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DEVELOPMENTAL PATTERNS IN TWO POPULATIONS OF THE MILLIPEDE *ARCHISPIROSTREPTUS SYRIACUS* (DE SAUSSURE) IN ISRAEL (DIPLOPODA)

by

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ABSTRACT

Comparison between two populations of the spirostreptid millipede *Archispirostreptus syriacus* reveals that there are no significant differences in the pattern of development between the xeric population (in Brosh) and the mesic one (in Megiddo). However, there is a difference in the duration of larval stages resulting in higher growth rates in the xeric population than in the mesic one. In Megiddo there are 11 larval stages and maturity is reached at the age of 8 years, following 3 adult stages. In Brosh maturity is reached at the age of 6 years after 12 larval stages, followed by 4 adult stages.

Eggs that are laid in Brosh during May are significantly heavier then those laid in Megiddo during July-August. Similarly, there is a significant difference in the caloric value of the eggs from both habitats and probably in their water content as well.

INTRODUCTION

Most studies concerned with millipede growth have dealt with species of Polydesmidae, Julidae and Blaniulidae that were mostly restricted to deciduous forests (Halkka, 1958; Blower, 1970; Striganova & Mazantseva, 1979; Snider, 1981). Baker (1978a, b) investigated julid growth in open grassland and dry sclerophyllous woodland in Australia. Only a few studies on spirostreptid growth (e.g. Mauriès, 1969; Demange & Mauriès, 1975) are known to us. In fact there are very few ecological studies on any spirostreptoids, in particular those inhabiting extreme habitats such as deserts (Toye, 1966; Crawford, 1976, 1978, 1979; Wooten & Crawford, 1974, 1975; Crawford & McClain, 1983).

The purpose of this study is to compare the post-embryonic development of a large spirostreptid, *Archispirostreptus syriacus* (De Saussure) (fig. 1), in a mesic and a xeric habitat. Elements of development considered here include: growth rate, energy allocated to growth, duration of each stage and time to reach maturity.

Studying the life cycle of long-lived animals depends on the possibility to determine the stages of individuals without following the entire cycle. Furthermore, there is a need to determine the duration of each stage. Fortunately, stages of development of many species of both julids and spirostreptids are easily determined by counting rows of ocelli (fig. 2) (Vachon, 1947) or serial groups of defence glands which are distinguished by their size and color (Halkka, 1958).

Translating stadial age to true age is more difficult. Most investigators agree that there are four or five molts during the first year and three during each of the following years. Thus,

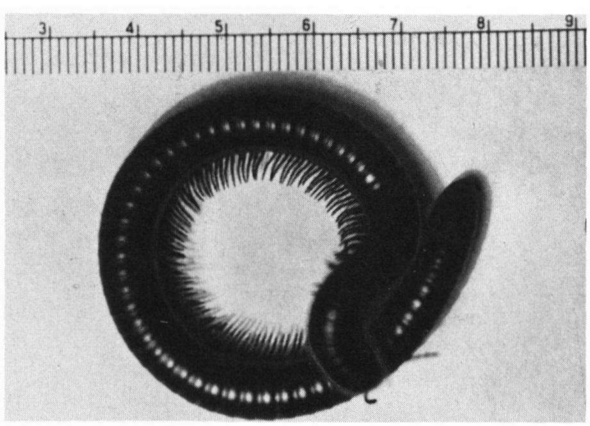

Fig. 1. An adult specimen of *Archispirostreptus syriacus* (scale figures in cm).

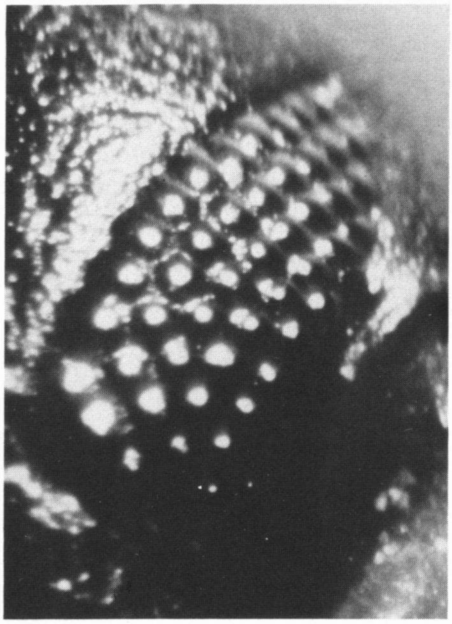

Fig. 2. Eye of adult *A. syriacus*.

calculations and observations on the first stages and on dormant stages have shown that life span of most long-lived millipedes is four to seven years (table I).

