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Role of Orthoporus ornatus millipedes in a Desert Ecosystem

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RESEARCH MEMORANDUM

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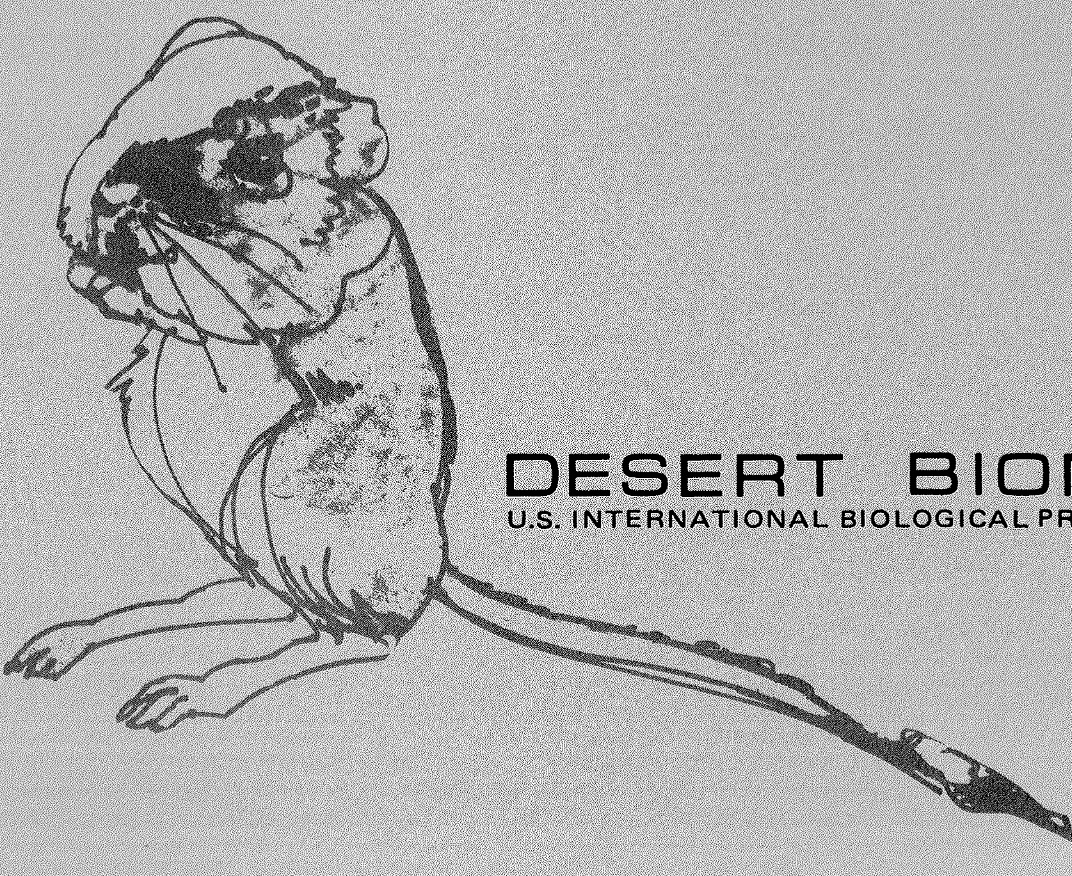

DESERT BIOME

U.S. INTERNATIONAL BIOLOGICAL PROGRAM

1972 PROGRESS REPORT

THE ROLE OF *Orthoporus ornatus* MILLIPEDES IN A DESERT ECOSYSTEM

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ABSTRACT

The role of the large and abundant desert millipede, *Orthoporus ornatus*, is being studied at the Jornada Validation Site, and also at sites in Big Bend National Park, Texas, and at Albuquerque, New Mexico. Because of its size and abundance *O. ornatus* is assumed to be an important detritivore, and therefore of consequence in nutrient cycling in the desert.

Periods of major activity coincide with rainfall occurring during the warmer months of the year. Early warm-season rains appear to trigger annual molting and surface appearance. Once on the surface, the opportunity exists for dispersal, mating, oviposition, and feeding. Eggs are laid in underground caches and small instars are seldom seen above ground. During most of the year *O. ornatus* remains underground in a relatively quiescent state. A substantial proportion of the Jornada population overwinters in the nests of the harvester ant, *Novomessor cockerelli*.

Potential fecundity ranges from about 330 eggs to 400 eggs. Mature females usually represent only a small portion of a population. Age structure as determined by frequency distributions of midsegment widths varies considerably with different populations.

Surface density estimates range from a mean of 67/ha (Jornada) to 733/ha (single Big Bend estimate). Standing crop in the latter estimate compares favorably with published values for dense populations of woodland millipedes.

The desert millipede ingests mainly dead organic material (often including bark of desert shrubs), as well as moist soil. It feeds most often between about 20 C and 30 C; ingestion rates more than double in this range. Assimilation percentages are high for a detritivore, ranging from about 24% to 38% at these temperatures. Monthly respiratory metabolism is somewhat temperature dependent, but rises out of proportion to temperature increase during surface activity, when respiratory energy expenditure is nearly 500 cal/g.

INTRODUCTION

The role of soil invertebrates in turnover of organic matter and nutrients is beginning to be understood, especially in mesic ecosystems (Edwards et al., 1970). These animals are instrumental in disintegrating, chemically changing, and increasing the surface area of plant litter so that it can be utilized by decomposer organisms and thereby recycled within the system.

Prominent among the detritivorous soil invertebrates are millipedes (Arthropoda: Diplopoda). These can reach vary high population densities (Banerjee, 1966; Blower, 1970; Dowdy, 1968; Saito, 1967; and Shaw, 1968). Although complete life histories are known for relatively few millipede species (Blower and Gabbut, 1964; Blower and Fairhurst, 1968), there have been a number of studies detailing aspects of their population energetics (Byzova, 1967; O'Neill, 1968; Phillipson, 1967; and Saito, 1967).

Little is known of invertebrate soil detritivores in desert ecosystems; however, IBP-supported process studies on ants will probably reveal that some desert species play an important role in the turnover of organic materials. Extensive work on termite activity is now being conducted in the Sonoran Desert by Nutting, as part of an IBP process study.

One of us (C.S.C.) acted as a consultant for the IBP/Desert Biome on preliminary studies of the desert millipede *Orthoporus ornatus* (Diplopoda: Spriostreptidae) during the summers of 1970 and 1971 at the Jornada Validation Site. From observations made then it was concluded that *O. ornatus* was large and abundant enough to warrant further investigation as a desert detritivore of considerable potential. It has a unique ability (for a millipede) to resist desiccation (Crawford, 1972), which enables it to remain on the desert surface and feed for a matter of days following summer rains. Consequently, we began to study its general role in the desert, assuming that when sufficiently abundant it could play an important part in the flow of nutrients in the desert.

Because of information herein reported, we continue to adhere to the view that *O. ornatus* can be an important desert detritivore. In the coming year we hope to obtain data that will show the extent to which a population actually removes and processes nutrient material in a desert ecosystem.

OBJECTIVES

These are essentially the same as in the original process study proposal. They are given below, together with qualifications more recently added.

