SALAMANDRA SALAMANDRA
AT THE SOUTHERN LIMIT OF ITS DISTRIBUTION

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CHAPTER ONE

DESCRIPTION, DISTRIBUTION AND SPECIATION

THE SPECIES

The fire salamander, *Salamandra salamandra* L. belongs to the order of Urodela, amphibians with tails. There are two species of this order in Israel: the spotted salamander, *S. salamandra* L. and the striped newt, *Triturus vittatus* (Jenys). Most of the work on salamanders has been conducted in Europe, where the species is common: research has dealt with the life cycle, distribution, division into subspecies, the development of the embryo and environmental factors. The few comprehensive publications that have appeared are those by Eiselt (1958), Joly (1968) and Gasser (1975, 1978a,b). Since then, much new knowledge on the species has accumulated, though there are many environmental and physiological aspects of the species that are still unknown.

In the matter of nomenclature, we will refer to the newly-born salamander as a larva, although this word may be thought to imply the absence of legs: the salamander is born with fully-formed legs.

HABITAT

Salamanders live in a number of different areas in Europe, in a variety of habitats. In central Europe, they are to be found mainly at 100–250 m above sea level, while in southern Europe and in the eastern Mediterranean they live in areas at elevations above 250 m. They can be found at heights of as much as 2000 m (Joly, 1968; Gasser, 1975).

Their natural habitat is in wooded areas. Joly (1968) describes the salamander as finding hiding places in the holes of small animals, especially that of the field mouse, *Apodemus sylvaticus*, and also in cracks in rocks, especially between terrace stones. Szabo (1959) gives the same description of using cracks between rocks for shelter in Hungary, and Feldmann (1964) writes the same of salamanders in Germany. According to Eiselt (1958), finding salamanders in non-wooded areas is a sign that these areas were forests in former times. During the cold of winter, the salamander burrows under moss or leaves, or finds shelter underground (Hecht, 1933; Eiselt, 1958). They are totally terrestrial, but they need to find pools or other bodies of water during their period of reproduction, and on the whole travel only relatively short distances. Hence, they never establish their habitats more than a few hundred metres from a hind part in water. Greven (1976) also describes the process, together with a picture, as it takes place in Europe. Degani (1976), Degani and Warburg (1995), and Warburg et al. (1979a) have described the breeding of the species in Israel in detail.

Most of the populations of the order are ovoviparious, although the larvae sometimes emerge from the embryonic sac a shortly before or immediately after breeding, which makes them viviparious. There is a small number of viviparious populations, in which the larva are even bred after metamorphosis, such as *Salamandra atra* (Joly, 1968; Fachbach, 1969); these are populations that live in high mountains, such as the Pyrenees.

With regard to brood sizes, Joly (1968) gave the number of larvae per brood at between 10 and 72. Schreiber (1912) put the number at up to 70, while Gasche (1939) wrote of 30–40 larvae per brood.

The dimensions of the larvae at the time of breeding were measured by Szabo (1959), who described them as 22.5–33.5 mm in length. Joly (1968) gives similar figures, finding that the larvae measure 25–33 mm and weigh 0.1–0.17 g. Larvae bred at various later stages of metamorphosis are bigger. Metamorphosis takes place at 3–12 months after birth, depending on the availability of food and on environmental conditions, and consists principally of the process by which the gills wither away, leaving the animal exclusively terrestrial.

It is generally accepted that in Europe salamanders reach sexual maturity at 4 years old, when the body length is 14–15 cm and weight 17 g (Joly, 1968).

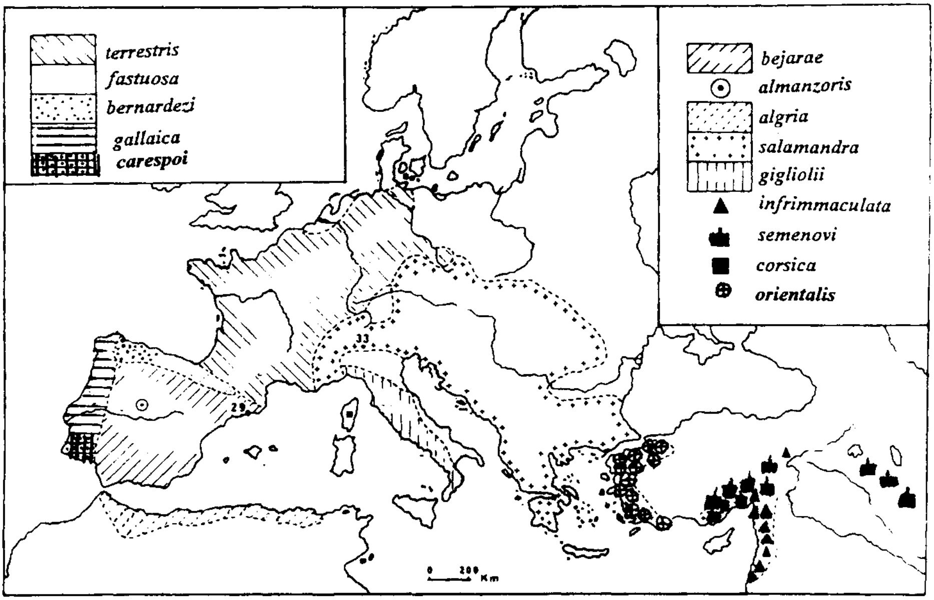


Figure 1.1. Distribution of salamander species in Europe (Eiselt, 1958; Gasser, 1975; Joger and Stenfaritz, 1985; Degani, 1986; Veith et al., 1994).

TERRESTRIAL ACTIVITY

The terrestrial activity of the salamander comprises its egress from its shelter and movement over the ground; it is influenced by climatic conditions (temperature, relative humidity and rainfall) and physiological factors, such as the reproductive cycle, controlled by hormones, and hunger.

In Europe, salamanders take shelter during the harsh winter, coming out on to the land during the spring months, March and April (Mertens, 1947; Szabo, 1959). In France, in the warmer regions, they are active in winter also (Joly, 1959; 1968). Evidently, these differences in activity are the result of differences of climate among the various regions of the salamander's distribution. Thus, Joly (1959) gives the temperature range for their activity as 2–8°C, and the relative humidity range as 80–90%. Bright moonlight and strong winds inhibit their activity. The electric field in the air and the degree of ionization are also linked to the salamander's activity on the ground (Joly and Landry, 1964).

Joly (1968) studied salamanders' territorial range and concluded that they spend most of their time in shelter, not moving any great distance except when they need to find places to breed. The males move within a range of only 9.8 m, on average, and the females 12.8 m; the greatest distances recorded were 135 m for males and 88 m for females. However, Joly (1968) found that salamanders possess a homing ability that enables them to travel up to 300 m to return to their own habitat.

POPULATION STRUCTURE

There are a number of difficulties in studying salamander populations: they are nocturnal animals, their period of terrestrial activity is relatively brief, and, as yet, no satisfactory method has been found for trapping them. Nor has a satisfactory way been found to estimate their age. A way to estimate the age of other members of the Urodela was found, e.g. for *Desmognathus* sp., by Organ (1960), based on the size of the testis; by which details elucidated in the laboratory are compared with findings in nature, but this method is not applicable to the salamander.

In France, Joly (1968) used the Lincoln Index for estimating populations, to measure the population density of the subspecies *S. s. terrestris*, and found 128 individuals in an area of 10,800 m^2, an average of 842 m^2 for each individual. These measurements were made in October-November 1958 and 1959; in another study, made in a different area of France in March 1962, he found 166 individuals in an area that gave each one an average space of 63 m^2.

The same author found differences in body length and weight between colonies in different parts of France and that the males were smaller than the females. In two colonies he found that males formed 58% and 62% of the population, respectively. This phenomenon evidently arises from the much greater activity of the males during the reproduction season. According to Gasche (1939), 75% of the specimens he trapped were males. Further support for the hypothesis that the preponderance of males over females is due to the greater activity of the males during the mating season was provided by studies on the sex ratio, at different times of year, in the Bercy Forest, in France: during October, 103 males and 43 females were caught, whereas in March only 9 males were caught, compared with 27 females. The percentage of young specimens (under 9 cm in length) was 7.2–11.6%.

FOOD AND NATURAL ENEMIES

Salamanders are carnivorous, identifying their prey mainly through movement. Studies on their food have concentrated mainly on the period after metamorphosis. According to Freytag (1955), *Salamandra salamandra* lives principally on snails (Gastropoda), insects (Insecta) and millipedes (Diplopoda). Szabo (1962) found that the salamander's prey consists of 61.16% jointed-leg animals (Arthropoda), 31.39% gastropods (Mollusca), especially shell-less snails, and 7.45% segmented worms (Annelida), especially earthworms.

The jointed-leg animals, which represent the main source of food, can be divided into insects (Insecta), 35.64%, spiders (Arachnida), 11.17%, multi-legged animals (Diplopoda) (8%), equal-legged crabs (Isopoda) (3.72%) and centipedes (Chilopoda) 2.66% (Szabo, 1962).

Fachbach et al. (1975), on the other hand, found that in the Girad district of Austria the salamander's main food consisted of snails, with insects only second in importance. This difference apparently arises out of the availability of different types of food in the different habitats.

Little is known about the salamander's natural enemies. Certainly adult salamanders have few predators, owing to the poison glands on their backs. Larvae are the main victims, e.g., Joly (1968) notes that the water beetle, *Ditiscus marginalis* is capable of eating large numbers of salamander larvae. However, even the adult salamander is preyed on by the European hedgehog, otters and water snakes. In Israel, too, Prof. Mendelssohn has observed water snakes feeding on adult salamanders (personal communication).

SOUTHERN LIMIT OF DISTRIBUTION

The southernmost occurrence of the salamander is in Israel, where there are three entirely separate habitats: in the Carmel Range, in the Segev and Tefen areas of Western Galilee, centered on Mount Meron, and in the north-east of the country, centered on Tel Dan (Fig. 1.2).

THE GALILEE RANGE HABITATS

This area includes one of the highest mountains in Israel, Mount Meron, which reaches a height of 1208 m. The height and particular location of this area have created a variety of conditions that influence flora and fauna, typical flora being oak and terebinth scrub. The winter is longer and rainier than in most of the country, with annual precipitation reaching 1000 mm. The summer is comparatively cool and comfortable, except on "hamsin" days (a meteorological condition comparable with

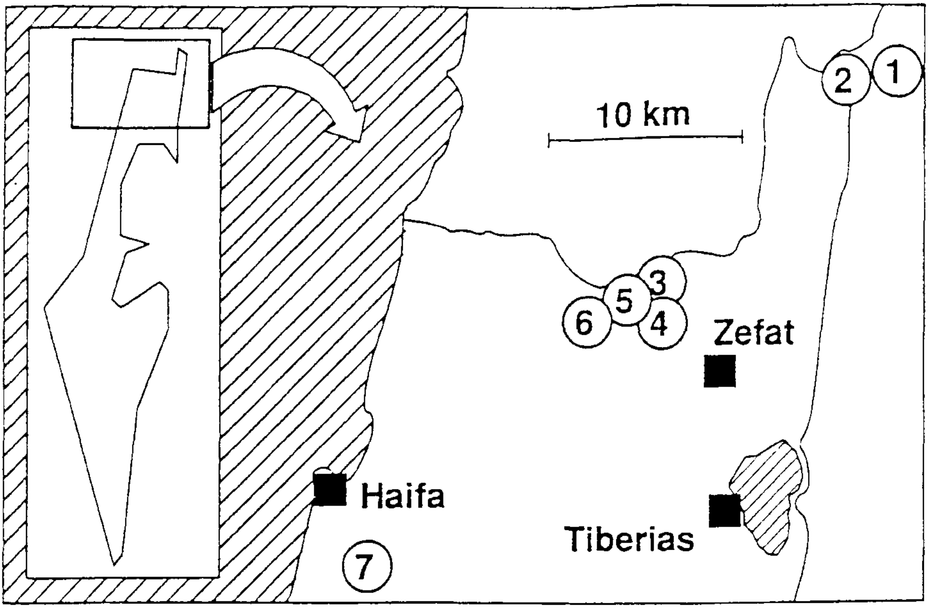


Figure 1.2. Distribution of *S. salamandra* in Israel. 1 = Mount Hermon, 2 = Tel Dan, 3 = Dovev Pond, 4 = Mount Meron, 5 = Gush Halav, 6 = Sasa Rock pool, 7 = Mount Carmel. (Veith et al., 1992).

the Föhn, the Sirocco and the Santa Ana, in other parts of the world).

The terrain consists of chalk and dolomite, which the plentiful rainfall dissolves readily, creating a varied and rocky landscape, characterized by cracks and holes. Strata of impermeable marl and clay allow the formation of pockets of water and such small springs as the Zakan, the Shvil, the Roc, etc., which are typical of the area. On the other hand, the nature of the soil precludes the formation of large springs in the Galilee region: the greater proportion of the water seeps deep into the ground.

Other water sources exploited by the amphibians found in this area are mainly rain pools, such as the Sasa, Gush Halav and Gevim Ponds, which are characterized by shade, where the amphibians can be found during most of the day. The water collected in these pools generally lasts for a number of months before they dry up, but can last the whole year round. Other sources are winter pools, which are generally smaller, and dry up only a few weeks after the end of the rainy season.

THE CARMEL RANGE HABITAT

The upper Carmel is a complex habitat, formed of two vaulted ridges, with notable karst features. The upper ridge consists of Kanoman chalk, with a general height of 500 m, reaching its maximum of 548 m near Ussefiya; the second, running

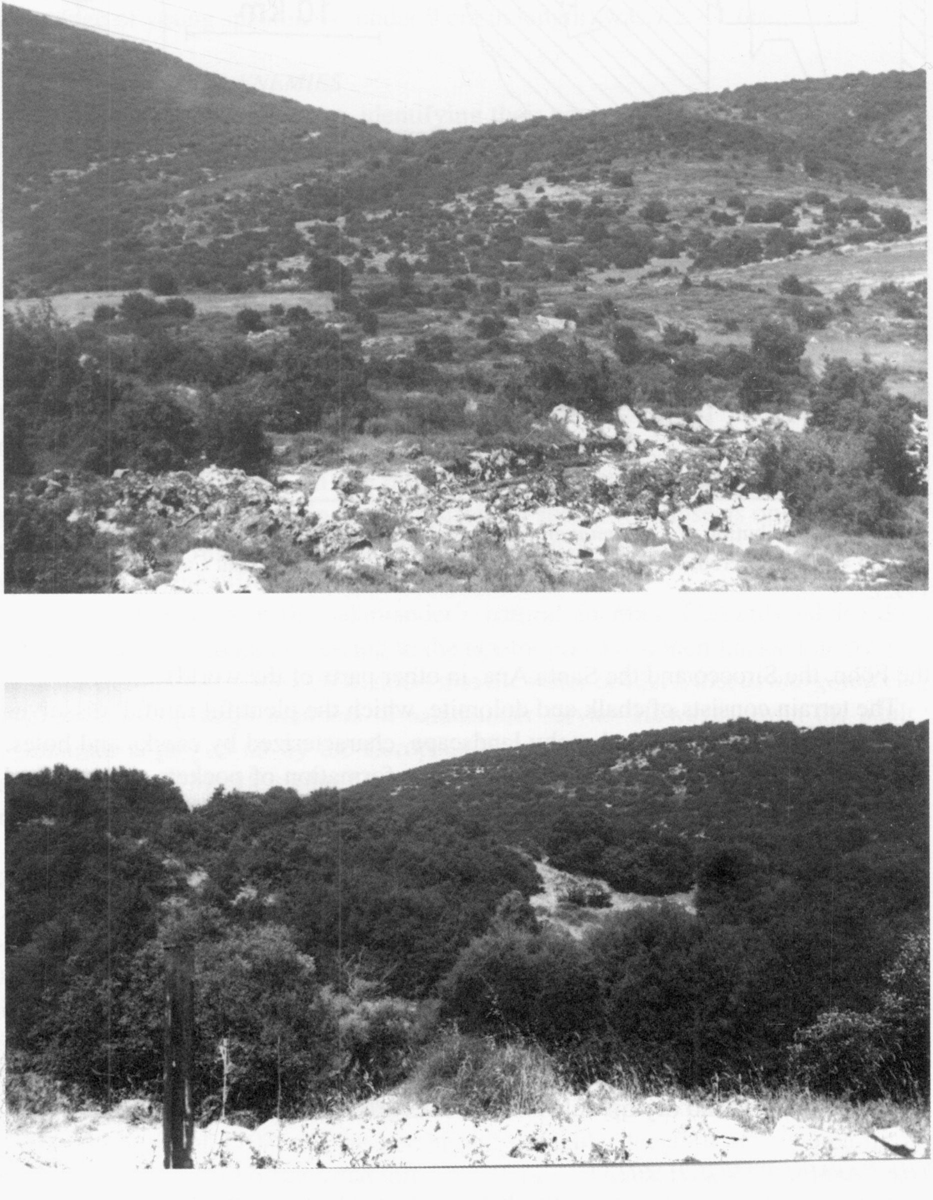


Figure 1.3. Habitats of salamander populations near Mt. Meron (Galilee) (Degani, 1980).

parallel to the first, consists of chalk and marl of the Lower Kanoman. This ridge runs from Tirat Hacarmel, via Bet Oren, to Daliat el Carmel, and is crossed by brooks, which carry rainfall down from the watershed; it is 450 m high, with a 497-m peak at Mt. Shekef.

As a result of its closeness to the sea and the steepness of its seaward slope, the area receives a rainfall comparable with that of Upper Galilee: upward of 800 mm annually. The natural flora, which have been preserved over large parts of the range, consist of typical Mediterranean scrub. Communities of *Quercus calliprinos* and *Pistacia palaestina* mingle with communities of *Genista fasselata* and *Pinus halepensis*, the former predominating at Kfar Damun and the latter at Bet Oren.

The salamander population in this area is concentrated around pools and springs, as in the Galilee region. Plentiful rainfall, acting on the local chalk, has given rise to a profusion of caves, holes and other settings for standing and running water. These are the water sources in which salamander larvae are to be found: winter pools, ponds, springs and streams. Some of the winter pools dry up in summer and many of the other sources are exploited by man, including reservoirs cut into the rock, which are in use mainly in the summer. As a result of human activity, many of the springs and streams which once ran all year round are now dry in summer, or polluted.

The dense scrub and rocky terrain form a habitat that provides the salamander with numerous hiding places.

THE TEL DAN HABITAT

The Tel Dan Nature Reserve is in the north-east of the country; it lies among hills and is bounded by mountains to the north, but is itself only 180 m above sea level. The area as a whole is characterized by numerous spring-fed streams running water, and is the only such area in Israel. The Nature Reserve is full of such brooks, which are spring-fed and run all year round, giving rise to the development of rich flora. Most of these brooks are shallow (usually 5–10 cm). This constant presence of water and dense growth has created an optimal and stable environment for wild life; the flora include northern species, such as *Farxinus syriaca*, and *Paliurus spina-christi*, as well as species more typical of the Mediterranean region, such as *Laurus nobilis*, *Rhamnus alaternus*, *Quercus ithaburensis* and *Styrax officinalis*.

This habitat remains constant throughout the year, and is totally different from those in Galilee and Carmel. The year-long availability of water, the constant moisture and the stable temperature combine to produce conditions which are very different from those found in Europe. In European habitats of the salamander species, the winters are cold, often below freezing, and summers are often relatively hot, although accompanied by rain and moisture.

GENERAL DESCRIPTION OF ISRAELI SUB-SPECIES

The salamanders in Israel, which are of the spotted, or blotched, variety, are unusually large. The head is round and the tail, the legs and digits unusually long.

Their spots are usually round or oval, and are distributed along most of the body, either in a single or double row, or scattered all over. Only rarely are the spots distributed across the breadth of the body. The dominant pattern on spots on the head is of four large spots, generally not joined, though examples have been found on which two spots joined together to form a single or double stripe along the head; there have even been examples on which all the spots were joined to form a horseshoe-shaped blotch on the head (Fig. 2-4). On most of the specimens, from all three habitats, there were no spots on the lower jaw, although a few examples of spotted lower jaws were found. These spots were pale yellow in colour, unlike the ordinary, larger spots, which were deep yellow or orange-yellow. Spots on the ventral side were rarer still. No special arrangements of spots that might distinguish one population from another were found.

SPECIATION

The polymorphic species *Salamandra salamandra* L. is a particularly suitable example for an approach to the study of the nature of speciation and micro-evolutionary differentiation. Salamanders are to be found throughout Europe, except in the British Isles and the most northerly countries (Fig. 1.1). Their distribution extends from Denmark in the north to West Africa in the south (Eiselt, 1958). There are two major types: the striped salamander, characterized by two yellow stripes running along its back, and the spotted salamander, marked by yellow spots or blotches. Differences in the arrangement of the spots represent transitions from the spotted to the striped varieties. In addition, variations in the background color exist, from almost entirely black to shades of yellow (Freytag, 1955; Eiselt, 1958). This variability has resulted in the division of the species into a large number of subspecies.

Hecht (1933) offered and interesting hypothesis on the cause of these variations: that the spotted salamander was spread widely throughout Europe before the last ice age and that during the ice age, the populations were driven to areas which were less cold, to western and south-western Europe. The south-western population developed into the spotted variety, while the western population developed into the striped variety. Then, after the ice age, both varieties returned to repopulate Central Europe, the striped salamander to the area bordered by the Elbe, and the spotted salamander to southern and western Germany, with an overlapping area of intermediate varieties.

Division into subspecies has undergone a number of changes. Originally, subdivision of the species was made according to external features, such as the size and arrangement of spots, the shape of the head, and the length of the body, digits and tail. Freytag (1955), summing up a large body of research, placed *Salamandra salamandra salamandra* in Germany, the Balkans, Central Europe and Italy, with *S. s. terrestris* in Germany, Belgium, Holland and France, and many subvarieties in the Iberian Peninsula. He described two subvarieties at the southern limit of distribution: *S. s. alegria* in North Africa and *S. s. infraimmaculata* in the Lebanon and Israel. A further subspecies, *S. s. semenovi*, inhabits Kurdistan.

In 1958, Eiselt introduced a number of changes into the subdivision and nomenclature of the species, on the basis of different morphological characteristics, some quantitative and others qualitative. Among these features, the most important are the number and arrangement of spots, the shape and size of the head, the length of the tail, limbs and digits, and spotting on the parotid area. The disadvantage of this method is that a number of the characteristics which Eiselt (1958) used to differentiate among subspecies change with the age of the individual, especially where the length of an organ is concerned; and hence conclusions as to the subspecies can only be drawn by measuring a large number of adults in every case. Eiselt divided the species into only 12 subspecies, and redefined their distribution. According to him, for example, the salamander population in Israel consists of *S. s. salamandra*, with *S. s. infraimmaculata* to be found only in the Lebanon. He introduced a number of changes into the nomenclature of subspecies in the Iberian Peninsula, and named a new one in Italy: *S. s. gigliolii*.

Then, in 1975, Gasser introduced further changes, in his map of the distribution of the various subspecies. In addition to morphological differences, this researcher included differences in plasma protein, as detected by electrophoresis. Thus, he separated one of the subspecies, named by Eiselt as *S. s. fastuosa*, into two distinct subspecies: *S. s. fastuosa* and *S. s. bernardezi* (Table 1.1). Although he examined salamanders in the Lebanon, Gasser did not reach Israel, and therefore gives no opinion on the identity of its subspecies. The Israeli variety was again redefined as *S. s. infraimmaculata* by Degani (1986), on the basis of morphological findings and electrophoretic analysis of its blood plasma. On the basis of different electrophoretic serum protein patterns Gasser (1978a,b) separated the subspecies *S. s. infraimmaculata* from species *S. salamandra* because of its fundamental differences in serum proteins and regarded as a full species *S. infraimmaculata*. Joger and Steinfartz (1995) were the studies the blood serum samples of *Salamandra* populations from Greece, Turkey and Israel. At investigated loci, Asia *Salamandra* is separated as a different species, *S. infraimmaculata* separated as a three different subspecies: *S. i. infraimmaculata* in Israel, Lebanon, Syria and Southwestern Turkey, *S. i. semenovi* in eastern Turkey and the bordering regions of Iraq and Iran, *S. i. orientalis* in south and center Turkey. This was confirmed by the findings of Veith et al. (1992), who examined the larvae of several populations by electrophoresis, found no differences in 14 loci, and concluded that, despite minor variations, the several different populations are monomorphic. Electrophoretic studies were also carried out by Fachbach (1971, 1976) in the Iberian Peninsula, and by Alcobendas et al. (1994) in northern Spain. Like Gasser, Veith (1994) also catalogued the species according to electrophoretic variations. He added *S. s. beshkovi* and *S. s. crespoi*, as separate subspecies, to the list drawn up by Gasser (1975), which is presented in Table 1.1.

Table 1.1. The distribution of subspecies of salamander in Europe (Gasser, 1975; Veith, 1994; Degani, 1986).

Subspecies	Distribution
S. s. terrestris	Western & Central Europe, France, Belgium, Holland, Germany
S. *s. salamandra*	Central & Eastern Europe, Asia Minor, the Balkans
S. s. gigliolii	Italy
S. s. infraimmaculata	Lebanon, Turkey, Israel
S. s. semenovi	Kurdistan
S. s. corsica	Corsica
S. s. algira	North Africa
S. s. bejarae	Central & Northern Spain
S. s. almanzoris	Spain
S. s. gallaica	Portugal
S. s. fastuosa	Northern Iberia
S. s. bernardezi	North-west Iberia
S. s. beshkovi	The Balkans
S. s. crespoi	South Portugal

For a later re-assignment of the species in Israel, see text.

CHAPTER TWO

MORPHOLOGICAL AND GENETIC DIFFERENCES AMONG SUBSPECIES

BODY SIZE

Eiselt (1958), who examined examples of the species in Israel (Galilee and Carmel) already noted that at this limit of their distribution, salamanders are particularly big. He reported that Mendelssohn had found a specimen in the Carmel area that reached 31.6 cm in length. In the series of investigations on which the present book is based, and even larger specimen (32.4 cm) was found in Galilee.

Eiselt (1958.) and Gasser (1975) observed that there are differences in size among the various subspecies, but examined only a small number of examples from each subspecies. However, Joly (1968) examined large numbers of salamanders of the subspecies *S. s. terrestris* from various habitats, and found that their length varied from 10 to 20 cm and their weight from 10 to 20 g. Although body size is an unreliable criterion for differentiation among subspecies, especially when only a small number of samples is measured, salamanders in Israel are demonstrably much larger than those in Europe. Samples of the populations in on Carmel and in Galilee show no great differences in length and weight from one another, but the population at Tel Dan is significantly smaller ($p<0.01$) in both length and weight than these two groups.

The subspecies *S. s. infraimmaculata* is smaller than *S. s. salamandra*, according to Eiselt (1958) and Gasser (1975), but the former investigator measured only 10 specimens in the Lebanon area and the latter only 15 specimens, so it is hard to be certain from their reports. It appears that the Tel Dan population, which is geographically nearer to the groups reported on by Eiselt and by Gasser, resembles them more closely in size than the other two groups in Israel. Differences in size between males and females described in the present studies are typical of *S. salamandra* generally, including the subspecies *S. s. terrestris* (Joly, 1968), with females longer and heavier than the males. Although Joly made no statistical comparison, his research shows a significant difference in weight between males and females, in all populations, while the difference in length is significant only in the Carmel, but not in the Tel Dan and Galilee populations (Tables 2.1, 2.2).

It seems, then, that differences in size alone are not enough to establish the existence of a separate subspecies, but that there is a gradual transition in the development of salamanders from one population to another that separates the Israeli specimens form other subspecies in Europe.

Table 2.1. Weights of salamanders from three locations (Degani, 1980).

Location	Number of specimens	Weight Sex	g	±	SD
Tel Dan	144	m & f	32.75	±	13.92
Galilee	161	m & f	69.54	±	26.43
Carmel	64	m & f	68.16	±	22.95
Tel Dan	104	m	31.78	±	13.21
Galilee	68	m	61.33	±	21.12
Carmel	40	m	65.70	±	18.11
Tel Dan	41	f	38.32	±	14.81
Galilee	56	f	79.51	±	27.79
Carmel	24	f	88.14	±	20.25

m = males; f = females

Table 2.2. Net body lengths of salamanders from different locations (Degani, 1980).

Location	Number of specimens	Weight Sex	g	±	SD
Tel Dan	144	m & f	11.06	±	1.82
Galilee	161	m & f	14.00	±	1.32
Carmel	64	m & f	14.32	±	1.53
Tel Dan	104	m	10.97	±	2.02
Galilee	68	m	13.73	±	2.00
Carmel	40	m	14.13	±	1.48
Tel Dan	41	f	11.38	±	1.79
Galilee	56	f	14.24	±	1.87
Carmel	24	f	14.85	±	1.60

m = males; f = females

Table 2.3. Total length of salamanders from different locations (Degani, 1980).

Location	Number of specimens	Weight Sex	g	±	SD
Tel Dan	144	m & f	17.45	±	2.72
Galilee	161	m & f	23.51	±	2.30
Carmel	64	m & f	24.42	±	2.69
Tel Dan	104	m	17.35	±	2.58
Galilee	68	m	23.01	±	2.91
Carmel	40	m	23.91	±	2.63
Tel Dan	41	f	17.69	±	2.37
Galilee	56	f	23.69	±	2.08
Carmel	24	f	25.32	±	2.62

m = males; f = females

DIFFERENCES AMONG POPULATIONS IN ISRAEL

In 1986, Degani measured 369 adult specimens form three separate populations. The average weight of the specimens from Tel Dan was 32.75 g, with a standard deviation of ±13.92 g; the Galilee specimens weighed 69.54 ±26.43 g, and those from Carmel weighed 68 ±22.95 g. Thus, the first group was significantly lighter ($p<0.001$) than the other two, which, in turn, showed no significant difference one from the other at $p>0.05$.

Taken separately, the males from Tel Dan, at 31.38±13.21 g, weighed considerably less than those from Galilee (61.33 ±21.12) and Carmel (65.70 ±18.11). As with the overall figures, there was no significant difference ($p>0.05$) between the males from the latter two habitats. Among the females, the picture was the same, with those from Tel Dan (38.32 ±14.81 g) significantly lighter than the females from Galilee (79.51 ±27.79 g) or Carmel (88.14 ±20.25 g). In all three populations, the females were significantly heavier then the males (Table 2.1).

The largest specimen, at 156 g and with a length of 32.4 cm (body length 17.8 cm) was from Galilee. However, no significant difference ($p>0.1$) in average body length was found between Galilee salamanders (14.00 ±1.32 cm) and Carmel salamanders (14.32 ±1.53), whereas those from Tel Dan were significantly smaller ($p<0.001$), at 11.06 ±1.82 cm. The same applied to separate measurement of males and females, both as to body length and total length (Tables 2.2, 2.3). There was, however, a significant difference between the body length (and hence the total length) of females from Carmel and females from Galilee (the former were longer, on average), but this difference was not significant among the males. When the total lengths of males and females within populations were compared, only in the case of the Carmel population was there a significant difference, the females being longer.

EXTERNAL APPEARANCE AND MARKING OF SUBSPECIES

It has been difficult to define the subspecies of *S. salamandra* in the Near East (Freytag, 1955; Eiselt, 1958, 1966; Fachbach, 1971). A number of specimens were studied in Israel, with the result that Freytag assigned them to the subspecies *S. s. infraimmaculata*, and Eiselt to the subspecies *S. s. salamandra*, though the latter based his findings on a sample of only six individuals from Galilee and Carmel. Gasser, in his more recent work (1975) did not examine any local specimens. The most recent study, by Degani (1986), gives a clearer picture, because a large number of individuals was examined. Where Gasser found wide variations in the markings of *S. s. salamandra*, the characteristic marking of *S. s. infraimmaculata* consists of a small number of relatively large, round spots, generally arranged in a sing row (Degani, 1986). In the Israeli salamander, there seems to be an intermediate stage between these two subspecies, as far as marking is concerned. Although many specimens had consistent with the characteristics of *S. s. infraimmaculata*, many others have a large number of spots (Table 2.4). Almost no arrangement of spots was found that is consistent with the description by Gasser (1975) of some *S. s.*

infraimmaculata in Europe, on which the spots are not round, and run across the breadth of the body (Fig. 2.1). No great difference in markings was found among the various populations in Israel, although the single row pattern was more common in Tel Dan than in the hilly areas of Galilee and Carmel. At the same time, a pattern of scattered spots was by no means unusual on specimens from Tel Dan (Table 2.4).

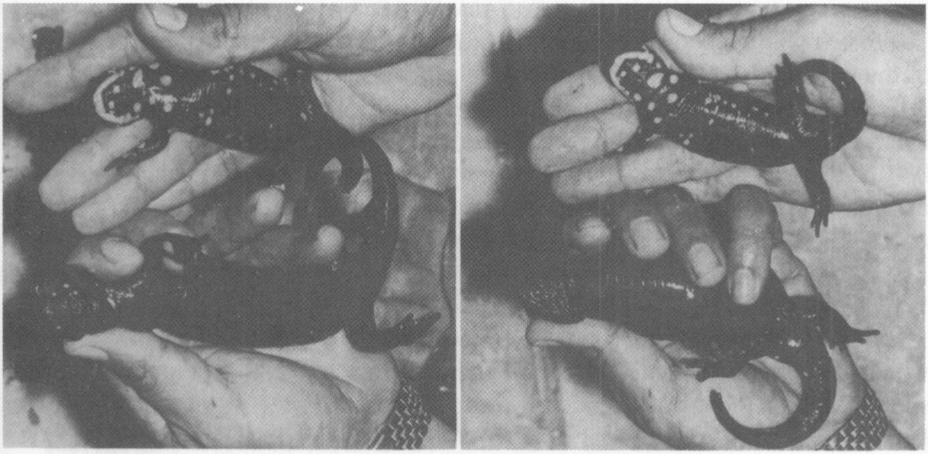
In the Israeli subspecies, the pattern of head marking is closer to that of *S. s. infraimmaculata*, in which the marks do not cover the parotids, or only partly cover them, with no differences among populations, whereas in contrast, on *S. s. salamandra* from Europe, the parotids are covered with spots (Gasser, 1975).