MATERIALS AND METHODS

Approximately 500 surface active millipedes were collected once a month, when possible, from September 1980 until September 1983 in Megiddo, a mesic habitat in the Jezreel valley (fig. 3). In Brosh, a xeric habitat in the Jordan valley (fig. 4). the collection (of about 300 specimens) began one year later at irregular intervals. During that period annual rainfall in Megiddo and Brosh ranged between 500-750 mm and 200-400 mm, respectively (figs. 5-6). Millipedes were measured immediately after arrival from the field; they were weighed at an accuracy of ± 0.1 mg on a Mettler H311 balance. Their mid-segment width was measured with calipers at an accuracy of ± 0.05 mm, while their length was measured by a ruler accurate to 1 mm. Segments were counted and divided into podous and apodous ones with the collum included in the podous segments and the telson included in the apodous ones.

Most of the specimens were kept on moist soil and fed on lettuce till they were released during the next visit. Some specimens of each stage and sex were kept for calorimetric measurements. They were oven-dried at 60° C on silica gel for five or six days. Samples of the dried bodies, excluding ovaries, weighing 0.25-0.50 g were ground to powder and burned in a Ballistic Bomb Calorimeter CB-370 (Gallenkamp) at an oxygen pressure of 25 atmospheres.

The egg-laying period in the field was determined by observing the disappearance of large oocytes (0.25-0.30 cm in diameter) dissected from ovaries of freshly killed females. In order to determine the onset of the egg-laying period and its duration, 17 pairs of millipedes of each

TABLE I

Life cycle data on some millipede species.

Species	Number of larval stages	Age of female at maturity (yr.)	Total number of stages	Lifespan (yr.)	Reference
Polydesmus inconstans Latzel	7	0.6	8	1	Snider, 1981
Ophyiulus pilosus (Newport)	9	2	11	3	Blower, 1974
Tachypodoiulus niger (Leach)	7	2	10	4	Blower & Fairhurst, 1968
Julus scandinavius Latzel	9	3	11	4	Blower, 1970
Ommatoiulus moreleti (Lucas)	9	2	16	~ 5 *	Baker, 1978a
Ommatoiulus (= Schizophyllum) sabulosus (Linnaeus)	8	3	11	6	Halkka, 1958
Cylindroiulus nitidus (Verhoeff)	8	4	12	7	Blower & Miller, 1977
Proteroiulus fuscus (Am Stein)	8	3	16	7	Rantala, 1974; Peitsalmi, 1981
Glomeris marginata (Villers)	7	3	16	10-11	Heath et al., 1974
Archispirostreptus syriacus (De Saussure)	11	8	15	11	present study

*Based on Baker (1978b).

Fig. 3. Habitat in Megiddo. The millipedes are confined to the ruins in the foreground.

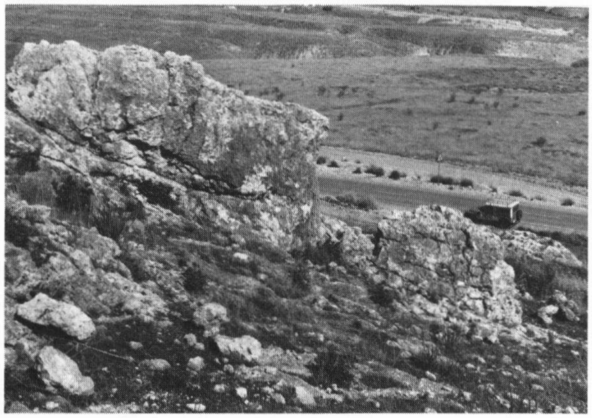

Fig. 4. Habitat in Brosh, a typical xeric habitat in the Jordan Valley.

population were kept in the laboratory from about one month prior to the expected egg-laying. Each pair was placed in a separate container (10.5 × 10.5 × 10.5 cm) and kept on moist soil at room temperature and in natural daylight until no more eggs were laid. Females were not separated from males so as to prevent effects of absence of males or copulations on development of oocytes or egg-laying. Each egg is laid in a capsule made largely of soil.

