

Energy Allocation and Life History Strategy of the Desert Isopod *H. reaumuri*

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Summary. Population characteristics of the desert isopod *H. reaumuri* and its energy allocation during each phenophase were investigated in the Negev desert, Israel.

It was found that on the individual level, 52% of the energy is allocated to the prereproductive, and 48% to the reproductive phenophases. On the population level, only 10–23% is devoted to isopods which are involved in reproduction. Assuming that the energy allocation pattern in *H. reaumuri* is the consequence of its life history strategy, two unique evolutionary lines were suggested. One suggestion is the evolution of the family mode of life which increases the probability of the individual's survival. This is due to parental investment and co-operation between siblings. The other suggestion is the evolution of high energy utilization for burrowing, in order to solve the low and unpredictable nature of water resources in the desert.

1. To determine the energy allocation per phenophase on the individual and on the population level in the desert isopod, *Hemilepistus reaumuri*.

2. To find the relationship between energy utilization and life history characteristics.

The desert isopod, *H. reaumuri*, was selected for this study because I was surprised at the evolution of an unflexible, time dependent life cycle in this species (Shachak et al., 1976, 1979). These characteristics were evolved in a desert in which the main water input factor – rainfall, has a high degree of unpredictability, while the desert isopods are highly water dependent (Edney 1968). Therefore, a detailed investigation into the life history strategy of the annual, semelparus *H. reaumuri* may contribute to our limited knowledge of the diversity of life history strategies of desert invertebrates.

Introduction

One of the approaches to the study of life history is that of energy budget. Calow (1973) provided ample justification for the utilization of that approach for the investigation of life history variables. The energy budget approach assumes that every individual assimilates a finite and limited amount of energy and that this must be divided into broad compartments devoted to growth, maintenance and reproduction. The allocation of energy is the product of natural selection and therefore, an integral part of the life history strategy (Giesel, 1976). According to Randolph et al. (1977) there are two aspects to the problem of assessing resources, physiological and demographic. The physiological aspect focuses on resource requirements of the individual and the demographic aspect deals with resource turnover in a population. Study of the individual's resource allocation provides data on the phenotypic and/or genotypic plasticity in resource budgeting. This is in relation to life history characteristics such as: body size, age of first reproduction, mode of reproduction, rate of development, clutch size, offspring size and life span. The study of resource exploitation, on the population level, provides additional information on the relationship between resource allocation, birth rate, survivorship and population size. Thus, the two aspects are complementary in respect of the study of the life history strategy of an organism.

In the present investigation, I have tried to integrate the two aspects of resource utilization with the energy budget approach. The specific purposes of the study were:

The Life Cycle of H. reaumuri

The basic unit of the *H. reaumuri* population is that of monogamous pairs living with their offspring in completely closed family communities (Linsenmair, 1972). The family lives in a subterranean burrow with only one entrance. The entrance is characterized by a pile of feces pellets surrounding it. Every burrow contains only one family unit. The development of the family unit and their burrow is described in a previous paper (Shachak et al., 1979). Only a brief summary of the life cycle is given here (Table 1).

Five distinct phenophases are recognizable in the life cycle of *H. reaumuri* (Shachak et al., 1979):

Pair Formation. From February until the end of March pair formation occurs. At this time the 9 months old isopods vacate the burrows in which they hatched. The females select sites for burrowing and begin to excavate new burrows. Pairing takes place after acceptance of a male by the female. Surface activity is between 1200 to 1600 and is comprised mainly of feeding on annual bushes and soil crust.

Gestation. The gestation period is during the month of April. During this phenophase most of the females are gravid, carrying either eggs or young within their brood pouch. Surface feeding activity is bimodal, mainly from 0700–0900 and from 1700–1800.

Hatching. In May, the young isopods hatch from the brood pouch while the female is in the tunnel of the burrow and then crawl into the chamber. Only the parents are active on the soil surface. The young remain in the burrow until the next phenophase. When

Table 1. Summary of family structure, activity and microclimatic conditions throughout the annual life cycle of *H. reaumuri*

	Duration of phenophase (days)	Family structure		Age (months)		Hours ^a of activity	Air ^a temperature (°C)	Burrow ^a temperature (°C)	Air ^a humidity (%) on soil surface	
		1	2	1	2					
Pair formation	Feb. ↓	♂+♀	0	9	—	1200–1600	10–25	11–17	15–35	
Gestation and hatching	Apr. ↓	♂+♀ ^b	0	11	—	0700–0900	15–30	16–24	50–95	
	May ↓	♂+♀	80–90	♂+♀	12	0	1700–1800	15–30	16–25	50–95
Growth	Nov. ↓	0	40–50	♂+♀	—	7	0700–0900	15–25	15–24	85–100
Stationary	Jan. ↓	0	30–40	♂+♀	—	8	0500–0700 ^c	—	7–13	—

1 = parents; 2 = offspring

^a Shachak et al., 1979

^b Gravid

^c At the end of November no above ground activity

active, the parents go on foraging expeditions and carry back pieces of soil crust and dead plant material for the young.

Growth. The growth phenophase is the longest in the life cycle of the isopods. The period from May to November is a period of rapid growth for the young. In November a 27 times increase in body weight was recorded. Surface activity is comprised of foraging, climbing on bushes and over the soil surface to feed upon branches, twigs and soil crust.

Stationary. From November to February, no feeding or above ground activity was observed. The ambient temperature is lowest at this time of the year and the isopods remain underground until the pair formation phenophase.

The Study Area

The study area is situated on a loessial plain about 500 m above sea level in the central Negev, 34°46'E, 30°50'N. The plant association was classified by Danin (1970) as *Hammadetum scopariae loessium*. It is composed mainly of *Hammada scoparia*, *Artemisia herba-alba* and *Reaumuria palaestina* shrubs.