In the European *S. s. salamandra*, the ventral area is partly or largely covered with spots, especially on the lower jaw. In *S. s. infraimmaculata*, on the contrary, the ventral side is unmarked (Gasser, 1975). Just over half (54%) of the Israeli specimens had no markings on the ventral side (Table 2.4), while the rest have smaller and fainter marks than those described for this subspecies in Europe. Again, there were no clear differences between one population in Israel and another, in this respect. At Tel Dan, very few specimens carried ventral spots, and those that do have only one or two dots. This is much the same as the accepted description of *S. s. infraimmaculata*. On the Carmel and in Galilee, most of the salamanders had black bellies, free of any marks, as in Tel Dan, though some had dots on the lower jaw. Hence, all three populations of salamanders in Israel more closely resemble the subspecies *S. s. infraimmaculata* than the European *S. s. salamandra* (Fig. 2.1). Lastly, the long tail and digits found on the Israeli salamanders also characterize them as belonging to the subspecies *S. s. infraimmaculata.*

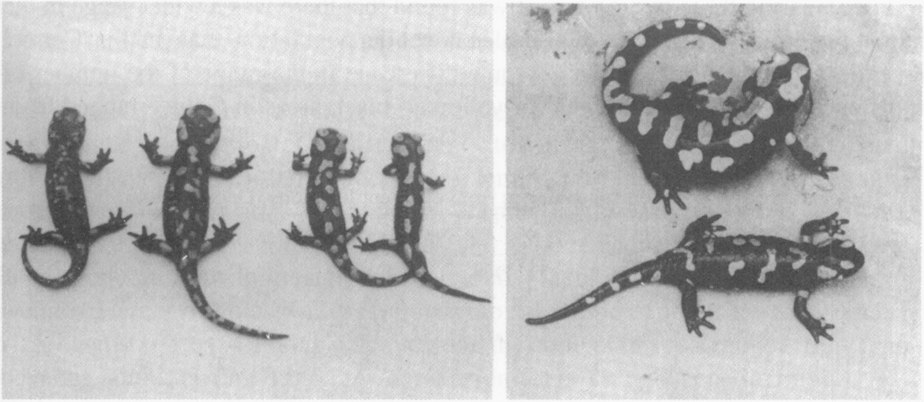
DIFFERENCES IN MARKING BETWEEN ISRAELI POPULATIONS

The difficulty of establishing criteria for classifying spot arrangements lies in the absence of a quantitative method. The yellow blotches on the back and ventral side of each salamander were counted. To determine the ratio between yellow and black areas, the color pattern was traced from photographs on tracing paper and the paper areas corresponding to the two colors were counted out and weighed separately. The ratio of these weights were taken to be equal to the ratio of the areas of the two colors. This is particularly true in the case of the spotted subspecies to which the salamander populations in Israel belong. The method developed in the series of studies on which this section is based, and the relatively large number of specimens examined, permits better analysis of differences, where they occur, than earlier studies.

Spot arrangements on a large number of specimens were examined quantitatively in two populations, in Tel Dan and in the Galilee area, with 64 adult specimens in Galilee and 30 in Tel Dan. The results show no great differences between the two populations in the numbers of spots — although there was a tendency for Galilee salamanders to have more (Figs. 2.3, 2.5). In both populations, the number of spots was consistent with the number that appears in the pictures of *S. s. infraimmaculata*



Europe (above) Carmel, Israel (below) Europe (above) Tel Dan, Israel (below)



Europe (left) Israel (right) Tel Dan, Israel (above) Europe (below)

Figure 2.1. Comparison of order of spots between Israeli and European (Austrian) salamanders (Degani, 1986).

presented by Eiselt (1958) and by Gasser (1975), although there were individuals with more spots than are shown in the pictures. To assess the ratio of yellow to black in the Tel Dan and Galilee specimens was difficult. It seems that yellow occupied a larger area of the back in the former, but the ratio was of the same order of magnitude in both cases. There were no great differences between juveniles and adults, in spot arrangement, in either population (Figs. 2.5, 2.6).

SPOTTING: ADULTS AND YOUNG IN GALILEE AREA

Findings of the study by Degani (1986) showed that in a comparison of the ratio of the total area of yellow spots to that of black background color there is no great difference between adults and juveniles in the Galilee populations. The overall ratio lies between 0.1 and 0.5, with the ratio among juveniles generally between 0.3 and 0.4 and that among adults between 0.2 and 0.3. In the number of spots, there is again no great difference: within a total range of 10 to 40 spots, the number among both adults and juveniles generally falls between 20 and 25.

SPOTTING: GALILEE AND TEL DAN ADULTS

Again, no great differences were found, either in the ratio of yellow to black, which in most adults from Tel Dan fell within a range of 0.2–0.4, or in the number of spots, although there was a tendency for the number of spots to vary less in the Tel Dan population. Within a total range of 10–35 spots on Tel Dan salamanders, the majority fell within a range of 15–19.

SPOTTING: GALILEE AND CARMEL JUVENILES

In comparing these two groups, it was found that there was a wider range in the ratio of yellow to black in the Galilee juvenile population than in the Carmel juvenile population and, similarly, some difference in the range of the number of spots encountered. Thus, the ratio of yellow to black areas in Galilee ranged from

Table 2.4. Spots on salamanders from different locations (Degani, 1986).

	No. of salamanders		
No. of spots	Tel Dan	Galilee	Carmel
1	4	1	–
2	19	14	2
3	23	16	6
4	70	213	50
5	3	9	–
	119	253	58
Order of spots			
1 line	49	71	9
2 lines	23	33	12
scattered	47	149	37
Ventral view			
Black	24	17	10
Small spots on jaw	12	11	5
Blotches on jaw	–	3	2
Ventral blotches	4	3	2
	40	34	19

0.1 to 0.5, with a tendency to fall between 0.3 and 0.4, while on Carmel, the tendency was to fall between 0.2 and 0.3, within a total range of 0.1–0.4. The number of spots in the Galilee population tended to be 20–25, within extremes of 10–40, compared with 25–30, within extremes of 20–35, on Carmel (Figs. 2.4, 2.5).

Both Gasser (1975) and Fachbach (1976) address spot arrangement as a criterion for the determination of subspecies with great caution. The latter showed that the number of spots and the plasma protein data, as revealed by electrophoresis, are not always co-ordinated. The work described here shows that the black/yellow ratio and the number of spots have an identical genetic origin. Larvae from a single brood have similar spot arrangements, which are always within a narrower range than those of the population as a whole (Degani, 1986).

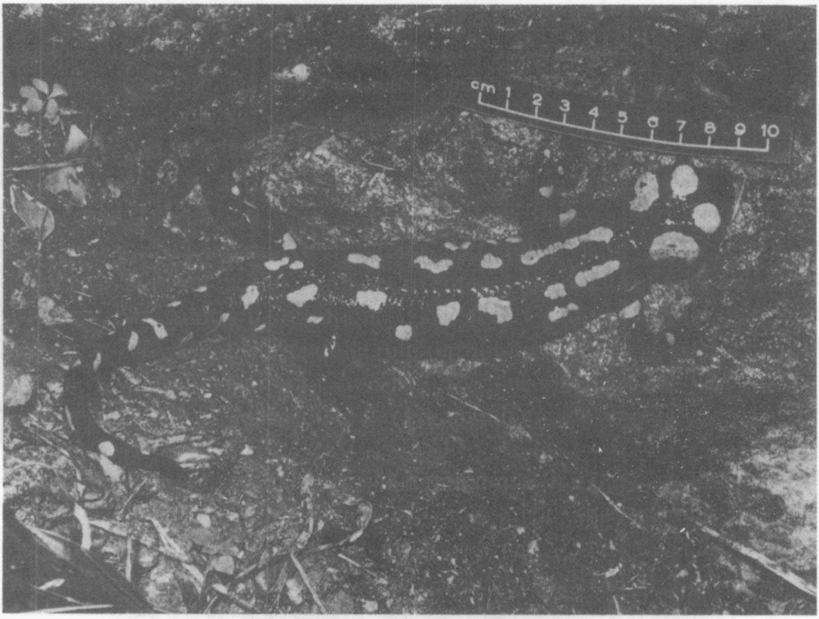
GENETIC INFLUENCE ON MARKING

A comparison between juveniles from a single brood at Tel Dan and juveniles from a single Mt. Meron brood, in which the groups were maintained under identical conditions, showed that while the broad range of marking was similar, there was a considerable difference in the majority tendency between the groups (Degani, 1986).

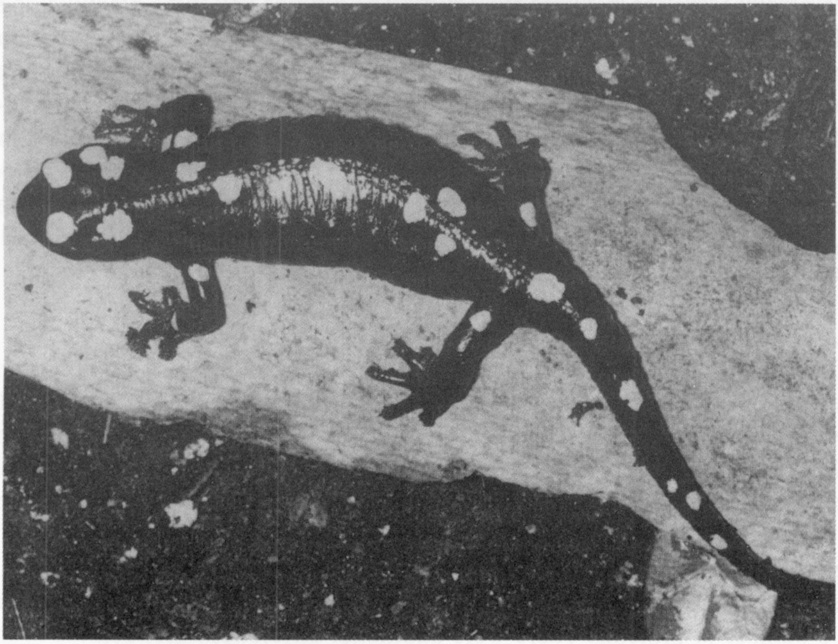
When adults and juveniles from Tel Dan were compared, it was found that, while the juveniles of a single genetic origin were alike as regards marking, there was a much greater variation between the adults. The ratio of yellow to black among the adults ranged from 0.1 to 0.5, with a tendency to fall between 0.2 and 0.3, compared with a total range of 0.1–0.5, with a strong tendency to fall into the 0.1–0.2 range among juveniles. Similarly, in the number of spots, adults showed a range of 10–40, while the range for juveniles was 25–35. The same phenomenon was noted in the Galilee population, with greater variation among adults than in a single brood of juveniles. Here the figures were as follows: the color ratio of adults ranged from 0.1 to 0.5, against 0.2 to 0.4 among juveniles, and the number of spots ranged from 10 to 40 among adults, against 15 to 35 among juveniles of a single genetic origin.

DIFFERENCES IN PLASMA PROTEIN BETWEEN POPULATIONS

Differences in the proteins found in blood plasma are likely to point to genetic differences between populations. Such differences are to be found particularly between one subspecies and another, although according to Gasser and Fachbach (1976), there may also be differences within a single subspecies. The former author writes that, in the subspecies, *S. s. salamandra* the two albumens were very clear and close to each other: more so than in *S. s. infraimmaculata*. The sample that was taken from populations in Israel (Degani, 1986) resembled those described for *S. s. infraimmaculata*, with separated albumens, and with the first albumen (A_1) divided into a number of proteins. There were additional differences between the proteins found in *S. s. salamandra* and those found in specimens of salamanders in Israel:



Galilee salamander with double line of spots (length 32.4 cm).



Galilee salamander with single line of spots.

Figure 2.2. Arrangement of spots in different populations (Degani, 1986).

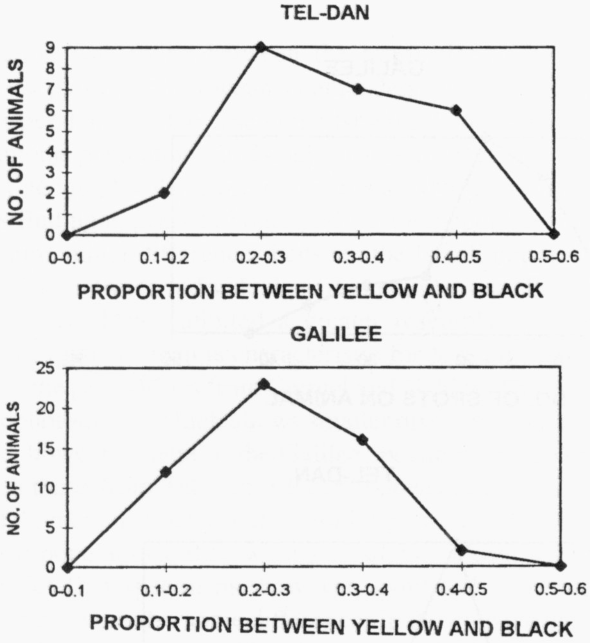


Figure 2.3. Ratio of yellow to black: Tel Dan and Galilee (Degani, 1986).

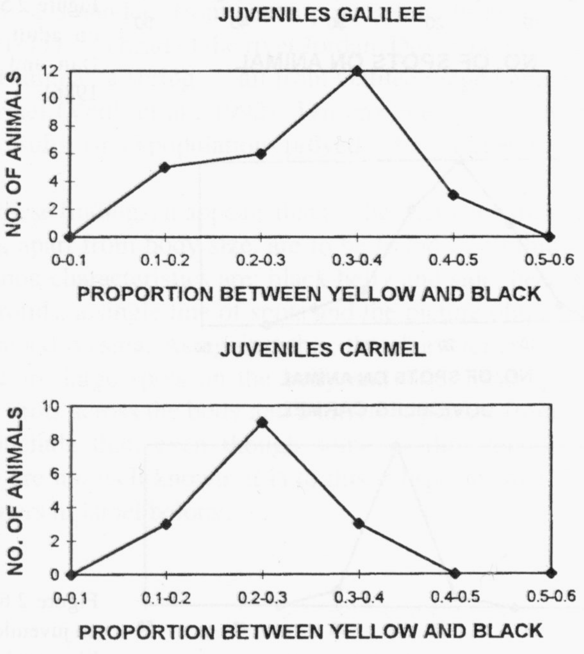


Figure 2.4. Ratio of yellow to black: Galilee and Carmel (Degani, 1986).

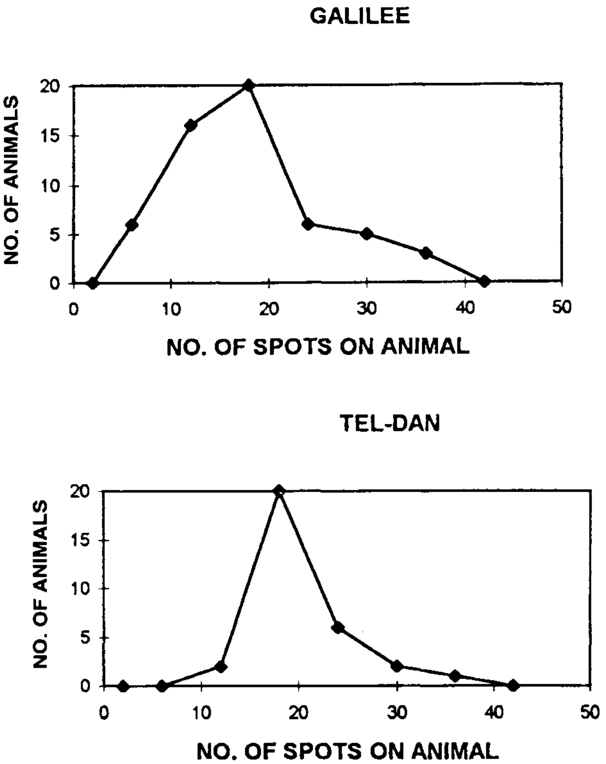


Figure 2.5. Number of spots on adult salamanders: Tel Dan and Galilee (Degani, 1986).

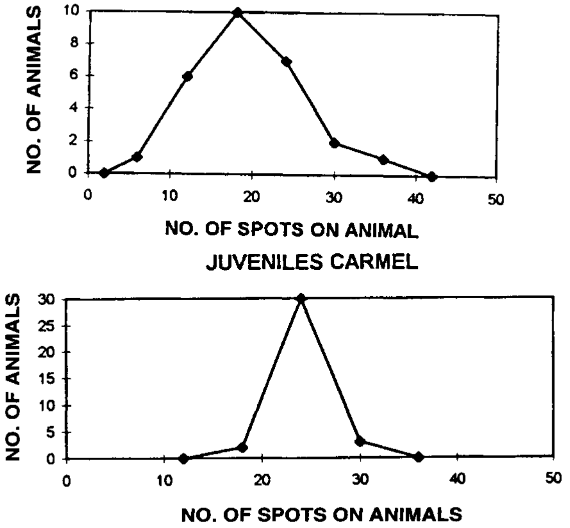


Figure 2.6. Number of spots on juvenile salamanders: Galilee and Carmel (Degani, 1986).

greater segmentation was found between the tranferrines (Tf) and the second albumen (A_2) in the plasma of European salamanders, and its macroglobuline was narrower and sharper than was the case in the Israeli salamander.

Differences among populations in Israel, in this respect, are small. Fachbach (1976) noted that geographically close populations exhibit similar electrophoretic patterns, and this finding appears to hold good for the populations in Israel. There were, however, some minor differences between the Israeli populations, as indeed there sometimes were between individuals within populations (Fig. 2.7).

Specimens from Tel Dan exhibited a greater resemblance between the two albumens and their segments than is characteristic for *S. s. infraimmaculata*; more than was found for the populations from Carmel and Galilee. This can be seen more clearly by spectrophotometry, which allows smaller differences to be distinguished. At the same time, however, some of the Galilee specimens exhibited very similar protein patterns to those from Tel Dan. Electrophoresis of plasma always showed albumens A_1 and A_2 more distinctly in that from the Carmel specimens than in that from the other two populations; they were also slightly closer together (Fig. 2.7). The Galilee and Tel Dan specimens, however, exhibited more segments in the albumen region. There were also some differences in the transferrins and macroglobulins, an area which has been studied less intensively. In this area, Galilee and Tel Dan specimens exhibited more proteins than did those from Carmel.

Horizontal starch gel electrophoresis was carried out on tail lip homogenatic of 173 larvae of the salamanders from seven populations in north Israel (Fig. 1.2): Mount Hermon, Tel Dan, a head of the river Jordan, Dovev pond, Gush Halav pond, Sasa rock pool, Hammama spring — all from Galilee range habitats, and the pond from Mount Carmel (Veith et al., 1992). Ten enzyme systems with 14 loci altogether provided results. Israel populations proved to be completely monomorphic of these 14 loci.

Summing up these findings, it appears that all the characteristics attributed to*S. s. infraimmaculata*, apart from body size, are to be found in all three populations in Israel. The common characteristics are: black belly and side, head spots which do not cover the parotids, a single line of spots and the picture obtained from electrophoresis of the blood plasma. As against this, the characteristics of the European *S. s. salamandra* are large spots on the belly and side, head spots covering the parotids, narrow spots across the body and a different picture from electrophoresis. From this, I conclude that, even though some of the characteristics of *S. s. infraimmaculata* are not well known, it is to this subspecies that all three populations of salamanders in Israel belong.

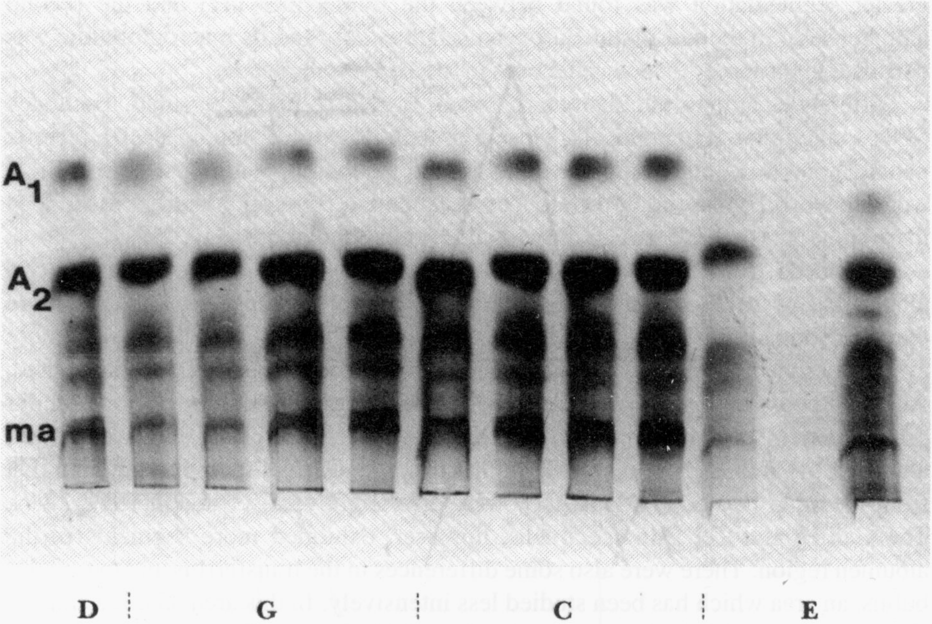


Figure 2.7. Electrophoretograms of plasma protein in salamanders from several localities (Degani, 1986).
A_1, A_2 = albumens; ma = macroglobulin.
E = Europe, C = Carmel, G = Galilee, D = Tel Dan.

CHAPTER THREE

SEASONAL ACTIVITY OF SALAMANDERS

The activities of Urodela species are dependent on environmental and seasonal factors: relative humidity, rainfall and temperature are important factors in their behavior. In addition, Joly and Landry (1976) found a connection between the electric charge in the atmosphere and the behavior of *S. salamandra*. Observation of their activities at different times of year has enabled researchers to gain a picture of the adaptation of various Urodela species to their habitat and of their life cycle.

Most of the information on this activity in Urodela concerns species in America; it has been accumulated by a large number of researchers: Hairston (1949), Heatwole (1962), Hurlbert (1969), Jaeger (1972), Shoop and Doty (1972), Huheey and Brandon (1973), Healy (1975), Orser and Shure (1975), Wells and Wells (1976) and Hall (1977).

Two principal categories of behaviour have been noted: movement in the vicinity of the habitat and movement to the breeding or laying locality. These two kinds of movement are directly linked to the mating season and the sexual maturity of the individuals. Research has been conducted in two principal ways: One is to trap the specimens in their habitat and release them elsewhere after tagging them, to enable the movements of the animal to be tracked; the second involves removing the amphibian from its habitat or breeding site (a water source), in order to study from what distance it is able to travel back to these places, i.e., the homing distance (Twitty, 1959).

Comparitively little is known specifically about the activity of *S. salamandra,* although Joly (1968) studied the activity of the subspecies *S. s. terrestris* in France. It is, therefore, of great interest to study how habitat and invironment affect the distances over which the salamander moves. In hill environments, particularly, where water sources are point located, there is a great deal to be gained from studying the distances that the salamander is able to cover in order to adapt itself to its environment.

RESEARCH METHODS

For the purposes of tracking the movements of salamanders in Israel, Degani and Warburg (1978) selected a number of populations, in the Galilee area, in Tel Dan and on Mt. Carmel (Fig. 1.3). The areas studied in Galilee consisted of the 3.2 ha site on which Kibbutz Sasa is built, 0.1 ha around the Hammama spring and 800 m^2 on the aproaches to the spring, and a further 0.1 ha around the pool at Gush Halav. In

Tel Dan, a route was selected that comprised a permanent path within the nature reserve, measuring 736 long × 4 m wide, partly in the lower and partly in the upper parts of Tel Dan. On the Carmel, populations were chosen that inhabitat, respectively, a pool, a spring and a stream, each area being approximately 0.1 ha. In addition, permanent routes of water approach to the water points were studied, one of $300 \times 4\ m^2$ other of $800\ m \times 4\ m^2$. Two larger areas, each of some 3.6 ha were also studied for one season, but were abandoned , when no specimens were found. Each animal that was caught was marked by clipping its digits (which are regenerative), and photographed; a card was prepared, with the date, the photograph, an identification number, the sex, weight and length of the specimens and the place it was caught. This method of marking was used in all the areas that were studied. Animals were released in the area where they were caught.

The route in Tel Dan was divided into areas (Fig. 3.1) and each animal that was caught was put into a cloth bag marked with the area in which it was found. In Sasa, the animals were all placed in separate containers, each marked with a note of where the animal was found. There, too, they were released where they had been found, after marking (Degani and Mendelssohn, 1982). Each habitat was examined once every two weeks during most of the year; from October to January, the active months, checks were made every week.

The behavior of adult salamanders was also studied in captivity, in two enclosures measuring 10 m^2, located at Sasa and Tel Dan (Fig. 3.2). Three to six local salamanders were put into each enclosure. Burrows of various depths, up to 80 cm, were dug in the enclosures. A little pool was built into the Sasa enclosure, while the Tel Dan enclosure was built on a braid of running water. Next to the main enclosure in Sasa, a smaller one of 4 m^2 was built, into which juvenile salamanders aged 1–2 years were put.

Relative humidity (RH) was measured with a psychrometer with an accuracy of ±0.5% RH, and ground and air temperatures were measured by a thermometer with an accuracy of ±1°C. The distance that salamanders are capable of covering to return to their breeding place was determined by releasing marked adults from the Hammama spring at 200, 300, 400 and 600 m from the spring.

RESULTS

The activity of salamanders is largely nocturnal and takes place mainly during the months October to December. The greatest numbers of specimens were caught during this period (Figs. 3.3 to 3.8), characteristically moving to water sources to breed (Figs. 3.8 and 3.9). In the Tel Dan population, unlike those from the hilly regions (Carmel and Galilee), there was no great difference between the beginning and the end of winter in the numbers of specimens caught (Fig. 3.5). Generally, in the early months of winter, more males were generally caught than females, in all the populations (Figs. 3.6 and 3.7).

Figure 3.1. Area of Tel Dan.

Figure 3.2. Enclosure at Sasa (Degani, 1980).

There are two main forms of activity: moving to a water source to breed, which occurs among both males and females (Figs. 3.8, 3.9), and in and around the salamander's hiding place.

The salamanders from Tel Dan were not observed to travel any great distance, unlike those from the hilly areas: most of the movement in Tel Dan was within limited spaces. Among the Sasa salamanders, 71% did not travel more than 10 m from where they were caught, a further 12.2% travelled 10–40 m, and the remainder travelled over 40 m (Fig. 3.9). In Tel Dan, specimens were recaptured close to where they were first captured, i.e., within 20 m, showing that they travelled less than their counterparts from the hills. However, in Tel Dan, this activity within a limited area takes place throughout the year, and is commoner during the summer. In general, however, activity is greater during the winter than during the summer (Figs. 3.3 to 3.6).

Most activity took place at a relative humidity of 90–100% and at temperatures of 4–9°C. In Galilee, activity was observed under more extreme conditions: occasionally at a temperature as high as 20°C and a relative humidity of 60% (Figs. 3.11, 3.14). In Tel Dan, activity took place under less extreme conditions, generally within a temperature range of 8–13°C and relative humidity of 90–100% (Fig. 3.13).

In comparing the activity of adult salamanders with that of juveniles, it was observed that the former are more active and are capable of leaving their hiding places under more exteme conditions then the latter (Fig. 3.14). Young salamanders were observed to be active within a temperature range of 4–14°C and a relative humidity range of 80–100% (Fig. 3.15). Rain has a marked effect on activity, more so among young than adult salamanders (Fig. 3.16).

Salamanders are capable of homing to their breeding place at distances up to 400 m (Table 3.1, 3.2). A number of salamanders were observed as far as 1–2 km from their breeding place, but none of them were marked specimens. In the Sasa area, the maximum recorded distance from the breeding area was 160 m. Although activity is generally nocturnal, daytime activity was observed in all three populations during rain and during the winter, especially during the breeding period and in the rain.

Table 3.1. Homing of salamanders from point of capture (Degani, 1980).

Distance of release from original capture	No. of males	No. of females returned	% recaptured returned
200 m	5	1	87.71
300 m	3	1	57.14
400 m	2	0	33.33
600 m	0	0	0

Table 3.2. Time taken by salamanders to return to original point (Degani, 1980).

Distance of release from original capture	Average time (months)
200 m	9.88 ± 4.28
300 m	4.67 ± 6.35
400 m	10.00 ± 2.52

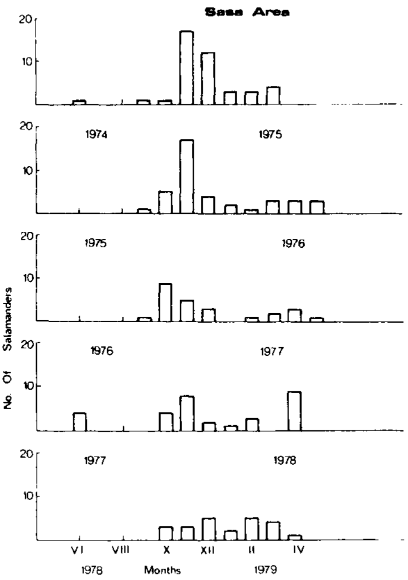


Figure 3.3. Distribution of salamanders collected in the Sasa area from 1974 to 1979 (Degani, 1980).

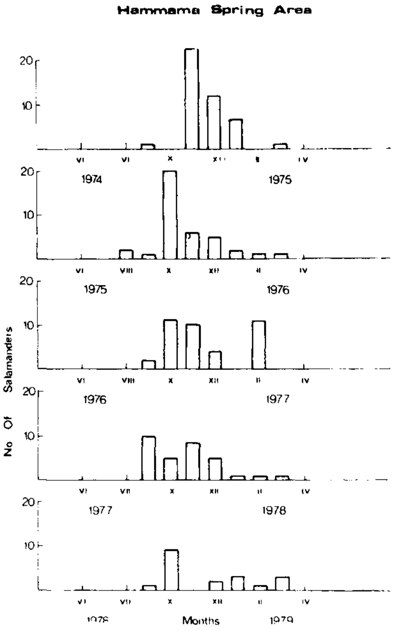


Figure 3.4. Distribution of salamanders collected in Hammama Spring from 1974 to 1979 (Degani, 1980).

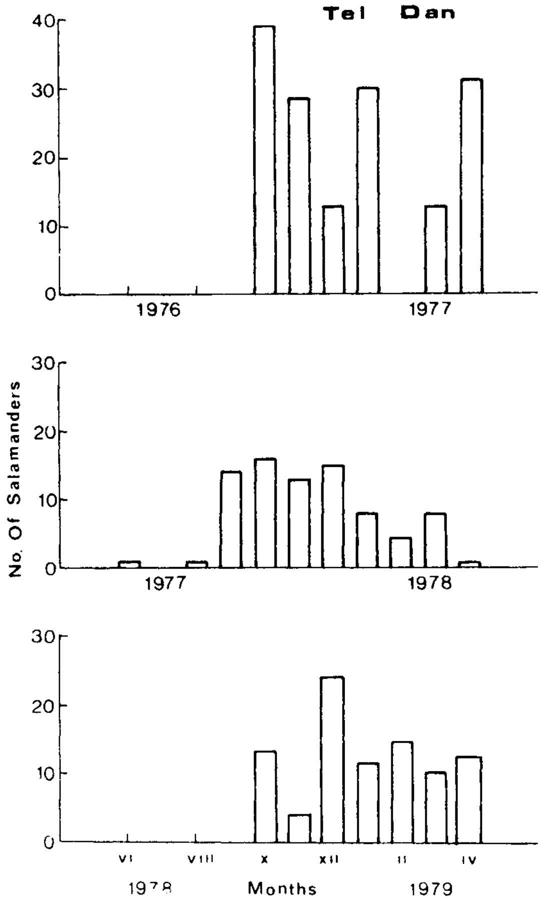


Figure 3.5. Distribution of salamanders collected in Tel Dan from 1974 to 1979 (Degani, 1980).

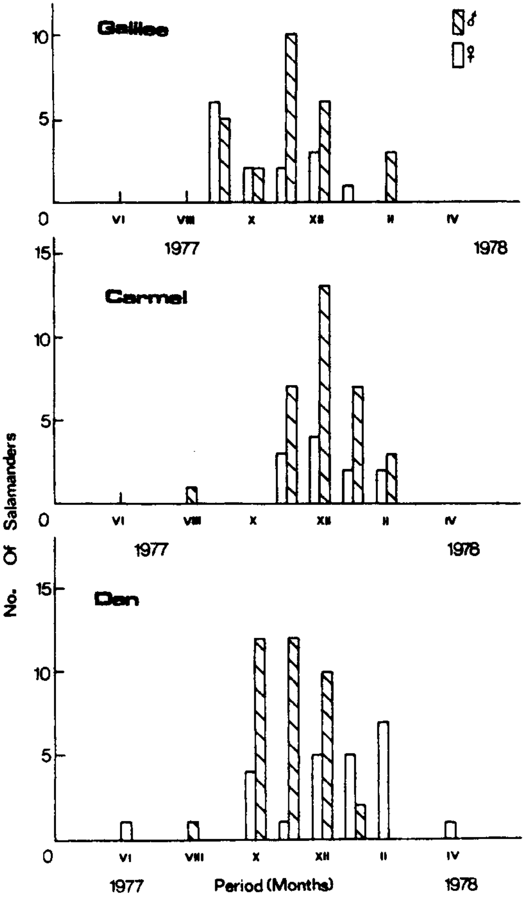


Figure 3.6. Distribution of male and female salamanders collected from different localities from 1977 to 1978 (Degani, 1980).