Egg diameter was measured using a measurement grid placed in the ocular of a dissecting scope. Each freshly dissected egg was weighed on a Cahn Gram Electrobalance at an accuracy of ± 0.001 mg. For calorimetrical measurements a sample of 70-170 eggs was treated in the same manner as the millipedes.

Most of the capsules laid in the laboratory were kept in moist soil at a depth of about 5 cm. Observations on post-embryonic development were made every two or three weeks.

RESULTS

Large oocytes disappeared from ovaries of Brosh specimens during May-June and from Megiddo specimens during July-August. These periods coincide with the egg-laying periods observed in the laboratory. There were significant differences ($P<0.001$) in both caloric values and net weight of the eggs from the two populations. Based on measurements of dry and wet weight and on the average water content of the egg, it would be justified to assume a significant difference in the water content as well, but not in the caloric values of 1-gram samples of dried eggs (table II).

Each egg is laid in a capsule made largely of soil in which the first three larval stages develop within the egg capsule. The third larval stage emerges by making a hole in the capsule (figs. 7-8). Discrimination between the sexes is possible from the 7th stage when the original ambulatory pair of legs on the 7th segment in males disappears. Following growth increment of the first six larval stages (with sex undetermined) live weight is doubled between molts (table III). The number of segments and of defence glands is characteristic of each of the first seven larval stages. There is no overlap in either segment or defence gland numbers between these earlier stages (table III). Live weights of the pupoid stage and the first three larval stages are similar in both habitats, but weight of stages 4-8 is less in Brosh specimens. From stage 9 onwards, the weight of each stage is significantly higher in Brosh specimens. Growth rate is higher in the xeric habitat. The cause of the latter fact is the shortening of the duration of each larval stage (till the 10th stage) in Brosh (table IV). For the purpose of calculation we used the actual growth period till hibernation. Although part of the population molts only after hibernation, no growth takes place during this period. Thus, there was no justification to include the hibernation period in calculating the growth rate.

There is no significant difference in growth

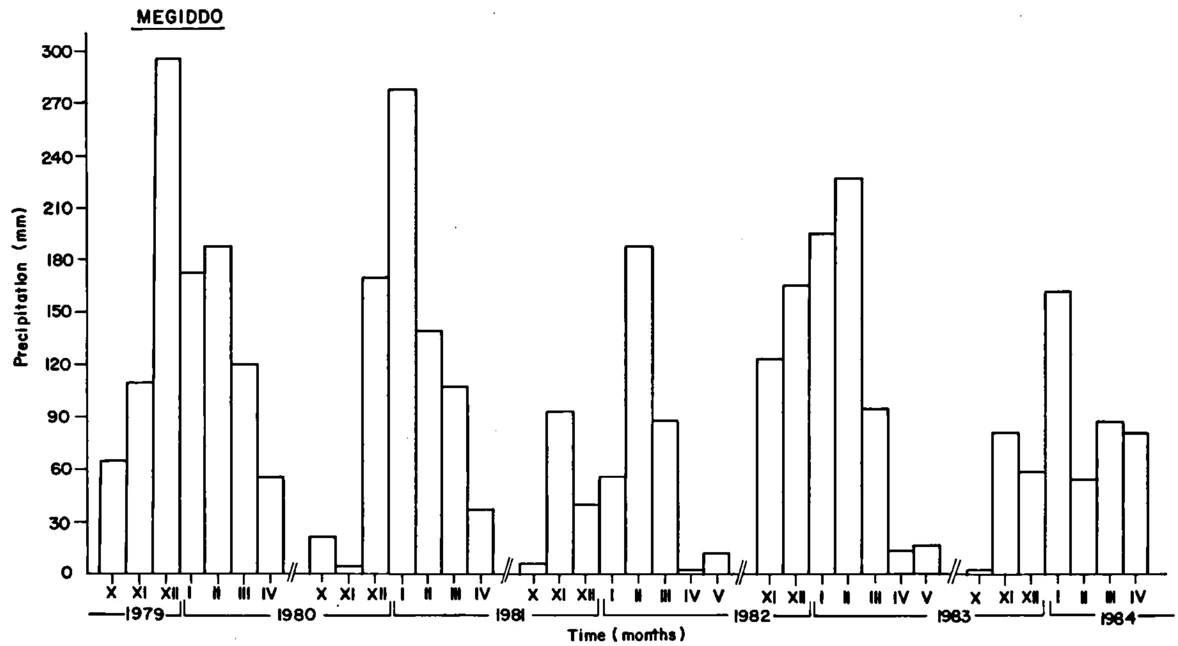

Fig. 5. Annual rainfall in Megiddo.