The Central Negev Highlands have the climate of a temperate desert, i.e. cool winter and hot summer months. This conforms with the definition of a desert, as a region where the moisture index is less than -40, and is characterized as BW by Koppen's formula (Evenari et al., 1971). Rainfall is low and highly irregular, with a quotient of variation of 5.0 or more. The rainfall figures for Sede Boqer (average 76 mm, max. 137, min. 23 mm quotient of variation 6.0) are typical of this area.

Due to the very dry air, evaporation values are very high. Values of 1,700–2,700 mm per annum are quoted, whilst relative humidity and solar radiation are 40–60% and 195–201 kcal cm⁻² year⁻¹ respectively (Evenari et al., 1971). An important factor in the desert is dew, which falls most heavily during the months of September, October and November. Up to 37 mm can be precipitated annually, but this figure is deceptive as the dew evaporates as soon as the sun rises (Evanari et al., 1971).

Methods

Burrow Structure and Soil Moisture

To determine the development of a burrow, throughout the life cycle of the isopods, an average of 10 burrows were dug up every month during one year. A deep hole was dug to one side of the entrance to trace the burrow downward. Soil samples for soil moisture determination were taken every 5 cm within and outside the burrows and at sites in which isopods were found.

Population Variables

Two rectangular grids, each comprising 4,000 m² (80 × 50 m), were used for the determination of the density of *H. reaumuri* families. Each grid was sub-divided into 80 rectangles of 10 × 5 m. This grid system made it possible to count the number and pinpoint the sites of the isopod burrows.

At the onset of the study, the population density was determined every month. As the study progressed, it was found that the study of isopod families in September yields information on the survival of families from the onset of pair formation phenophase (February) to the end of the growth phenophase. The following key was used in order to classify burrow survivorship from February to September:

1. Burrows surrounded by a small pile of faeces (10–30 g) with two distinguishable sizes of faecal pellets (small 0.3 mm³, large 4.4 mm³) indicates families that became extinct during the beginning of the growth phenophase (May, June).

2. Burrows surrounded by a large pile of faeces (150–350 g), dominated by large faecal pellets (4.4 mm³) indicated families that survived the growth phenophase.

The total number of burrows found in the area in September (1 and 2) are the number of families formed during the pair formation phenophase in February.

The number of isopods within a burrow (family size) was calculated using the Lincoln Index. Preliminary studies were done to compare the estimated number of isopods per burrow, using the Lincoln Index, with the actual number of isopods found in excavated burrows. This showed that the Lincoln Index is applic-

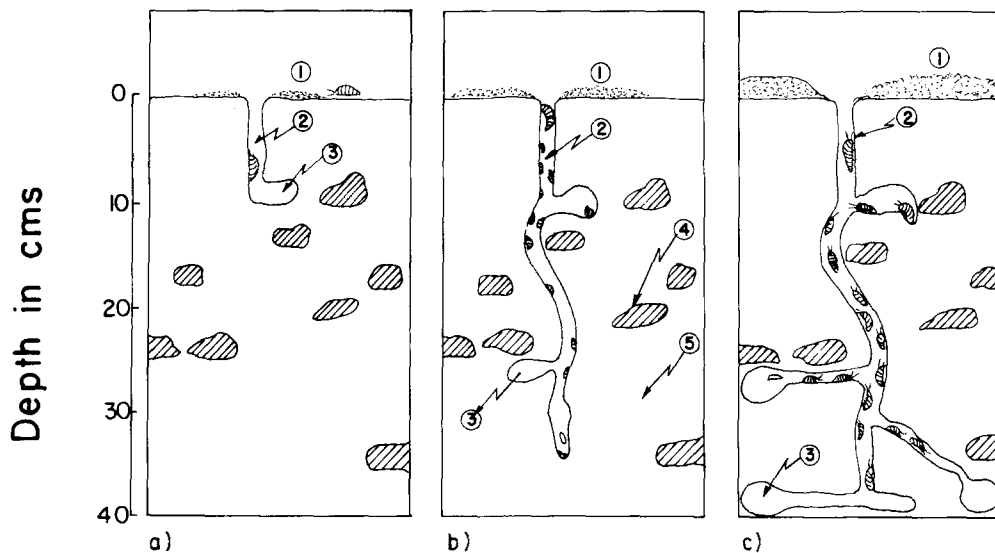


Fig. 1a-c. The development of *H. reaumuri* burrow throughout the annual life cycle of the family. a Pair formation and gestation phenophases. b and c Growth phenophase. 1. fecal pellets 2. tunnel 3. chamber 4. stone 5. soil

able. For the determination of family size an enclosure made of P.V.C. (30 cm in diameter and 20 cm height) was erected surrounding the burrow. The isopods that were active on the surface a few hours later, were marked with a coloured dot on the second pereonite. On the following day, the number of marked and unmarked active isopods was recorded. Data collected on the two consecutive days was used to calculate the family size.

Growth

For growth curve construction, 100 active isopods were collected during May, June, July, August, November 1972 and February, March and April, 1973. Average live and dry weight was determined.

Predation

During the study period, many field observations were made in order to identify *H. reaumuri* predators. The only observed predator in the field was found to be the burrowing scorpion, *Scorpio maurus palmatus*. Thus, an intensive study on the ecology of this scorpion is under investigation. Relevant to the study of *H. reaumuri* is the population density of *S. maurus palmatus* and its predation rate during the growth phenophase of the isopods.

Determination of the scorpion density – *Scorpio maurus palmatus* lives individually in subterranean burrows with a semi-circular entrance (diameter ranging from 0.5 to 2.2 cm) easily identified in the field. The number of scorpion burrows in the study area were recorded twice during the period of May to November.