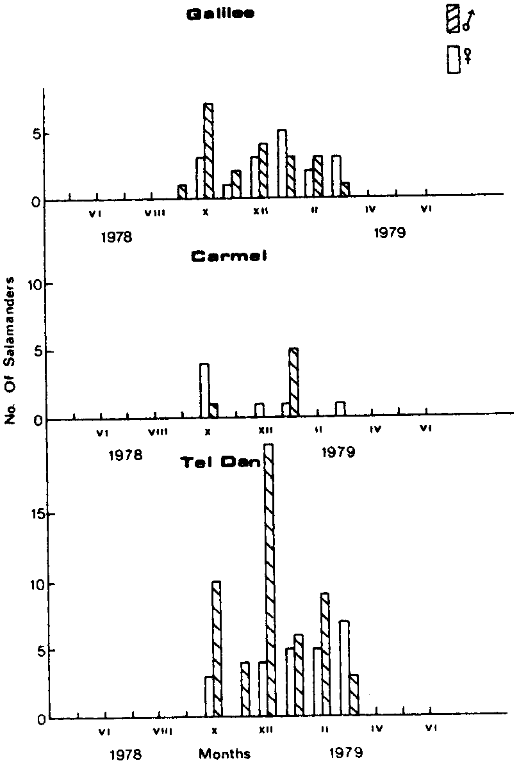


Figure 3.7. Distribution of salamanders collected in Galilee, 1974 to 1978 (Degani, 1980).

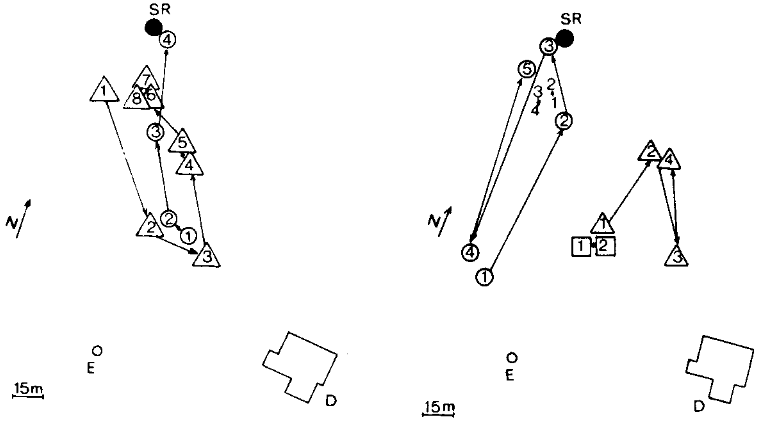


Figure 3.8. Map of Sasa: activity of adult salamanders over 3-ha area.
SR = Sasa rock pool; E = enclosure; D = dining hall (Degani, 1980).

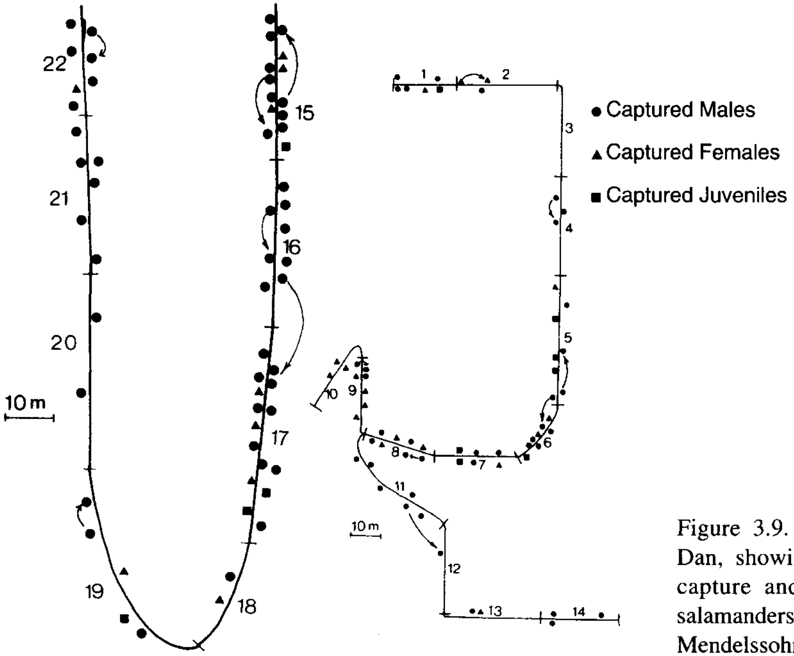


Figure 3.9. Map of Tel Dan, showing places of capture and activity of salamanders (Degani and Mendelssohn, 1982).

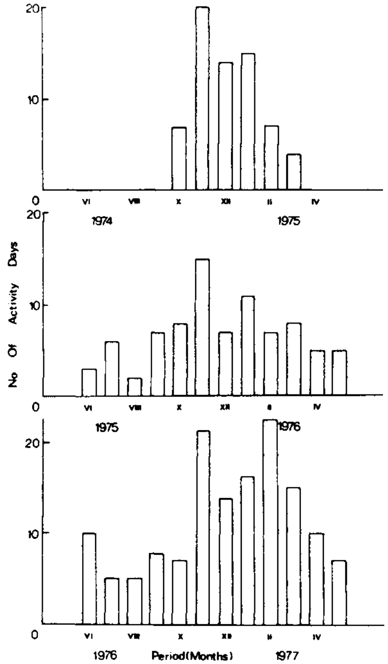


Figure 3.10. Local activity in Sasa enclosure throughout the year (Degani, 1986).

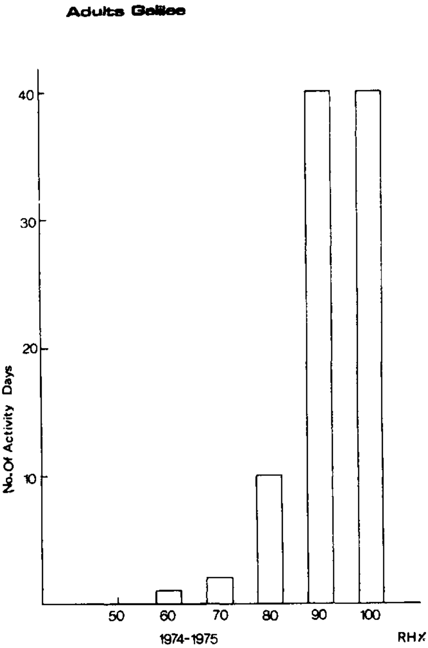


Figure 3.11. Activity of salamanders as a function of relative humidity in Sasa (Degani and Warburg, 1978).

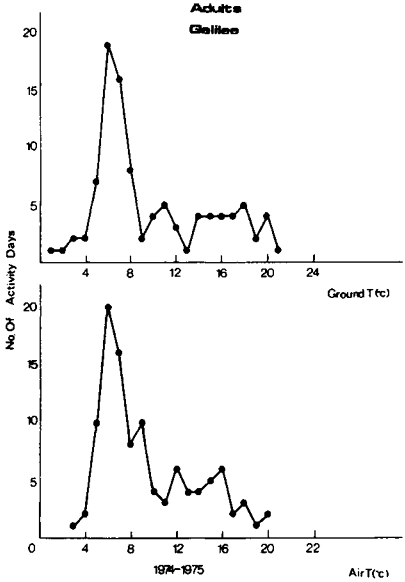


Figure 3.12. Activity of salamanders as a function of temperature in Sasa (Degani and Warburg, 1978).

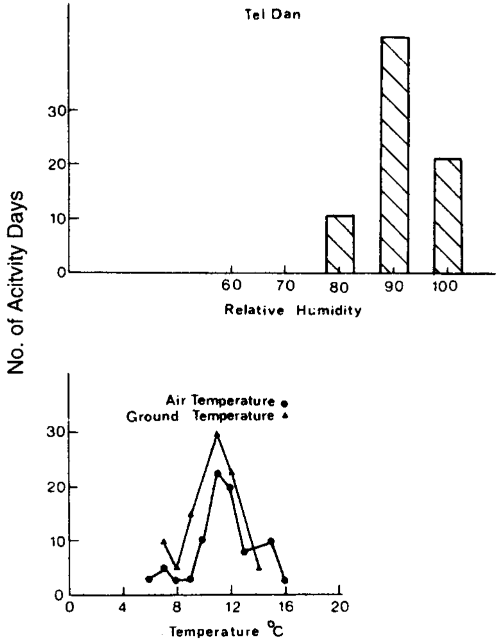


Figure 3.13. Activity of salamanders as a function of temperature and relative humidity in Tel Dan (Degani and Mendelssohn, 1980).

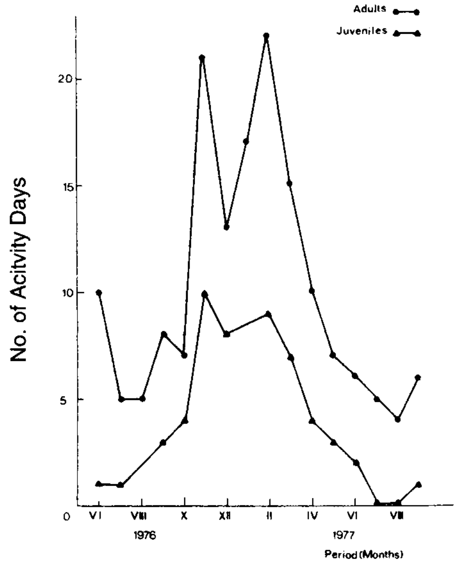


Figure 3.14. Comparison of activity of adult and juvenile salamanders in various seasons (Degani and Mendelssohn, 1980).

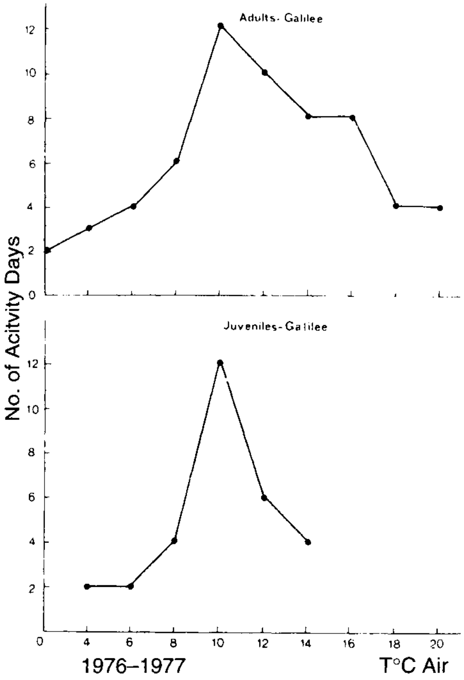


Figure 3.15. Comparison of activity of adult and juvenile salamanders as a function of temperature (Degani, 1980).

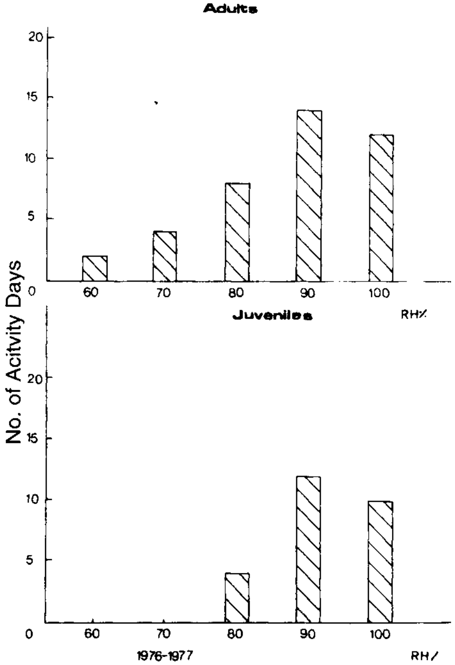


Figure 3.16. Comparison of activity of adult and juvenile salamanders as a function of relative humidity (Degani, 1980).

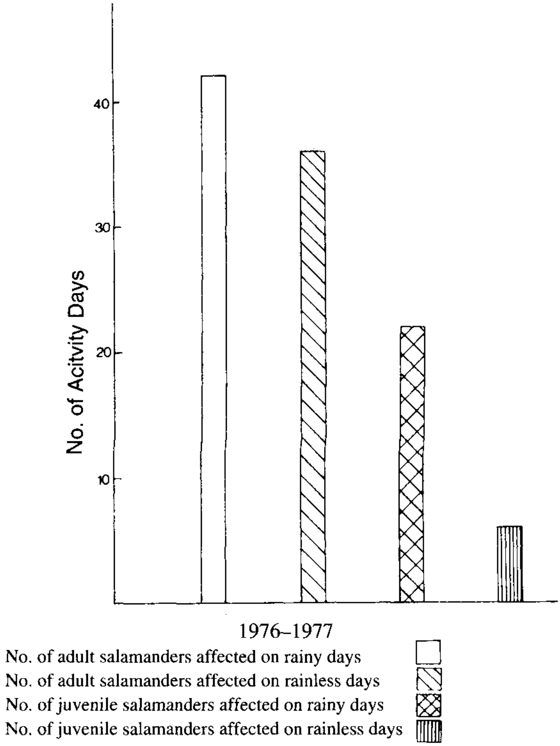


Figure 3.17. Correlation between incidence of rain and activity of adult and juvenile salamanders in Mt. Meron area (Degani, 1980).

The adaptation of *S. salamandra* to the environment of the southern limit of its distribution, as shown by the results of the study described in this chapter, can be seen in the nature of its activity, local and migratory, in the season of activity, in the climatic conditions in which it is active, in the influence of the habitat and in the differences between the activity of adult and juvenile salamanders.

There have been many research reports on the activity of species of Urodela in the New World: it takes place mainly in the spring and summer months, with little during the autumn, though in the southern United States activity has been observed in winter (Table 3.3). In the same way, summer activity also characterizes *S. salamandra* in the cooler climates of Europe (Mertens, 1947; Szabo, 1959). In Israel, on the contrary, with its warm, dry climate, activity takes place mainly in the winter, continuing into spring (Figs. 3.3 to 3.8). The adaptation of *S. salamandra* to this region is through the transfer of its seasonal activity to the winter, from the spring and summer when it occurs in cooler climates. This hypothesis is further supported by Joly (1968), who found that there is a transitional stage in France, with

Table 3.3. Period of activity of various Urodela.

Species	Date	Activity & Reference
Notophthalamus viridescens	Apr.–May	Migration to breeding places
	Aug.–Dec.	(Hurlbert, 1969).
	Aug.–Nov.	Juvenile migration from ponds.
	Mar.–May	Limited migration (Healy, 1975).
Triturus helveticus	Oct.–Nov.	Adult migration to water.
	March	ditto (von Gelder, 1973).
	June–July	Leave water.
Ambystoma opacum	End autumn	Migration to dry ponds, nesting & spawning (Shoop & Doty, 1972).
Plethodon glutinosus	July	Most activity (Hairston, 1949).
Desmognathus wrighti	August	Most activity (Hairston, 1949).
D. ochrophaeus carolinensis	August	Most activity (Hairston, 1949).
Salamandra salamandra	Mar.–Apr.	In Germany.
	Feb.–Oct.	In Germany (Klewen, 1985).
S. s. terrestris	Oct.–May	In France (Joly, 1968).
S. s. infraimmaculata	All year	Tel Dan — local activity only.*
	Aug.–Apr.	Hammama — migration to breed.*
	Nov.–Jan.	Gush Halav — ditto.*
	Sep.–Feb.	Carmel — ditto.*
	Nov.–Jan.	Carmel (Warburg, 1986).
	Oct.–Jan	Carmel (Warburg, 1994).

*Degani, 1980.

winter as the active season in some areas and spring and summer in others. It seems, therefore, that this phenomenon is a general one, and it applies to many species of Urodela. In North America, with its cold winters that prevent the animals from leaving their hiding place in the winter, these species are active principally in spring and summer.

In most cases, the activity of the male *S. Salamandra* betweeen October and December is greater than that of the female (Fig. 3.6), apparently because this is the period during which the male seeks a mate to fertilize (Degani, 1976). Joly (1968) also describes seasonal differences between the numbers of acitve males and females of *S. salamandra*, a phenomenon noted in other Urodela by Gelder (1973), Healy (1975) and Rose (1976).

Activity above ground is greater among adult than among juvenile salamanders (Figs. 3.14, 3.15), which may explain the demographic structure described by Joly (1968) for the subspecies *S. s. terrestris*, with the juvenile population apparently much smaller than the adult population.

No great differences were found in the season of activity between the different populations in Israel, though that of the Mt. Meron area (Sasa) migrates to its breeding place at the beginning of winter (Degani, 1980) and Carmel salamanders are mostly active between October and January (Warburg, 1986), whereas in Tel Dan, where water temperatures are relatively constant (16°–17°C), the population is active all year round. However, there is a considerable difference in the distances of migration. In Sasa, 70.7% of the specimens recaptured were found 10 m from their original place of capture, whereas no migration at all was observed in the Tel Dan area (Fig. 3.9). It is reasonable to suppose that the constant presence of water in the entire habitat of Tel Dan, as opposed to the point sources in the hilly areas, is what causes this difference in migratory habits.

Joly (1968) also observed migration to a breeding place in France. There, most of the activity takes place in the vicinity of the hiding place: males travelled an average of 9.8 m and females an average of 12.8 m. In Sasa, the corresponding figures were 19.8 and 28.7 m, respectively. Where Joly noted the longest homing distance for a salamander to be 300 m, in the study described in this chapter it was found that both salamanders were capable of returning from as far away as 400 m, to the breeding place. This migration was observed both in the Mt. Meron area and in Carmel, among males and females equally.

Migration distances have been studied in many Urodela. In *Plethodon glutinosus*, there is no significant difference between males and females, the migration distance usually being 0–3 m and occasionally reaching 9 m, although Wells and Wells (1976) noted rare occurrences in which this species travelled as far as 90 m. Shoop and Doty (1972) described *Ambystoma opacum*, which migrates in summer and autumn, laying its eggs in dry water holes, where they hatch when the holes fill up with rainwater. The migration of *Triturus helveticus* to water sources was described by von Gelder (1973), while Hurlbert (1969) described the activity of *Notophthalmus viridescens*. The homing phenomenon has been described for a number of species, and can shed a light on distances that they travel: Twitty (1959) found that the newt *Taricha* can travel up to a mile to return to its habitat. In another study, Twitty et al. (1964) found that in water, specimens can return from far greater distances to the original point of capture.

In most cases, the activity of the male *S. salamandra* is greater between October and December than is the case with the female (Figs. 3.6), apparently because this is the period that the male seeks out a mate to fertilize (Degani, 1976). Joly (1968) also describes differences between the number of active males and females during the seasons of the year in *S. salamandra* a phenomenon noted in other Urodela by Gelder (1973), Healy (1975) and Rose (1976).

Activity above ground is greater among adult than juvenile salamanders (Figs. 3.14, 3.15), which may explain the demographic structure described by Joly (1968) for the sub-species *S. s. terrestris*, by which the juvenile population appears to be much smaller than the adult population.

Salamanders in Israel are capable of activity at a wider range of temperatures than their European counterparts: 0–20°C (Fig. 3.12, 3.13) against 2–8°C (Joly, 1968), though their preference is for a range of 4–8°C, like the European salamander. Activity at higher temperatures was observed occasionally in summer in all three Israeli populations studied. In Carmel and Tel Dan, where observations were taken only once every two weeks, only a few examples of summer activity were recorded, whereas for the Sasa enclosure, where observation was conducted on most days of the week, so a greater body of data is available.

Rain has a considerable affect on activity (Fig. 3.17): most activity takes place on rainy days. Adults are more active than juveniles on rainless days. The link between activity above ground and rainfall has been described in many species of Urodela (Joly, 1968; Hurlbert, 1969; Jaeger, 1972; Shoop and Doty, 1972; Healy, 1975).

To sum up this chapter, salamanders at the southern limit of their distribution are active mainly in the winter. Activity is mostly local, and such activity can also be found in summer. Migration to breeding places is limited to the hill populations, since the specific environmental conditions at Tel Dan greatly reduce the need for it. Activity takes place in conditons of 0–20°C and 60–100% RH, which are more extreme than those described for specimens in Europe. Males are more active at the beginning of winter; and juveniles are less active than adults, which may explain the low percentage of juveniles caught by Joly (1968).

CHAPTER FOUR

DEMOGRAPHY OF POPULATIONS IN DIFFERENT HABITATS

Research scientists have shown great interest in demographic aspects of species of Urodela, concentrating on two primary topics: size and density of the population (Feldman, 1964; Joly, 1968; Huheey and Brandon, 1973; Rose and Armentrout, 1974; Burton and Likens, 1975; Orser and Shure, 1975; Hall, 1977); and on the structure of the population, i.e., the male to female and adult to juvenile ratios (Whitford and Vinegar, 1966; Joly, 1968; Hurlbert, 1969; Shoop and Doty, 1972; von Gelder, 1973; Healy, 1975; Rose, 1976).

However, the influence of the habitat on the population size and structure of a given species has been given little attention. This topic is of particular interest in *S. salamandra* at the southern limit of its distribution, a region where great differences can be found between one habitat and another. It is also of interest to compare the population structures of salamanders in Israel with what is known of them in Europe.

Population density was examined in the Galilee, Tel Dan and Carmel habitats by catching specimens, marking them and freeing them again in the same location, and then conducting a second sweep of catching. The population in marked sections of the habitat can then be estimated with the aid of the Lincoln Index, as applied by Joly (1968) to European salamanders: in the formula $P = M \times N/m$, P = number of animals in the population; M = number of specimens first caught; N = number caught on second sweep; m = number of marked animals caught on second sweep.

This formula was adapted by Jolley (see Roff, 1973) for the number of adults in a stable, but small population. The estimate of a population over a given time is given by $P_i = N_i \times M_i/m_i$, where N_i represents the number of animals marked and released up to time i; M_i is the total number caught during time i; m_i is the number of marked animals among those caught during time i. This was the formula employed for our study.

The population size was directly related to the type of habitat. The density in Tel Dan was greater than those of the Hammama and Sasa populations, both of the latter being in the Galilee region (Table 4.1). In the Gush Halav pool (in the same region), the density was low, but the low percentage of recapture prevented an estimate of the size of the population. This phenomenon occurred also in Carmel. These findings also indicate that there is a direct relationship between population density and the conditions of the habitat, namely suitable hiding places and the availability of water. At the southern limit of its distribution, the harder the conditions, the lower the size and density of the salamander population.

Table 4.1. Estimates of adult populations of salamanders in three habitats in the Galilee (Degani, 1980).

Sasa Date	Hammama (3 ha)	Tel Dan (0.1 ha)	Sasa (3 ha)
Nov. 1974	37	48	
Dec. 74	48	45	
Jan. 75	48		
Feb. 75	37		
Mar. 75	101		
Oct. 75	33		
Nov. 75	66	91	
Dec. 75	50	43	
Jan. 76	78	46	
Mar. 76	123		
May 76	123		
Oct. 76	189		
Nov. 76	122	78	546
Dec. 76	871		
Jan. 77	52	1151	
Mar. 77	53	98	
Sep. 77	1161		
Oct. 77	81		
Nov. 77	102	77	
Dec. 77	134	108	
Jan. 78	103		
Mar. 78	900		
Oct. 78	126		
Nov. 78	129		
Dec. 78	88	87	780
Jan. 79	141	130	1253
Average ±SD	90.81 ± 41.0	77.9 ± 32.7	951.7 ± 250.8

However, caution must be exercised over the question of population density, because most of the salamanders were caught during the migration season, making it more reasonable toase conclusions on size of the population, without regared ot the area. During the migration period, large concentrations of salamanders in hill populations can be found near the breeding sites and convenient routes to them. In measuring the sizes of the populations, it was again found that the highest was at Tel Dan, where it varied from 546 to 1161 salamanders, compared with Sasa, with a population of 37–189 and Hammama, with 33–108 (Table 4.1).

There were more males than females at Sasa, though the difference was small (53.49% males), while at Hammama there were slightly more females (47.62% males) (Table 4.2). Observations were made over a long period of six years at these locations, with frequent checks. In Tel Dan, the preponderance of males was greater: 71.53%. Similarly, in his studies of salamanders in the Mt. Carmel area, Warburg (1986, 1994) found that males formed 63.36% of the population. The more frequently observations were made, the nearer the ratio of males to females approached 1:1 (Table 4.2).

The percentage of juveniles that had not reached sexual maturity and were smaller than 12 cm was low in all the populations studied (Table 4.3). This finding

Table 4.2. Percentages of males and females in various populations (Degani, 1980).

Population	No.	% Males	% Females	Reference
Sasa	43	53.49	46.51	Degani, 1980
Hammama	63	47.62	52.38	ditto
Gush Halav	10	70.00	30.00	ditto
Pond on Carmel	19	68.42	31.58	ditto
Spring on Carmel	24	62.50	37.50	ditto
Galilee (total)	161	54.48	45.52	ditto
Carmel (total)	64	65.12	34.88	ditto
Carmel (total)	131	63.36	36.64	Warburg, 1994
Tel Dan	144	71.53	28.47	Degani, 1980

Table 4.3. Percentages of adults and juveniles in various populations (Degani, 1980).

Locality	No.	% Adults	% Juveniles
Galilee	187	86.10	13.90
Carmel	79	81.01	18.99
Tel Dan	160	90.00	10.00
Hammama	84	75.00	25.00
Sasa	58	74.14	25.86

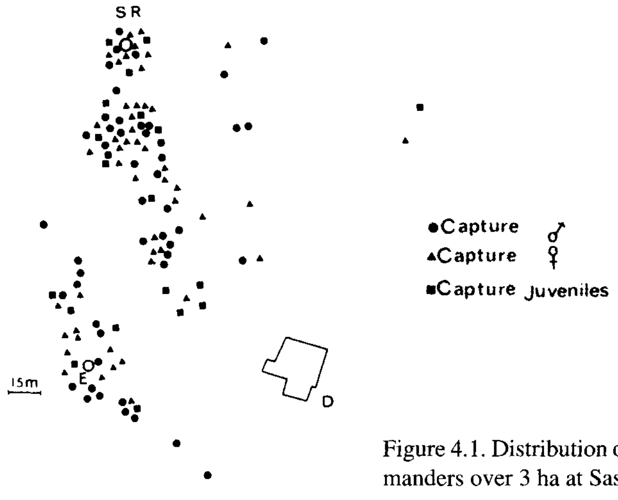


Figure 4.1. Distribution of male, female and juvenile salamanders over 3 ha at Sasa 1974–79 (Degani, 1980).

relates only to the number of juveniles that were caught, so the data must be considered with caution, but it is worth remarking that the percentages of such juveniles were within a fairly limited range (10–25%) in all populations. Furthermore, as noted in the previous chapter, the lower activity of juveniles could result in a lower proportion being caught, thereby explaining discrepancies, in part at least. Joly (1968) also found similar, though somewhat lower percentages, in France (7.2–11.6%). Intensive observation leads to the capture of a higher percentage of juveniles, giving a more accurate picture of the true population balance, and showing that the low percentage of captured juveniles is the result not only of their actual numbers in the population, but also of their lower activity.

Population density in Europe was studied in the subspecies *S. s. terrestris* by Joly (1968), who found one specimen per 84 m^2 in the Bercy Forest, in France, while in La Fleche Park, a hilly habitat in the same country, the population density was lower. Sasa, another hill population, showed only one specimen per 330.36 m^2, whereas in Tel Dan the highest density was found, with one specimen for every 3.13 m^2. Here, too, caution must be observed, because observations in Tel Dan were made on paths, whereas in Hammama a high density was found in the immediate vicinity of the spring (one specimen per 12.87 m^2), and only four specimens were caught on the routes to the spring, an area of 800 m^2, i.e., one specimen per 200 m^2, not very different from the density found at Sasa. The Sasa population was smaller (N = 128) than that found by Joly, but the Tel Dan population was larger (N = 166).

It is reasonable to deduce from these results that the nature of the habitat and the availability of water are the main factors governing the size and density of the population. This deduction is strengthened by the low percentage capture around a winter pool, such as those at Gush Halav and a number of seasonal springs on the Carmel: these populations were small. On the Carmel, in a total approach area of 3,200 m^2, only a single specimen was found, and in another area of 1,200 m^2, on the approaches to a winter pool, one additional salamander was caught.

Population density has been studied in many other species of Urodela (Table 4.4). Among most of the small species in North America, the density is far higher than among *S. salamandra*. However, there are a number of methods for the estimation of populations, and it has been found in some cases that they may give differing results in a given population, so some caution is required in discussing figures (Hueey and Brandon, 1973; Rose and Armentrout, 1974).

It is evident that habitat also influences population density in other species of Urodela. Thus, researchers have found differences between areas in the population density of the species *D. fuscus*, apparently due to differences in the habitats (Orser and Shure, 1975; Hall, 1977), as well as seasonal variations in population density.

As among other species of Urodela, such as *Eurycea bislineata* (Burton and Likens, 1975), the larva density exceeds the adult density in *S. salamandra* (Joly, 1968). It should be noted that Burton and Likens (1975) found that the density of *E. bislineata* was far lower than that of *Plethodon cirereus*, giving rise to the

Table 4.4. Population density of Urodela species.

Species	Season	Density	Reference
Desmogthanus fuscus	spring	1.12/m^2	Orser & Shure, 1975
D. fuscus	summer	0.05/m^2	Orser & Shure, 1975
D. fuscus		0.82/m^2	Hall, 1977
D. ochrophaeus	Jul–Aug	35-229 (total)	Hueey & Brandon, 1973
Eurycea bislineata adult	1970	0.037/m^2	Burton & Likens, 1975
E. bislineata adult	1971	0.022/m^2	Burton & Likens, 1975
E. bislineata larvae	1970	0.498/m^2	Burton & Likens, 1975
E. bislineata larvae	1971	0.756/m^2	Burton & Likens, 1975
Ambystoma tigrinum		1/4.8 m^2	Rose & Armentrout, 1974
S. s. infraimmaculata (Sasa)		1/3485 m^2	Degani, 1986
S. s. infraimmaculata (Tel Dan)		1/3.6 m^2	Degani, 1986
S. s. terrestris		1/48 m^2	Joly, 1968

conclusion that, in studying the influence of habitat on population density, it is necessary to study this topic in a single species.

Studies of the ratio of males to females in populations in France found 58% males in one location and 65% in a second. Similarly, more males than females were caught in most of the Israeli populations (Table 4.2). It is reasonable to assume that this apparent imbalance arises from differences between the activities of males and females. During the period of migration, which in Israel is also the mating period (Degani, 1976), the males are more active than the females (see Chap. 2). This hypothesis is strengthened by the fact, noted above, that in populations that were studied all the year round over a number of years (Sasa and Hammama), the male-female ratio more nearly approaches 1:1. Similarly, of the salamanders caught in the

Table 4.5. Proportion of males and females among various Urodelas.

Species	Males	Females	Reference
Notophthalmus viridescens	47%	53%	Hurlbert, 1969
N. viridescens (aquatic)	55%	45%	Hurlbert, 1969
N. viridescens	36-60%	64-40%	Healy, 1975
Triturus helveticus		M>F	von Gelder, 1973
T. helveticus (neotenic)		M<F	von Gelder, 1973
Plethodon wehrlei	65-74%	26-45%	Hall & Stafford, 1972
S. s. infraimmaculata (Galilee)	54.5%	45.5%	Degani, 1986
S. s. infraimmaculata (Carmel)	65%	35%	Degani, 1986
S. s. infraimmaculata (Tel Dan)	71.5%	28.5%	Degani, 1986
S. s. terrestris (Oct.)	103%	43%	Joly, 1968
S. s. terrestris (Mar.)	9%	27%	Joly, 1968

Bercy Forest in October, 103 were males and 43 females, whereas in March the corresponding figures were 9 and 27 — a total of more males than females, but quite differently distributed in different seasons.

If, then, we accept this hypothesis, it would explain the relatively high percentage of males caught in Tel Dan. Due to the nature of the habitat, there is no migration to a breeding place, with the result that the movement of females is lower than that found in hill-country populations. Hence, fewer females are caught. Among other Urodela species, the ratio of males to females varies: in some species there are more males than females, in others the opposite (Table 4.5).

These results, then, show that the nature of the habitat influences population density. In Tel Dan, where water is constantly available, there was a higher density than in the hilly regions. The fact that, in general, more males than females were caught arises from the nature of their respective activities. There was no significant difference between the Sasa and Hammama populations, with their similar habitats, in the male:female ratio. Finally, the small number of juveniles caught arises from both of their true numbers and the fact that they are less active than adults.