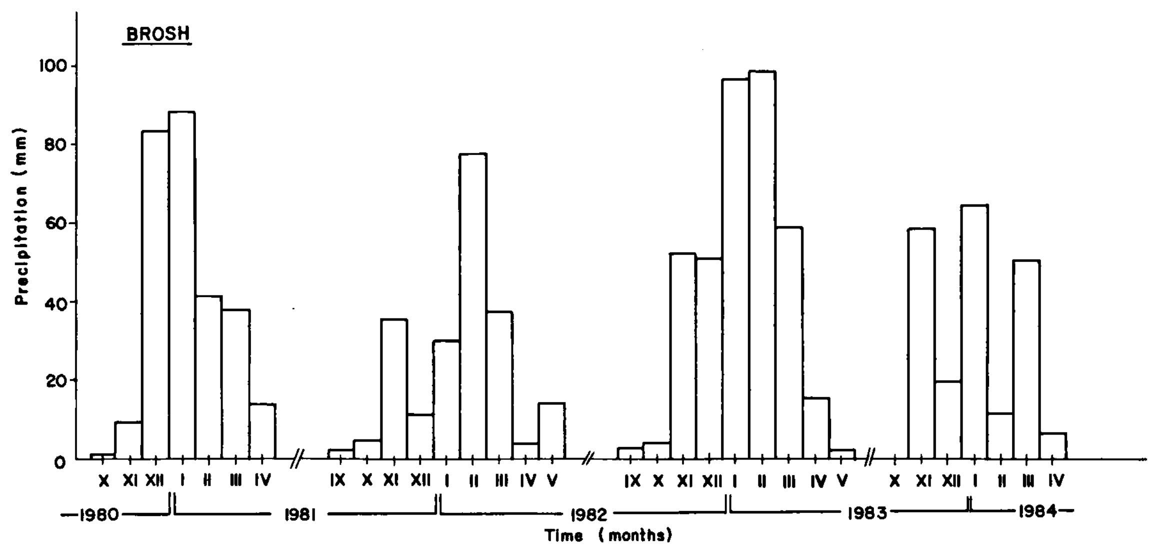

Fig. 6. Annual rainfall in Brosh.

rate between females and males in either habitats until the 10th larval stage. Thereafter growth rate of larval females exceeds that of larval males. Growth is accelerated at the transition from larval to first adult stages, but is considerably greater in females than in males. Maturity is associated with a considerable increase in weight. The weight increase in Megiddo males is 110% as compared with 93% in Brosh males, whereas in females from Brosh weight increase is 80% compared with almost 200% in Megiddo females (figs. 9-10).

Maturity of males is easily determined by the appearance of external gonopods. In Megiddo,

TABLE II

Eggs of *Archispirostreptus syriacus*: parameters and their measurements (n = number of specimens).

Parameters	Parental origins and parameter values of eggs studied (the latter given as $\bar{x} \pm$ S.E.)	
	Megiddo (n)	Brosh (n)
Wet wt. (mg)	5.96 ± 0.14 (7)	7.26 ± 0.10 (10)*
Dry wt. (mg)	3.85 ± 0.05 (7)	4.28 *
Water content (%)	35.23 ± 1.24 (7)	41.00 †
Ash content (%)	7.58 ± 0.16 (12)	6.53 ± 0.20 (12)*
Caloric value/egg (cal)	22.12 ± 0.60 (10)	25.93 ± 0.91 (10)*
Caloric value/egg (J)	92.55 ± 2.51 (10)	108.49 ± 3.81 (10)*
Caloric value of 1 dry gram (kcal)	5.86 ± 0.08 (12)	6.05 ± 0.09 (11)
Caloric value of 1 dry gram (J)	24518.2 ± 334.7 (12)	25313.2 ± 376.6 (11)

* Significant difference at P = 0.001 using Mann-Whitney U test.
† Not tested.

most males mature at stage 12, but some mature at stages 11 or 13. In those stages where both immature and mature males exist simultaneously, there is an obvious difference in weight between them. Furthermore, mature males at stage 11 are heavier than immature ones at stage 12 and even 13 (fig. 9). In Brosh, males mature at stage 12 and some mature at stage 13 (fig. 10).

