should be a predictor of the other, which would allow use of the simpler, gravimetric method. Duplicate samples were analyzed for carbon by each method and the results were compared by regression analysis. The relationship was found to be

$$Y = 2.028X - 2.337$$

where Y = percent organic matter as determined by wet oxidation (Walkley) and X = percent organic matter determined by ignition. Loss-on-ignition proved to be an excellent predictor of organic matter content ($r^2 = 0.730$, $P < 0.001$). The regression equation was of the same form as found for a range of soils by Davies (1974) but both the slope and Y-intercept were quite different. Consequently, it is considered prudent to make a calibration curve for each soil before relying on the gravimetric method.

SUMMARY

The ground-dwelling beetles, of which *Eleodes armata* is representative, remain poorly understood in Rock Valley. Population assessment remains an enigma although Sleeper and his associates have tried a wide variety of approaches. From our own attempts to rear tenebrionid beetles in the laboratory, we have found them to be enthusiastic omnivores. Larvae are cannibalistic as well as detritivorous. Adults sample anything put into the cage, including

Table 5. Distribution of nitrogen under shrubs in Rock Valley

Species	SAMPLE POSITION								
	1	2	3	4	5	6	7	8	9
Larrea (July)	.088	.068	.059	.058	.057	.058	.043	.038	.044
Larrea (Sept)	.108	.066	.056	.056	.040	.039	.037	.033	.034
Ambrosia (July)	.069	.044	.034	.040	.030	.039	.048	.042	.040
Ambrosia (Sept)	.048	.030	.028	.029	.026	.025	.032	.032	.031
Lycium (July)	.116	.048	.030	.062	.044	.054	.048	.038	.040
Lycium (Sept)	.173	.145	.128	.090	.061	.059	.023	.030	.036
Krameria (July)	.073	.043	.038	.055	.040	.044	.050	.043	.046
Krameria (Sept)	.054	.039	.038	.035	.032	.038	.026	.028	.031

All values are % of dry weight. Sample positions 1,2, and 3, respectively, refer to 0-10 cm depth, 10-20 cm depth, and 20-30 cm depth immediately under a shrub. Position 4,5, and 6 are corresponding depths at the canopy margin. Positions 7,8, and 9 are corresponding depths at 2 mean shrub radii away from the canopy margin.

Table 6. Distribution of carbon under shrubs in Rock Valley

Species	Sample Position								
	1	2	3	4	5	6	7	8	9
Larrea (May)	1.790	.942	.939	.756	.383	.631	.390	.340	.523
Larrea (July)	1.384	.930	.744	.849	.767	.715	.308	.314	.308
Larrea (Sept)	.801	.507	.391	.328	.293	.305	.259	.293	.323
Ambrosia (May)	1.174	.779	.492	.886	.808	.610	.636	.581	.538
Ambrosia (July)	.907	.546	.395	.482	.337	.267	.279	.256	.256
Ambrosia (Sept)	.367	.258	.295	.244	.240	.266	.243	.289	.295
Lycium (May)	.913	.538	.558	.430	.462	.523	.401	.386	.439
Lycium (July)	1.587	.663	.360	.767	.512	.512	.366	.349	.378
Lycium (Sept)	1.050	.739	.676	.581	.360	.419	.183	.249	.304
Krameria (May)	1.704	-	.436	.567	.392	.395	.445	.340	.375
Krameria (July)	1.070	.628	.430	.756	.453	.372	.372	.326	.395
Krameria (Sept)	.408	.297	.291	.242	.245	.271	.187	.206	.211

All values are % of dry weight. Sample positions are as in Table 5.

creosotebush, and might alternately be classified as herbivorous, detritivorous or necrovorous.

It is quite obvious that the potential exists for rapid population growth under favorable conditions, but occasional individuals, at least, are long lived. High priority should be placed on finding an effective means of sampling populations so that response to perturbations can be measured. These organisms may be important in rapid mobilization of nutrients following periods of unusually high plant production.

Procedural problems remain to be solved before the functional roles of soil microarthropods in the Mohave Desert are known. The microcosm approach tried here was not successful. With the time remaining, it is highly unlikely that IBP-supported research will be able to define those roles.

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