CHAPTER FIVE

REPRODUCTION OF *S. s. infraimmaculata*

SEXUAL BEHAVIOR

Little has been published on the sexual behavior and reproduction of *S. salamandra.* In Europe, it has a long reproductive season, from April to July (Joly, 1966; Thiesmeier et al., 1994); in Israel, the season is shorter, extending from October to March (Degani, 1976). Joly, who reviewed all the work that had been published previously on the salamander's sexual behavior, was the first to photograph the various stages of the behavioral cycle of *S. s. terrestris.* He identified the spermatophore (sperm sac) and observed the manner of its transferral, and described the entire process of courtship and reproduction, dividing sexual behavior into 10 distinct stages. Figures 5.1.1 to 5.1.10 show these stages in *S. s. infraimmaculata,* as photographed by Degani (1976), who gave a detailed account of the sexual activity of the local salamander, on the basis of 18 couples who went through the entire process, in all its stages. Degani (1976) identified some minor differences from the process as described by Joly (1966), the most prominent being that the first amplexus stage was not observed in the Israeli salamander. The stages of sexual behavior are:

Stage 1: The male assumes a characteristic stance, raising his body on his front limbs, while his rate of breathing accelerates. From time to time he changes his position. This stance has also been observed in nature on a number of occasions when the male adopted it on a rock or other piece of high ground for the purpose of observation (Fig. 5.1.1).

Stage 2: The male follows a female who is passing near him. On infrequent occasions, he may follow another male. This stage may continue for a long time. Couples have frequently been caught in their natural surrounding while moving together in this form of pursuit.

Stage 3: This stage ensues if the female followed is ready to breed, a state which she signals by coming to a standstill. In some cases, the male mounts her rear quarters (Figs 5.1.2, 5.1.3), but usually he penetrates beneath her from behind (Figs. 5.1.6 to 5.1.8).

Stage 4: The male pushes himself under the female until he reaches her head (Fig. 5.1.9).

Stage 5: The female grasps the male with her front limbs, and he raises his front limbs to the sides, a position known as amplexus (Figs. 5.1.9, 5.1.11).

Stage 6: The male moves his head from side to side, rubbing the ventral epidermis of the female's jaw. The female moves her head reciprocally in the opposite direction. At the same time, both move their tails and cloacal regions in a scissor-like motion. This motion of heads and tails sometimes moves the couple forward.

Stage 7: The male ceases his movements and ejects his cone-shaped spermatophore to the ground (Fig. 5.1.10). The base of the spermatophore is elliptic, measuring some 8 × 6 mm in diameter, with a height of 8 mm. It is transparent, with white spots on the upper part. The movements of the female continue, especially as regards the tail and cloacal region.

Stage 8: The male turns his body at 60–90° to that of the female (Fig. 5.1).

Stage 9: The female continues the movement of the lower part of the body and tail, makes contact with the upper part of the spermatophore, and continues her movement until it penetrates the entrance to the cloaca. Her movement then ceases, and the spermatophore is drawn into the body.

Stage 10: Amplexus ceases and the couple parts.

This process may be repeated more than once. On one occasion it was observed to take place only a few days before breeding. It is not clear how the male identifies the female; Mertens (1947) hypothesized that it is through the secretion of a pheromone by the female.

SAMPLES STUDIED

Reproduction was studied in female salamanders from two habitats: Tel Dan (11 specimens) and Mt. Meron (seven specimens). These animals were captured over a year and a half, between May 1993 and November 1994. However, although the first specimen was caught in May, no more were found that summer, so that the next one was captured after October 1993 (Sharon, 1995).

Most of the salamanders were caught on rainy days, in most cases after a number of rainy days. Little success was obtained in finding salamanders after rain or during dry weather. All specimens were caught after dark, near water sources.

The average length of the salamanders was 11.77 ± 1.75 cm, with a maximum of 15 cm and a minimum of 9.5 cm. The average weight was 52.31 ± 20.12 g; maximum 108.2 g and minimum 30.2 g.

Table 5.1. General data on specimens caught.

	Mt. Meron	Tel Dan	Combined data
No. specimens	7	11	18
Length (cm)*	13.5 ± 1.17	10.66 ± 0.96	11.7 ± 1.75
Weight (g)	70.06 ± 20.22	41.03 ± 9.07	52.31 ± 20.12

*Body length, not including tail (Sharon, 1995).

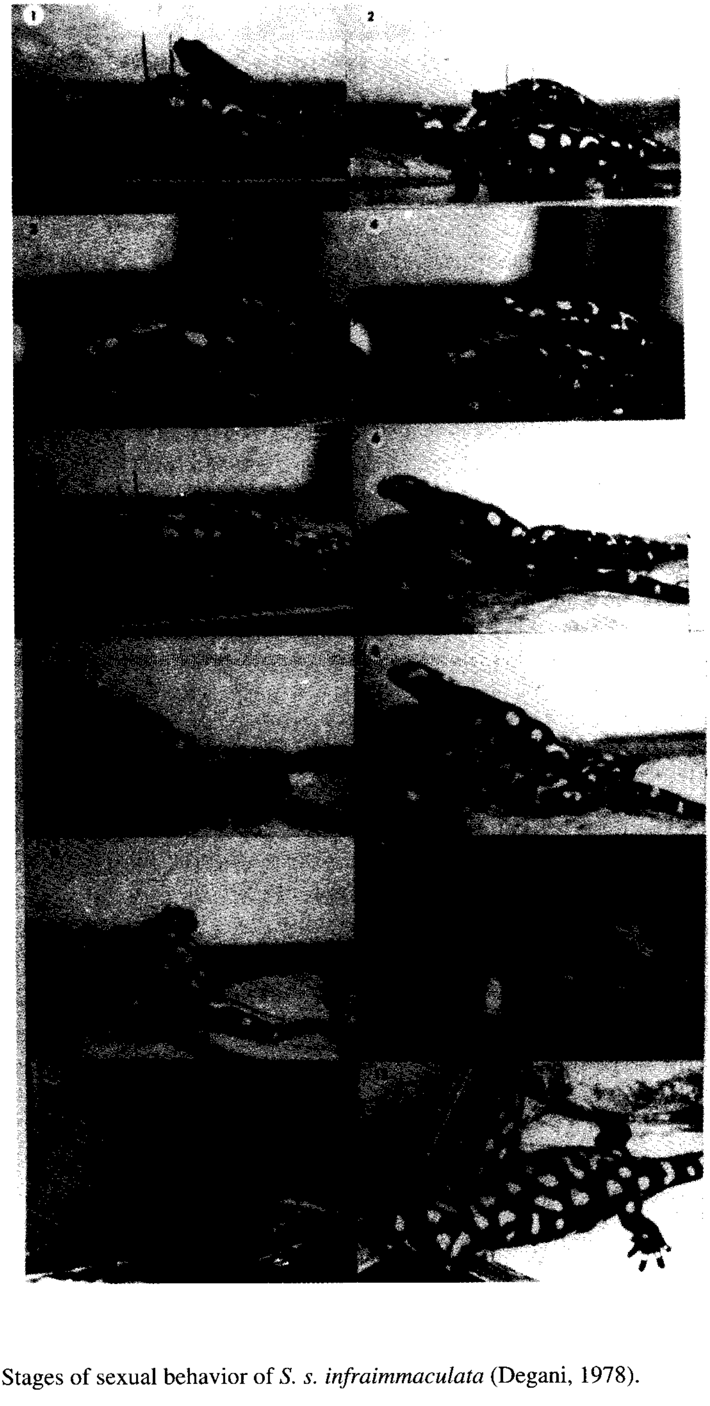


Figure 5.1. Stages of sexual behavior of *S. s. infraimmaculata* (Degani, 1978).

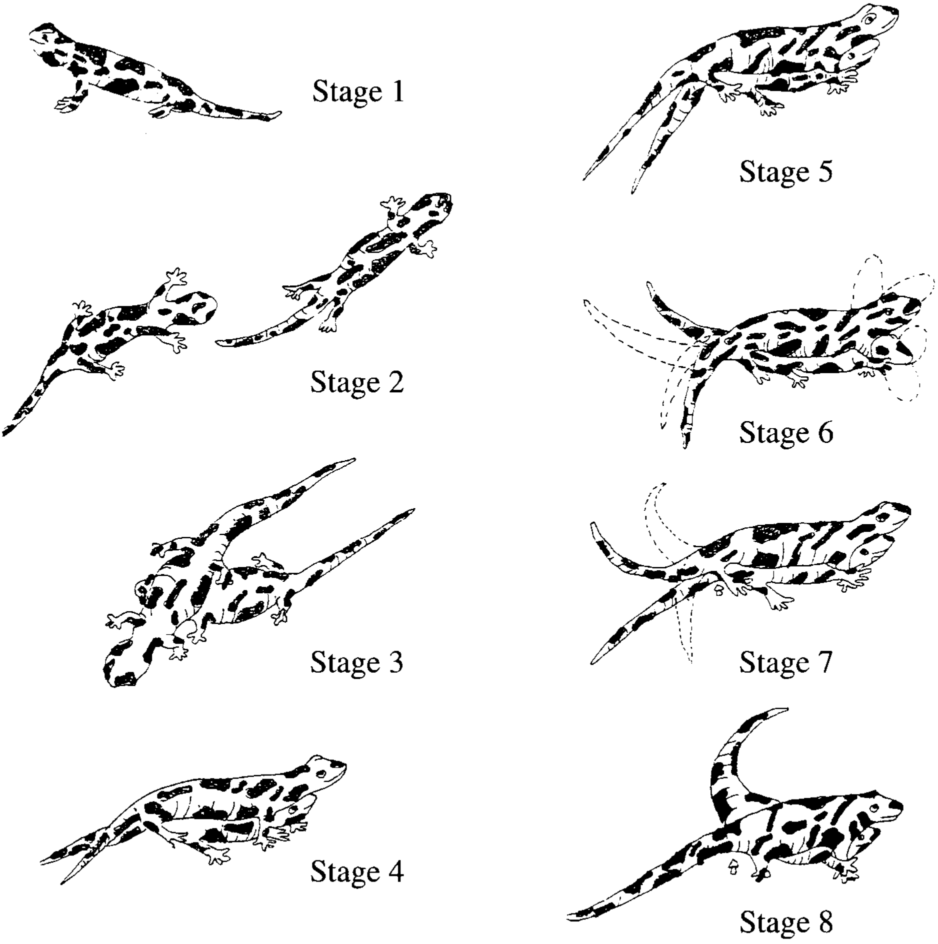


Figure 5.1a. Stages of sexual behavior of *S. s. infraimmaculata* (Degani, 1976).

REPRODUCTORY ORGANS

The reproductive system of the female salamander consists of two elongated ovaries, located on either side of the stomach cavity. Two oviducts, leading from the pulmonary area, pass near the ovaries, widen toward the uterus and reach the cloaca (Fig. 5.5).

OVARIES

The ovary of the salamander is enveloped in a thin transparent membrane, with the oocytes (ova) on its inner surface, attached to a connective collagen tissue (Sharon, 1995). Granular cells are scattered between the fibers of the connective

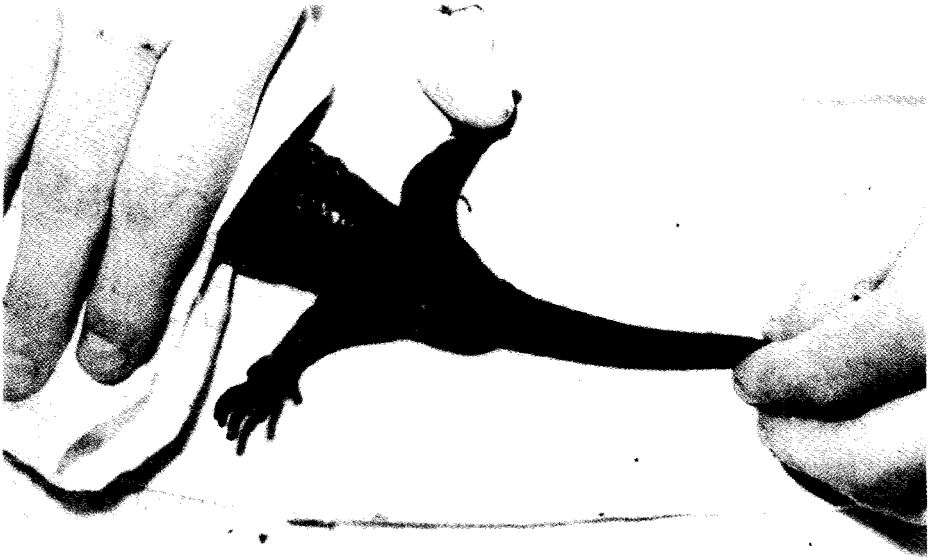


Figure 5.2. Cloacal region of female *S. s. infraimmaculata* (Degani, 1976).

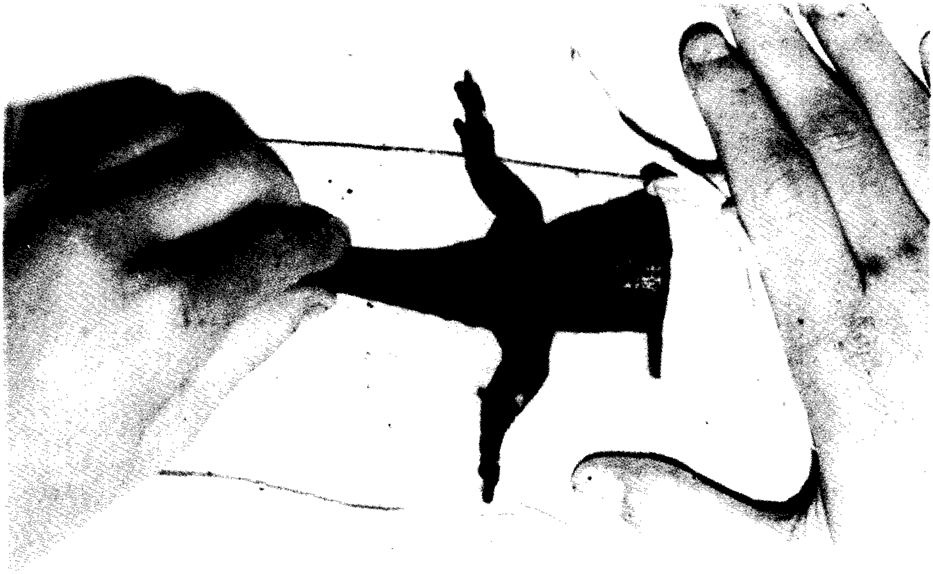


Figure 5.3. Cloacal region of male *S. s. infraimmaculata* (Degani, 1976).

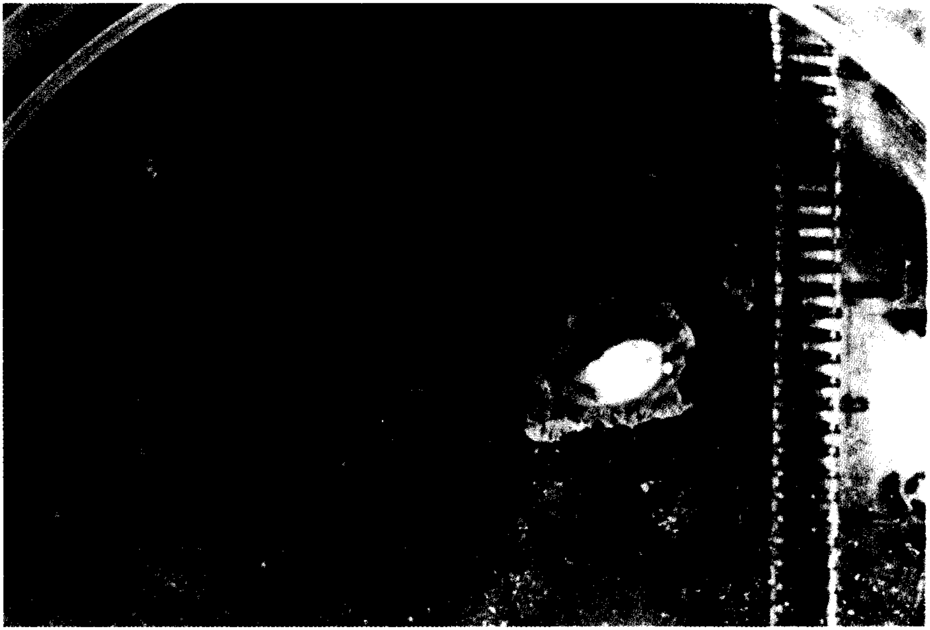


Figure 5.4. Spermatophore of *S. s. infraimmaculata* (Degani, 1976).

tissue, with round large nuclei, and small cells of oogonia, with round nuclei. Cells with flat nuclei, apparently those of thecal cells, can also be seen, but since these resemble the nuclei of the fibroblast, it is difficult to be certain. This is the germinal epithelium.

OVARIAN CYCLE

Sharon (1995) describes the ovarian cycle starting from autumn and continuing to spring, since no salamanders were found in the summer. The cycle is based on examination of all the ova in each animal and drawing up a scale of the diameters appropriate to each stage of oocyte development. All research papers on amphibians, except that of Masood-Parveez and Nadkarni (1993), describe the ovarian cycle of *Ichthyophis beddomei* according to oocyte diameter. Our research on the Israeli species has shown that this diameter does not provide a reliable differentiation between the final stages of vitellogenesis. An attempt, during the present work, (Sharon, 1995) to draw up a growth curve showed that there is no connection between the weight of the ovary and the season or the stage of the reproductory cycle, in contradiction to the findings of Jorgensen (1973) in *B. bufo*.

Joly et al. (1994) consider that the ovarian cycle is seasonal (oocytes growing through the year to reach maximum size before ovulation) and dependent on

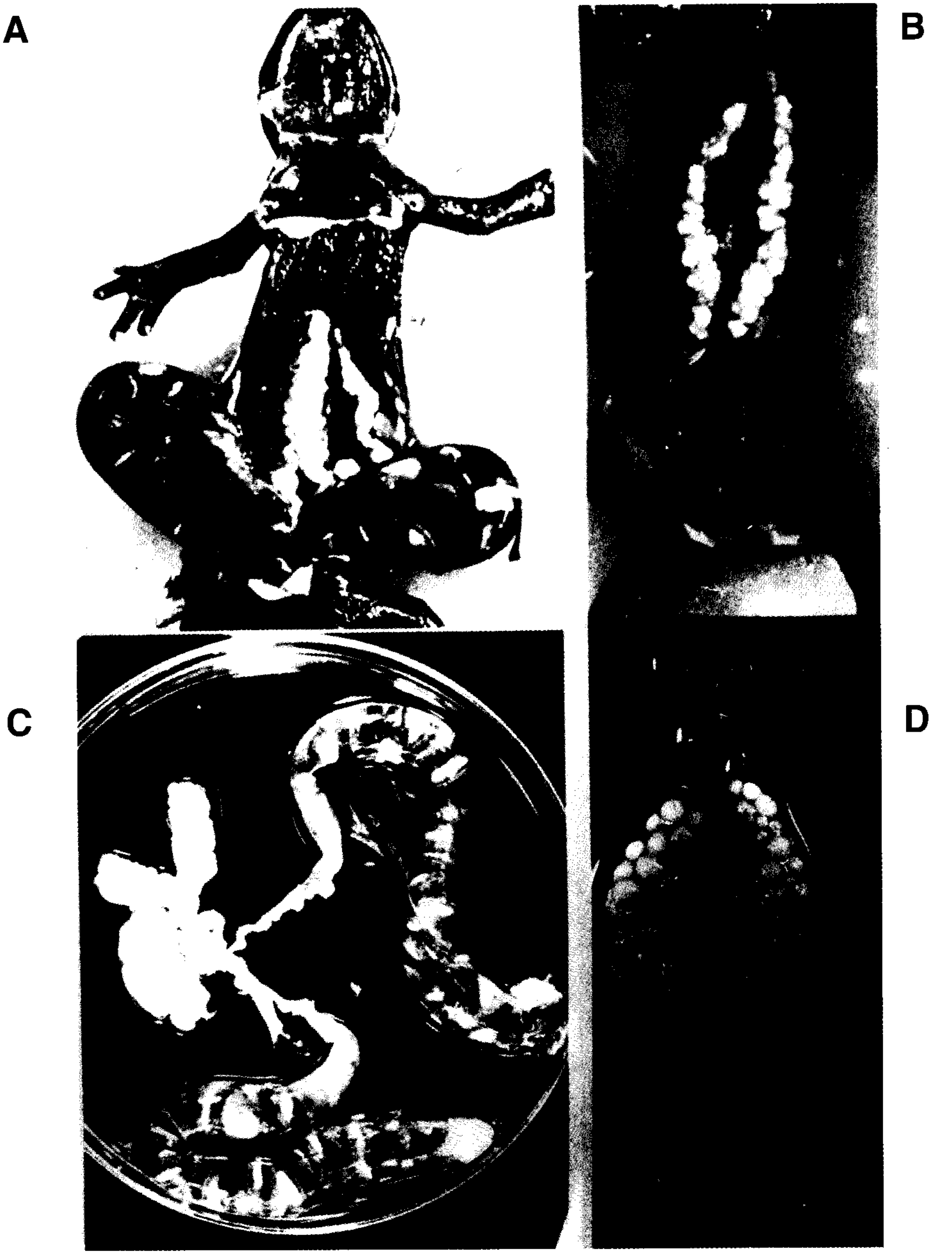


Figure 5.5. Reproductive system of *S. s. infraimmaculata* (Sharon, 1995). A. pregnant; B. Non-pregnant; C. Pregnant ; D. Non-pregnant (vitellogenesis) (Sharon, 1995).

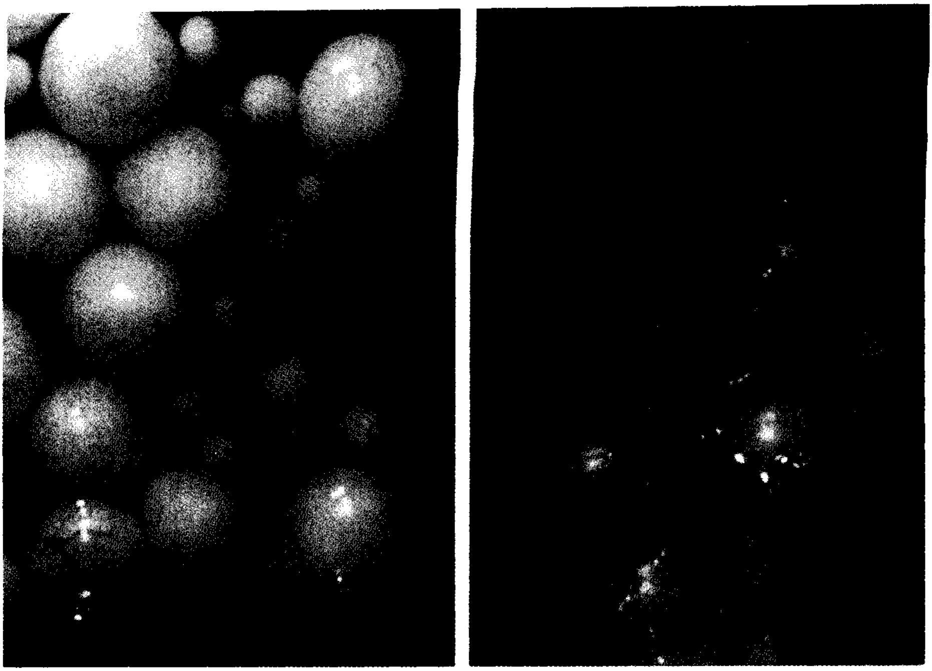


Figure 5.6. Reproductive system of *S. s. infraimmaculata* (Sharon, 1995). Right ovary wrapped in a thin transparent membrane, through which the oocytes can be seen.

subspecies and geographical location. *S. s. terrestris* completes its cycle in a year, whereas in *S. s. fastuosa*, the oocytes develop to a certain point of vitellogenesis and diameter in a gestation, and the development of the oocyte to maximum size takes place during the following year. Our work showed that in the ovarian cycle only the last stage of vitellogenesis and maturation of the oocytes depends on season. Even the influence of the reproductory cycle on the salamander appears to depend on the habitat. As mentioned above, it was observed that oocyte development takes place constantly, in contradiction to the findings of Joly et al. (1994), so that the ovary is prepared to progress to the last stage (preparation for ovulation) as soon as stimulation takes place. This stimulation, which evidently depends on the habitat, as will be explained in detail below, may be of heavy rainfall or a change of season: the end of winter and lengthening days (Sharon, 1995).

Pre-vitellogenic and vitellogenic oocytes were found together in the ovaries of all the female specimens examined. No change in the length or weight of the ovary was found during the months of the reproductory cycle, nor was any correlation found between the weight of the ovary and the number of oocytes present, whether previtellogenic, vitellogenic or post-vitellogenic. The correlation between the number of oocytes in vitellogenesis and the total number of oocytes was high. Significant correlation was found between pre-vitellogenic and vitellogenic oocytes (Sharon et al., 1996).

COMPARISON OF OVARY SIZE IN DIFFERENT HABITATS

The parameters which were used to study the influence of habitat on the size of the ovary were length, weight and number of oocytes present. Ovaries of salamanders from Mt. Meron were significantly bigger than those from Tel Dan, in all three parameters (Sharon et al., 1995). In Tel Dan, the ovaries examined were more homogenous in length and weight: the SD of ovary length in Tel Dan was 0.34, compared with 0.67 on Mt. Meron, and the SDs of weight were 0.15 and 0.26, respectively. In the number of oocytes, the Mt. Meron population showed greater homogeneity, with SD = 35, compared with 43.27 in Tel Dan.

COMPARISON BETWEEN THE DEVELOPMENT OF OVA IN DIFFERENT HABITATS

Specimens for examination of the ovary were taken from two habitats. Fourteen salamanders were collected from moist habitat, of which 11 were examined and the remainder released. Four of the specimens examined carried embryos. Nine salamanders were collected in January at Mt. Meron, of which two died before examination. All seven remaining specimens carried embryos. Collection was more difficult here, a fact that is expressed in the lower number of specimens caught and the wide span of time during which they were collected (Sharon, 1995).

COMPARISON BETWEEN OVARIAN CYCLES IN DIFFERENT HABITATS

As can be seen in Table 5.3, the variation in the number of ova per ovary was greater on Mt. Meron (xeric habitat) than in Tel Dan (moist habitat). The ovaries of the Mt. Meron salamanders contained significantly more oocytes that those of Tel Dan salamanders, both pre-vitellogenic and vitellogenic, and therefore, of course, in total. However, the Mann-Whitney test indicated that there was no significant difference in the percentage of oocytes in vitellogenesis between the two populations. Thus, habitat is not an influence on the percentage of oocytes in vitellogenesis, which remains constant in both habitats (Sharon et al., 1996).

THE RELATIONSHIP BETWEEN BODY SIZE AND OVARY SIZE

Since there is a significant difference between the two populations, in body size, and since there is a degree of correlation between body size and ovarian mass, Sharon et al. (1996) examined whether the difference in ovary size was maintained when the effect of body size was eliminated, by dividing the ovary size by the body size. The result is shown in Table 5.2, below.

The relative ovary length of the Mt. Meron salamanders (after elimination of the influence of body length) is greater than in the Tel Dan population, and analysis by the Mann-Whitney test determined that the difference is significant. While the relative ovary weight in the Mt. Meron salamanders is also greater than in salamanders from Tel Dan, the difference is not significant.

These results establish the fact that ovary weight is influenced by body weight, and not directly by habitat, as such. On the other hand, ovary length is not influenced by body length, and differences in habitat may, therefore, be the deciding factor in ovary length.

The percentage of oocytes in all stages of vitellogenesis was higher in the Mt. Meron salamanders. There was no significant difference between the populations in the percentage of mature oocytes, but it would appear that in Tel Dan the period of fertilization was season-dependent, since the percentage of mature oocytes rose towards March. On the other hand, when post-vitellogenic oocytes alone are considered, their percentage was higher in Tel Dan.

The data in the following table were obtained from both ovaries of all the salamanders examined (18 specimens). Weight and length were measured before opening the membrane, while oocytes were counted after opening it.

From the division of the presence of post-vitellogenic oocytes according to months, mature oocytes were found from October on Mt. Meron, meaning that the female was ready for fertilization by the beginning of the winter at the latest, whereas in Tel Dan, post-vitellogenic oocytes were seen only in February. It will require more detailed study to establish the exact onset of fertility.

Summarizing the comparisons between habitats, we see that the Tel Dan population is more homogenous in most parameters measured. The Mt. Meron salamanders are bigger, as to both body size and ovary size; their ovaries contain more oocytes, and they breed a greater number of larvae, as we shall see in the next

Table 5.2. Difference in ovary size after elimination of effect of body size (Sharon et al., 1996).

	Length of ovary ÷ body length	Weight of ovary ÷ body weight
Mt. Meron	0.33 ± 0.055	0.092 ± 0.03
Tel Dan	0.25 ± 0.028	0.095 ± 0.037

Table 5.3. Average measurements of salamander ovaries (Sharon et al., 1996).

	Mt. Meron	Tel Dan
Length (cm)	4.35 ± 0.67	2.77 ± 0.34
Weight (g)	0.64 ± 0.26	0.37 ± 0.15
Ova per ovary	265.35 ± 35	184.5 ± 43.27

Minimum length: 2.0 cm; maximum length: 6.2 cm; Minimum weight: 0.17 g; maximum weight: 1.13 g; Minimum no. ova: 108; maximum no. ova: 406.

chapter. These findings could indicate an adaptation of Mt. Meron salamanders to severer conditions, resulting from the absence of available water for most of the year. Contrary to this interpretation is the finding that a greater number of post-vitellogenic oocytes were found in Tel Dan salamanders, where one would expect the higher number of ova at Mt. Meron to produce more larvae. The number of post-vitellogenic oocytes found at Mt. Meron was much lower than the number of larvae (with averages of 9.16 and 86.4, respectively) and can, therefore, serve as a qualitative measure of readiness for fertilization, but not as a quantitative measure. At the same time, the small number of specimens studied — none at all during the summer — makes it very difficult to determine oocyte development in the different habitats exactly.

The courtship ceremony, prior to coupling, was observed in salamanders from Mt. Meron before and during breeding, suggesting that coupling can take place at any time, and that the period of period of migration to a source of water is also exploited for coupling by this population. Sexual behavior was observed at the beginning of winter, after breeding, fertilization of oocytes towards the end of winter, and embryonic development was found to occur during spring and summer.

Salamanders from Mt. Meron were able to mate during the heavy rains. Gestation did not inhibit sexual behavior, which can apparently also take place during the migratory period. Salamanders from Tel Dan, on the other hand, were ready for fertilization only at the end of the winter, judging by their oocyte development (Sharon, 1995) , and only when they were not gravid. However, no observed sexual behavior has been recorded for Tel Dan, and larvae are born throughout the year (Degani and Warburg, 1995).

The reproductive cycle of salamanders from Mt. Meron is similar: they begin to breed at the beginning of the rainy season, and they are ready for mating and breeding during the rains even if temperatures have not yet dropped. In the Mt. Carmel area, Warburg (1995) found that larvae are born every year, apparently depended on precipitation.

No correlation was found between length and weight, or between weight and number of ova (oocytes). A weak correlation was found between length and number.

OVIDUCT

Four strata of cells were found in the oviduct. From the central cavity outward (Sharon, 1995). These are:

(a) An epithelium surrounding the cavity and comprising epithelial cells and large round cells, with a large nucleus and some of them have cilia on the surface facing the oviduct cavity. The ends of these inner cells can be stained with a number of histochemical stains, suggesting that they either perform a specific function or have on them a chemical compound which is different from the interior of the cell. This layer of cells is common to both gravid and non-gravid salamanders.

(b) Connective tissue forms the major layer of the oviduct. Collagen fibres create a tendril-like structure. Two types of fibroblast cells were observed, one with a spindle-shaped nucleus, and the other with a large, round and granular nucleus. These cells were frequently seen in various stages of fission, sometimes with two nuclei and sometimes with the chromosomes visible.

(c) A layer of peripheral muscle attached to the connective tissue, with no clear boundary between the two layers. Among the muscle cells are neurosecretory cells which react to PF stain.

(d) A scaly peritoneal epithelium envelops the oviduct. Its cells are flat and elongated and have flat nuclei (Fig. 5.8).

The staining of the oviduct shows a high presence of mocopolysaccharides. Large blood vessels are visible outside the scaly epithelium, with capillaries in the connective and muscle tissues.

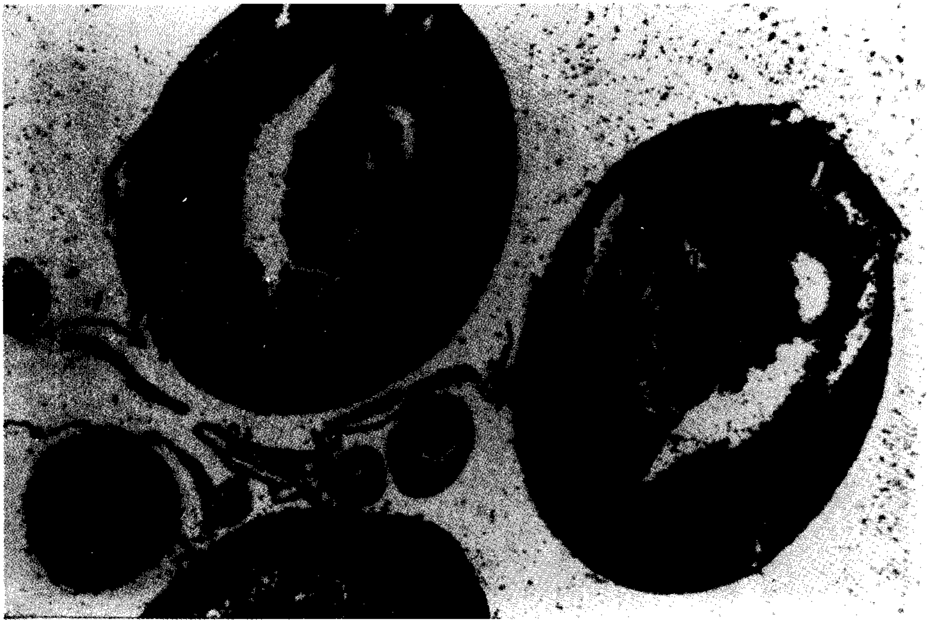


Figure 5.7. Oocytes attached to enveloping membrane by connective tissue. Ovary of non-gravid salamander, stained by Barrett stain. (× 25). C = connective tissue; V = oocyte in vitellogenesis; Pr = in previtellogenesis; Po = in post-vitellogenesis (Sharon, 1995).