Maturity of females is difficult to determine as it is not visible externally. Thus it is difficult to distinguish between young adult females and heavy larvae. Dissection confirming the existence or absence of developing oocytes during

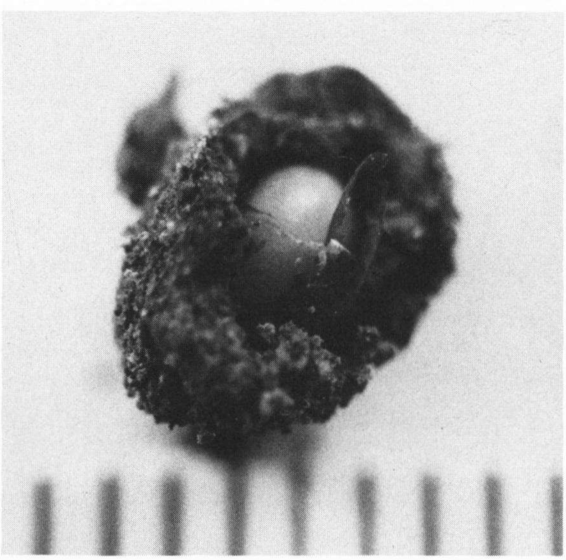

Fig. 7. A young larva in a capsule (scale in mm).

Fig. 8. A perforated capsule.

TABLE III

Morphology of early larval stages originating in Megiddo (n = number of specimens; values are given as $\bar{x} \pm$ S.E.).

Stage	n	Live weight (mg)	Mid-segment diameter (mm)	Length (cm)	Total number of segments	Number of apodous segments	Number of defence glands
Pupoid	4	5.2 ± 0.17			6 + abdomen*		
1					6 + abdomen*		
2	7	7.2 ± 0.16	1.24 ± 0.01	1.0 ± 0.1	26 ± 0.0	20	1 ± 0.0
3	17	15.9 ± 0.40	1.24 ± 0.01	1.2 ± 0.1	32 ± 0.2	6	21 ± 0.2
4	12	29.7 ± 1.00	1.50 ± 0.00	1.5 ± 0.0	37 ± 0.3	6	26 ± 0.2
5	3	59.0 ± 5.58	1.81 ± 0.01	1.9 ± 0.1	42 ± 0.0	7	30 ± 0.3
6	17	120.7 ± 4.00	2.18 ± 0.03	2.6 ± 0.0	49 ± 0.2	7	37 ± 0.3

* Number of abdominal segments not clear.

TABLE IV

Growth rate of larvae in Megiddo and Brosh.

	Megiddo			Brosh		
Stage	Live weight (mg)	Duration of the stage (weeks)	Growth rate (mg/week)	Live weight (mg)	Duration of the stage (weeks)	Growth rate (mg/week)
Pupoid		5				
1		8				
2	7.2 ± 0.16	8		8.0 ± 0.23	6	
3	15.9 ± 0.40	12	0.72	13.9 ± 0.58	6	0.91 ± 0.14
4	29.7 ± 1.00	25	0.55	25.6 ± 0.98	6	1.95
5	59.0 ± 5.58	25	1.17	50	6	4
6	120.7 ± 4.00	25	1.18			

the reproductive period solved this problem. Females mature in Megiddo at stage 12 and in Brosh at stage 13.

A. syriacus molts at least twice as an adult. It gains slightly in weight and length, but its segment numbers do not increase. Maximum segment number is reached during the last larval stage.