Determination of predation rate – feeding experiments for the determination of predation load of *S. maurus palmatus* on *H. reaumuri* was carried out from 5.10.73 to 31.10.73. Twenty scorpions that were collected from the field on 3.10.73 and were individually put in plastic boxes (30 × 20 × 12 cm). At the beginning of the experiment every scorpion was supplied with a live isopod. As soon as the scorpion predated upon the isopod, a new one was provided. The number of isopods eaten by the scorpion was recorded every day.

Egg Production

Samples were collected from the field in April, 1973, 1974, 1975 and 1976. Each sample consisted of 50 females with brood pouches. In each case, the ova were removed from the pouch and were counted and weighed.

Determination of Respiration

Oxygen consumption was measured with volumetric respirometers according to Scholander et al. (1952) at air temperatures corresponding to average burrow and surface temperatures in which the isopod lives. The isopods collected in the field, were acclimated to the test temperature for 5–7 h. Newell et al. (1974) regards this interval as sufficient for adaptation.

Results

The Burrow

1. Burrow Development

The desert isopods spend most of their time in subterranean burrows (Shachak et al., 1979). The construction of the burrow by the family of isopods is a continuous process. To illustrate this, the development is divided into three distinct states. The first stage (February to May), starts when the 9 month old females start digging new burrows and terminates when a vertical burrow of about 10 cm deep is dug (Fig. 1 a). During the second stage (June to July) further expansion of the burrow is carried out by the members of the family. This stage ends with a vertical burrow of 40–50 cm in depth having been developed (Fig. 1 b). Stage 3 is characterized by horizontal expansion. Horizontal branches terminated by small chambers are found in the fall before the isopods stop their above ground activity for the winter (Fig. 1 c).

2. Estimation of the Digging Effort

Except for a very short period, at the onset of the pair formation phenophase, the isopods do not dig with their pereopods. Most of the expansion of the burrow is carried out by feeding on the underground soil and clearing faeces out of the burrow. The faeces are almost completely made up of soil. A typical behavioural pattern of *H. reaumuri* is to carry from the burrow a few faecal pellets in their maxilliped and drop them on the soil surface at a distance of 10–20 cm from the entrance of the burrow. A direct method of observation and measurement of the feeding-digging activities was not developed. However, with the available data on the burrow structure and the soil made faeces accumulation, it is possible to estimate the number of isopods in a family which are involved in the feeding-digging process. The following equation was used to estimate the number of the digging isopods (N).

$$N = \frac{S}{DR \cdot D}$$

where:

S – The weight of soil removed from an average burrow as faecal pellets;

DR – Average feeding-digging rate/day/individual;

D – Number of feeding-digging days.

The weight of soil removed (S) was calculated from the length and radius of the burrow's tunnels and the number and volume of chambers (Table 2). It is estimated that 111.6 g of soil are removed by an isopod family during the excavation of a burrow (average volume 62.3 cm², soil density 1.8 g·cm⁻²).

Table 2. Average dimensions of a fully developed (Stage 3)^a *H. reaumuri* burrow ($N=28$)

Length of tunnels ^a	145 ± 28 cm
Radius of tunnels	0.35 ± 0.05 cm
No. of chambers ^a	3 ± 1
Volume of chambers	6.2 ± 0.9 cm ³

^a See Fig. 1

Assuming soil consuming rate (DR) of 37 mg·isopod⁻¹ day⁻¹ (Shachak et al., 1976) and 90 days (D) of intensive feeding – digging activities (June to September) the calculated minimum number of isopods which participate in the digging-feeding process is about 34.

3. Burrow Depth and Soil Moisture Regime

Figure 2 summarizes the variation of soil moisture content at a given burrow depth from February to September. It can be seen that during the reproductive phenophases (pair formation, gestation and hatching) when the burrow depth varies from 5 to 20 cm, the soil moisture content is within the range of 5 to 18%. During the growth phenophase the soil moisture content at the burrow's depth is lower – from 2 to 10.4%.

Determination of soil moisture content in the burrow's chambers, in which the isopods live, shows that the moisture content is always higher than 6% within the range of 6–13% (Fig. 2).

There isn't any direct evidence that *H. reaumuri* cannot survive in burrow chambers with a soil moisture level less than 6%. However, due to the fact that live isopods were not found within burrow chambers with less than 6% soil moisture content it was assumed that 6% is the lowest limit for the survival of these isopods. If the 6% soil moisture content assumption is valid, then the probability of reaching this value of soil moisture content by the feeding-digging activities is very high during the reproductive phenophase and much lower during the growth phenophase (Fig. 2).

Population Variables

1. Density

Population density, families and individuals, was estimated three times during the annual life cycle of the isopods. First, the maximum density after hatching in May; second, the density of families and individuals that survived from hatching in May to September; third, the density after pairing in February. These three densities show the within generation fluctuation from maximum in May to minimum in February. The density in September is of the isopods that survived the pre-reproductive phase. Figure 3 shows the fluctuation in population size (families and individuals) for six generations of *H. reaumuri* from 1972–1978. In the analysis of the fluctuation of the population size, within and between generation variations, should be distinguished. Within the same generation the general pattern is a decrease of 2–8 times in the population size from May to September (pre-reproduction phase) and a decrease of 3–42 times during February (Reproductive phase). Comparison of the variation in population size from 1972–1978 shows that maximum density was recorded in May 1976; 4,800 isopod·100 m⁻² is about 8 times higher than the minimum density in May, 1975. The variation of the minimum densities in February is about the same from 14 iso/100 m² in 1974 to 120 iso/100 m² in 1976. On the family level, no general pattern of variation in density was found. In the six generations studied 3 increased and 3 decreased in the density of families, within the same generation. This was determined from the pre-reproductive to the reproductive phases. The most intensive build-up of families occurred in the 1975–1976 generation. The density of families was 8 in September, and 60 new families were established in February – an increase of 7.5 times in families size. The lowest number of pairings occurred in February 1974 when the recorded density of new families was only 7 per 100 m².