1. To reveal various details in life history. Recent emphasis has been on phenology and reproductive attributes.
2. To estimate potential fecundity.
3. To estimate diel activity in terms of periodicity and surface dispersal.
4. To estimate density and biomass. Preliminary density estimates have been made; biomass studies are being deferred until next year. Age structure estimates have been and will be made in connection with these studies.
5. To record kinds of food eaten in the desert and to measure attributes of ingestion.
6. To determine assimilation values as a prerequisite for the establishment of an energy budget. This objective was not specifically stated as such in the original proposal.

METHODS

Life history

Field observations at the Jornada Validation Site, on the West Mesa in Albuquerque, N.M., and at Big Bend National Park, Texas, were used to record life history data. Phenological information was made possible in large part by monthly excavations with shovels of *Novomessor cockerelli* harvester ant nests (except for July) at the Jornada site in order to obtain samples for respiratory metabolism (DSCODE A3UCF01). In addition, a trip was made in late May and early June to Big Bend to study density and to make observations on life history. Excavations in the soil were made with spoons and revealed sites of egg chambers.

Potential fecundity

Estimates of potential fecundity were accomplished by dissecting large females and counting enclosed eggs when present. Size categories of these eggs were based on measurements with an ocular micrometer (see DSCODE ACU3F01).

Diel activity

Aside from general observations on this phenomenon with respect to ambient conditions, one of us (R.C.W.) spent two diurnal sessions recording millipede activity in a marked hectare plot near the Jornada playa. Indirect evidence from laboratory feeding experimants was used to demonstrate nocturnal feeding.

Density

Density estimates were made by the following methods: 1) ant nest excavation mentioned above, 2) single counts of surface-located specimens made on 1.6 km of dirt road (3.5 m wide) near the Jornada playa, 3) single counts of all specimens in a given plot on either the Jornada site or in Albuquerbue, and 4) a regression method in which cumulative removal is plotted against numbers removed each time from a sealed-off area (Petrusewicz and Macfadyen, 1970, p. 73).

Age structure has so far been estimated by width measurements of middle segments made with a micrometer (see DSCODE A3UCF01).

Food, ingestion, and assimilation

Field observations were made of different materials eaten.

Ingestion rates were studied in experiments also designed to measure assimilation percentage. The procedure first involved drying sections of *Ephedra* (Mormon tea) stems at 60 C for 24 hr. These were previously cut to equal lengths. *Ephedra* bark is a common food of *O. ornatus* at the Jornada site, where all specimens used in feeding tests were obtained.

Each experimental unit was treated in the following manner: After being placed in a desiccator until a constant weight was reached, 4 *Ephedra* sections were then placed, together with a millipede and 2 g of soil (treated initially as was the *Ephedra*), in a large plastic shoe box. Several series of millipedes were so treated; they had been initially conditioned to an identical situation for 5 days. Twice a day 1 cc of water was added to the soil in each box. Temperatures and photoperiods were controlled.

Ephedra bark consumption over the ensuing 5-day period was determined by weighing the *Ephedra* sections before and after the experiment. A correction factor for atmospheric absorption of water was obtained from control sections and used to adjust ingestion values. Soil consumption was measured by weighing the uningested soil following drying at 60 C for 24 hr.

A muffle furnace was used to determine the ash-free weights of food consumed and feces produced. *Ephedra* bark collected at the same time as that used for food was ashed at 500 C for 18 hr, and feces produced were ashed under the same conditions after first being ground in a Wiley mill. The ash-free value of soil was determined similarly, but without grinding. All ash-free values were determined from material that was previously at a constant dry weight.

Methods of calculating ingestion rates and assimilation percentages are indicated in Table 6.

Respiratory metabolism

Monthly metabolic rates were determined by use of a Gilson differential respirometer (see DSCODE A3UCF01). Specimens to be tested were acclimated for at least 48 hr in soil maintained at approximately mean ambient soil temperature for that time of year. Specimens were then each exposed to three, 1-hr respirometer runs at that temperature. When the runs were complete each specimen was acclimated for another 48 hr at 20 C, and then tested in the respirometer as before, but at 20 C. Averages of the 3-hr runs were used in expressing respiration rates.

Measurement of carbon dioxide production for respiratory quotient (RQ) estimation was accomplished by recording pressure changes in the respirometer in the absence of the ususal carbon dioxide absorbent (Ascarite) from the reaction vessels. The difference between oxygen consumption (in microliters) and the change recorded in the absence of Ascarite constituted carbon dioxide production.

Conversion of recorded values of oxygen consumption to caloric values was performed by using the estimated RQ value and tables of caloric values in Brody (1945).

RESULTS

Life history

Mating was observed on several occasions in the daytime on the soil surface and in shrubs at Big Bend in late May. It was also seen once in mid-August on the soil surface 56 km west of Lordsburg, N.M. On both occasions heavy rains had fallen the previous day and many millipedes were on the surface. Mating can proceed for at least 0.5 hr. Mating pairs were intermittantly noted when many mature *O. ornatus* were kept together in a collecting container.

Oviposition by a captive female (from Big Bend) occurred once. She deposited about 30 eggs, each covered with a fecal coating, in a group beneath the soil. At

Big Bend 3 caches of between 100 and 200 eggs were discovered in separate chambers about 15 cm beneath the surface of a mound that was probably formed at the base of an old *Opuntia* cactus plant. All of the eggs at Big Bend appeared to be old, many having small holes in the fecal covering. Attempts to properly incubate eggs have not yet resulted in hatching.

Emergence of early instars from the mound described above took place in late May following heavy rains. These small specimens appeared too large to have just emerged from the eggs found in the mound and may have hatched a year earlier. These and other groups of small instars exhibited a decidedly clumped dispersion. They were feeding on debris and on dead leaves of a plant tentatively identified as *Senecio*. They were only present on the surface when the surface was moist.

Overwintering takes place underground; in fact, as Table 1 shows, about three-fourths of the year is spent in subterranean residence. As is indicated below, a diapause-like state exists during the coldest part of the winter. At the Jornada site probably no more than half of the specimens over 3 cm in length overwinter in nests of *Novomessor cockerelli* (see Table 4), where they are coiled adjacent to galleries. Sexually mature specimens are rare in these nests but extensive digging has not revealed them elsewhere.

Molting at the Jornada site occurred in late spring following the first major precipitation of the year (Table 1). Just prior to that time appears to be a critical period relative to survival: all 12 premolt specimens collected on June 5 died within 2 days in Albuquerque, whereas the 6 postmolt specimens simultaneously collected did not.

The relationship of precipitation to surface phenology of *O. ornatus* is depicted in Table 1.

Potential fecundity (see DSCODE A3UCF02)

Mature females were not common in *Novomessor* nests. Therefore, the apparent progression of maturity with season shown in Table 2 may be somewhat misleading. Table 2 does suggest, however, that egg maturation occurs significantly only after molting has occurred (see also Table 1).

Data from Tables 2 and 3 indicate that mean potential fecundity in this species over a wide geographical range approximates 400 eggs, with the value for Jornada specimens being about 330. At times of collection no more than about half of those eggs were mature.