Duration of the first stages (1-4) of *A. syriacus* was determined through our laboratory observations, while duration of the following stages (5-16) was based on newly molted specimens and on the phenology of millipede growth as observed in natural populations from the field (figs. 11-12). Thus, in Megiddo, most of the larvae emerge from the capsules after about eight months from the time of egg-laying, while in Brosh they already emerge after four and a half months. Stages 6 or 7 are one year old in Brosh, but three years old in Megiddo. Maturity of females is reached at six years in Brosh, while in the mesic habitat in Megiddo maturity is reached at eight years. No specimen at stage 15 was seen in Megiddo and none of stage 17 in Brosh. Thus, we assumed that they die prior to these stages. Based on calculations and observa-

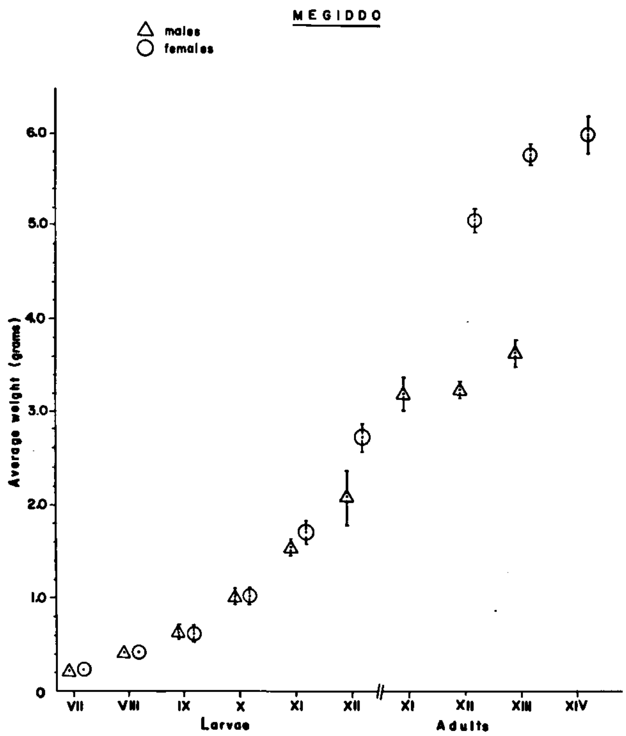

Fig. 9. Average weight of each stage (in which the sex could be determined) in Megiddo.

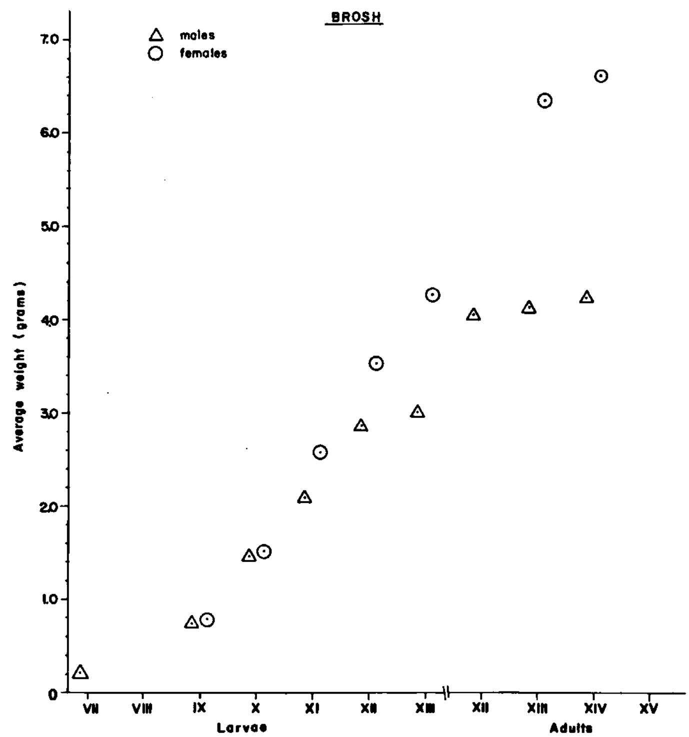

Fig. 10. Average weight of each stage (in which the sex could be determined) in Brosh. In all cases ± S.E. was very small (<0.25) so it was not drawn.

tions of first larval stages, life span in Megiddo is 11 years, while in Brosh it is nine years.

DISCUSSION

Significant differences exist in the entire life cycle between the population of millipedes from Brosh and that from Megiddo, but the pattern of development is similar. Similarity is expressed in the emergence from the capsule at the same stage and in the external difference between sexes at stage 7 in both populations. The number of segments and defence glands of each stage shows a similar pattern during development in the two populations as well.