2. Survivorship

Life tables were constructed for five generations of *H. reaumuri* (Table 3).

The study of survivorship of the five generation mortality (dx) and mortality rates (qx) revealed similar trends. Highest mortality occurred in the growth phenophase 471–842 died out of 1,000 individuals entering the phenophase. Total mortality during growth phenophase is the sum of whole families extinction and mortality of individuals in families that survived. Mortality of whole families causes higher losses to the population than mortality of individuals. Highest rates of mortality occurred during pair formation phenophase out of 1,000 isopods entering the phenophase 630–966 died.

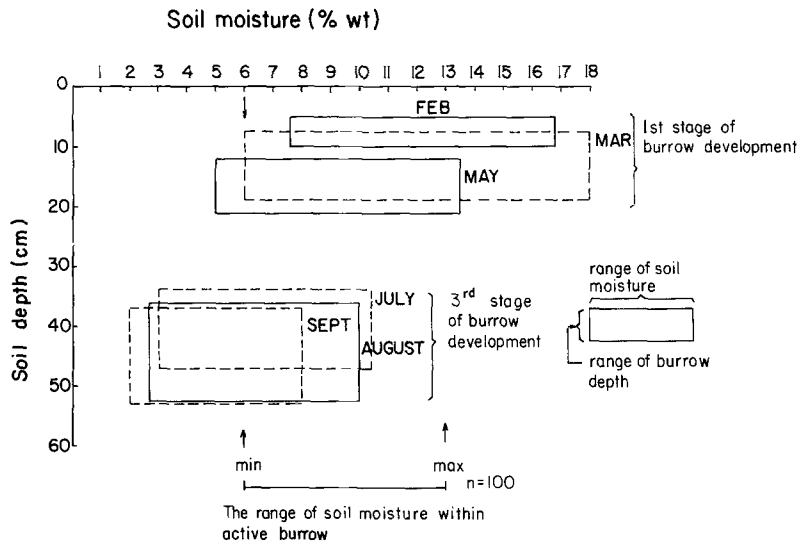


Fig. 2. The temporal variation in the range of soil moisture at the depth corresponded to the various stages of *H. reaumuri* burrows

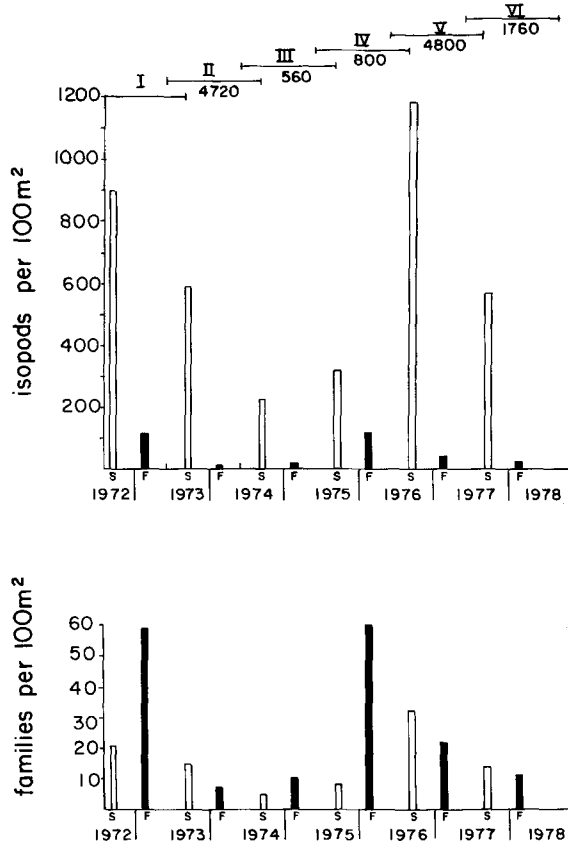


Fig. 3. Changes in density in six generations of *H. reaumuri*. I-VI generations (number under the generation line - maximum population size in May)

3. Fecundity

H. reaumuri is single brooded and the gestation period is always in April. The frequency distribution of number of ova per brood for four generations of isopods is shown in Fig. 4. The number

Table 3. Life tables for five generations of *H. reaumuri* in a loessial plain in the Negev desert

	Phenophase	# Living at beginning of phenophase (<i>lx</i>)	# Dying in pheno-phase (<i>dx</i>)	Mortality rate per 1,000 alive at beginning of phenophase (<i>qx</i>)
G1	Growth	1000	842	842
	Stationary	158	31	196
	pair formation	127	124	976
	gestation	3	—	—
G2	Gr	1000	571	571
	S	429	85	198
	PF	344	309	898
	Ge	35	—	—
G3	Gr	1000	471	471
	S	529	105	198
	PF	424	267	630
	Ge	157	—	—
G4	Gr	1000	664	644
	S	336	67	199
	PF	269	260	966
	Fe	9	—	—
G5	Gr	1000	594	594
	S	406	81	200
	PF	325	312	960
	Fe	13	—	—

of eggs produced by a single female varied from 30-150 eggs per brood. No correlation was found between female weight and clutch size. In spite of the wide distribution of number of ova per female, the annual variation of the mean is very small, ranging from 88.06 (± 16.56) in 1975 to 92.38 (± 21.52) in 1973.