Table 1. Surface phenology of Jornada *Orthoporus ornatus* in 1972

Date	Events observed	Recent precipitation*	Soil conditions (means) Date of measure	Temp (C)** 15cm	Temp (C)** 45cm	Moisture pot. (bars) 15cm	Moisture pot. (bars) 45cm
6/3	First surface specimens		5/16	19	23	-112	-43
6/4	First molts	31mm 6 days before, 103mm 20 days before	6/16	21	24	-26	-55
Late June	Few large surface specimens	606mm in June (total)	6/21	28	28	-7	-37
7/7	Few small surface specimens	75mm 3 days before, 62mm 15 days before	7/6	27	29	-93	-63
7/21-24	Maximum surface specimens	246mm 2 days before, 426mm in previous 10 days	7/28	29	30	-17	-11
8/24	All subterranean	31mm in previous 16 days	8/16	29	28	-108	-86

*Between 1/1 and 5/13 only 59mm were recorded.

**45cm soil temperatures previously recorded were 23C (5/13), 20C (4/08), 16C (3/11), and 6C (2/4).

Table 2. Egg counts from dissected female *Orthoporus ornatus* dug from *Novomessor cockerelli* nests on Jornada Experimental Range, N.M. (DSCODE——A3UCF02)

1972 Collection dates	No. of females collected & examined	Mean diam. width (mm)	Mean no. of eggs/female Immature (<0.5mm)	Developing (0.5-1.5mm)	Mature (>1.5mm)	Mean total no. of eggs/female
March 18	1	5.1±0.0	299.0±0.0	----	----	299.0±0.0
April 15	4	4.8±0.2	312.5±27.6	----	----	312.5±27.6
May 20	0	----	----	----	----	----
June 9	2	8.3±0.0	332.5±4.5	43.0±9.0	----	375.5±4.5
July 6	9	7.1±0.7	258.7±36.3	97.3±3.0	121.0±29.7	331.4±13.5

Table 3. Egg counts from dissected female *Orthoporus ornatus* in 1972 (DSCODE——ACU3F02)

Places & dates on collection	No. of females collected & examined	diam. width (mm)	Mean no. of eggs/females			Mean total no. of eggs/female
			Immature (<0.5mm)	Developing (0.5-1.5mm)	Mature (>1.5mm)	
Big Bend, 5/30-6/2	9	9.3±0.2	106.6±17.3	65.0±9.4	215.0±19.7	389.9±33.0
Jornada*, 3/18-7/6	16	6.5±0.5	283.9±22.2	75.6±13.9	121.0±51.4	330.2±10.9
Lordsburg, 8/11	3	8.1±0.0	124.0±3.8	127.0±12.7	216.0±6.8	467.7±19.8
Albuquerque, 7/25	4	8.0±0.0	201.5±10.7	167.5±4.8	80.0±13.7	449.0±5.6

*All specimens from Jornada Experimantal Range, N.M., were dug from harvester ant (*Novomessor cockerelli*) nests.

Diel activity

Hourly counts of numbers of *O. ornatus* on the ground, inactive, and feeding are given in Fig. 1. Values were recorded on a 1-ha plot on the playa fringe at the Jornada site on July 24. Activity information recorded the next day was similar. Figure 1 probably represents typical millipede activity on a hot day shortly after heavy rainfall. Feeding activity did not occur between 1000 hours and 1400 hours, and about half of the above-surface population was feeding at any one time. Laboratory and field observations have confirmed that feeding also takes place at night.

Density and biomass

A mean of 2.67 ± 0.27 millipedes was excavated from *Novomessor* nests (excavation depth: 1m; diameter at top of hole: 1.5m) in monthly trips between January and September (except for July) to the Jornada site. Eighty three nests were excavated and 222 specimens found. An approximate calculation of the dispersion parameter k (Southwood, 1966) by the formula $k = \frac{\bar{x}^2}{s^2 - \bar{x}}$ shows k = 2.066, where k is about 70% efficient. Although this is a relatively low density population, this information suggests that the millipedes in ant nests assume a clumped dispersion and are therefore not dispersed among the nests on the basis of chance alone.

Density estimates from the Jornada site, from Albuquerque, and from Big Bend are given in Table 4. Standing crop estimates from counts made in 2 areas are given in Table 5 and are compared with those from published studies.

Age distribution expressed in terms of midsegment width is given for counts made at the Jornada site and Big Bend (Fig. 2), and for counts made on two 929 m^2 plots and a single hectare plot in Albuquerque (Fig. 3). At each site the frequency distributions are different, reflecting possible differential mortalities in the past. Arrows indicate approximate midsegment width of the smallest females in each population found to contain some mature eggs.

The relationship between live and dry weights shown in Fig. 4 indicates a respective 3:1 ratio of these basic units of biomass. This and all other regression relationships shown in this report have highly significant correlation coefficients ($p < 0.01$). Specimens obtained for this comparison came from surface collections at the Jornada site in late July.