Dissimilarity is expressed by the shortened duration of each larval stage in the xeric habitat compared with longer durations occurring in the mesic one. As a result, the time until reproduction in the former habitat is relatively short. Since larval mortality is affected by the duration of development, the shorter this period is, the higher is the survival rate. Harsh conditions may cause reduction in the survival rate. In the xeric habitat a combination of shorter larval life and dry conditions presumably result in an equal replacement rate as in the mesic habitat where external conditions are mild and larval life is longer.

Baker (1978a) assumed, however, that moisture conditions act in a different way for populations of *Ommatoiulus moreleti* (Lucas) in Australia. He concluded that increased moisture prior to the breeding season may have allowed greater feeding and thus may have caused early maturation in females from the wetter habitat.

Male maturation at a stage prior to that of females is known in many julids (Blower & Miller, 1977; Baker, 1978a; Blower, 1974). According to Snider (1981), males and females of

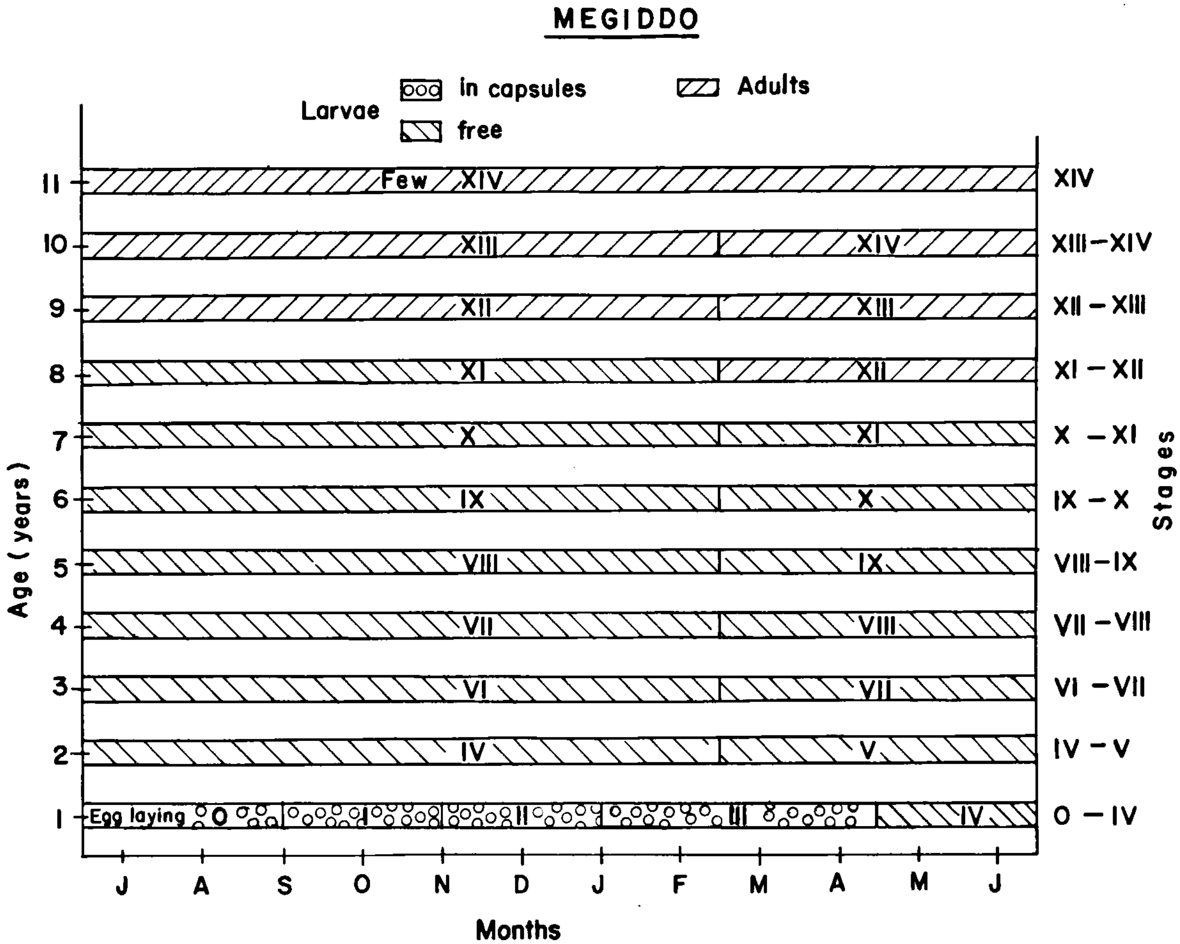

Fig. 11. Life cycle of *A. syriacus* in Megiddo.