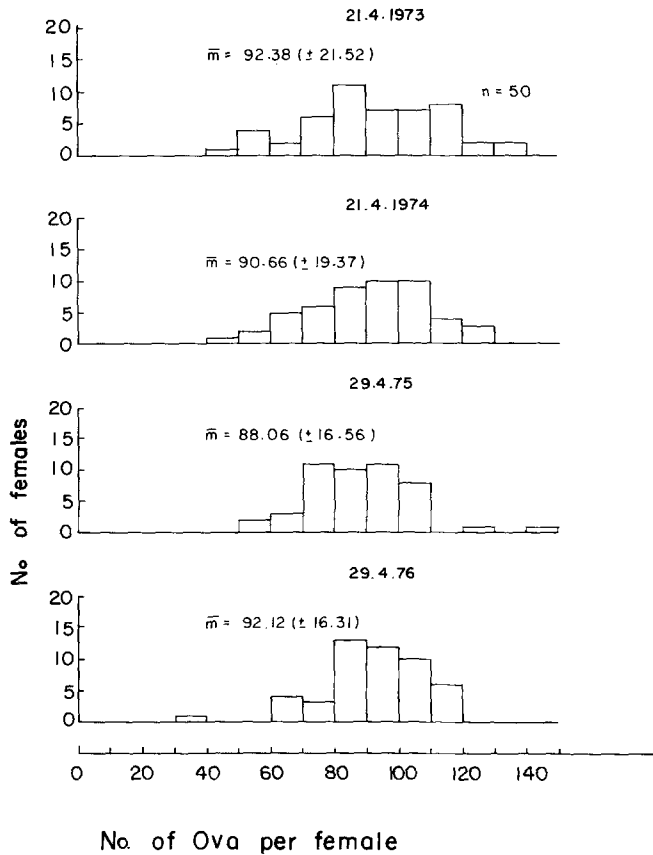


Fig. 4. Frequency distribution of ova number per female for four generations of *H. reaumurii*

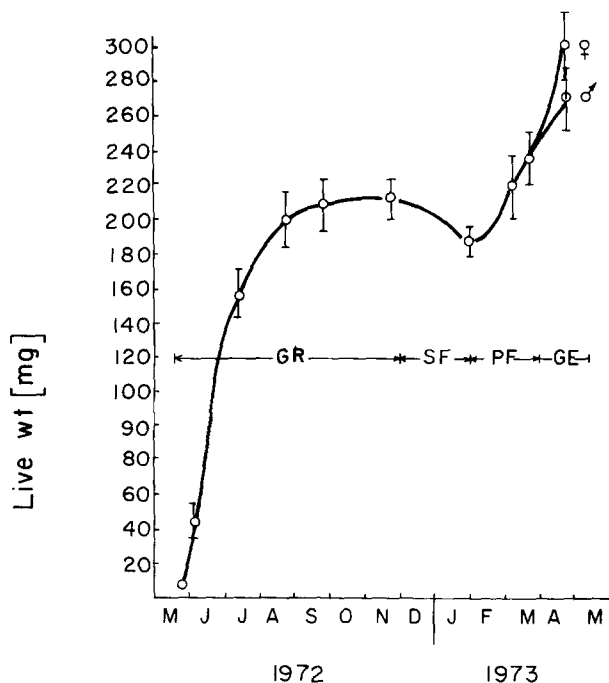


Fig. 5. Growth curve for the 1972-73 generation of *H. reaumurii*. GR, ST, PF, GE - Growth, stationary, pair formation and gestation phenophases, respectively

Growth

Throughout the life cycle of *H. reaumurii* there are two periods of increase and one of decrease in body biomass (Fig. 5). Increase in body weight was recorded during growth, pair formation, and gestation phenophases. Decrease in biomass occurred in the stationary phase. The most intensive biomass gain is from May to August about 2.85 mg live weight per isopod per day. Toward the end of the growth phenophase growth rate is low. A mean of 0.15 mg live weight · isopod⁻¹ day⁻¹ was recorded. In the stationary phenophase, when the isopod stops soil surface activity, the average decrease in body weight is 0.34 mg live wt · isopod⁻¹ day⁻¹. With the renewal of surface activity, during pair formation, the rate of gaining biomass is about 1.31 mg live weight · isopod⁻¹ day⁻¹. In the gestation period, females gain about 1.7 mg live wt. per day.

Predation

The scorpion *S. maurus palmatus* is the predominant predator of *H. reaumurii*. Its density in the study site varied from 3-13 scorpions per 100 m² during the period of 1973-1977. The annual fluctuation in the scorpion population size during the growth phenophase of *H. reaumurii* is given in Table 4. *Scorpio maurus palmatus* is eurytopic and eats various small arthropods in addition to isopod it eats mainly ants and beetles. Evidence that the scorpion preys upon these arthropods was found after rainfall when the burrows were cleaned by the scorpions, and prey remains were easily identified. From the field data it is impossible to estimate the allocation of the predation effort of the scorpion among the various species of arthropods. However, it seems that about 20-60% of the remains are antenna, heads, pereonites, pereopods and urpods of *H. reaumurii*. The laboratory feeding experiments show that when *S. maurus palmatus* feeds entirely on isopods, the average predation rate is 0.15 isopod · day⁻¹. Field densities of the isopods and scorpions combined with the predation rate from the laboratory study of the estimation of predation load, in the field is given in Table 4. It can be seen that if the scorpions would feed only on isopods they would eat from 1.7-19.3% of the total population during the growth phenophase.