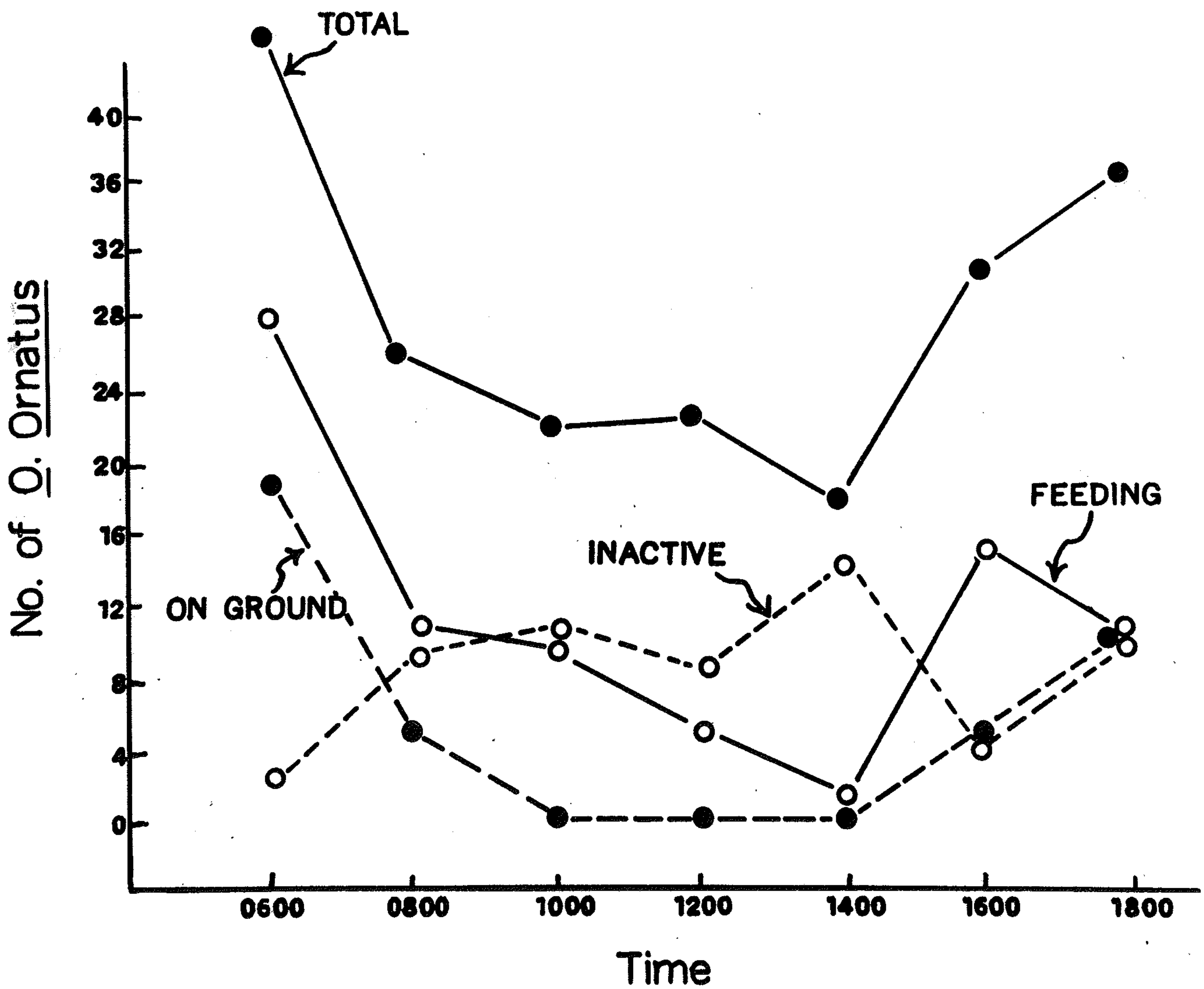

Figure 1. Hourly counts of *Orthoporus ornatus* engaged in different activities on a 1-ha plot (Jornada Validation Site; July 24, 1972).

Table 4. Preliminary density estimates of *Orthoporus ornatus* >3mm width

Place	Method	No. ha^{-1}
Jornada	Mean 1972 *Novomessor* nest count	17
"	Highest 1972 playa fringe count	44
"	Highest 1971 road count	85
"	Single 1972 $900m^2$ enclosure estimate	121
	Mean estimate: 67	
Albuquerque	Single 1972 hectare count	183
"	Mean of 2, 1972 $929m^2$ counts	387
	Mean estimate: 258	
Big Bend	Single 1970 $900m^2$ enclosure estimate	733

Table 5. Some comparative standing crop (live weight) estimates

Species	Individual wt. (mean or range in g)	Standing crop ($g\ m^{-2}$)	Situation	Source
Japonaria laminata	0.044	0.323	Adults, Jan. 1966-Jan. 1967	Saito, 1967
Iulus scandinavius	0.028-0.077	0.801	Overwintering instars VIII-XI	Blower, 1970
Orthoporus ornatus	1.95 (n=35)	0.003	Highest single 1972 Jornada road count	Present study
Orthoporus ornatus	6.31 (n=63)	0.763	Single $900m^2$ Big Bend enclosure	Present study

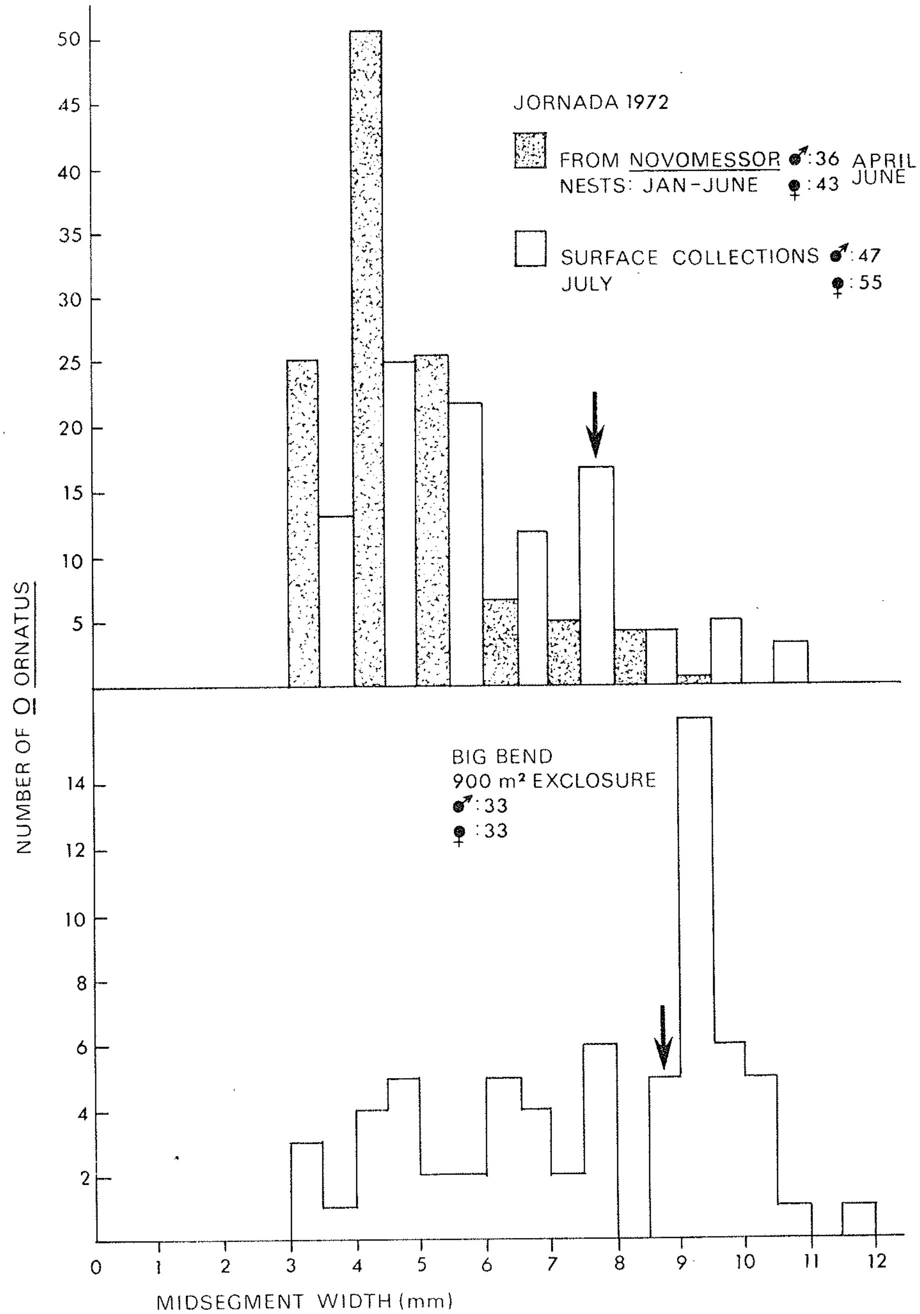

Figure 2. Age distribution expressed in terms of midsegment width of *Orthoporus ornatus* populations from the Jornada Validation Site and from Big Bend National Park. Arrows indicate approximate midsegment width of smallest females found to contain mature eggs.