TABLE V

Summary of main differences between the two habitats.

Parameter	Megiddo (mesic)	Brosh (xeric)
Larval stages in the first year	3 - 4	6 - 7
Age at maturity (yr.)	8	6
Life span (yr.)	11	9
Egg wet weight (mg)	5.96 ± 0.40	7.26 ± 0.10
Caloric value of an egg (cal)	22.12 ± 0.60	25.93 ± 0.91
Caloric value of an egg (J)	92.55 ± 2.51	108.49 ± 3.81

Polydesmus inconstans Latzel mature at the same stage, but the duration of the last larval stage of the females is longer. The earlier maturation in males is explained as a mechanism ensuring fertilization. *A. syriacus* males mature one stage earlier than females, but as the proportion between sexes is about 1 : 1, the above explanation does not seem adequate.

Table V summarizes the differences in postembryonic development between the two habitats.

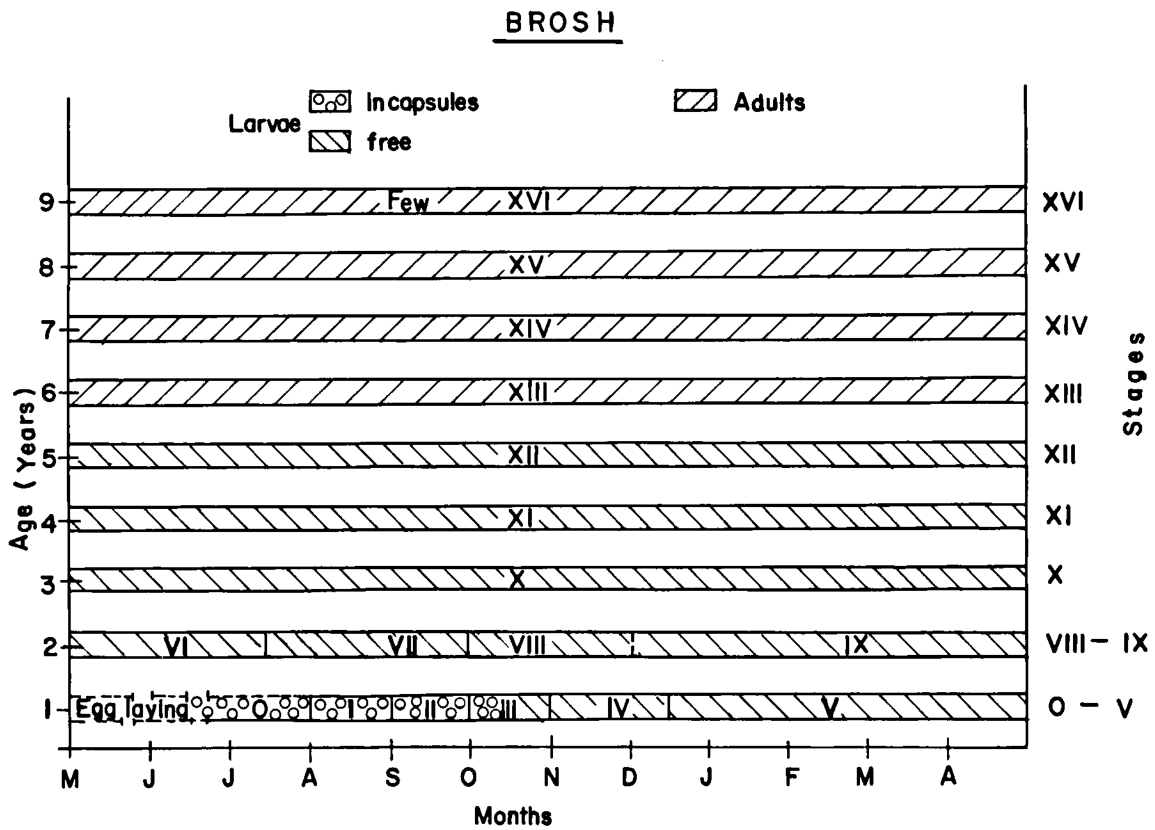

Fig. 12. Life cycle of *A. syriacus* in Brosh.

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