Table 4. Estimated maximum predation load on *H. reaumurii* by the scorpion *Scorpio maurus palmatus*

	# of scorpions per 100 m ²	# of isopods ^a hatched 100 m ²	Predation load (estimated max.)	
			iso/100 m ² ^b	%
1973	3	4720	81	1.7
1974	4	560	108	19.3
1975	5	800	135	16.9
1976	13	4800	351	7.3
1977	6	1760	162	9.2

^a # of pairs × 80

^b Per growth phenophase 180 days, predation rate = 0.15 iso/day from feeding exp. 5. 10. 73-31. 10. 73

Table 5. Oxygen consumption of *H. reaumuri* in the laboratory at air temperature corresponded to average burrow and surface temperature during the various phenophases (see Table 1)

Phenophase	O ₂ consumption (cal · g ⁻¹ · h ⁻¹) ^a	
	Surface activity	Burrow inactivity
Growth	1.5 ± 0.3 ^b	1.1 ± 0.3
Stationary	—	0.4 ± 0.1
Pair formation	1.0 ± 0.2	0.5 ± 0.1
Gestation and Hatching	1.6 ± 0.3	0.7 ± 0.2

^a 1 μlO₂ = 0.005 cal

^b S.D.

Respiration

Oxygen consumption of isopods in the laboratory at air temperature, corresponded to average burrow and surface temperatures during five phenophases is shown in Table 5.

Phenophases and Energy Allocation

The Approach

It was assumed that every individual isopod assimilates throughout its life cycle a finite amount of energy. The allocation of this amount of energy between phenophases is a product of the evolution of life history strategy and adaptation to life in the desert. Thus, the basic equation used to calculate energy allocation was:

$$E = E_{GR} + E_{ST} + E_{PF} + E_{GE} \quad (1)$$

where:

E – Total energy turnover for an individual isopod;

E_{GR} , E_{ST} , E_{PF} , E_{GE} – Energy turnover throughout the growth, stationary, pair formation and gestation phenophases respectively.

Every phenophase has two components of energy flow: maintenance energy (E_m) and energy for growth and/or reproduction (E_r). Thus, the energy turnover throughout a given phenophase (E_{PH}) is:

$$E_{PH} = E_m + E_r \quad (2)$$

Two methods were used for E_{PH} determination. In the first method E_{PH} was calculated according to Eq. (2) when E_m was calculated using oxygen consumption data (Table 5) and E_r was determined from growth curve (Fig. 5). E_m was calculated as follows:

$$E_m = \text{DOC} (W_0 + 1/2 \Delta W) \Delta t \quad (3)$$

where:

DOC – average daily O₂ consumption in a given phenophase;

W_0 – average body weight at the onset of a given phenophase;

ΔW – average increase in body biomass during a given phenophase;

Δt – the duration of the phenophase.

Energy from growth and/or reproduction (E_r) was calculated

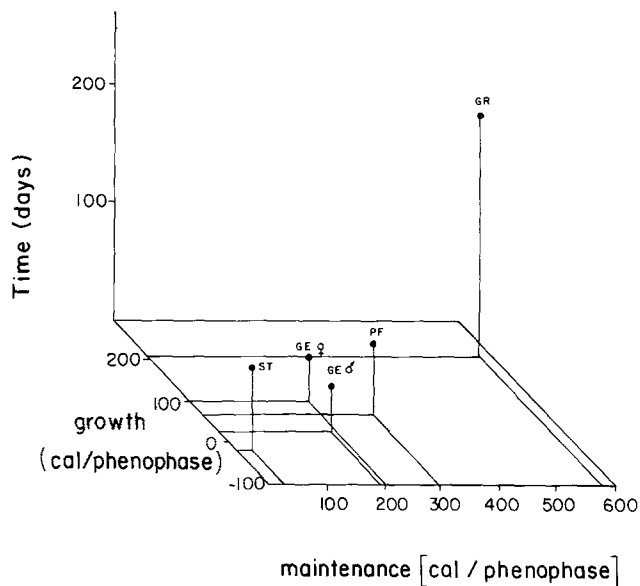


Fig. 6. Allocation of time and energy for maintenance and growth of the desert isopod *H. reaumuri* on the individual level. GR, ST, PF, GE – see Fig. 5

as the product of increase in biomass during a given phenophase (ΔB) times the caloric value of the isopod tissues (CV)

$$E_b = \Delta B \cdot CV \quad (4)$$

The second method for E_{PH} determination used assimilation rates of *H. reaumuri* from feeding experiments in the laboratory (Shachak et al., 1976). E_{PH} was calculated as follows:

$$E_{PH} = DA (W_0 + 1/2 \Delta W) \Delta t \quad (5)$$

where:

DA – average daily assimilation rate.

The population aspect of energy partition integrates individual energy allocation with the population density. Thus, the product of the individual energy turnover per phenophase (Eqs. 1–5) times the population density in a given phenophase gives the energy turnover of the population.

Energy Allocation

The following four questions were raised in order to understand the energy allocation pattern of *H. reaumuri*:

(1) Within a given phenophase, how much of the total amount of energy assimilated by the individual is devoted to maintenance and to change in body biomass?

(2) Out of the total amount of assimilated energy consumed by the individual, how much is devoted to each phenophase?

(3) Within a given generation, what is the allocation of energy, on the population level, between phenophases?

(4) What is the similarity and difference in the energy allocation pattern between generations?

The allocation of time and energy for maintenance and increase in body weight on the individual level, is given in Fig. 6. Figure 6 can be analyzed by integrating the individual phenophases into pre-reproductive and reproductive periods. In the growth and sta-