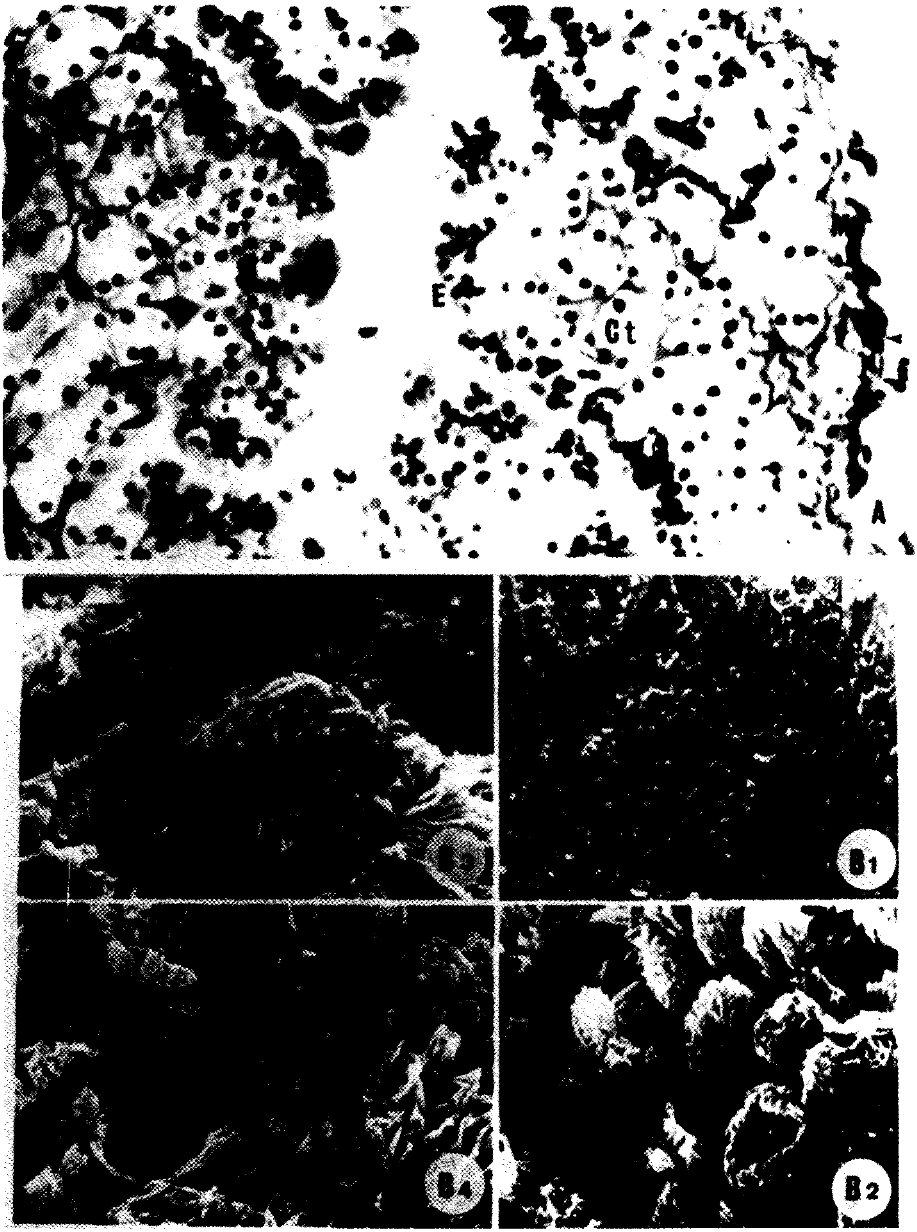


Figure 5.8. Oviduct of salamander under the microscope (Sharon, 1995). A. Oviduct of non-gravid salamander (×20). E = epithelium near lumen; CT = connective tissue; M = muscle (arrow: peritonal epithelium); B1. Diamond-shaped cells with microvilli; B2. Cilia-covered glands (×3500); B3. Cells with cilia (×3500); B4. Dense ciliated cells (×3000).

UTERUS

Four strata of cells were observed in the uterus, as in the oviduct. In non-gravid salamanders, the epithelium produces folds which penetrate the uterine cavity, and the muscle and connective tissues are thicker than those in gravid specimens, in which the uterine wall becomes stretched, obliterating the folds in the epithelium, whose cells grow flatter, while the muscle and connective tissue become narrower and almost disappear. Approximately a week after breeding, the epithelium is shed and a new one layer epithelial layer grows underneath. The uterus is rich in blood cells, which are seen in the connective tissue next to the epithelium (Fig. 5.9).

The boundaries between the four strata of cells in the uterus can be seen clearly, unlike those in the oviduct. The cells of layers differ from those of the oviduct:

(a) The epithelium is made up of an even layer of cells, placed wall to wall. No fibrous cells were observed, but two types of nuclei were revealed by staining, one darker than the other. As in the oviduct, the part of the epithelium cell facing the cavity takes a different histochemical stain from the rest of the cell. Microvilly was also seen on the surface of the cells. Two types of cells were recognized — rounded and flat.
(b) The connective tissue. Cells were observed among the fibroblasts with long, granular nuclei, which stained violet with PF, indicating that they were neurosecretory. There were also cells, possibly mast or plasma cells.
(c) The muscle tissue is split by collagen fibers.
(d) The scaly outer epithelium appears the same as in the oviduct (Fig. 5.9A).

OOGENESIS

The process of oogenesis takes place in three main stages: (1) the formation of the pre-vitellogenic oocyte from the oogonium, and its growth to the stage (Fig. 5.10); (2) vitellogenesis — the stage at which the oocyte fills up with vitellogen, secreted from the blood, and grows to its maximum size, when vitellogen ceases to enter it (Fig. 5.11); (3) the formation of the post-vitellogenic oocyte, (maturation) (Fig. 5.12). The mature oocyte ovulates before parturition. Each of these stages is divided into a number of substages.

PREVITELLOGENESIS

The formation of the previtellogenic oocyte has three substages. (a) The oogonia divide and form "cell nests". Division takes place in a kind of compartment, enveloped in germinal epithelium, so that a number of oogonia can be seen in each nest cell compartment at a certain stage. (b) The germinal epithelium becomes differentiated into a layer of granular cells and two layers of thecal cells, inner and outer. The follicle is formed, with the oocyte enveloped in the granular thecal layers. (c) The size of the oocyte is increased by a rise in the quantity of cytoplasm and increase in the size of the envelope. Although the thecal envelope is next to the oocyte, it is possible to distinguish between them.

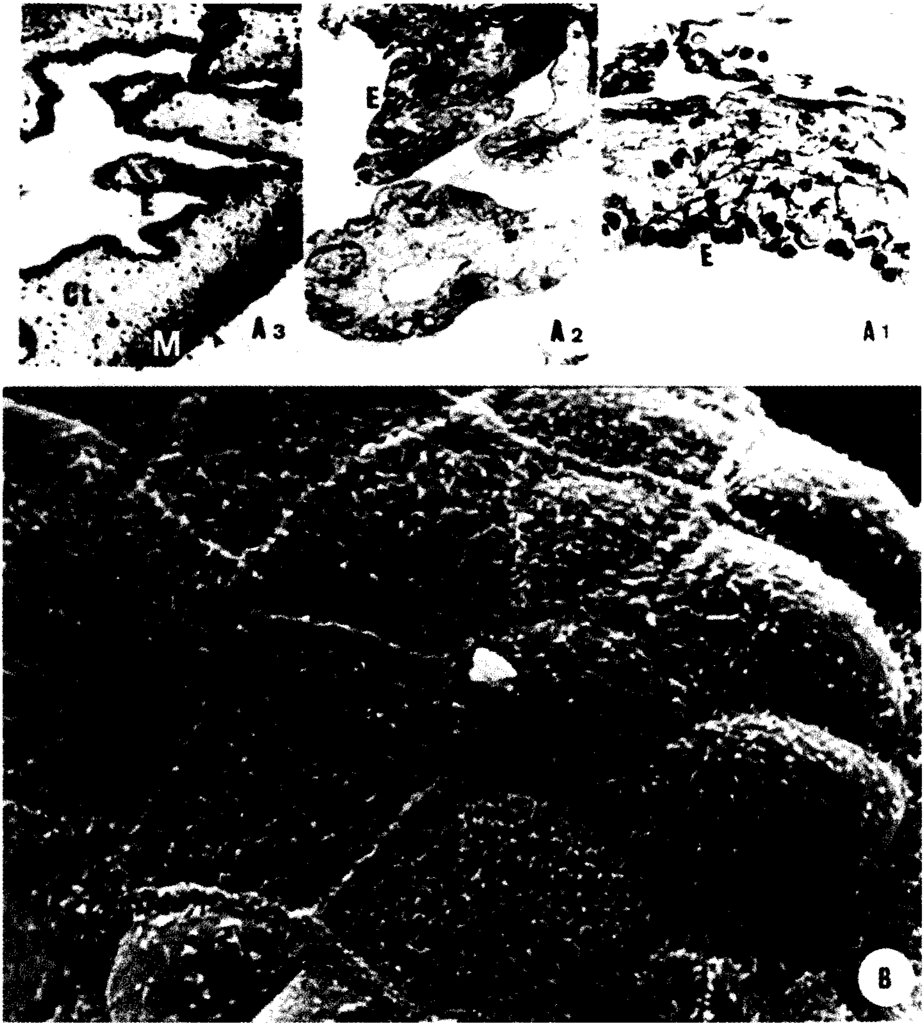


Figure 5.9. Uterus of salamander (Sharon, 1995). A1. pregnant female (×40); A2. After delivery (×20); A3. Non-pregnant (×10). B. Epithelial cells of non-pregnant female (F = diamond-shaped cells; S = round cells). E = Epithelium near lumen; CT = connective tissue; M = muscle tissue, peritoneal epithelium.

The entire process of oogenesis, with all its stages, had not been described in *S. s. infraimmaculata* until the present series of studies. A general classification of the stages of oogenesis, according to their observations, was made by Duellman and Trueb (1986), who noted that oogenesis is similar in all species of amphibians: division of the oogenia by meiosis, followed by differential division to form oocytes (ova). The stages of development of the oocyte are: a large number of "cell nests" supply the follicles, previtellogenic follicles appear, the vitellogenic follicles grow rapidly and add nutrients, and the ovum reaches its maximum size at postvitellogenesis. The oocytes have a single nucleus (Duellman and Trueb, 1986).

All stages of oogenesis, from the division of the oogenia to the postvitellogenic oocyte, have been described in our citations, including the diameter of the oocyte at all stages and changes in the enveloping layers. In these layers, two thecal layers can be seen at each stage, a granular layer and a membrane which surrounds the oocyte. Masood-Parveez and Nadkarni (1993a,b) give a more detailed description of the stages of oogenesis in *Ichthyophis beddomei*, from the division of the oogenia (maximum diameter 1 mm) to the end of vitellogenesis (0.2–7.5 mm), but without detailing the changes that take place between the various stages. They also mention only a single thecal layer.

Bonnanfant-Jais and Mentre (1983) begin their description of oogenesis in *Pleurodeles waltlii from the previtellogenic oocyte (maximum diameter 0.3 mm)*, through vitellogenesis (maximum 1.1 mm), to the stage of the postvitellogenic oocyte (maximum 1.6 mm) when it begins to migrate. They give no description of the enveloping layers of the oocyte or of the changes they undergo. Joly and Picheral (1972) have described the oocyte layers before and after ovulation, in *S. s. terrestris*, without describing other stages of oocyte development. The oocyte diameter in *S. s. infraimmaculata*, as measured by Sharon et al. (1995), was bigger than that of *I. bedommei* and *P. waltlii*, at all stages. We found the development of the oocyte, through its various stages, to be similar to *P. waltlii*. Differences were found, such as changes in the appearance of pigment between the two types of cytoplasm. Judging by the various descriptions of oocyte development through vitellogenesis and postvitellogenesis, the salamander is closer to the triton that to the *Caecilia*. Joly and Picheral (1972) give the maximum diameter of the mature oocyte as 5 mm, which is confirmed by Grodzinski (1976) and Joly et al. (1994). We found the maximum diameter of the oocyte of *S. s. salamandra* to be 3.9 mm. This smaller diameter may be due to a shorter period of gestation, however, no difference in larvae site was found.

VITELLOGENESIS

Vitellogenesis can be divided into four substages. (a) pockets of lipids first form on the edges of the cytoplasm, probably precursors to albumen sacs. Scattered drops of albumen can be seen. The diameter of the oocyte is ≈0.2–0.6 mm. (b) Enough albumen sacs are formed to create a uniform layer at the edge of the cytoplasm, which is still not uniform: the granulosity which divides the two types of cytoplasm still exists. The thecal envelopes form folds, and spaces between the theca and granulosity appear. The average diameter of the oocyte at this stage is 1.125 ± 0.069 mm, with a minimum of 0.4 mm and a maximum of 1.6 mm. (c) The oocyte grows in size rapidly. Virtually no intermediate stage can be seen during the transition from substage (b) to substage (c). The yolk now fills half the volume of the oocyte, with small sacs round the edges and larger sacs in the middle. The cytoplasm has become uniform. Nucleoli are visible around the nucleus. The average diameter of the oocyte at this point is 2.0 ± 0.22 mm, with a minimum of 1.0 mm and a maximum of 2.9 mm. (d) The oocyte continues to grow until it reaches its maximum size and is full of albumen. The cytoplasm is visible only around the nucleus. The layer of sacs around the edges grows smaller. The thecal layers come close to the oocyte, while the granular cells are stretched and become flat. The average diameter of the oocyte is now 2.66 ± 0.32 mm, with a minimum of 2.1 mm and a maximum of 3.6 mm.

POSTVITELLOGENESIS

The only change observed in our study was the movement of the nucleus to one of the ends of the oocyte. Average diameter: 3.19 ± 0.29 mm (minimum 2.0 mm, maximum 3.9 mm). The size range of the oocyte at this stage overlapped that in the final stages of vitellogenesis.

The averages given are based on measurements in all the salamanders found, but taken individually, it was observed that there were large variations in oocyte diameter at stage 2 of vitellogenesis. There was no overlap in oocyte diameter between stages 2 and 3, with a significant increase in size at the transition to stage 3. From then on there were no great variations in size.

Sharon et al. (1996) examined whether there were changes in the percentage of vitellogenic oocytes at different times and months, relative to breeding: the data are given in Table 5.5.

Analysis of the significance of the differences (Mann-Whitney Test) showed that there were no significant differences among the percentages of vitellogenic oocytes during different months. Nor were there significant differences among the stages of the reproductory cycle. These results show that the percentage of oocytes reaching vitellogenesis remained constant and independent of these factors.

According to Degani and Warburg (1995), the reproductory cycle of the salamander in Tel Dan differs from tha t of the European salamander, insofar as it breeds all year round. The gestatory period of the Tel Dan salamander is 7–12 months, as against 4–12 months for the species in France (Joly et al., 1994). In the last breeding of Tel Dan salamanders, the average length of the larvae was 3.7 cm and the average weight 0.27 g. This compares with the findings of Joly (1968) in *S. s. terrestris*, in which the length of the larvae was 3.1 cm and the weight 0.25 g. Furthermore, although the ovum of the Israeli salamander contains less albumen, the period of gestation is no shorter. The larvae are born at the same size or larger than those in France, for reasons which are not clear.

Sharon et al. (1995) give a detailed description of the stages and substages of oogenesis, making it possible to determine the stage in the animal's ovarian cycle reliably, according to the state of development of the oocyte within the cycle, as well

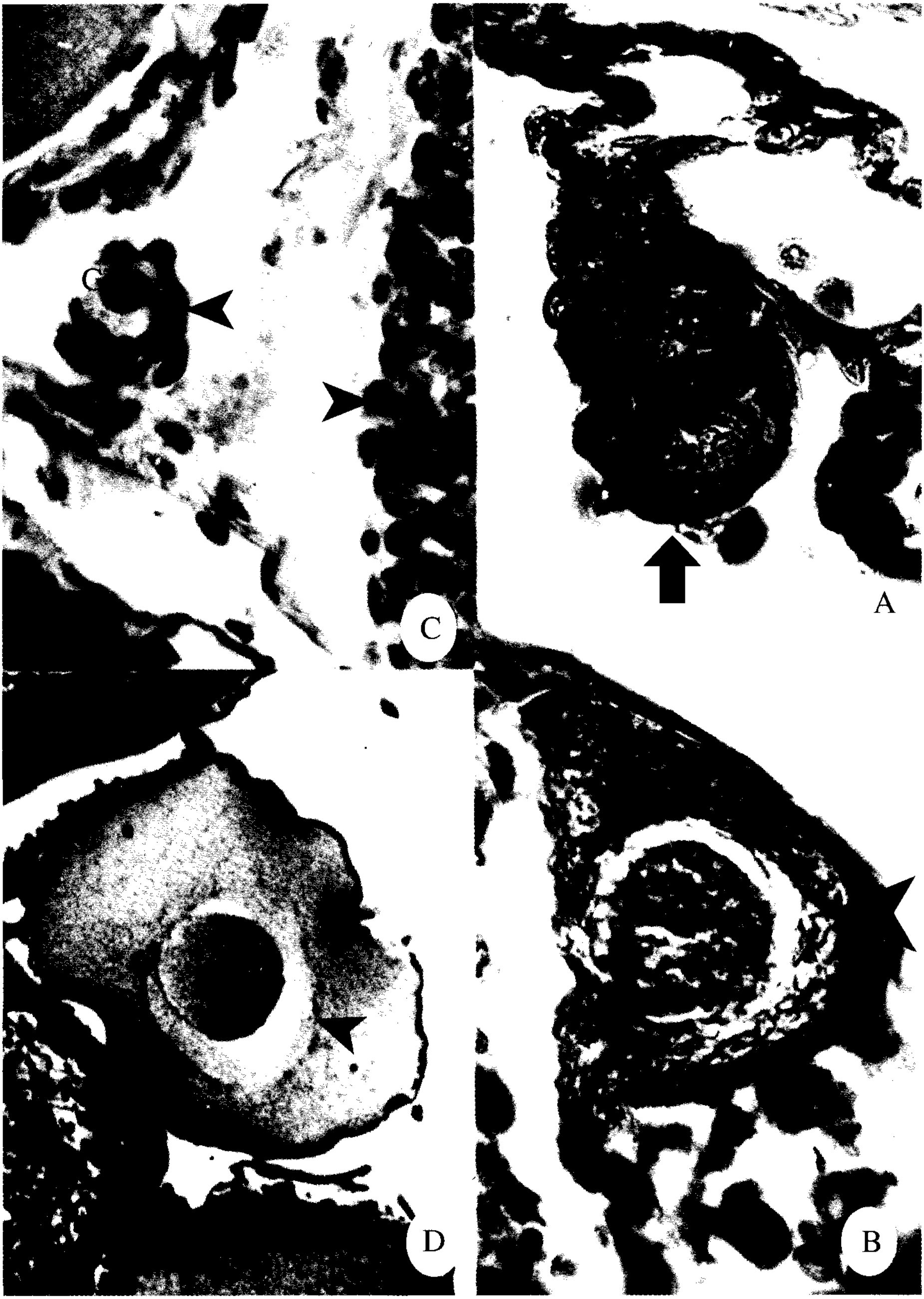


Figure 5.10. Previtellogenic oocyte development (×40) (Sharon, 1995). A. Creation of cell-nest (small arrow); B. Oogonia divide (big arrow); C. Differentiation into oocyte (small arrow. granulosa; G = nucleus); D. Size of oocyte increases (small arrow. pigmentation; G = nucleus).

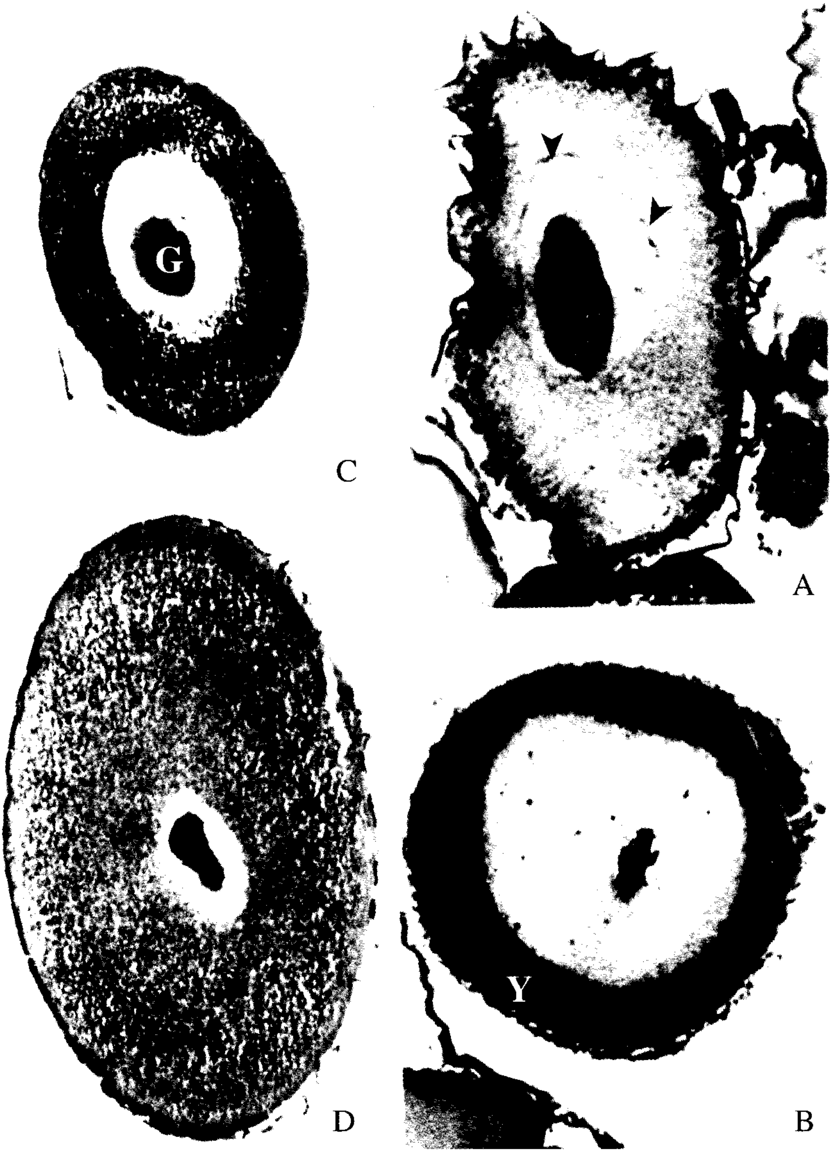


Figure 5.11. Vitellogenesis of oocytes (×15) (Sharon, 1995). A. Lipids accumulate at periphery of cytoplasm (× 100); B. Yolk accumulates at periphery of of cytoplasm (× 42); C. rapid increase in size of oocyte, half-filled by yolk (×40); D. Yolk fills entire oocyte (arrows. pigmentation, lipids; G = nucleus; Y = yolk).

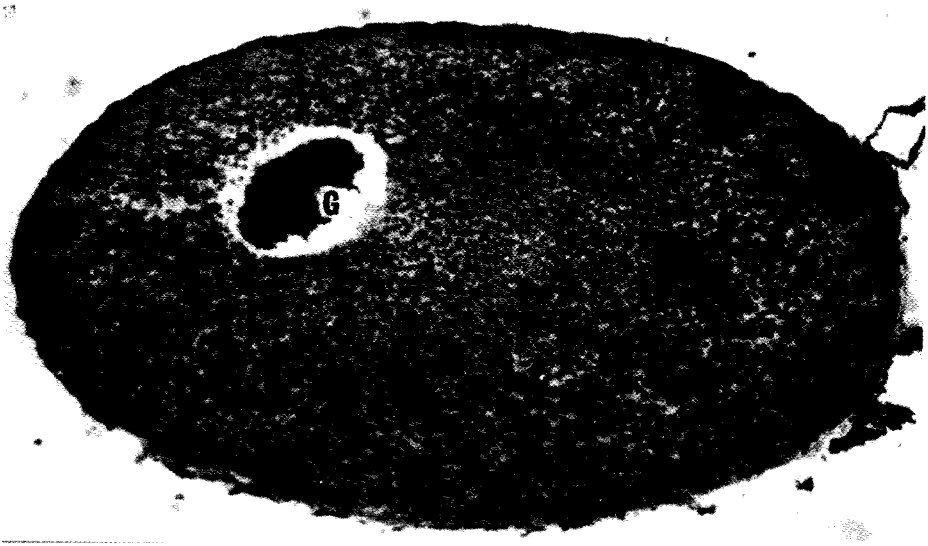


Figure 5.12. Postvitellogenic oocyte. Nucleus moves to to pole (Sharon, 1995). (G = nucleus; v = yolk) (×40).

Figure 5.13. Changes in enveloping layers of oocyte (Sharon, 1995). Po = post-vitellogenic oocyte. The envelope is attached to the oocyte, with no clear boundary between the layers (arrowhead); and the vitellogenic oocyte (v) in which the theca forms folds and granulosa cells are large and round (arrow).

Table 5.4. Distribution of oocytes in ovary (Sharon, 1995).

	Mt. Meron	Tel Dan	Total
Total no. of oocytes	265.35 ± 35	184.50 ± 43.27	217.79 ± 56.5
Previtellogenic	180.00 ± 50.12	112.80 ± 28.13	140.0 ± 50.49
Vitellogenic	88.92 ± 12.88	66.25 ± 18.64	75.59 ± 19.74
% in vitellogenesis	33.20 ± 6.46	36.02 ± 4.6	34.86 ± 5.44

Table 5.5. Percentage of vitellogenic oocytes out of total according to month and stage of reproductory cycle (Sharon, 1995).

Month	No. of specimens	Vitellogenesis %	Breeding stage	Number	Vitellogenesis %
October	1	48.5	Gravid	7	33.8 ± 5.7
November	2	33.4 ± 2.5	Post-breeding	3	35.0 ± 7.5
December	4	35.6 ± 6.3	Late post-breeding	1	38.7
January	5	32.3 ± 7.6	Non-gravid	6	35.2 ± 5.2
March-April	5	36.4 ± 1.9			

as by its diameter. At the same time, the diameter of the oocyte at a specific stage varies from variety to variety within the species. For example, in one variety, an oocyte of 2 mm diameter is postvitellogenic, while in another variety the oocyte does not reach this stage until its diameter measures 3.6 mm. Furthermore, there is some overlapping in diameter between one stage and the next in all salamanders. Since this overlapping in diameters exists within the individual animal, it can be found to an even greater extent between one animal and another, and between one habitat and another. In previous studies on the variation of the diameter of the oocyte during the ovarian cycle of the salamander, quoted above, the researchers regarded

Table 5.6. Vitellogenic and postvitellogenic oocytes in ovary (Sharon, 1995).

	Vitellogenesis					
Location	Stage II		Stage III		Stage IV	
	Number	%	Number	%	Number	%
Mt. Meron	101.5 ± 13.56	57.9	31.66 ± 10.95	18.1	32.83 ± 22.57	18.8
Tel Dan	69.11 ± 27.90	53.7	22.30 ± 16.8	17.3	19.80 ± 20.55	15.4
Total	82.06 ± 27.90	55.0	27.90 ± 27.9	18.7	25.06 ± 21.60	16.8

	Postvitellogenesis	
	Number	%
Mt. Meron	9.16 ± 8.84	5.2
Tel Dan	17.3 ± 21.50	13.46
Total	14.06 ± 17.60	9.4

the diameter of the oocyte as an indication of its oogenesis stage; the present work shows that this approach is not exact. Furthermore, it is not possible to relate the oocyte diameter of a salamander specimen from one area to the stages of oocyte development in salamanders from another area.

DISTRIBUTION OF VITELLOGENIC OOCYTES IN OVARY

Oocytes in the three first stages of vitellogenesis were found in all the ovaries examined; in *S. s. infraimmaculata* Sharon et al. (1995) found oocytes in all stages in most of the specimens they examined.

Table 5.7. Mature oocytes as percentage of vitellogenic oocytes (Sharon et al., 1996).

	Mt. Meron	Tel Dan
Mature oocytes (%)	22.2 ± 11.6	31.9 ± 20.4

Table 5.8. Percentage of mature oocytes by month of examination (Degani et al., 1996).

Month	Number of specimens	% Mature oocytes (average per ovary)
October	1	18
December	4	21.6 ± 15.3
Jan.–Feb.	5	19.8 ± 14.6
March–Apr.	5	43.3 ± 16.1

The majority of vitellogenic oocytes were at Stage II (55%), with a drop in the percentage at Stage III, but no further significant change to Stage IV. All oocytes which reached Stage III appeared to continue to Stage IV, but the transition to post-vitellogenesis brought a sharp drop in the percentage present, with only approximately half of them reaching post-vitellogenesis (from 7% to 9.4%).

No correlation was found between the numbers of vitellogenic and postvitellogenic oocytes found, showing that the number of oocytes reaching postvitellogenesis is not dependent on the number in vitellogenesis; nor is it dependent on the length and size of the ovary, therefore, the factor involved in the transition remains unclear. The presence of postvitellogenic oocytes is a sign of preparedness for ovulation and reproduction.

There was an overlap between the two stages in oocyte diameter ranges, making it difficult to distinguish between the stages according to diameter, therefore, the two stages were taken together for the purposes of the present research work.

Analysis of significance (Mann-Whitney) shows that there was no significant difference in the percentage of mature oocytes between December and January–February, but there was a significant difference between both these and March–April. No analysis can be made regarding October, since only one specimen was examined during that month. It appears that March–April was the period of preparation for reproduction, but it must be borne in mind that not all the specimens collected at that time carried embryos. It is probable that the main factor in oocyte maturation is the stage of breeding, not the season. When the significance of the difference between the stages of the reproductory cycle were analyzed, it was found that there was a significant difference between gravid and non-gravid females, but not between gravid females and those immediately after breeding, nor between females immediately after breeding and non-gravid ones. It appears that fertilization takes place some months after breeding, and that gestation inhibits the maturation of oocytes.

The problem with this analysis is that most of the females examined in March-April were from Tel Dan, and none of them was gravid. It is possible that differences emanated from differences in habitat, which will be considered below. 'Only one female collected from Mt. Meron was pregnant.

REPRODUCTIVE CYCLE

A description of the reproductory cycle requires knowledge of times of mating, fertilization, oogenesis in the ovary, the breeding season and how these are related. The work described examined the ovarian cycle and breeding times. Two female salamanders from Mt. Meron were observed during the courting ceremony that leads to mating: one before breeding, the other in the middle of breeding.

REPRODUCTIVE MECHANISM

Different types of reproduction exist in different species of salamanders. Degani (1976) found that *S. s. infraimmaculata* breeds encapsulated larvae, though larvae without capsules have also been observed (Warburg et al., 1978; 1979a). Wake (1993) defines this form of reproduction in *S. s. infraimmaculata* as ovoviviparity.

Boujard et al. (1990) describe the larvae of *S. s. terrestris* whose birth was delayed, e.g., by lack of available water, as being thinner. This finding was not

Table 5.9. Mature oocytes in relation to breeding time (Sharon, 1995).

Breeding stage	Number of specimens	% Mature oocytes (average per ovary)
Gravid	6	13.7 ± 10.8
Post-breeding	2	26.4 ± 15.5
Late post-breeding	1	29.9
Unknown	6	42.6 ± 14.3

confirmed in our work in the laboratory in 1993/4, where larvae that were born earlier weighed less, even though some of them were already without a capsule. This finding may point to a different reason for delay, possibly nutrition by unfertilized eggs, as described by Dopazo and Alberch (1994) in the subspecies *S. s. bernardezi.*

In our work, we found that the period of gestation of the salamander in Israel is 8–12 months: salamanders from Mt. Meron which were dependent on the availability of water were able to lengthen gestation from 8 months to a full year, while in salamanders from Tel Dan, gestation was some 9 months, which they were able to lengthen to a year when temperatures were late in falling. Degani and Warburg (1995) note two occurrences of breeding by Tel Dan salamanders during the summer, and extrapolate from this finding that Tel Dan salamanders breed all year round. However, most published information shows that most breeding takes place in the winter, so that the two salamanders that were observed breeding in summer were probably exceptional. One of the two bred in May, and it is possible that temperatures in May that year were low, as sometimes happens.

REPRODUCTIVE STRATEGY

Boujard et al. (1994) write that temperature, availability of water and defence against predators in the water are the principle factors affecting adaptation to the environment. The same authors found that hormonal feedback in the control of the secretion of gonadotropin was a more significant factor than the environment. They compared a number of reproductive strategies, including the use of different types of reproduction (see Chapter 1). *S. s. fastuosa* lives in a habitat in which the availability ,of water is low: streams dry up in summer and freeze in winter. The larvae of this subspecies are larger and are bred at higher temperatures than those of *S. s. terrestris.* Sharon (1995) found that the rate of growth of Tel Dan larvae was lower than that of Mt. Meron larvae. These findings probably point to a more advanced stage of metamorphosis, resulting from the lack of water during most of the year. Warburg et al. (1979b) found that the rate of growth of larvae depended on the state of the pond: winter ponds were richer in organic materials, leading to a higher rate of growth. Nonetheless, in our work, larvae from two habitats were grown in identical conditions, and the larvae from Mt. Meron grew faster than those from Tel Dan. This could indicate the foremer ones were born at a more advanced stage of metamorphosis, even though the larvae from the two habitats were born at the same weight, or that genetic adaptation enabled them to grow faster, as demanded by the variable conditions of the Mt. Meron habitat, in contrast to the more comfortable and stable conditions at Tel Dan.