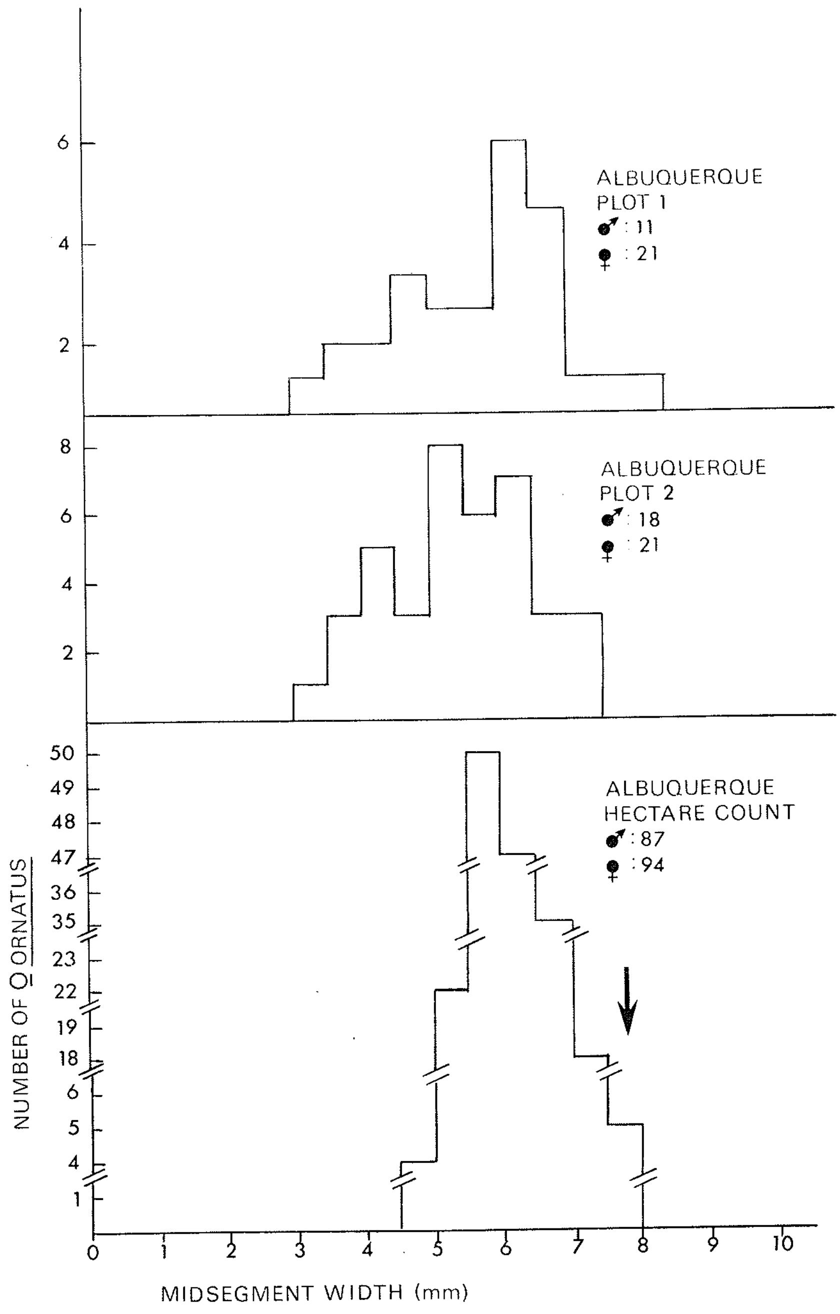

Figure 3. Age distribution expressed in terms of midsegment width of *Orthoporus ornatus* from 3 different plots on the West Mesa, Albuquerque, N. M.

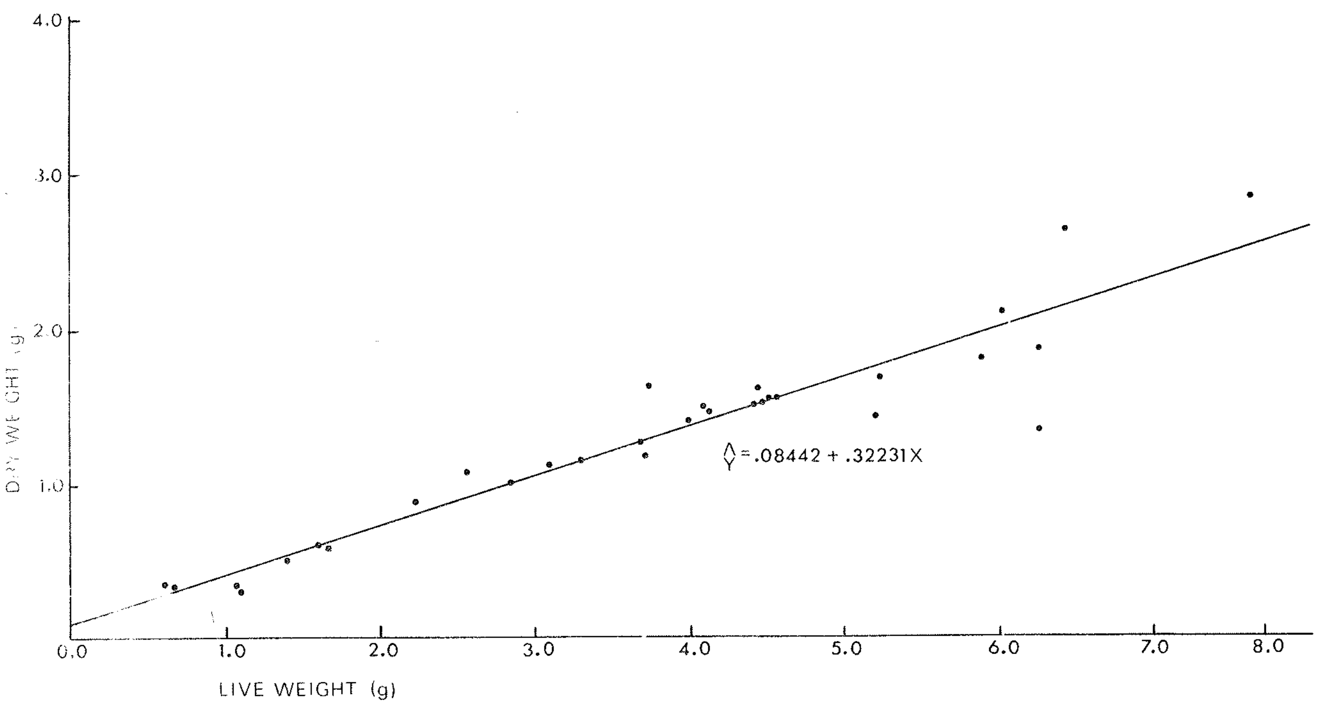

Figure 4. The relationship between live weight and dry weight of *Orthoporus ornatus* (collected from Jornada Validation Site; late July, 1972).

Food and ingestion

A complete list of food items seen in the process of being eaten is not as meaningful as the statement that diet in *O. ornatus* has considerable range. Diet in nature can be summarized as follows: new shoots of annuals and animal feces (infrequent); virtually any kind of dead plant tissue and superficial tissues of shrubs (frequent). The latter category includes mainly dead bark; however, the bark is not always dead and the tissue is not always bark. For instance, superficial tissues of a type of *Opuntia* are common food at Big Bend. In Albuquerque the bark of *Salsola* (tumbleweed) is a frequent food. At the Jornada site the barks of *Ephedra* and *Prosopis* (mesquite) are readily eaten. However, the bark of *Larrea* (creosote bush) appears rarely eaten.

Consumption of moist soil is a prerequisite for ingestion of dry *Ephedra* bark. Analysis of soil ingestion is not yet complete.

Ingestion rates of *Ephedra* bark are inversely related to dry body weight (Fig. 5). Expressed as g food ingested/g dry weight over a 5-day period, they more than double between 20 C and 30 C (Table 6). Such temperatures are considered a reasonable approximation of the range in which *O. ornatus* feeds in the field.

Assimilation

As shown in Table 6, assimilation percentage ranges from about 24 at 20 C to about 38 at 30 C.