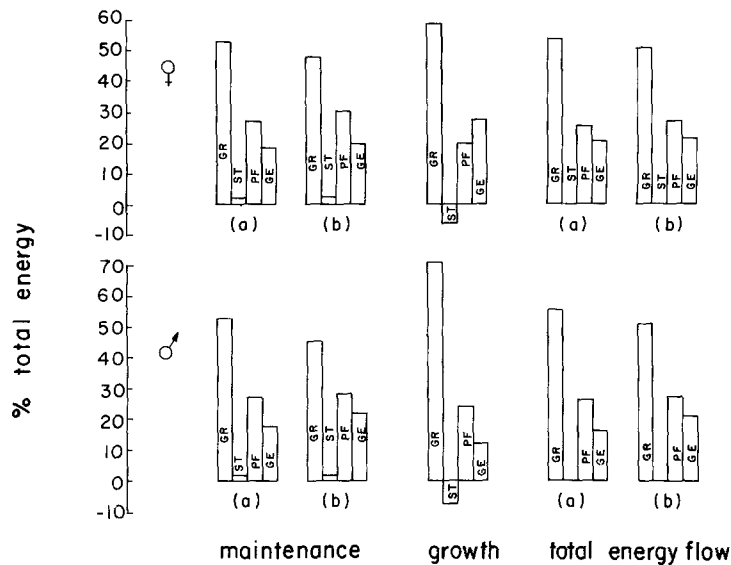


Fig. 7a and b. Allocation of energy among four phenophases of an average individual of *H. reaumurii*. a Calculated using oxygen consumption data. b Calculated using assimilation rates from feeding experiments GR, ST, PF, FE – see Fig. 5

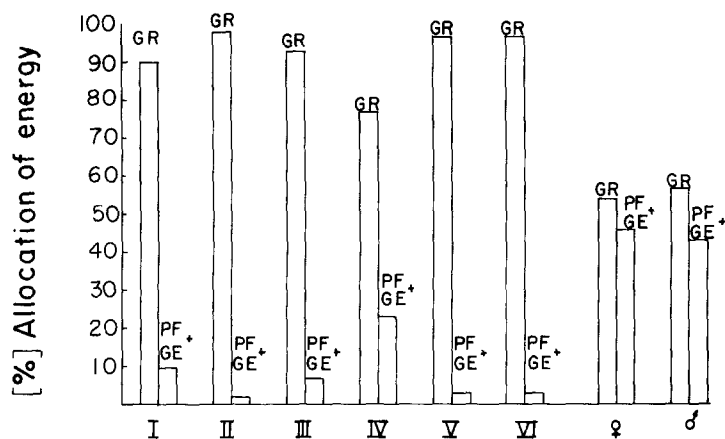


Fig. 8. Energy allocation in *H. reaumurii* between pre-reproductive and reproductive phenophases. I-VI, Energy allocation in six generations. ♀ ♂, Energy allocation on the individual level

tionary pre-reproductive phenophases 26–31% of the total energy turnover is devoted to increase in biomass and 74–69% for maintenance. In the pair formation and gestation reproductive phenophases, about 25% of the female energy flow is allocated to growth and ova production and 75% for maintenance. The male is devoted less of its total energy to growth and more for maintenance, 17 and 83% respectively.

Figure 7 shows the partition of the energy assimilated by the individual *H. reaumurii* between phenophases. From the total female energy flow throughout the four phenophases 50–54% is devoted to the pre-reproductive phases and 46–50% to the reproductive ones. The energy allocation of the male is very similar 51–57% of total energy flow is used in the pre-reproductive phases and 43–49% for the reproductive ones. Net production partition between pre-reproductive and reproductive phases shows the following pattern. Females allocated 58% and 42%, males 71% and

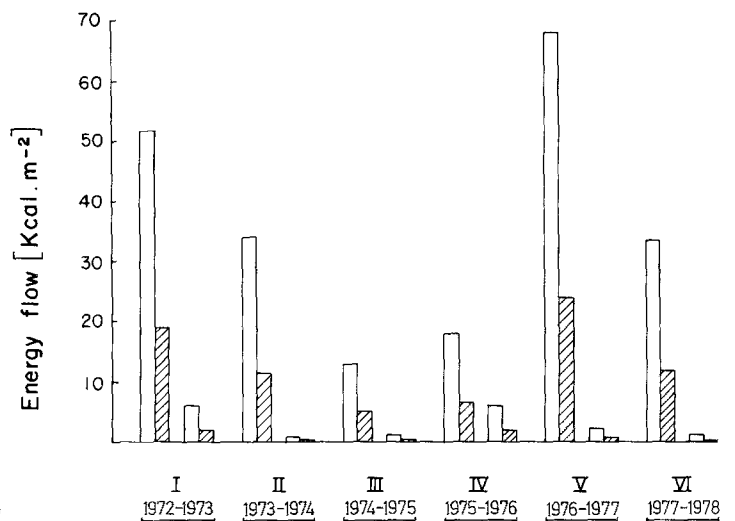


Fig. 9. Energy allocation for maintenance and growth in the pre-reproductive and reproductive phenophases of six generations of *H. reaumurii*. □ maintenance; ▨ growth. (The left and right bars of the six generations are for the pre-reproductive and reproductive phenophases, respectively)

29% of the net energy to pre-reproductive and reproductive phases respectively.

The energy flow on the population level in the six generations of this isopod, is given in Fig. 8. It can be seen that energy turnover in the same generation is mainly during the growth phenophase and the minority of energy flow is in the reproductive phenophases (Fig. 9). 77–90% from the total energy devoted to a given generation is allocated to the population in the pre-reproductive phase while only 10–23% is devoted to the population which is active in reproduction. It can be concluded that the pattern of energy allocation between phenophases on the population level is different from individual level. On the individual level, about equal amounts of energy are devoted to pre-reproductive. On the population level, more than 3/4 of the energy is devoted to the premature population.

Discussion

There is a growing body of knowledge concerning various aspects of isopod population biology in the field (Hatchell, 1947; Paris and Pitelka, 1962; Saito, 1965, 1969; Sutton, 1968; Standen, 1973; Sunderland et al., 1976). However, data necessary for comparative study of the life history strategies of the various species of isopods is still limited. Within the framework of the data available I shall discuss three aspects of the life history of *H. reaumurii*:

1. The differences between the life history of *H. reaumurii* and mesic isopods.
2. The relationship between family mode of life and the life history of *H. reaumurii*.
3. The relationship between energy and water resources allocation throughout the life cycle.