In the present work, it was found that salamanders from geographically close habitats employed different reproductive strategies: in each habitat, it was the local limiting factor that dictated the reproductive strategy. On Mt. Meron this factor was the seasonal availability of water. The differences in reproductive strategy involved numbers of larvae per breeding, times of readiness for reproduction and the dependence of breeding on the limiting factor. Warburg (1992) found that salamanders on the Mt. Carmel range manoeuvered between two contradictory strategies:early birth involved the danger of mortality, should the ponds dry up early as a result of too great a period between events of rainfall. The salamanders that breed later in the season, once the ponds have been more thoroughly established avoid this danger; however, this strategy involves the dangers that only a short time is left for the larvae to complete full metamorphosis, and that they are easy prey for larger larvae that were bred earlier.

Our work did not include observation of behavior over a period of years, so it produced no data as to whether salamanders from Mt. Meron, faced with similar problems, employed these strategies; but the ability to delay breeding that was observed certainly showed that there is such a possibility of manipulating breeding times.

Bentley (1972) showed that progesterone can delay larval growth in the uterus of the frog until conditions are suitable for breeding. In the present work, it was found that larvae can be bred at very different weights, without affecting their viability: smaller larvae compensate by faster growth. It is probable that adaptation in salamanders is not through a delay in the growth of larvae in the uterus, but by compensatory growth after early breeding.

The conclusion of Gasser and Joly (1972) with regard to *S. s. fastuosa*, that the reproductory cycle is two-yearly, is based on the finding that no oocytes in an advanced state of oogenesis were observed in gestating salamanders, and that the gonadotropin cells were inactive, whereas in non-gestating salamanders the opposite was found. In the same way, gravid Tel Dan salamanders were found not to be ready for reproduction, whereas non-gravid salamanders contained oocytes in late stages of oogenesis, including postvitellogenesis. These findings may point to a two-yearly reproductive cycle, but they may equally well point to an annual cycle, in which the oocytes resume oogenesis immediately after breeding. According to all researchers who have studied amphibians, the last stages of oogenesis are gonadotropin-dependent. It is probable that there is no negative feedback of oestrogen, progesterone or other factor that affects the secretion of gonadotropin of Mt. Meron salamanders, with the result that oogenesis can be completed, whereas in Tel Dan such a negative feedback affects the secretion of gonadotropin during gestation, with the result that the final stages of oogenesis take place only after breeding.

Boujard et al. (1990) explain the variation in estradiol level during oocyte maturation in amphibians, in terms of the organization of the ovary, and conclude in principle that the level drops, even though this is difficult to determine by measuring an individual ovary. This hypothesis is probably not generally applicable, but rather concerns variations from one animal to another and from one area to another, in the sensitivity of the tissue to negative feedback. In the absence of negative feedback, secretion of gonadotropin continues, leading to continued production of estradiol in the granular tissue. The effect of negative feedback of estradiol on gonadotropin would be a cessation in the production of estradiol. Another possibility is that the various effects of estradiol are due to the presence or absence of receptors in the follicle tissue.

The relationship among steroid levels, oogenesis and gestation was discussed by Degani et al. (1996). The levels of the steroids 17ß-estradiol and testosterone rose during vitellogenesis and maturation, and also during gestation. Differences between the Galilee and Tel Dan populations, in steroid levels, parallel the differences between the two habitats in oogenesis and the reproductory cycle.

PART II:

LARVAE

CHAPTER SIX

BIRTH OF LARVAE IN DIFFERENT HABITATS

Most varieties of salamander are ovoviviparous, with some neonates born wrapped in an embryonic membrane and others without it (Figs. 6.1. 6.2), there are subspecies in Europe which are viviparous. In the Pyrenees and in Spain, there are populations in which the young are born highly developed, even in a state after metamorphosis (Joly, 1968; Fachbach, 1969; Gasser, 1975).

Some researchers are of the opinion that the batch size per breeding in Urodela is in direct proportion to body size (Bruce, 1975; Rose & Armentrout, 1975; Anderson and Williamson, 1976). In *S. salamandra*, specifically, Eiselt (1958), Joly (1968), Degani (1976) and Degani and Warburg (1977, 1995) have compared the number of larvae per breeding in Israeli salamanders with that of their smaller counterparts in Europe. Joly (1968) reviewed the numbers of larvae born per batch, and found a range of 10–72. He based his data on the findings of a number of researchers, but it should be noted that these findings arose from samples of very limited numbers of breedings, in many cases only single ones. The work on the Israeli salamander is based on samples of a much larger number of batches (52) than is found in the literature on the European species.

Our findings were that the harsher the conditions, the larger the batches of larvae born, which agrees with findings for other species of Urodela in Europe. Thus, the Tel Dan salamander produces smaller batches than are found in hotter and more arid areas in Israel. Even within specific areas, salamanders which live near permanent water sources produce smaller batches than those which rely on seasonal sources: the batches in Sasa numbered up to 193, compared with a maximum of 72 at the nearby Hammama Spring.

Of the three habitats in Israel, Tel Dan has similar conditions to those in Europe, at least in summer, though the other two habitats (Mt. Meron and Mt. Carmel) have much harsher conditions, especially from the point of view of summer aridity. The difference between these habitats, which are in relatively close proximity to each other, makes it possible to assess the influence of habitat on the numbers born in a single breeding.

Adult female salamanders were collected from the five habitats. Specimens were collected in the early hours of darkness, as they come out of their hiding places and before they reached the water. They were transferred to plastic containers, measuring 40×20×20 cm, with 4 cm water, in laboratories located in all cases near to their natural habitats, and gave birth in these containers. Rates of birth were timed, and

Figure 6.1. Larva emerging from cloaca, enveloped in embryonic sac (Degani, 1976; Warburg et al., 1979a).

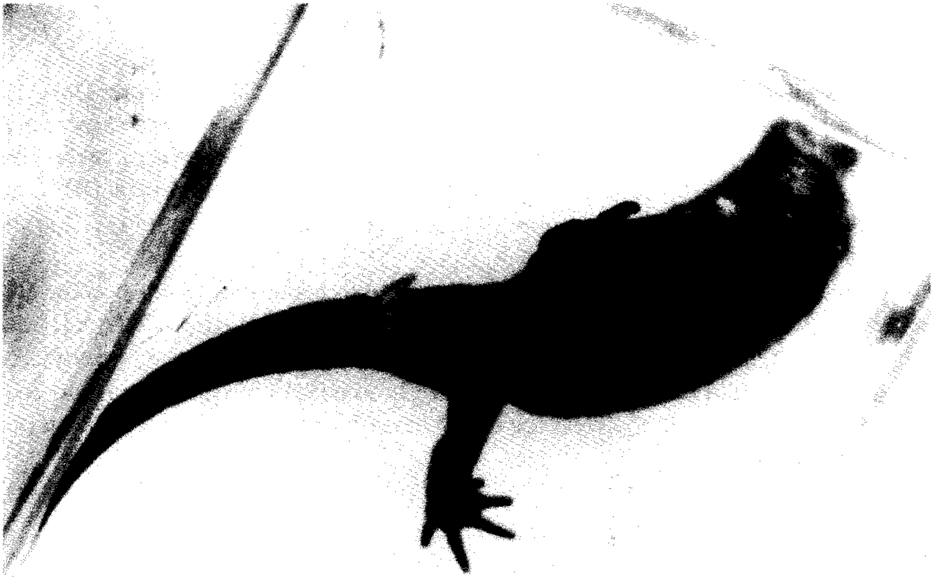


Figure 6.2. Larva born without embryonic sac (Degani, 1976; Warburg et al., 1979a).

the newly born larvae were counted. At least 25 larvae from each brood were slightly dried on filter paper, measured and weighed individually.

In the hilly habitats, breeding usually takes place in winter, whereas in Tel Dan it can take place at any time of year (Fig. 6.3; Degani and Warburg, 1995). At the Hammama spring, larvae were still small at the end of August and beginning of September, because of scarcity of food. Breeding continued until April. In the pool at Gush Halav, larvae were found only in December and January. On the Carmel Range, breeding took place during October–January (Fig. 6.3), but judging by the size of larvae found in various water sources on Carmel, breeding must occur in January too.

The number of larvae per batch ranged: in Galilee from 47 to 192, with an average of 83.73; on the Carmel from 30 to 158 (average 112.25); and in Tel Dan from 17 to 105, with an average of 53.73 (Tables 6.1 to 6.5). It is interesting to note that the average number in the batches born at Hammama, a perennial spring, was lower than (61.29) in the batches at Sasa (average 117.64) and Gush Halav (89.86). We will return to this matter below.

In general, there were no significant differences among populations in average length and weight of larvae (the figures are given in Tables 6.1–6.5), with the following exceptions: larvae from Sasa were lighter than those of some other populations, and there were significant differences in average length between Hammama, on the one hand, and Tel Dan and Sasa, on the other (Tables 6.6, 6.7). Although batch sizes varied considerably, larva sizes within populations showed only occasional significant differences, and sizes within batches were remarkably uniform. When comparing length as a function of weight in a population, it was found that the larvae from Tel Dan and Sasa were smaller than those of other populations, but the difference was not significant (Fig. 6.4).

The time taken to breed was much longer at Tel Dan (1–17 days) than elsewhere (Galilee and Carmel 1–3.5 days) (Fig. 6.5, Table 6.8).

Adaptation of salamanders to extreme conditions and the drying up of water sources involves adjustment of the breeding time, in this case to early winter, and the number of larvae per batch, a faster rate of breeding and slightly increased larval birth size.

S. salamandra is among the largest of the terrestrial Urodela species. However, the latter do not give birth to live young, but lay eggs' like most of the North American Urodela, which makes comparisons difficult (Table 6.9). At the same time, there are differences within the species itself: Tel Dan salamanders are smaller than those from hilly regions. In addition, the numbers born in Tel Dan are lower, but breeding is spread over the whole year. One of the interesting facts that came out of this work concerned differences among habitats, in breeding, even within a given region. The more stable the source of water and less extreme the climatic conditions, the longer the breeding season. It is reasonable to assume that under difficult conditions, selection favored a shorter breeding season. This ap-

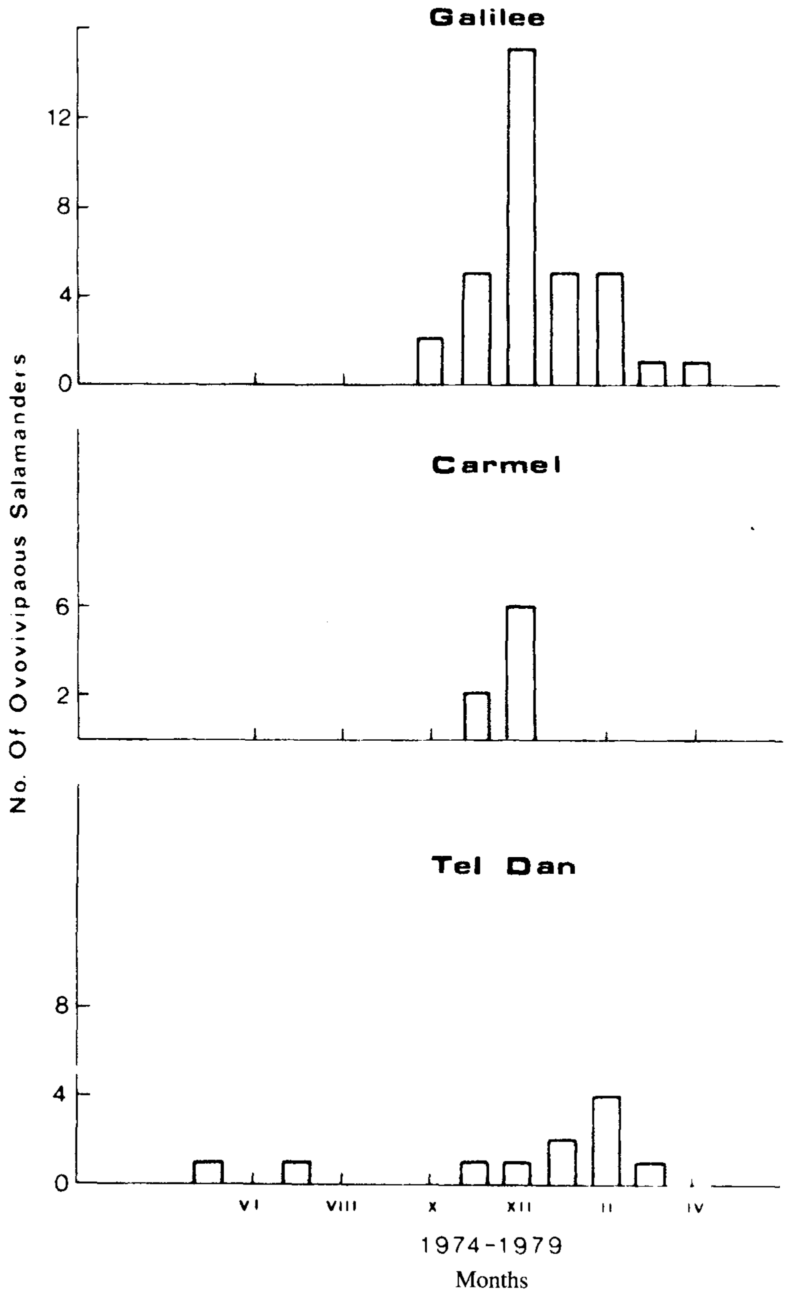


Figure 6.3. Number of larvae born between 1974 and 1979 (Degani, 1980).

Table 6.1. Larvae born on Mt. Carmel (Warburg et al., 1979a; Degani, 1980).

Larvae per batch	No. measured & weighed	Average length (mm ± SD)	Average weight (g ± SD)
74	74	35.9 ± 1.4	0.32 ± 0.04
121	121	34.5 ± 1.3	0.31 ± 0.04
100	30	28.1 ± 1.1	0.14 ± 0.03
130	30	33.3 ± 2.3	0.27 ± 0.03
30	30	34.5 ± 1.6	0.31 ± 0.04
129	29	35.2 ± 0.7	0.28 ± 0.02
156	25	31.1 ± 0.9	0.30 ± 0.02
158	25	29.9 ± 1.4	0.25 ± 0.02

Table 6.2. Larvae born at Gush Halav (Degani, 1980).

Larvae per batch	No. measured & weighed	Average length (mm ± SD)	Average weight (g ± SD)
42	25	32.9 ± 0.9	0.26 ± 0.02
90	25	38.0 ± 1.3	0.33 ± 0.03
104	44	38.1 ± 1.2	0.34 ± 0.03
71	25	35.6 ± 1.2	0.24 ± 0.02
73	25	25.3 ± 1.1	0.27 ± 0.02
117	25	34.0 ± 1.3	0.27 ± 0.03
132	25	38.6 ± 1.1	0.42 ± 0.01

Table 6.3. Larvae born at Sasa (Degani, 1980).

Larvae per batch	No. measured & weighed	Average length (mm ± SD)	Average weight (g ± SD)
164	164	27.2 ± 1.1	0.15 ± 0.02
193	193	29.7 ± 1.7	0.19 ± 0.03
142	142	30.6 ± 1.6	0.15 ± 0.02
49	38	31.7 ± 1.0	0.17 ± 0.02
51	51	32.7 ± 1.3	0.20 ± 0.02
99	97	37.3 ± 3.2	0.30 ± 0.03
128	125	30.0 ± 2.9	0.17 ± 0.02
90	25	32.0 ± 1.0	0.18 ± 0.01

Table 6.4. Larvae born at Hammama (Degani, 1980).

Larvae per batch	No. measured & weighed	Average length (mm ± SD)	Average weight (g ± SD)
64	64	36.4 ± 1.2	0.34 ± 0.04
72	72	33.9 ± 1.1	0.32 ± 0.02
55	24	33.3 ± 1.4	0.21 ± 0.02
65	25	34.7 ± 1.1	0.20 ± 0.02
55	26	37.3 ± 0.8	0.31 ± 0.03
57	25	35.8 ± 1.0	0.24 ± 0.02
62	25	37.1 ± 2.5	0.27 ± 0.04
61	25	32.2 ± 0.9	0.21 ± 0.01
53	25	33.4 ± 1.2	0.23 ± 0.02
47	25	32.4 ± 1.1	0.20 ± 0.02
59	25	31.0 ± 3.0	0.20 ± 0.02
69	24	36.1 ± 1.3	0.24 ± 0.01
82	25	29.5 ± 0.9	0.16 ± 0.01
60	25	36.0 ± 0.8	0.29 ± 0.02
70	25	32.3 ± 0.8	0.18 ± 0.01
52	25	34.9 ± 2.4	0.30 ± 0.05
59	25	36.1 ± 1.6	0.43 ± 0.03

Table 6.5. Larvae born at Tel Dan (Degani, 1980).

Larvae per batch	No. measured & weighed	Average length (mm ± SD)	Average weight (g ± SD)
17	17	31.7 ± 0.8	0.29 ± 0.02
35	12	31.0 ± 0.8	0.17 ± 0.01
27	24	32.6 ± 1.4	0.21 ± 0.02
20	10	34.4 ± 1.0	0.25 ± 0.01
57	18	33.5 ± 1.4	0.24 ± 0.02
15	15	31.7 ± 2.8	0.21 ± 0.08
85	25	34.5 ± 1.9	0.26 ± 0.02
96	25	32.2 ± 1.3	0.29 ± 0.04
105	25	33.9 ± 1.4	0.32 ± 0.03
55	25	33.6 ± 1.0	0.21 ± 0.04
97	25	29.0 ± 0.9	0.16 ± 0.01

Table 6.6. Comparison of larva weights from different locations (t-test) (Degani, 1980).

Location	No. of fem. specimens	Average weight (g ± SD)	P
Galilee*	33	0.25 ± 0.07	>0.1
Carmel**	8	0.27 ± 0.06	
Galilee	33	0.25 ± 0.07	>0.1
Tel Dan	11	0.23 ± 0.05	
Carmel	8	0.27 ± 0.06	>0.1
Tel Dan	11	0.23 ± 0.05	
Sasa	9	0.19 ± 0.05	<0.05
Hammama	17	0.26 ± 0.05	
Sasa	9	0.19 ± 0.05	>0.05
Tel Dan	11	0.23 ± 0.05	
Hammama	17	0.26 ± 0.05	>0.1
Tel Dan	11	0.23 ± 0.05	
Sasa	9	0.19 ± 0.05	<0.01
Carmel	8	0.27 ± 0.06	
Hammama	17	0.26 ± 0.05	>0.1
Carmel	8	0.27 ± 0.06	

*Galilee = Sasa, Hammama, Sasa rock pool, and Gush Halav.

**Carmel = Pond and Spring.

Table 6.7. Comparison of larva length from different locations (t-test) (Degani, 1980).

Location	No. of fem. specimens	Average length (mm ± SD)	P
Galilee*	33	33.94 ± 2.80	>0.1
Carmel**	8	32.81 ± 2.80	
Galilee	33	33.94 ± 2.80	>0.1
Dan	11	32.56 ± 1.67	
Carmel	8	32.81 ± 2.80	>0.1
Dan	11	32.56 ± 1.67	
Sasa	9	31.69 ± 2.76	<0.05
Hammama	17	34.26 ± 2.25	
Sasa	9	31.69 ± 2.76	>0.1
Dan	11	32.56 ± 1.67	
Hammama	17	34.26 ± 2.25	<0.05
Dan	11	32.56 ± 1.67	
Sasa	9	31.69 ± 2.76	>0.1
Carmel	8	32.81 ± 2.80	
Hammama	17	34.26 ± 2.25	>0.1
Carmel	8	32.81 ± 2.80	

*Galilee = Sasa, Hammama, Sasa rock pool, and Gush Halav.

**Carmel = Pond and Spring.

Table 6.8. Rate of birth of salamanders in various populations (Degani, 1980).

Location	No. days	Larvae born/hr
Sasa	3.5	2.26
Sasa	4	1.96
Sasa	1	14.71
Sasa	3	0.61
Sasa	2	1.36
Sasa	2.25	1.83
Sasa	2.5	1.74
Hammama	3	0.39
Hammama	1.67	2.38
Gush Halav	2.21	2.49
Gush Halav	0.67	7.31
Gush Halav	0.69	4.41
Carmel (pond)	3.17	2.08
Carmel (pond)	2.8	2.04
Carmel (spring)	2.7	1.34
Carmel (spring)	2.08	3.13
Tel Dan	9	0.30
Tel Dan	17	0.14
Tel Dan	2.7	1.34

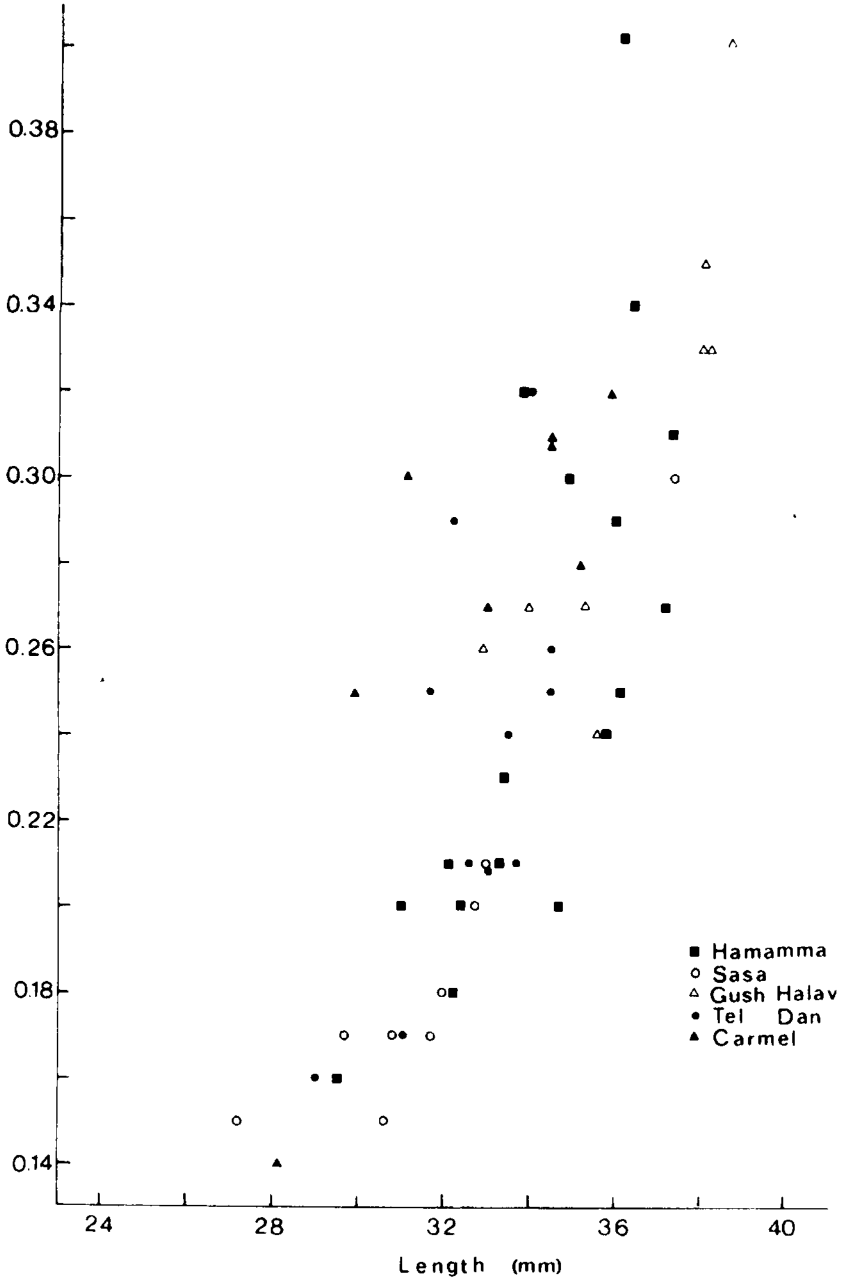


Figure 6.4. Weight as a function of length in newborn larvae of various populations (Degani, 1980).

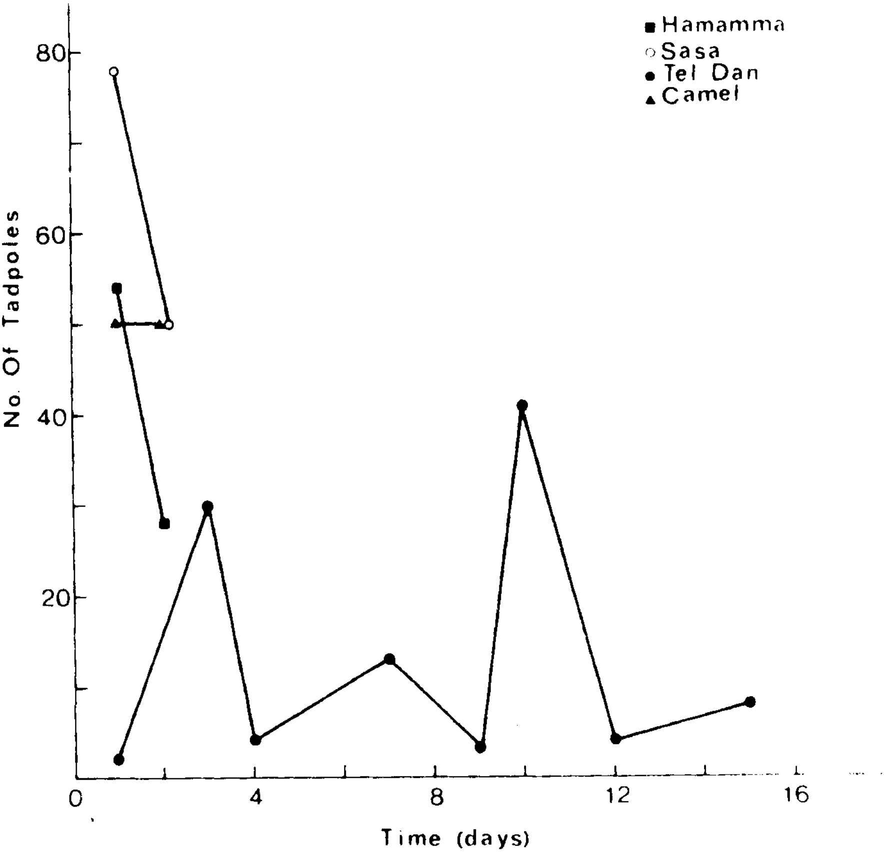


Figure 6.5. Rate of birth in various populations (Degani, 1980).

pears to be true of other species of Urodela, as can be seen in Table 6.10.

Marked differences between Israel and Europe, in larva size as well as breeding season, were found. Larvae at the southern limit of distribution were bigger: larvae bred in France measured 25–33 mm (Joly, 1968) and those in Hungary 22.5–33.5 mm (Szabo, 1959), while Mt. Meron larvae measured 27.2–38.6, Mt. Carmel larvae 28.1–35.9 and Tel Dan larvae 24.0–34.5 mm. There were no significant differences in averages among the three Israeli populations. Although the average weight was slightly lower at Sasa, this was probably because this population had a higher number of larvae per batch. However, the inference that larvae from southern populations are larger than their European counterparts can only be stated with caution, in view of the paucity of data from Europe.

The observed marked difference between Tel Dan and Mt. Carmel in breeding rate may arise from the natures of these habitats (Table 6.8, Fig. 6.5). It may be an advantage that breeding in Tel Dan is spread over a long period, insofar as the larvae are bred in a number of locations. This hypothesis is supported by the fact that no great concentrations of larvae were found in this habitat, though one cannot ignore the possibility that they were scattered by the stream. Salamanders in the hilly regions must migrate over relatively long distances, consequently the advantage lies in rapid breeding and large larvae, to minimize danger to the salamander and her brood.

The fact that larvae breeding was studied in the laboratory in containers, rather than in natural conditions, must be taken into account, and some caution must therefore be exercised in drawing conclusions from the results. Abnormal conditions may affect the breeding season and even the breeding rate. Thus, Gasche (1942) obtained early breeding under special conditions, especially under stress. On the other hand, a large number of breeding specimens was captured in our research and gave consistent results, while their breeding behavior did not differ from that of salamanders in the wild.

At all events, it is clear that the breeding seasons and larval sizes in Israel differ from those in Europe, and the differences are the result of environmental differences. In the hilly regions of Mt. Carmel and Mt. Meron, where the availability of water is seasonal, breeding took place at the beginning of winter, with larger batches and larger larvae than in permanent water sources (Tel Dan and Hammama) or in Europe. In the habitats with stable water sources, the breeding season lasts longer, and can continue into the spring or — in Tel Dan — even into the summer.

Table 6.9. Number of larvae or eggs per batch bred by various Urodela.

Species	No. per batch	Reference
Ambystoma maculatum	92–328 eggs	Shoop, 1974.
A. cingulatum	97–222 eggs	Anderson & Williamson, 1976
A. tigrinum (large)	139–142 eggs	Rose & Armentrout, 1975
A. tigrinum (small)	99–105 eggs	Rose & Armentrout, 1975
Desmognathus fuscus	11–36 eggs	Hall, 1977
D. ochrophaeus	8–24 eggs	Hall, 1977
Pseudotriton montanus	77–192 eggs	Bruce, 1975
S. s. infraimmaculata (Europe)	10–72 larvae	Joly, 1968
S. s. infraimmaculata (Sasa)	49–193 larvae	Degani, 1980
S. s. infraimmaculata (Hammama)	47–82 larvae	Degani, 1980
S. s. infraimmaculata (Carmel)	30–156 larvae	Degani, 1980
S. s. infraimmaculata (Tel Dan)	17–105 larvae	Degani, 1980

Table 6.10. Breeding season of various Urodela.

Species	Season	Reference
Desmognathus ochrophaeus	Spring–winter	Forester, 1977
Pseudotriton montanus	Autumn–winter	Bruce, 1975
Triturus helveticus	Aug., Sept.	von Gelder, 1973
Ambystoma tigrinum	End winter–spring	Rose & Armentrout, 1975
A. opacum	End summer–autumn	Shoop & Doty, 1972
A. cingulatum	Nov., Dec.	Anderson &Williamson, 1976
Bolitoglossa rostrata	May, June	Houck, 1977
Plethodon vehiculum	Autumn	Peacock & Nussbaum, 1973
Triturus vulgaris	Spring & summer	Hagstrom, 1974
Triturus vulgaris	Spring & autumn	Bell & Lawton, 1975
S. s. terrestris	Oct.–May	Joly, 1968
S. s. salamandra	Spring & summer	Szabo, 1959
S. s. infraimmaculata (Tel Dan, Israel)	All year long	Degani and Warburg, 1996
S. s. infraimmaculata (Galilee, Israel)	October–April	Degani and Warburg, 1996
S. s. infraimmaculata (Carmel, Israel)	October–April	Degani and Warburg, 1996

CHAPTER SEVEN

GROWTH RATE AND METAMORPHOSIS OF LARVAE

The rate of growth of *S. salamandra* larvae has been little studied in Europe. There, as in Israel, the larvae are to be found in both flowing and stagnant water (Joly, 1968). Other species of Urodela are also be found in different water habitats: *Ambystoma opacum* in seasonal pools (Shoop and Doty, 1972), *Dicamptodon ensatus* in small streams (Nussbaum and Clothier, 1973) and *Triturus vulgaris* in small pools and puddles (Bell, 1974), for example. In Israel, at the southern limit of their distribution, *S. s. infraimmaculata* can be found in every type of water: running streams (Tel Dan), springs (Hammama), winter ponds (Gush Halav, Sasa), seasonal water holes (Mt. Carmel) and even in large puddles that only fill up every few years (Prof. H. Mendelssohn, personal communication). Springs and winter pools characterize the Carmel and Galilee regions, while streams are typical of Tel Dan. Several papers have been published which deal with the growth rate of salamander larvae in Israel: Warburg et al. (1979b), Degani et al. (1980) and Degani (1982). The survival *and growth of larvae in different types of water body is a topic relevant to the study* of environmental influences on animals.

Little was previously known about the adaptation of the species to the type of water source and how this adaptation influences the rates of growth and metamorphosis of the species. The study of how long larvae remain in the water and their rates of growth and metamorphosis can shed light on how the larvae adapt to greatly differing habitats within this southern region.

Many water bodies in which salamander larvae are found were studied. All have been mentioned above, but it is now appropriate to describe them in detail (see map, Fig. 1.2).

1. The Gush Halav pool (Fig. 7.1), in central Galilee, is 725 m above sea level. It is a winter pool (December to April), which dries up in the summer; it measures 10 × 20 m and reaches depths of 10–80 cm, dependng on the amount of rainfall and extent of evaporation. The water temperature ranges from 1–27°C. Not infrequently, a shortfall of rain in drought years prevents the pool from filling up.
2. Also in central Galilee, at 880 m above sea level, is the Sasa Pond (Figs. 7.2, 7.3), which holds water from December to June. It may hold water all through the year, if rainfall has been plentiful in winter, but it dries up earlier in drought years. This pond measures 40 × 60 m, with depths of 20–100 cm and its water temperature is 1–16°C.
3. A second pond at Sasa (Fig. 7.4), at the same height above sea level, is cut into

rock and holds water for most of the year (7–12 months). It measures 2 × 6 m, reaches a depth of 100 cm and has a water temperature of 5–22°C.