Table 6. *Orthoporus ornatus*: estimates of ingestion and assimilation

Parameters	20 C (N=12)	24 C (N=15)	30 C (N=10)
Ingestion rate*	0.020±0.003	0.034±0.004	0.050±0.010
Assimilation %**	23.6±4.0	31.4±2.3	37.6±3.5

*g food ingested/g dry wt x 5 days
**calculated as $\frac{\text{food ingested - feces}}{\text{food ingested}}$ x 100; all values ash-free dry wt.

Respiratory metabolism

Oxygen consumption is inversely related to body weight (Fig. 6), as is Q_{10} from summer animals during a change from 25 C to 35 C (Fig. 7). Specimens weighing between 3.2g and 5.9g had a mean Q_{10} of 1.45, while those weighing between 0.8g and 1.8g had a mean Q_{10} of 2.38.

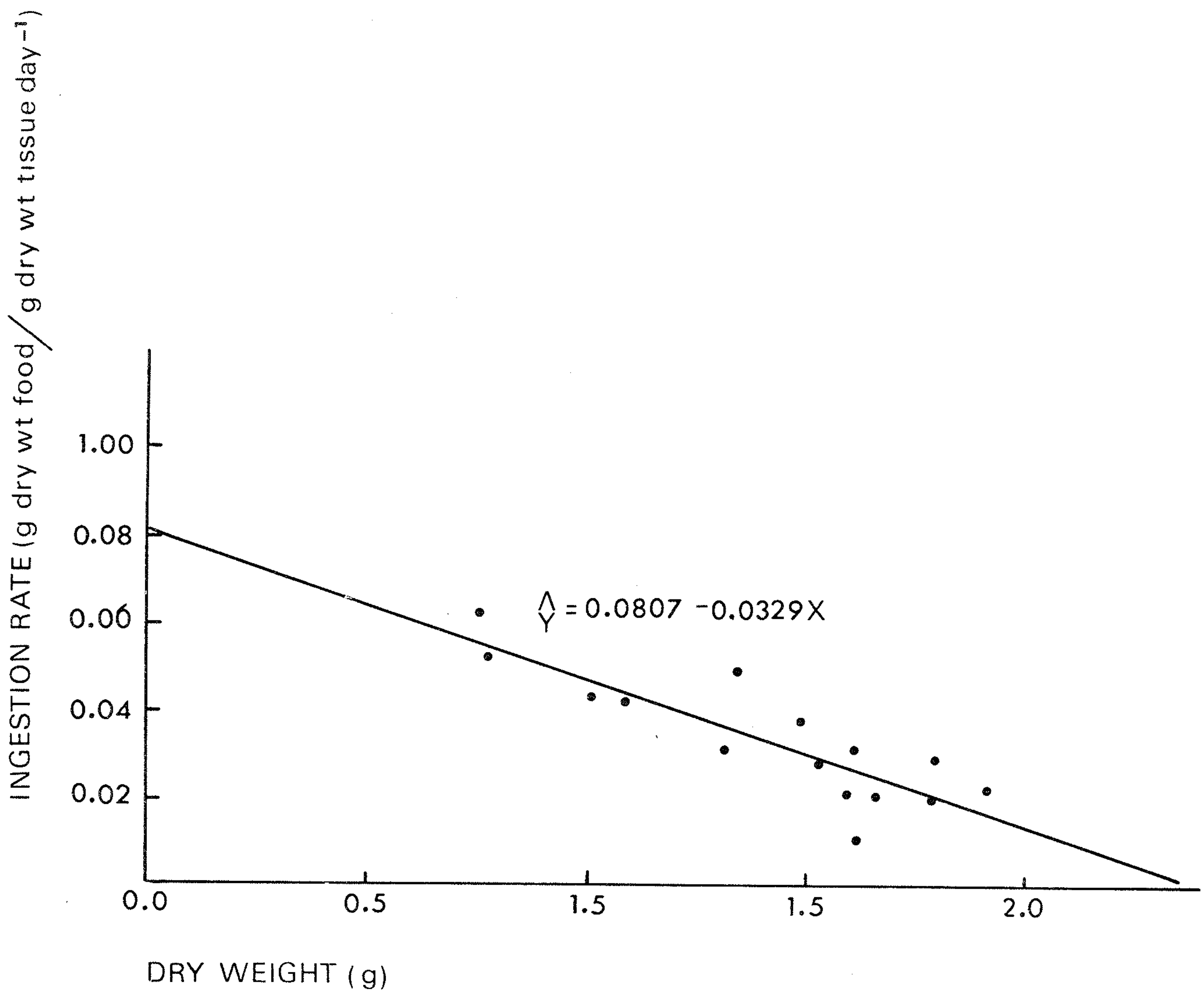

Figure 5. The relationship between ingestion rate of *Ephedra* bark and dry weight of *Orthoporus ornatus* at 24 C (collected from Jornada Validation Site; late July, 1972).