H. reaumurii vs. Mesic Isopods

A combination of previous works with the present study provides some evidence that the desert isopod *H. reaumurii* exhibits a life

history strategy which in many respects is different from the life history of isopods inhabiting mesic environments.

1. The life span of *H. reaumuri* is shorter, about 15 months, while the length of life of a *Armadillidium Vulgare*, *Porcellio scaber*, *Philosciamuscorum* from a mesic environment is 2–4 years.

2. *Hemilepistus reaumuri* is single brooded (semelparous) and many mesic species are multiple brooded (interparous).

3. No subsocial behaviour was found in the mesic species, *Oniscus asellus*, *Porcellio scaber* and *Armadillidium nastum* (Schneider and Jakobs, 1977). *H. reaumuri* lives in monogamous pairs together with their offspring in completely closed family communities (Linsenmair, 1972).

4. It seems that clutch size of *H. reaumuri* (mean 90 eggs/clutch) is higher than clutch size of mesic species. The clutch size reported for *A. vulgare* (Paris and Pitelka, 1962) and for *P. muscorum* 5–35 eggs per clutch (Sutton, 1968).

5. No data is available on parental care in mesic isopods. *H. reaumuri* exhibits a period of parental care after the young leave the brood pouch (Shachak, unpublished). The same behaviour pattern was found for *H. aphganicus* (Schneider, 1970).

The differences listed show that the evolution of *H. reaumuri* correlates with r-selection characteristics which are expected in the desert's extreme conditions (Pianka, 1970).

Family and Life History

An attempt to explain the evolution of the life cycle of *H. reaumuri* by a one dimensional scheme may greatly simplify the explanation of the process of evolution. Nevertheless, I would like to argue that the development of its life cycle strategy is a consequence of the evolution of the family community unit. As a consequence of the development of the family community, the survival of the individual isopod from hatching to reproductive age is a combination of its own fitness and the survival of his family. The family mode of life increases the probability of the individual's survival by parental investment and co-operation between siblings.

Parental investment which affects the survival of the offspring includes site selection for burrowing, protection of brood, and parental care during the early stages after hatching.

Selection of site for burrowing has high survival value. If the female selects a site in February which maintains high soil moisture with the expansion of the family burrow during the growth phenophase, the probability of her offspring maintaining their water balance increases (Fig. 2).

The protection of the brood by the marsupium which provides physical protection and nourishment for the young is typical for isopods (Vandel, 1943; Heeley, 1941; Pandian, 1972). It also has the same effect on *H. reaumuri* and increases the potential of the family members to survive. In addition to site selection and brood protection, *H. reaumuri* exhibits a period of parental care after the young leave the brood pouch (Shachak, unpublished). The same phenomena was found by Schneider (1970) for *H. aphganicus*. Parental care includes carrying food from the soil surface to the subterranean burrow which protects the young isopods from exposure to the harsh environmental conditions above ground. They also guard the burrow entrance which protects the young isopods from predation and competitors. A distinction should be made between the individual and population as far as parental investment in energy allocation is concerned. The individual female devoted 300 cal. which is about 42% of her total energy. On the population level, the energy utilization is comparatively low.

Only 8% of the total energy flow at the population level is devoted to parental investment.

The co-operation between the family members takes place mainly in two forms: expansion of the burrow and guarding. As was shown in the results a burrow can be dug only by the co-operation of at least 34 isopods. The expansion of the burrow has the following consequences on the survival of the individual:

(a) By utilizing the microclimate of the burrow and the complementary above ground activity pattern, *H. reaumuri* is able to regulate its heat balance (Shachak et al., 1979).

(b) The burrows microenvironment provides the isopods which comparatively high soil moisture which increases the air water pressure (Edney, 1968) and therefore, reduces water loss from the isopod. Further increase in water conservation may be reached by aggregation of the family members in the burrow's chambers.

During the phenophase in which burrow expansion takes place, energy consumption by the individual as well as on the population level is high. It is assumed that high energy utilization was involved because the regulation of radiation load and water balance can be achieved only by the high investment of energy by the family members in the construction of the burrow.

Energy, Water and Life Cycle

Within the limits set by our investigation of life history of *H. reaumuri* it may be hypothesized that the life history of this isopod evolved toward a set of co-adopted traits in order to solve the variation in energy and water flow relationship during its life cycle. In the reproductive phenophases, the probability that the environment will provide the individual isopod with its energy and water requirement is high. Plants standing crop is very high compared to the low *H. reaumuri* population in February. Soil moisture is also high, during this period, relative to the isopod's demands. In this setting of environmental conditions, the probability of successful reproduction is high. That could have been the main factor for the development of semelparity in this isopod. In the pre-reproductive phases, the probability that the environment will provide the individual with its energy requirements is also high (Shachak et al., 1976). However, probability of providing the isopod with its soil moisture requirement is low, because of the depth in which the soil moisture required can be found. Under such environmental conditions, the probability of the individual isopod surviving is low. It is assumed that the adaptive solution to the water flow problem was the development of the family as the basic unit of the population. Utilization of high energy for digging on the family level is the only solution for the individual's water requirements.

The evolution of semelparity, high fecundity and family mode of life creates a problem on the population level. In order to maintain a stable population size out of 1,000 eggs laid 22 isopods (11 ♀+11 ♂) have to survive and reproduce. During the pre-reproductive phases, the number of isopods remaining alive is high which may be explained by the high probability of the members of the family to survive. If all isopods that survive the pre-reproductive phases enter the reproductive phases, the population size would constantly increase. To counteract this trend, high mortality occurs during the onset of the pair formation phenophase (Table 3). The mechanism which regulates losses of individuals during pair formation, to solve the population dynamics consequences of the life history strategy is now under investigation.

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