4. Hammama Spring (Fig. 7.5), near to the Sasa ponds, at 926 m above sea level, is small but continuous all year round. It rises in a small cave and forms a pool (1 × 6 m) at the entrance to the cave, reaching depths of 6–20 cm; its temperature is 9–16°C.
5. Tel Dan (Fig. 7.6), to the north and east, in Upper Galilee, is a nature reserve that contains a number of heavily shaded springs and streams. Lower elevation (180 m above sea level), the constant temperature of the springs and the heavy shade of the natural plant growth maintain relatively constant water temperatures of 16–17°C.
6. The Carmel Range overlooks the sea, to the west. Here three points were chosen for study: a small stream that drains into a rock pool that dries up in summer, a rain pool that holds water all year round, and winter stream which contains water for only a month or two.

The results of Degani (1980) are presented in Figs. 7.7 to 7.12. They show that the rate of growth and length of stay in the water of the larvae vary from one type of water body to another: in seasonal water bodies, growth was rapid and the stay in water was short. Thus, larvae remained in the Gush Halav pool for 3.5–4 months (December to April) and in Nahal Ahzav for 1.5–3 months (December to March). In water bodies that are only dry for only 2–4 months, or remain full throughout wet years, the length of stay in the water was longer: 6–7 months (December to July) and sometimes even longer, in the Sasa rock pool and 4–5 months (December to May) in the other Sasa pool. Larvae in permanent water bodies remained in the water even longer: from August to June in Hammama, and for the entire year in Tel Dan. In such permanent water bodies, both large and small larvae can be found at the same time, during most of the year (Warburg et al., 1979b).

A regular growth curve, such as was found for the other water bodies, was not found for Hammama. Wide deviations from the average indicate large differences among larvae. At Tel Dan, it was difficult to capture specimens: although larvae could be seen all year round, they tended to appear singly and were hard to catch. Here too, big differences in larva size were measured. However, larvae from a single brood, grown in the closed container at Tel Dan, did not show any differences in size, suggesting that larvae of different sizes in nature grew from different broods. Growth from birth to metamorphosis took seven months.

There were significant differences in the sizes of larvae from different sources at any given time, though not between those from the pools at Sasa and Gush Halav (Tables 6.2, 6.3). A notably large difference in the rate of growth was found between Carmel larvae and those from Tel Dan. At most times, no significant differences in weight were found ($p>0.1$), but there were large differences in body length and length of stay in the water (Table 6.6–6.8).

Figure 7.1. Gush Halav pool, a seasonal rain pool (Degani, 1980).

Figure 7.2. Sasa pond, a winter rain pool (winter) (Degani, 1980).

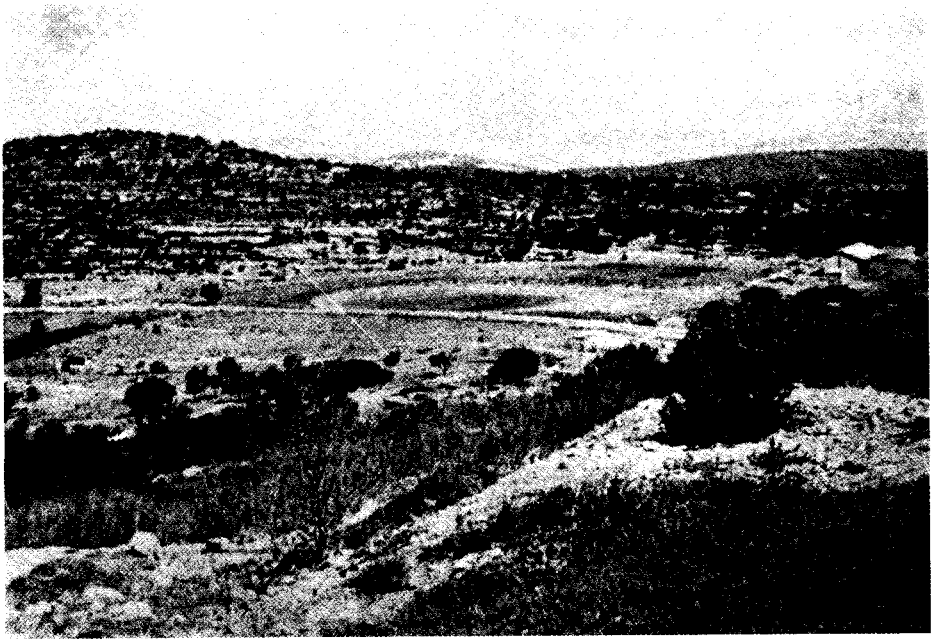


Figure 7.3. Sasa pond, a winter rain pool (summer) (Degani, 1980).

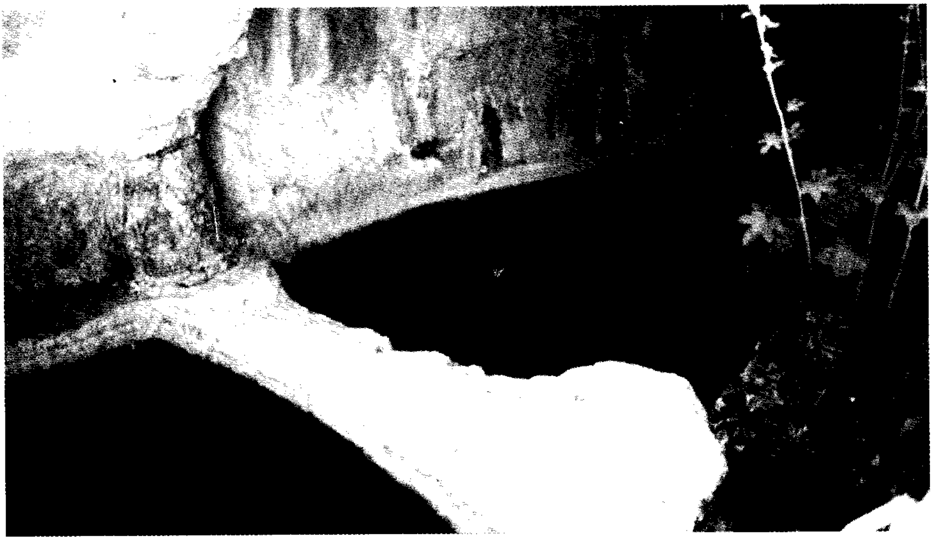


Figure 7.4. Sasa rock pool, a winter rain pool (Degani, 1980).

Figure 7.5. Hammama spring, originating in a small cave (Degani, 1980).

Figure 7.6. Tel Dan stream, perennial fast-flowing water (Degani, 1980).

Although no two years were exactly alike, there were no great differences in the growth rate, or the shape of the growth curve, from one year to another, throughout the years of study. The growth curve can be defined by the formulae $L = ae^{bt}$; $W = ae^{bt}$, where L = length in millimetres; W = weight in grams; e is the base of natural logarithms, and a and b are empirical coefficients (Tables 7.1, 7.2).

There were differences in the sizes of the young, according to whether they were caught near a spring, under stones or in various water bodies. The difference was particularly marked in the case of the young from Hammama, which were also particularly small. These completed their metamorphosis in the summer, and were then unable to leave the immediate area of the spring. Larvae that completed their metamorphosis in winter were much larger, though these were only caught and measured before leaving the water, not after metamorphosis. In winter, the young leave the spring immediately after completing metamorphosis.

The young from Mt. Carmel were particularly big, with an average weight of 3.22 ± 0.37 g and average length of 83.1 ± 2.7 mm. At the other extreme were the young from Tel Dan, which averaged 1.33 ± 0.17 g and 54.0 ± 2.0 mm immediately after metamorphosis. Differences in the types of water bodies produced further differences in size. In the seasonal water bodies, which dry up in summer, such as Gush Halav, Sasa and a stream on the Carmel, all the larvae achieved metamorpho-

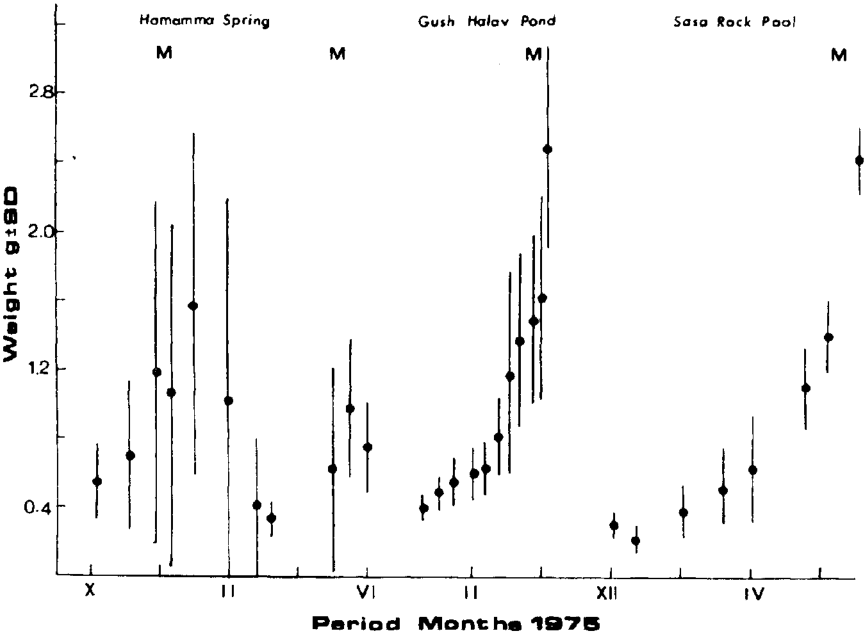


Figure 7.7. Growth rates (weight) of larvae from Galilee (1974–75). M = end of metamorphosis (Degani, 1980).

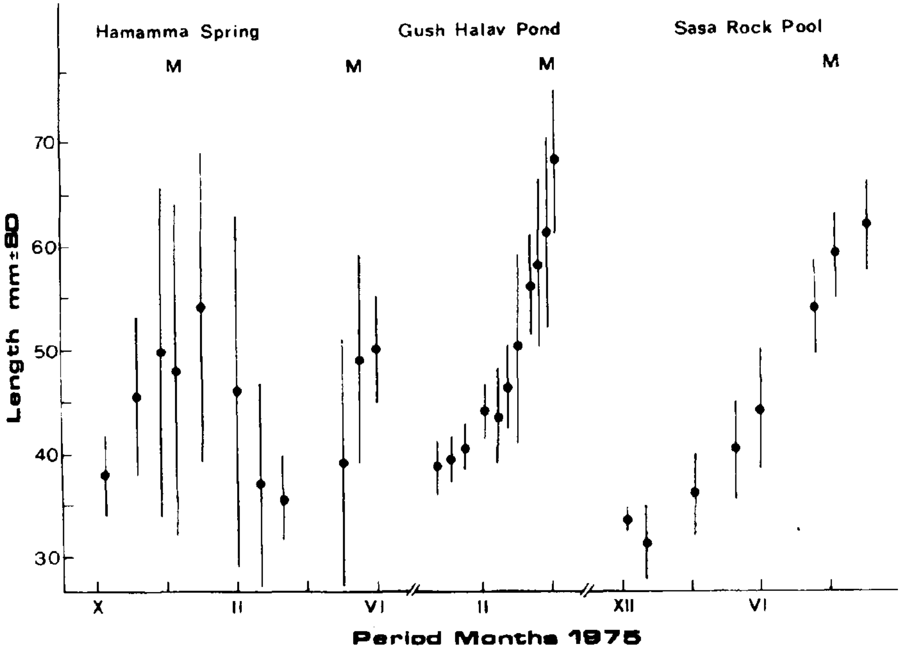


Figure 7.8. Growth rates (length) of larvae from Galilee (1974–75). M = end of metamorphosis (Degani, 1980).

sis at the same time. The time taken for it (from when the gills begin to wither to the time of their complete disappearance) was relatively short. In permanent water bodies, such as Tel Dan and Hammama, only some of the larvae complete metamorphosis at any one time, so that young salamanders and larvae in the last stage of metamorphosis were to be found simultaneously. Furthermore, in these locations the process of metamorphosis took up to a full month.

The size of the larva population was also measured in a number of places in 1975. In Gush Halav it averaged 113.3 (253–1782 individuals), in Sasa 695.8 (240–936) and in Hammama 266.2 (187–260), though in Hammama the figure must be treated with caution because cannibalism was noted among the larva population.

Density of larva population is hard to estimate, owing to the changes in many of the water bodies during the season. Thus, in Gush Halav, population density increases as the pool dries up, reaching a maximum between March and May, whereas in the permanent water bodies population density is stabler. In the Sasa stone rock pool, density was 40–170 larvae/m^2, and in Hammama it was 17–70 larvae/m^2.

It would appear that the main strategies which mark the adaptation of salamander

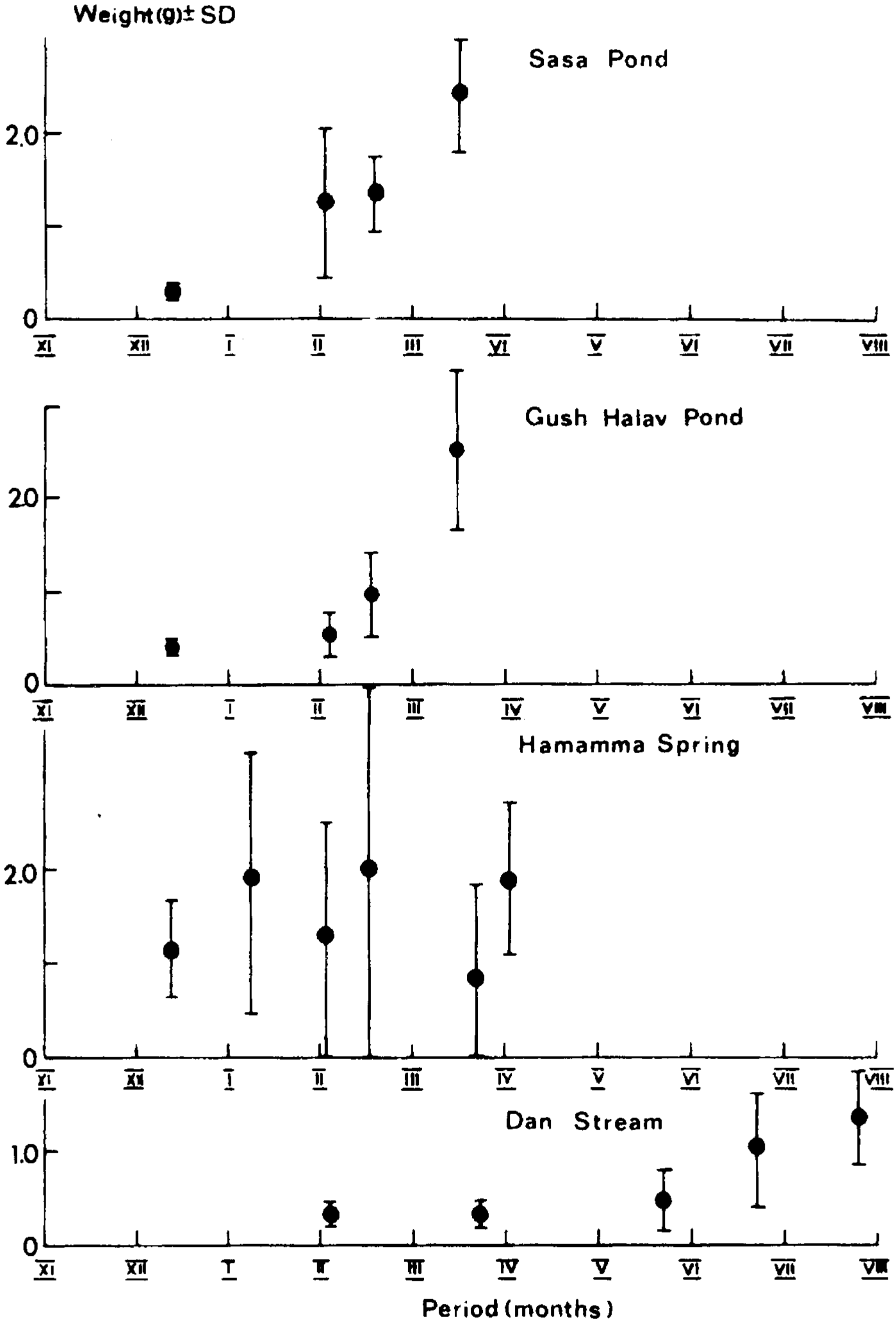


Figure 7.9. Growth rates (weight) of larvae from various locations (1977) (Degani, 1980).

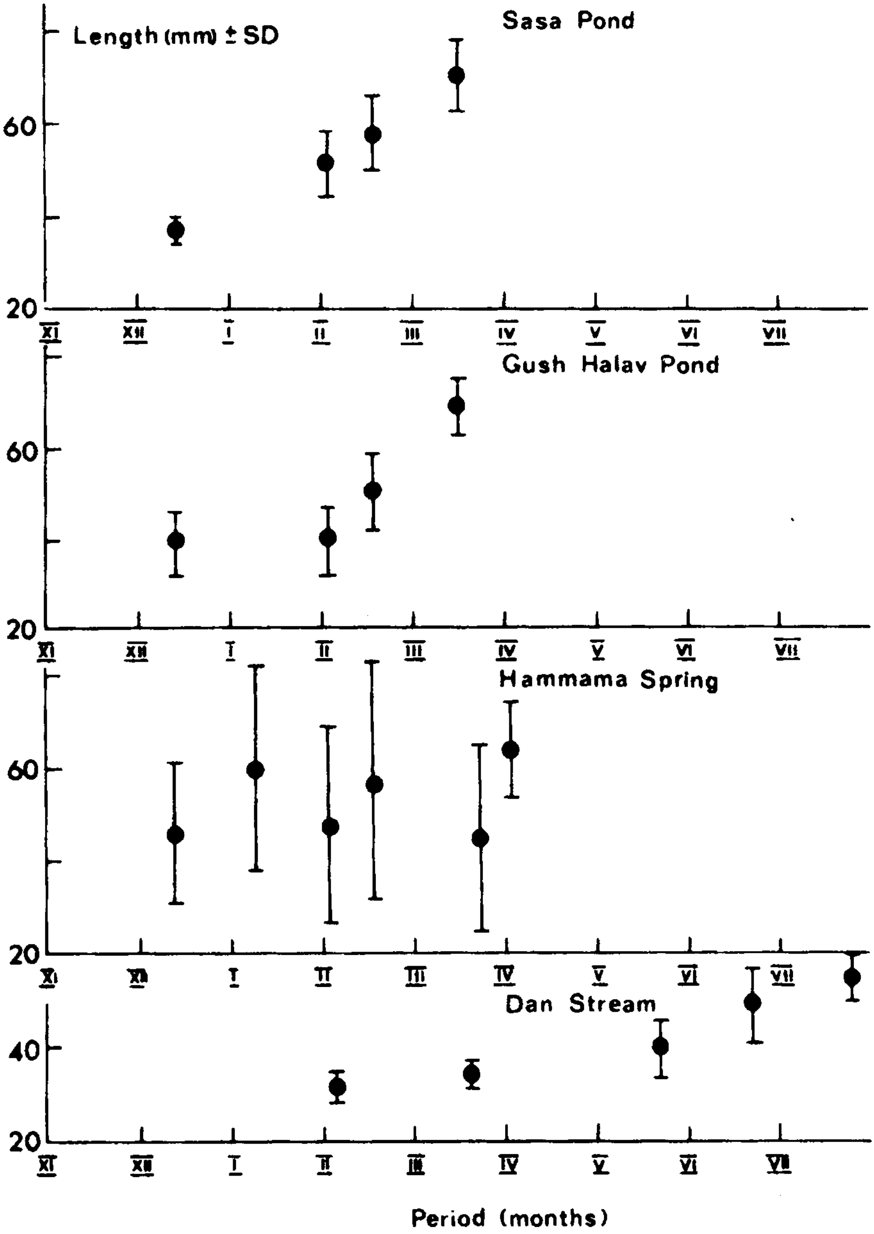


Figure 7.10. Growth rates (length) of larvae from various locations (1977) (Degani, 1980).

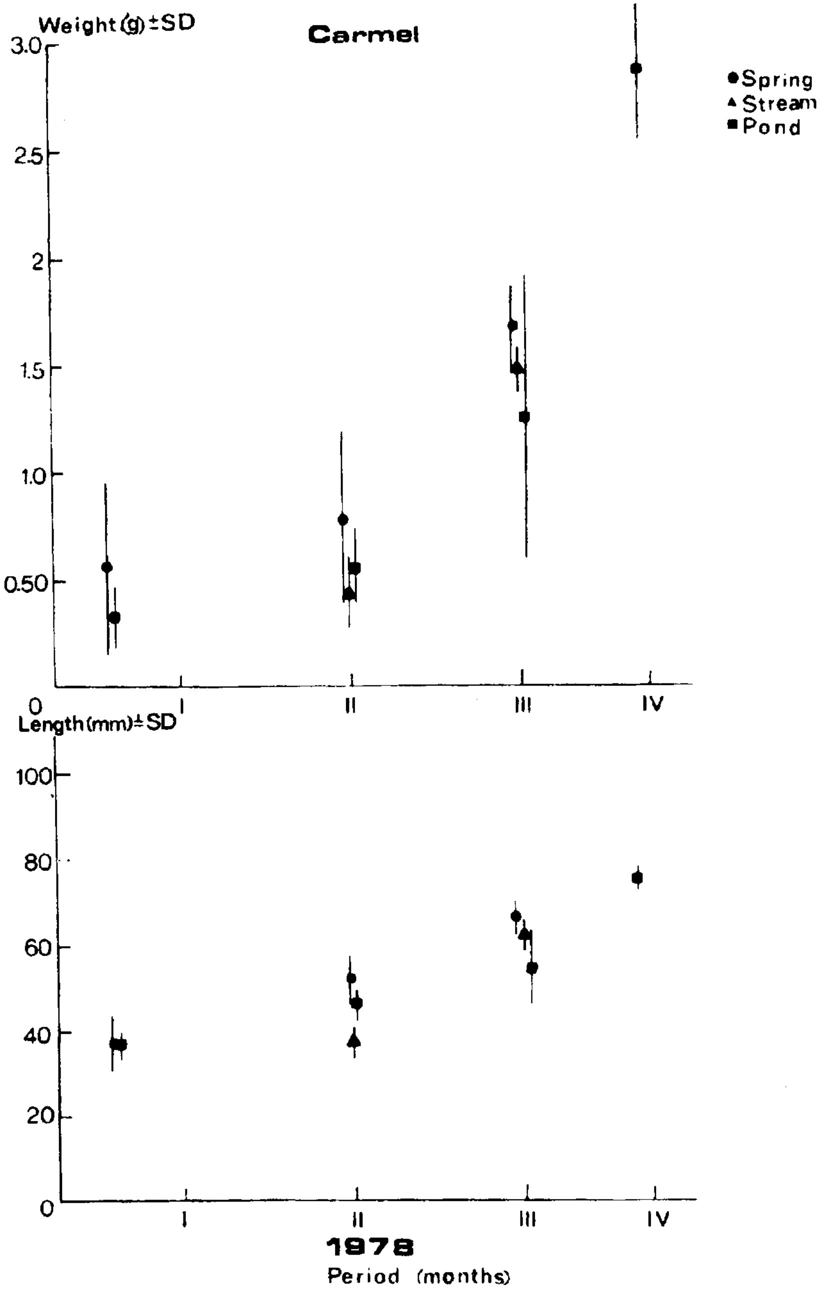


Figure 7.11. Growth rates (length and weight) of larvae from Carmel (1978) (Degani, 1980).

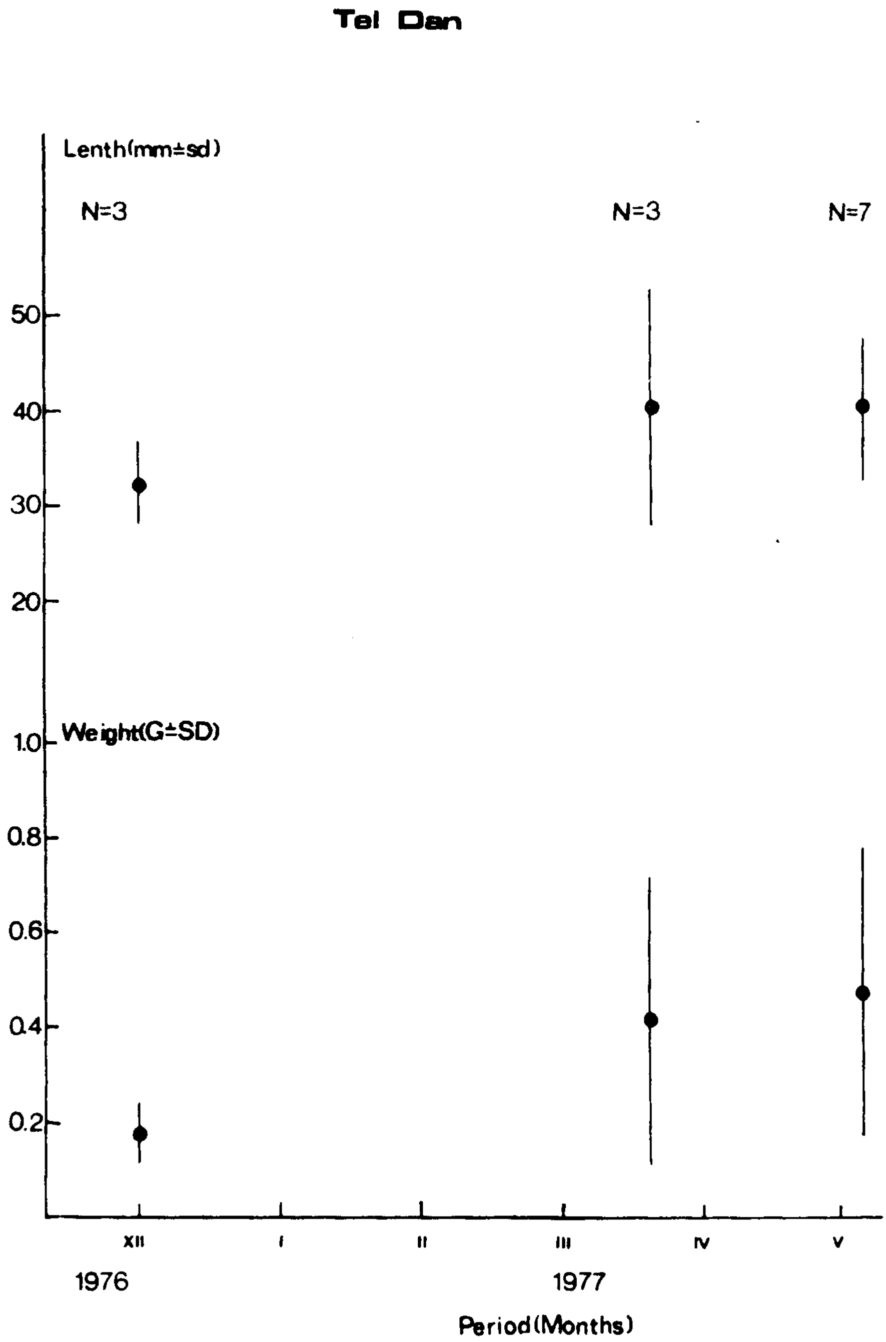


Figure 7.12. Growth rates (length and weight) of larvae from Tel Dan (Degani, 1980).

larvae to more difficult water conditions in this region are faster growth (especially toward the end of the season) and quicker completion of metamorphosis in temporary pools than in permanent water bodies. Both ensure that the larvae remain in water for a much shorter time. Population density is much higher in seasonal than in permanent water bodies, and this can only partly be attributed to shrinkage in the area of water. Breeding takes place as these pools fill up with rain water and not according to the ambient temperature. Metamorphosis of all the larvae is simultaneous. The higher rates of growth and development are facilitated by rising temperature and increasing concentration of food as the pools begin to dry up.

All these parameters differ in permanent water sources. Breeding takes place over a much longer period, up to the extreme case of all year round in Tel Dan. The larvae found are of uniform size, their growth is slower and metamorphosis does not take place at a single, defined time. There are, of course, intermediate states, between the extremes. Furthermore, the influences of temperature and availability of food were not studied thoroughly in this investigation, but the data are sufficient to support the generally expressed hypothesis that environmental factors influence the rates of growth and development.

Little information is available on the rate of growth of *S. salamander* larvae elsewhere, as noted above, though Szabo (1959) gives the size of Hungarian salamander larvae as 27.30 mm in April, 37.29 mm in May, 44.67 mm in June and 43.63 mm in July. In the work described here, only the populations in Tel Dan and Hammama (both permanent water bodies) showed similar sizes and rates of growth during the same period. In most of the other water bodies, growth took place mainly in winter, and the larvae reached much greater sizes. Further comparisons can only be made with other species of Urodela, in the absence of data.

Healy noted that, in the species *Notophthalmus visidescens*, young that grow in water grow faster than those that have completed metamorphosis. Nussbaum and Clothier (1973) found differences in the growth rates in different populations of *Dicamptodon ensatus*, some of which were found in small streams and others in large pools; these differences arose from temperature differences, as tentatively noted in our work. In his study of *Triturus vulgaris* in small ponds near Oxford, Bell (1974) noted that, where habitats are similar, rates of growth are also without significant differences, as we found for salamanders in winter pools. In another finding that parallels our work, Shoop (1974) noted a faster rate of growth of *Abystoma maculatus* in seasonal than in permanent water bodies.

A variation of growth behavior not previously reported in *S. salamandra* was noted in Hammama. Larvae were born at the end of summer and in autumn, and grew somewhat before winter. After this, they turned into cannibals, preying principally on smaller salamander larvae that had been born later, and completed their metamorphosis by the end of winter. Larvae born at the end of winter and in spring complete metamorphosis at the end of summer (Figs. 7.7–7.10). This cannibalism and changes in food will be discussed more fully in the next chapter. The larva

Table 7.1. Growth rate (weight) formula in various populations (Degani, 1980).

Location	Date	Growth Curve	N	r	p
Sasa pond	1975	$W = 0.47e^{0.01t}$	49	0.66	<0.001
Sasa pond	1976–7	$W = 0.38e^{0.02t}$	38	0.86	<0.001
Sasa rock pool	1974–5	$W = 0.25e^{0.01t}$	204	0.87	<0.001
Gush Halav	1975	$W = 0.41e^{0.02t}$	278	0.80	<0.001
Gush Halav	1976–7	$W = 0.35e^{0.01t}$	80	0.662	<0.001
Tel Dan	1976–7	$W = 0.14e^{0.01t}$	34	0.83	<0.001
Carmel spring	1977–8	$W = 0.40e^{0.02t}$	17	0.75	<0.001
Carmel stream	1977–8	$W = 0.42e^{0.04t}$	11	0.75	<0.001
Carmel pond	1977–8	$W = 0.28e^{0.02t}$	17	0.89	<0.001

Table 7.2. Growth rate (length) formula in various populations (Degani, 1980).

Location	Date	Growth Curve	N	r	p
Sasa pond	1975	$L = 40.99e^{0.003t}$	49	0.66	<0.001
Sasa pond	1976–7	$L = 38.99e^{0.01t}$	38	0.86	<0.001
Sasa rock pool	1974–5	$L = 30.51e^{0.003t}$	204	0.87	<0.001
Gush Halav	1975	$L = 36.46e^{0.01t}$	278	0.80	<0.001
Gush Halav	1976–7	$L = 38.61e^{0.03t}$	80	0.51	<0.001
Tel Dan	1976–7	$L = 29.42e^{0.02t}$	34	0.71	<0.001
Carmel spring	1977–8	$L = 40.11e^{0.0062t}$	17	0.72	<0.001
Carmel stream	1977–8	$L = 37.00e^{0.01t}$	11	0.95	<0.001
Carmel pond	1977–8	$L = 35.05e^{0.01t}$	17	0.92	<0.001

Key: W = weight (g); L = length (mm); t = time (days).

population in the Gush Halav pool was particularly large, despite the variable size of the pool. Although population density reaches its maximum from March onwards, the rate of growth remains rapid. The implication is that population density does not affect the rate of growth in salamanders. Further support for this hypothesis will be given in the next chapter.

CHAPTER EIGHT

FOOD OF LARVAE

A number of researchers have studied the nutrition of the various species of Urodela. In North America, the terrestrial species feed mainly on insects (Hamilton, 1932; Burton and Martin, 1973; Lynch, 1973; Burton, 1976; Fraser, 1976). Freytag (1955) found that after metamorphosis, *S. salamandra* feeds mainly on gastropods, insects and diplopods. Szabo(1962), studying the species in Hungary, noted that their main food consisted preferably of arthopods (mostly insects) and then molluscs, whereas Fasbach et al. (1975), on the basis of the contents of the digestive tract, placed gastropods first and insects second.

However, little work has been performed on the nutrition of the larvae of Urodela species. Cooke (1974) noted that during their acute phase, *Triturus cristatus* and *T. vulgaris*, feed on the frog larvae, whereas Avery (1968, 1971) found the larvae of dipterous insects to be the main source of nutrition for *Triturus* spp., as has also been found for *Desmognathus fuscus, Eurycea bislineata* and *Gyrinophilus porphyriticus.*

Regarding the food of *S. salamandra* larvae in particular, little has been published, except the study by Degani and Mendelssohn (1978), who focused particularly on the success of the species in adapting itself to a wide variety of habitats. In the study decribed in this chapter, the contents of the digestive tract were analyzed. The body that administers the strict laws for the protection of wild animals in Israel limited the study to the examination of only a few specimens from each of the five types of habitat selected. These were: a 3–4 month seasonal pool (Gush Halav), an 8–12 month pool (Sasa), an 8–12 month rock pool (Sasa), a perennial spring (Hammama) and a stream (Tel Dan), described in detail in the previous chapter.