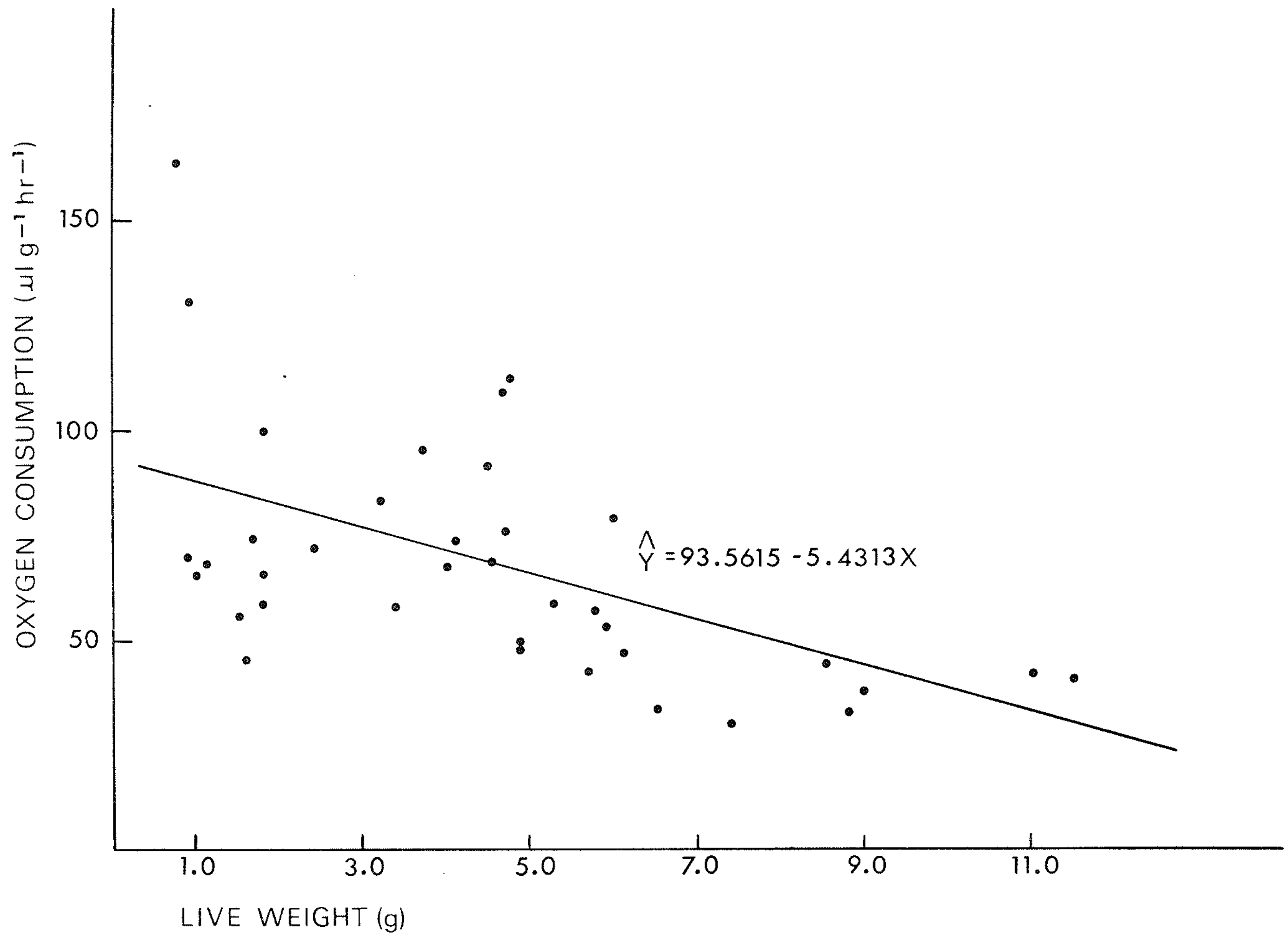

Figure 6. The relationship between oxygen consumption at 24 C and live weight of *Orthoporus ornatus* (collected from Jornada Validation Site; late July, 1972).

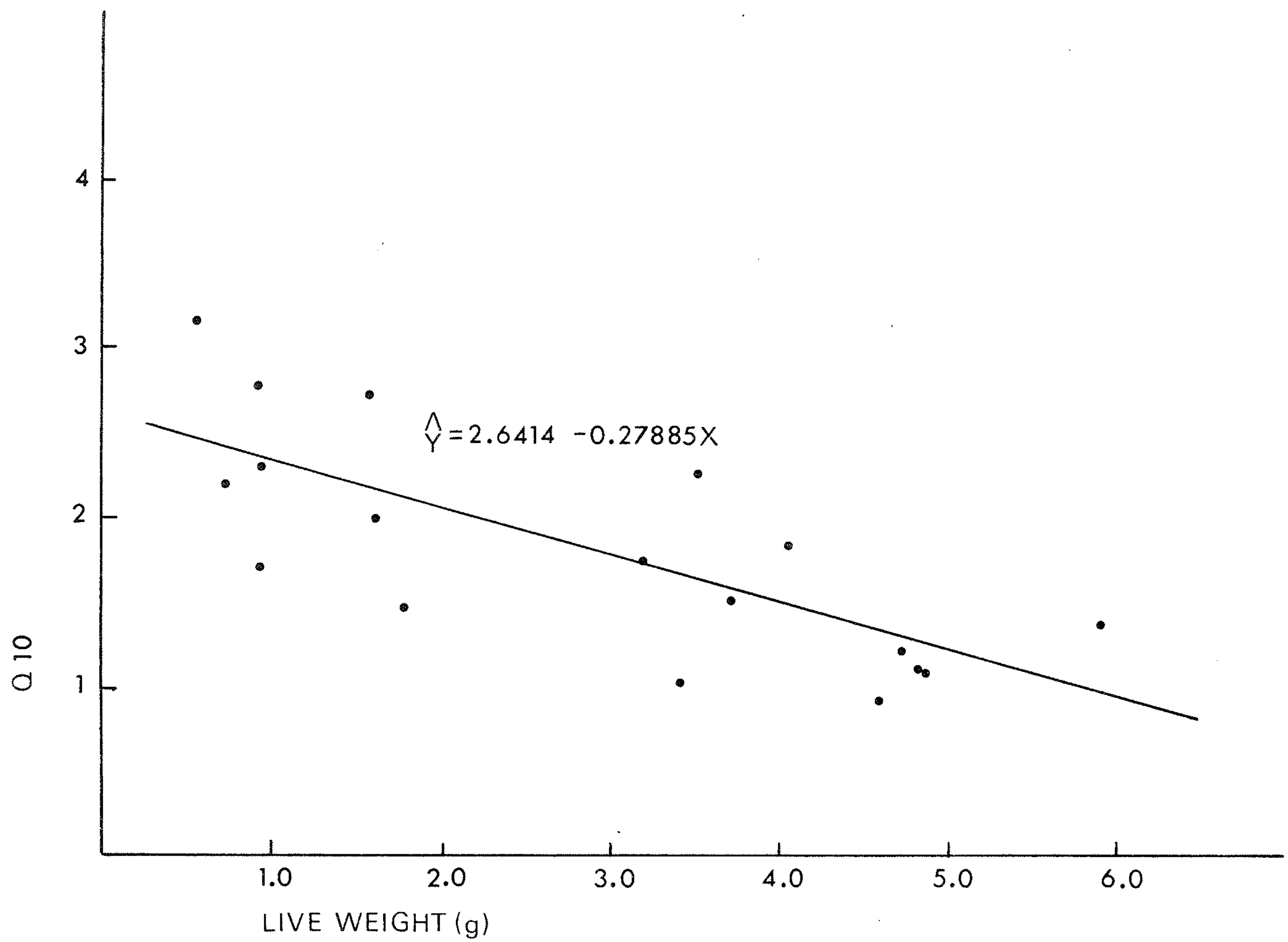

Figure 7. The relationship between Q 10 for a change from 25 C to 30 C and live weight of *Orthoporus ornatus* (collected from Jornada Validation Site; late July, 1972).

Monthly values for oxygen uptake are given in Fig. 8. Following relatively steady rates at 20 C between January and early June just prior to molt, *O. ornatus* appeared to depart from a diapause-like state between late June and September, at which time specimens had probably been underground for at least a month.

Oxygen uptake values of ambient temperatures reflected such temperatures to some extent; however, the increase after molting is out of proportion to a mean ambient temperature rise of only 3 C. October values suggest that the diapause-like state begins in late fall.

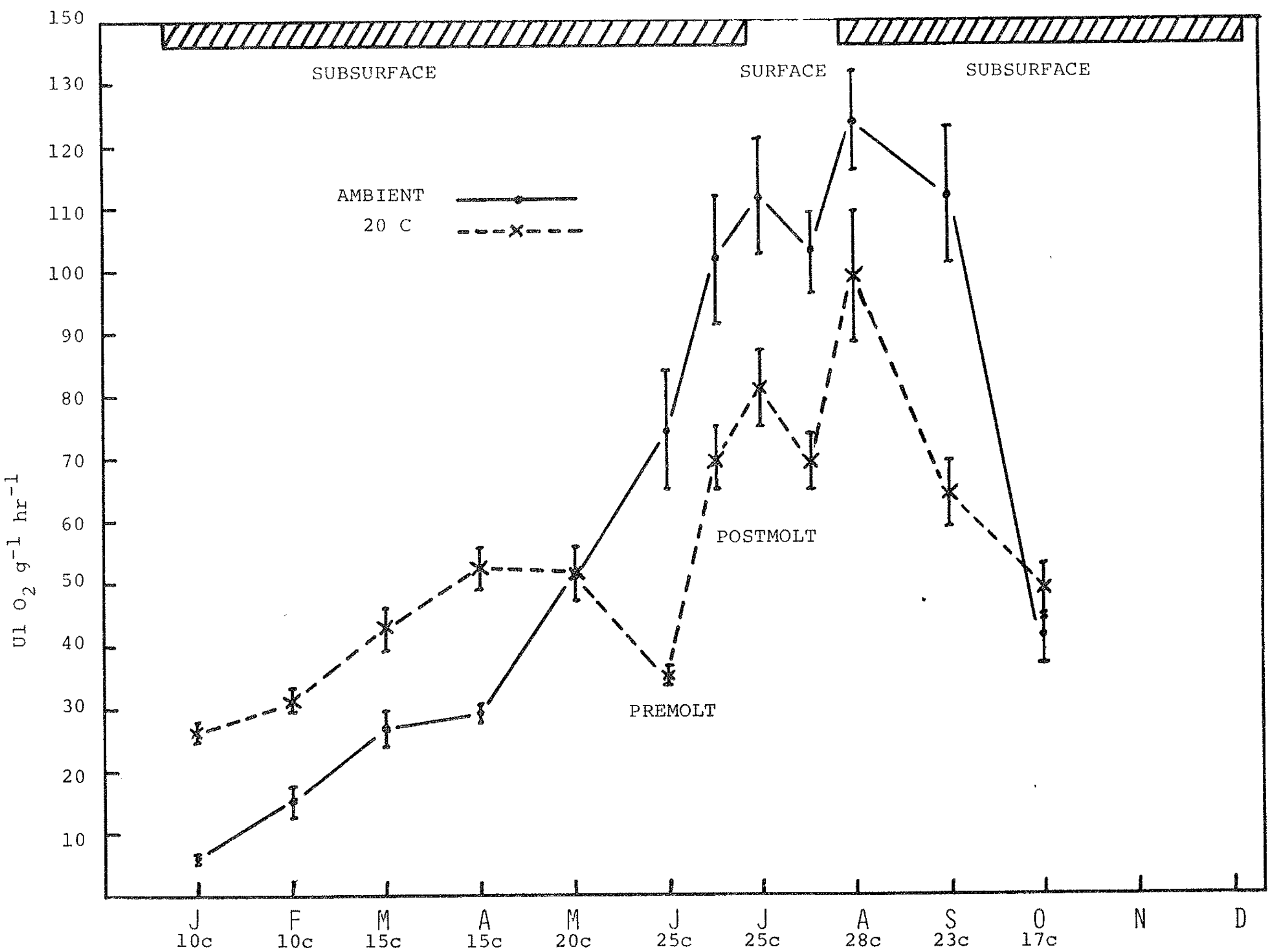

Figure 8. Monthly values of oxygen consumption per unit of live weight for *Orthoporus ornatus* collected from *Novomessor cockerelli* nests (except for July surface specimens) at the Jornada Validation Site (DSCODE A3UCF01).

When expressed in terms of cal g^{-1}, respiration at ambient field temperatures also showed an annual curve (Table 7). All values in Table 7, except for those of July, were calculated from one half of each of the recorded mean values of oxygen uptake (in $\mu l\ g^{-1}\ hr^{-1}$) that were recorded each month. The reason for this is that in reaction vessels specimens tend to move about, and therefore metabolize more than when in their soil-bound state. This procedure seems to give a reasonable estimate of oxygen uptake for an animal at rest.

Caloric values were calculated using a measured RQ value of 0.83.

Table 7. *Orthoporus ornatus:* annual respiratory metabolism (DSCODE A3UCF01)

Month	N	cal g^{-1}*	Temp. (C)
Jan.	12	27.8	10
Feb.	14	38.6	10
Mar.	15	48.1	15
Apr.	16	50.2	15
May	15	90.9	20
June	16	178.6	25
July**	33	470.6	25
Aug.	16	253.5	28
Sept.	17	222.3	23
Oct.	15	72.5	17

*Live weight
**Surface individuals

DISCUSSION

The results to date substantiate preliminary conclusions that *O. ornatus* is at times an abundant desert detritivore. The term "detritivore" is not completely appropriate, however. The desert millipede's diet is also to some extent that of a herbivore.

Perhaps the most striking aspect of this animal's life is that it appears to feed for a very limited part of the year, unlike millipedes living in forest litter. Several key adaptations seem to allow this kind of existence. First, responsiveness to a reasonably predictable rainfall pattern during the warmer part of the year has obviously evolved in this species. Early rains during late spring appear to trigger an annual molt and to arouse the otherwise quiescent millipedes to a state allowing later surface foraging. Responsiveness to early rains probably also involves ovarian maturation in large females.

Early and late rains can trigger movement to the surface, where dispersal, reproductive activities and foraging take place. For a detritivore, *O. ornatus* has relatively high assimilation efficiency; it is approximately twice that of a woodland millipede, *Narceus americanus*, that feeds on dead wood (O'Neill, 1968). This high rate, together with the ability to resist desiccation and to ingest water rectally (Crawford, 1972), enables the desert millipede to feed on the surface during periods that would be rapidly fatal to most other millipedes.

It is during these periods of surface foraging that *O. ornatus* probably makes its main contribution to nutrient flow in the desert, because after a short duration of high energy expenditure, a semi-dormant state is once again entered beneath the surface.

EXPECTATIONS

By December, 1972, monthly measurements of respiratory metabolism will be complete. These measurements, together with the new available assimilation and ingestion values, allow rough estimates of *O. ornatus* activity during the year. It remains to be demonstrated precisely how much nutrient material is processed by a given population in a feeding season, and also to what extent this produces additional millipede biomass. For IBP modelling purposes, we feel that a complete description of a millipede energy budget is desirable, but of secondary importance. Therefore, most of the emphasis during the coming year will be directed toward answering the two points raised above.

Basic to both points is a reasonable approximation of population density and age structure. More accurate measurements of biomass as seasons change are needed as well. In addition, daily feeding activity requires further analysis, and annual growth increments must be estimated. Finally, renewed attempts should be made to estimate potential and actual fecundity (birth rates and death rates are also desirable population parameters to know, but will be very difficult to ascertain).

In the coming year density at the Jordada site will be measured by making repeated daily counts of individuals on the surface of hectare plots. The regression technique will also be used at the Jornada site and will employ areas set off with lawn edging material. The same approaches will be used at Big Bend and perhaps at Albuquerque. Personnel will be present to make such measurements on days when millipedes are active.

Age structure will be analyzed after fixing millipedes in ethanol to obtain maximal body contraction (Blower and Gabbut, 1964). This seems the best remaining approach to the problem. The method will hopefully produce size discrepancies between any two instars and will therefore indicate longevity with relatively little error (recall that *O. ornatus* molts once a year).

Biomass will be estimated by drying specimens seasonally at 60 C until a constant weight is reached. Cuticular and gut-content components of biomass (as opposed to tissue biomass) will be estimated if possible.

Daily feeding activity will be estimated as before, and careful attention will be paid to the daily progression of ambient temperatures at different places in the feeding area.

Annual growth increments will be estimated by 1) weighing specimens kept in cohorts out of doors at yearly intervals (the first weighing has taken place), and 2) weighing laboratory specimens before and after molting.

Potential fecundity studies by dissection will be continued. Actual fecundity will be estimated where possible by counting eggs laid by females.

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