Specimens were caught with a hand net and immediately immersed in 70% alcohol. At the same time, the presence of invertebrates in the water was examined, by dragging a 11 × 17 cm net, with a 0.3 mm mesh, through a 1-m horizontal stretch of water, 10 times near the surface and 10 times near the bottom. The catch of invertebrates from each water body was transferred to 100 ml 70% alcohol, of which a 3-ml sample was examined. An additional examination of invertebrates was made by transferring them to 100 ml of water, drying them for 48 h at 65°C and determining the dry weight.

It was found that the larvae ate many kinds of invertebrates (Table 8.1). In the Sasa winter pond, at the beginning of its season, the principal food consisted of newts, species of *Hemidiaptomus*, while at the end of the season *Potamocypris almasyi*, *Ceriodaphnia* sp. and *Chydoridae* predominated.

In the Sasa rock pool, the same pattern of feeding was found, but in addition, the water snail *Melanopsis praemorsa* was eaten throughout the season.

In the Gush Halav pool, the main food of the larvae consisted of crustaceans, the most prominent being *Lynceus*, followed by *Ceriodaphnia* and *Hemidiaptomus*. Although many mud newts (*Cyzicus* sp.) were to be found in the pool, the larvae of salamanders can only eat them at the end of the season, because of their large size. At that time, there was also a rise in the proportion of *Eucypris lutaria* found in the digestive tracts.

In the Hammama spring, where salamander larvae can be found for most of the year, mosquito larvae (*Culex*) provide the main source of nutrition in spring, summer and autumn. In winter, *Culex larvae* are unavailable and other invertebrates are scarce, yet there is a large number of salamander larvae in the water. Under these circumstances, the main source of nutrition is through cannibalism (Degani and Mendelssohn, 1978).

The principal food in the streams of Tel Dan consisted of *Gammarus* sp., with the water snail *Melanopsis praemarsa* second in importance. These species are available for most of the year.

The salamander larvae from the Mt. Carmel area were taken mainly from water bodies in which larvae of the toad, *Bufo viridis*, are also to be found: in the seasonal Achsav stream, a number of such larvae were found in the digestive tracts of the salamander larvae examined. In addition, at the source of the stream, a salamander larva was found to have been eaten cannibalistically. This phenomenon was also found in the Neviya pool, downstream.

Generally speaking, salamander larvae ate any invertebrate species that was to be found in their habitat, the exceptions being those that were too big or moved too fast. This was tested and confirmed in the laboratory, by providing larvae with a wide variety of invertebrates for food, including larvae of *Bufo viridis*: the only appetite limitations were found to be the size and speed of movement of potential prey. However, some caution must be observed in extrapolating the findings of the study on salamanders to other Urodela, since in most cases the potential food populations in the habitats were not sampled.

The digestive tracts of salamanders examined during metamorphosis were found to be empty. This was especially noticeable in the Gush Halav pool, because the process takes place in a shorter time there than elsewhere (Degani and Mendelssohn, 1978).

The study of the dry weight of invertebrates found in each 0.15 m^3 water yielded the following results: Sasa pond, 6.0–73.0 mg; Sasa rock pool, 1.0–35.1 mg; Gush Halav, 1.0–10.0 mg; Tel Dan, 150–360 mg; Hammama, none, or below limit of significant measurement. The relatively high weight at Tel Dan resulted from the weight of *Melanopsis* shells.

Degani and Mendelssohn (1978) showed that salamanders can make use of a wide range of invertebrates for their nutrition, a fact that enables them to live in

Table 8.1. Prey found in the stomach of salamander larvae (Degani and Mendelssohn, 1978).

Sasa Pond		3. 12. 77	15.2.77	15.3.77	9.4.77
Hemidiaptomus gurney		54	415	11	
Potamocypris almasyi		25		48	60
Ceriodaphnia sp.				57	9
Chydoridae				80	2
Oligochaeta				1	
Cypris pubera (juv.)				12	
Cypris pubera (adult)				30	
Candona sp.			1	3	
Arctodiaptomus similis			2	4	1
Dytiscid larvae					1
Hemiptera larvae				1	1
Eucypris sp.					2
Chironomidae larvae					1
Hemiptera					1
Sasa Rock Pool		13.1.77	20.2.77	1.4.77	17.5.77
Hemidiaptomus gurney		10	2	4	20
Potamocypris almasyi		4	5	3	6
Ceriodaphnia sp.			17	800	20
Melanopsis praemorsa		2	2	1	1
Chydoridae				7	20
Oligochaeta			1		
Ephemeroptera				3	
Daphnia				3	
Cyclops				6	
Diaptomid				3	
Gush Halav Pond		17.12.77	10.1.77	15.3.77	3.4.77
Hemidiaptomus gurney		4	3		
Lynceus		30	54	257	
Ceriodaphnia sp.		33	20	3	
Cyzicus sp.			1	2	
Eucypris lutaria				40	
Cyclops			1	1	
Arctodiaptomus similis				1	
Chironomidae larvae				4	
Coleoptera larvae				1	
Tel Dan		20.3.77	21.5.77	24.6.77	21.7.77
Melanopsis praemorsa		2	2		2
Gammarus sp.		7	10	9	8
Ilydromus sp.			3		
Insecta		1	1		
Hammama	4.12.77	8.1.77	3.2.77	22.3.77	1.4.77
Culex larva	1				2
Insecta	4				
Salamandra larvae	4	1	2	3	2

Table 8.2. Invertebrates in water (Degani and Mendelssohn, 1978).

Sasa Pond	3. 12. 77	15.2.77	15.3.77	9.4.77
Hemidiaptomus gurney	94	153	3	2
Potamocypris almasyi	3	1	30	50
Ceriodaphnia sp.	2	4	20	24
Chydoridae		3	5	5
Corixa	2	1	1	3
Cypris pubera		12	20	
Arctodiaptomus similis		1	4	
Dytiscid larvae			1	2
Hemiptera larvae			1	1
Eucypris sp.			1	2
Chironomidae larvae		1	2	1

Sasa Rock Pool	3.1.77	20.2.77	1.4.77	17.5.77
Hemidiaptomus gurney	10	12	11	10
Potamocypris almasyi	4	5	50	255
Melanopsis praemorsa	2	2	1	1
Ephemeroptera		1		
Ceriodaphnia sp.		1	73	165
Chironomidae larvae		1	1	
Chydoridae			7	25
Daphnia		1	2	
Cyclops		1	6	2
Culex			2	3
Corixa	1	2	1	1

Gush Halav Pond	20.1.77	17.2.77	15.3.77	3.4.77
Hemidiaptomus gurney	2	38	2	
Lynceus sp.	3	2	30	25
Ceriodaphnia sp.		5	2	5
Cyzicus sp.	2	1	3	4
Eucypris lutaria			10	4
Cyclops			2	
Arctodiaptomus similis			1	
Chironomidae larvae		2	1	1
Coleoptera larvae			3	
Corixa		1	1	1

Tel Dan	20.3.77	21.5.77	24.6.77	21.7.77
Melanopsis praemorsa	2	2	1	2
Gammarus sp.	1	2	1	1
Ilydromus sp.		1		
Odonata larvae	1	1		
Planaria	1			

Hammama	3.2.77	17.2.77	22.3.77	1.4.77	12.4.77	1.8.77
Culex		1		3	2	

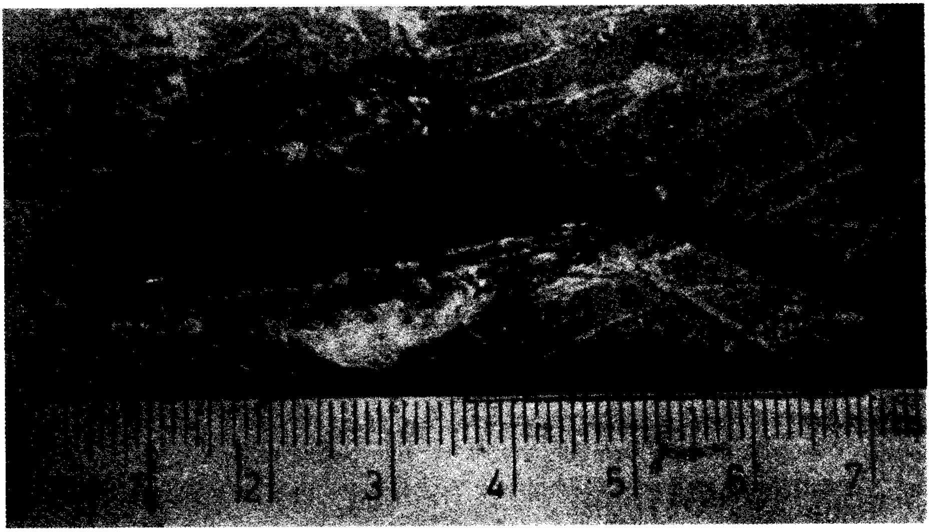


Fig. 8.1. Cannibalistic larva and its prey (Degani, 1980).

Fig. 8.2. Small larva in stomach of large larva (Degani, 1980).

widely differing habitats, with regard to both the variety and quantity of invertebrates available. The assumption that this absence of selectivity in feeding also applies to many other species of Urodela is backed up by the work of Avery (1968; 1971) on the newts, *T. helveticus*, *T. vulgaris* and *T. cristatus*, and by studies on the larvae of American Urodela such as *Ambystoma tigrinum, Eurycea bislineata* and *Desmognathus fuscus* (Houtcooper, 1973; Caldweel and ; Rose and Armentrout, 1975; Burton, 1976). The phenomenon applies also to Urodela in their terrestrial phase: Szabo (1962) and Fachbach et al. (1975) report it for *S. salamandra*, Rose and Armentrout (1975) for *A. tigrinum*, Jeayer (1972) for *P. richmondi shenandoah* and *P. cinereus*, Fraser (1976) for other varieties of Plethodon, Hairston (1949) and Huheey and Brandon (1973) for other varieties of *Desmognathus*.

Regarding availability, the disagreement over preference, between Szabo and Fassbach et al., mentioned earlier in this chapter, is probably a matter of relative availability in the respective habitats, rather than selectivity. Avery (1968; 1971) also mentions size and speed as limiting factors in the prey of varieties of newts, of the Triturus family. As far as size is concerned, the case is strengthened by the fact that the mud crustacean *Syzicus*, which is to be found in the Gush Halàv pond all year round, was eaten only by large salamander larvae (Tables 8.1, 8.2).

Cannibalism in the salamander at the southern limit of its distribution was studied by Degani and Mendelssohn (1978), Degani et al. (1980) and Degani (1993). The practice of cannibalism that was found in the Hammama spring and, to some extent, in the Carmel spring, enables salamander larvae to survive in bodies of water that are poor in nutrition sources, but otherwise thoroughly suitable for salamanders after metamorphosis. In the Mt. Meron area, where there are rock pools and shaded water holes, which apparently have low productivity of fauna, energy is transferred from the adult salamanders to their larvae by the latter preying on smaller larvae. The cannibalistic larvae complete metamorphosis in winter, and are, therefore, not exposed to the danger of dehydration, unlike the larvae in other water bodies that undergo metamorphosis in spring and summer. Our research on cannibalism in *S. salamandra* revealed certain morphological difference between cannibal larvae and those that feed normally on invertebrates: the former are particularly large and have wider heads.

Joly (1968) describes the phenomenon of intra-uterine cannibalism in *S. salamandra*. In this form of cannibalism, the larvae break out of their embryonic envelope inside the uterus and feed, not only on infertile ova, but also on undeveloped larvae. Rose and Armentrout (1975) also describe cannibalism in larvae of *A. tigrinum*.

Although there is not enough evidence to prove it, it is a plausible hypothesis that cannibalism develops readily in varieties of Urodela, since they prey on such a wide variety of species, especially though not only, on invertebrates. For example, newts of the Triturus family prey on Anura larvae (Cooke, 1974a), which also serve salamander larvae for food. In the laboratory, we successfully fed salamander larvae on the larvae of *Bufo viridis*, indicating that although only a few examples of *B. viridis* larvae were found in their digestive tracts in nature (in the Carmel area) there can be no doubt that they are suitable food for the species.

It is notable that no cannibalism was found in the Sasa pool, nor in the pool at Gush Halav, where the larva populations were particularly dense. The reason is evidently that other food is plentiful in these locations. Furthermore, no Anura larvae were found in the digestive tracts of salamander larvae from Sasa, even though such larvae are to be found there: the implication is that these represent a low preference as prey. Both these findings suggest that there is some degree of selectivity in the feeding habits of the salamander.

CHAPTER NINE

INFLUENCE OF FOOD AND TEMPERATURE ON GROWTH OF LARVAE UNDER CONTROLLED CONDITIONS

Salamander larvae grow in water bodies in which conditions such as food supply and temperature vary considerably. As we have seen, this is particularly true of the environment at the southern limit of its distribution. Thus, the larvae are able to flourish in winter pools that dry up after the rains (Gush Halav and Sasa), in which there is an abundance of food, and also in springs where there is little food (Hammama); in places where the temperature is virtually constant all year round (Tel Dan), as well as in water bodies in Galilee and Carmel where, by way of contrast, the temperatures are very low in winter and very high in summer, with differences of up to 30°C.

Thus, it was important to examine the influence of variations in food and temperature on the growth of the larvae in the laboratory, under controlled conditions, isolated from other factors that influence growth. No such work on salamanders had been done previously, nor had such data been available for other species of Urodela, apart from those published by Brandon (1976), prior to the studies by Degani and Mendelssohn (1978), Warburg et al. (1979), and later by Degani (1993).

The aim of the study (Degani, 1993) was to gain a better understanding of how salamander larvae survive and grow in their various habitats, by determining the influence of the following parameters on growth and development:

1. The temperature range;
2. Whether there were regional differences;
3. Water quality;
4. Population density;
5. Cannibalism as an alternative to normal food;
6. The length of time that larvae could exist without food, while still completing metamorphosis.

To this end, a number of experiments were conducted in the laboratory. The results were analyzed statistically, with significance of differences between means examined by t-test, the equations of the best-fit lines connecting groups of variables were calculated by regression, and the accuracy of fit of the lines to the experimental points was analyzed by means to the correlation coefficient r and by t.

EXPERIMENT 1

To test the influence of temperature under conditions of food shortage, 60 larvae from a single brood of a Galilee female were divided into three groups, with each group of 20 placed into a separate glass aquarium, measuring 60 × 20 × 40 cm, with a water depth of 10 cm. One group was maintained at 20°C, the second at 25°C. These temperatures were maintained to an accuracy of ±0.5°C. The third group was maintained at winter room temperature, which varied between 10–15°C, as determined by a maximum-minimum thermometer (Fig. 9.2). The groups were fed once a day, with a constant and equal quantity of invertebrates, taken from pools or other water bodies by means of a 20 × 10-cm net with 1-mm mesh. Equal distribution of invertebrates was ensured by mixing the catches thoroughly in a single water container, and dividing the water into three equal parts. The rates of growth of the larvae were determined by weighing them and measuring their length.

EXPERIMENT 2

To find out whether larvae are able to grow at a temperature of 5°C, 50 larvae were taken from a single brood in Galilee and 50 from a brood on the Carmel. Each of these two groups was subdivided into two groups of 25 larvae, one of which was maintained at 18°C and the other at 5°C. The weights and lengths of the larvae were measured once a month.

EXPERIMENT 3

This experiment studied the effect of different temperatures on the rate of growth and completion of metamorphosis, under conditions of abundant food. The larvae were supplied with an excess of food, in the form of invertebrates, throughout their development. Three groups of five larvae, all from a single brood from Galilee, were maintained at 10°C, 16°C and at ambient temperature (10–20°C). Each group was subdivided among three containers, measuring 35 × 20 × 15 cm, which received two, two and a single larva, respectively. The weights and lengths of the larvae were measured approximately once every 2 weeks.

Larvae were able to complete their metamorphosis within 35 days, under conditions of excess food, in a wide range of temperatures 16–30°C (Fig. 9.1). However, when food was limited, a rise in temperature became a handicap, not an advantage. Thus, with a limited food supply, larvae grew more quickly at 20°C than at 25°C. Interestingly enough, the time taken to complete metamorphosis was identical in the two cases, so that the larvae kept at the higher temperature were smaller on completion (Fig. 9.2). When the food supply was limited, there was a significant difference in growth between larvae maintained at 10–15°C and those maintained at 20° or 25°C. In the trial with excess food, there was also a significant difference in growth between larvae grown at 10°C and those grown at 15–20°C or at 16°C. Larvae from both Galilee and Carmel failed to develop or achieve metamorphosis at 5°C, up to the time the experiment was terminated, after one year. At 10°C, growth was slow, and metamorphosis took from 1 to 1.5 yr. The experiment therefore

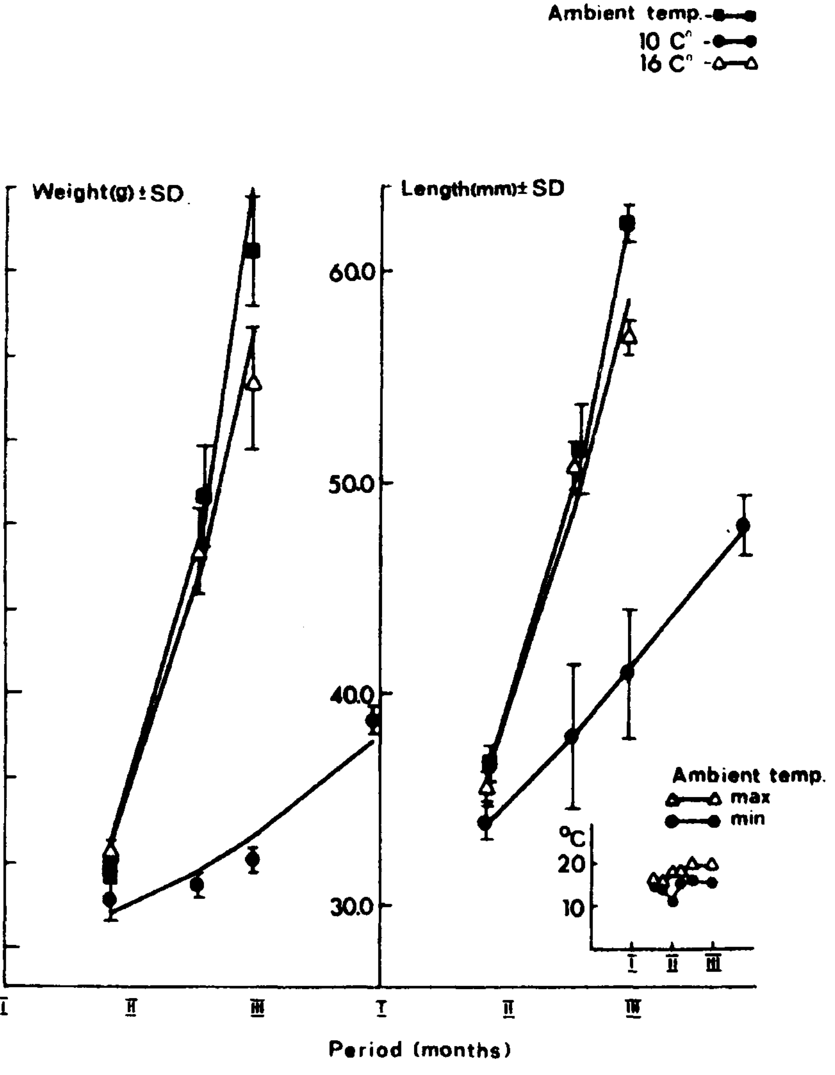


Figure 9.1. Rate of growth under different temperatures and with abundant food (Degani, 1993).

established that larvae require a minimal temperature of 10°C to develop and complete metamorphosis in a single season.

EXPERIMENT 4

This experiment aimed to compare the rates of growth and metamorphosis of larvae from Galilee (Gush Halav) with those of larvae from Carmel, using 20

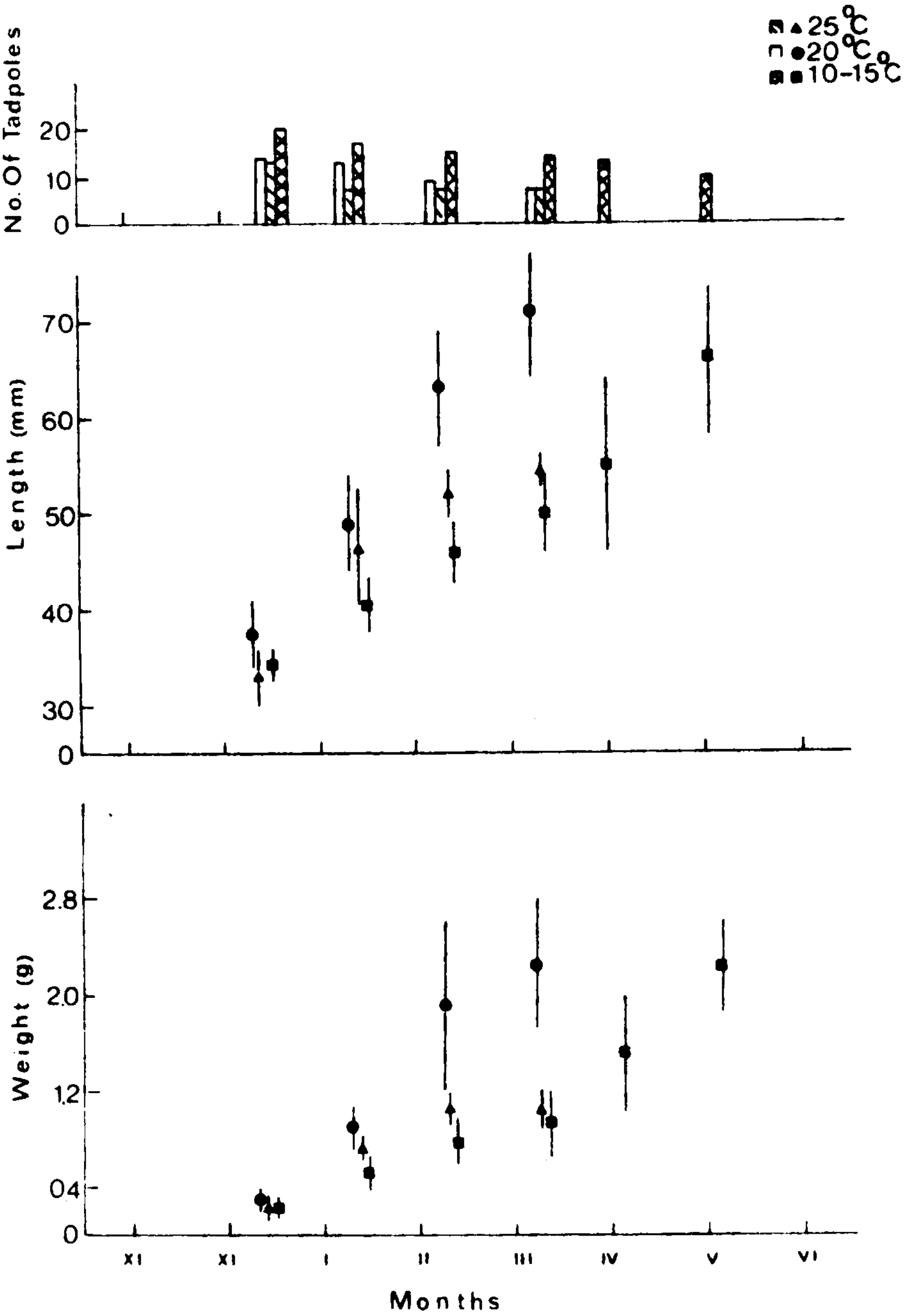


Figure 9.2. Rate of growth under different temperatures with limited food (Degani, 1993).

specimens from single and contemporary broods in each case. Each group was subdivided into two equal sub-groups, with one maintained at 28–30°C and the other at 20°C. The larvae were fed to excess throughout the experiment, and they were weighed and measured every 3 weeks.

No significant difference was found between these two sites of origin (Galilee and Carmel), in rates of growth, but in a comparison between larvae from Galilee and from Tel Dan, a significant difference emerged at most of the stages of development, with the Galilee larvae larger than the Tel Dan larvae, on average (Fig. 9.3).

EXPERIMENT 5

The aim in this experiment was to examine the effects of food shortage on the rate of growth and on cannibalism. Twenty-six larvae of a single brood from Galilee were equally divided between two containers, measuring 35 × 20 × 15 cm. In the first container, there was enough invertebrate food for half a week, after which the larvae were given no food for 4 days; in the second container, half this quantity of food was provided. The larvae were weighed and measured once a month. The results of this experiment are shown in Fig. 9.4. Larval growth was approximately the same in the two groups: partial cannibalism developed in the second group, thereby supplementing the relative lack of food.

EXPERIMENT 6

This experiment examined the growth of larvae whose only source of food was other salamander larvae. On 13th December, 1977, 10 large larvae from Hammama were caught and put into two plastic containers (40 × 20 × 10 cm), five larvae to each container. Fifteen small larvae, immediately after birth, were put in with the first group. Each day, the larvae that remained were counted, and the numbers made up to the starting point by adding more recently born small larvae. The second group was kept without any form of food. Measurements were taken at intervals ranging from 2 weeks to a month.

Cannibalism developed whenever there was a lack of food. Larvae tried to eat each other even when they were of the same size, but successful cannibalism, i.e., one larva actually ingesting another, only took place when one larva was bigger than the other (Fig. 9.5). Such differences in size were not confined to earlier and later broods: during growth, the time when cannibalism was observed, larvae grew at different rates, to the point that cannibalism within a single brood took place. The phenomenon increased with increasing temperatures, but where food was abundant, no cannibalism occurred.

Larvae from Hammama, where cannibalism occurs in nature, are able to survive and grow by preying on smaller salamander larvae. Under the conditions of the experiment, five cannibalistic larvae ate 116 smalller larvae in a period of 3 months. The larger they grew, the higher the rate of cannibalism became. Cannibalism ceased when clear signs of the beginning of metamorphosis appeared.

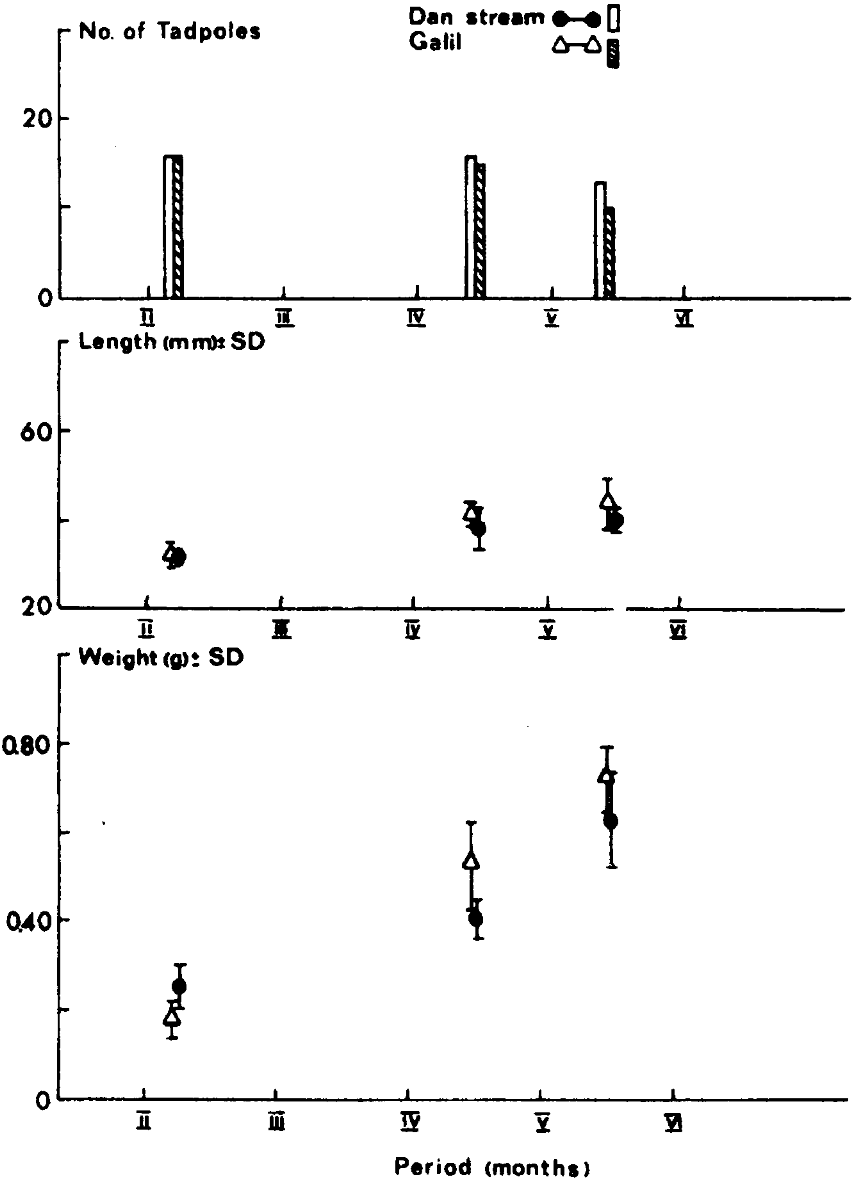


Figure 9.3. Rate of growth of larvae from Hammama (Galilee) and from Tel Dan. The former were cannibalistic and the latter not (Degani, 1993).

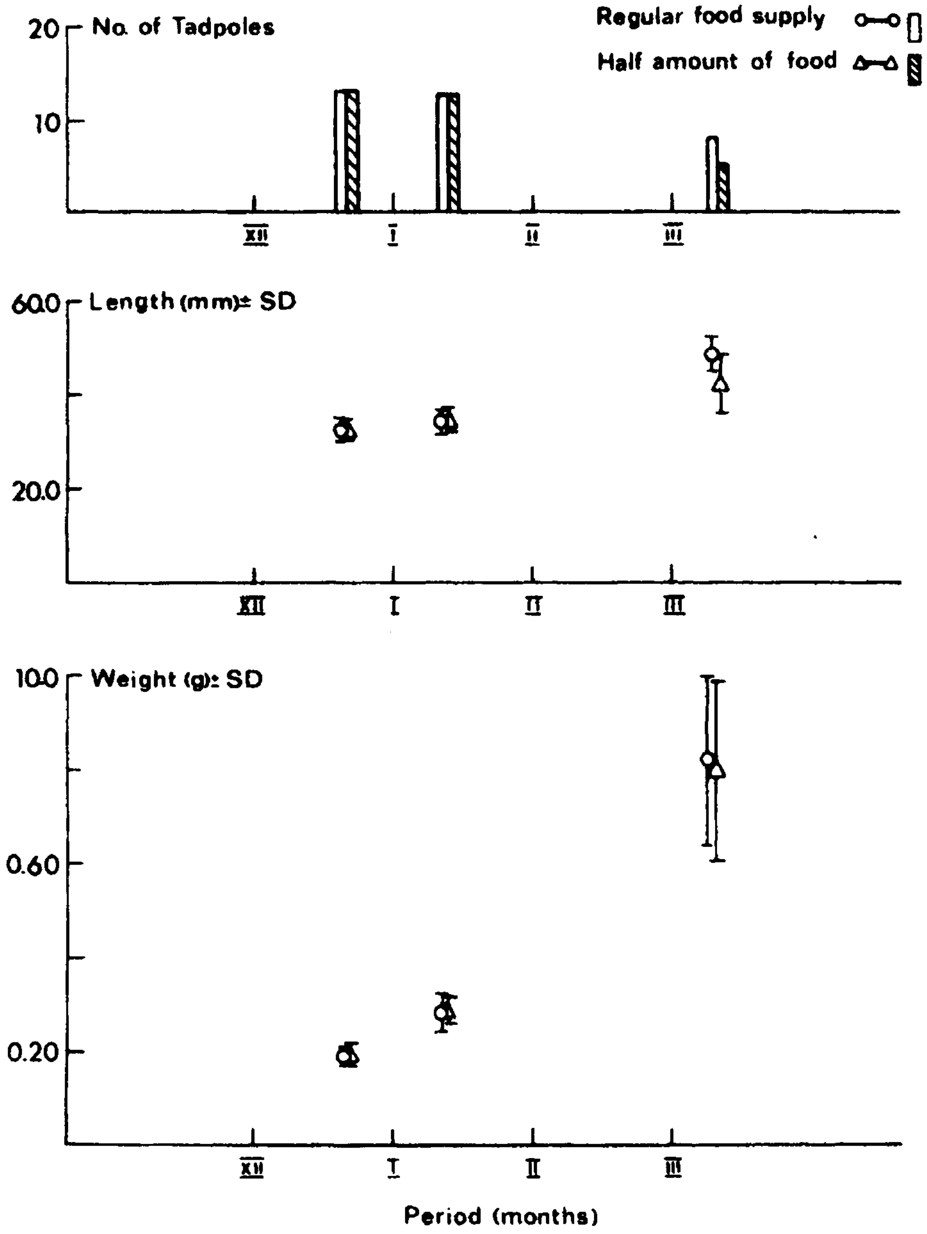


Figure 9.4. Influence of lack of food on growth rate and cannibalism (Degani, 1993).

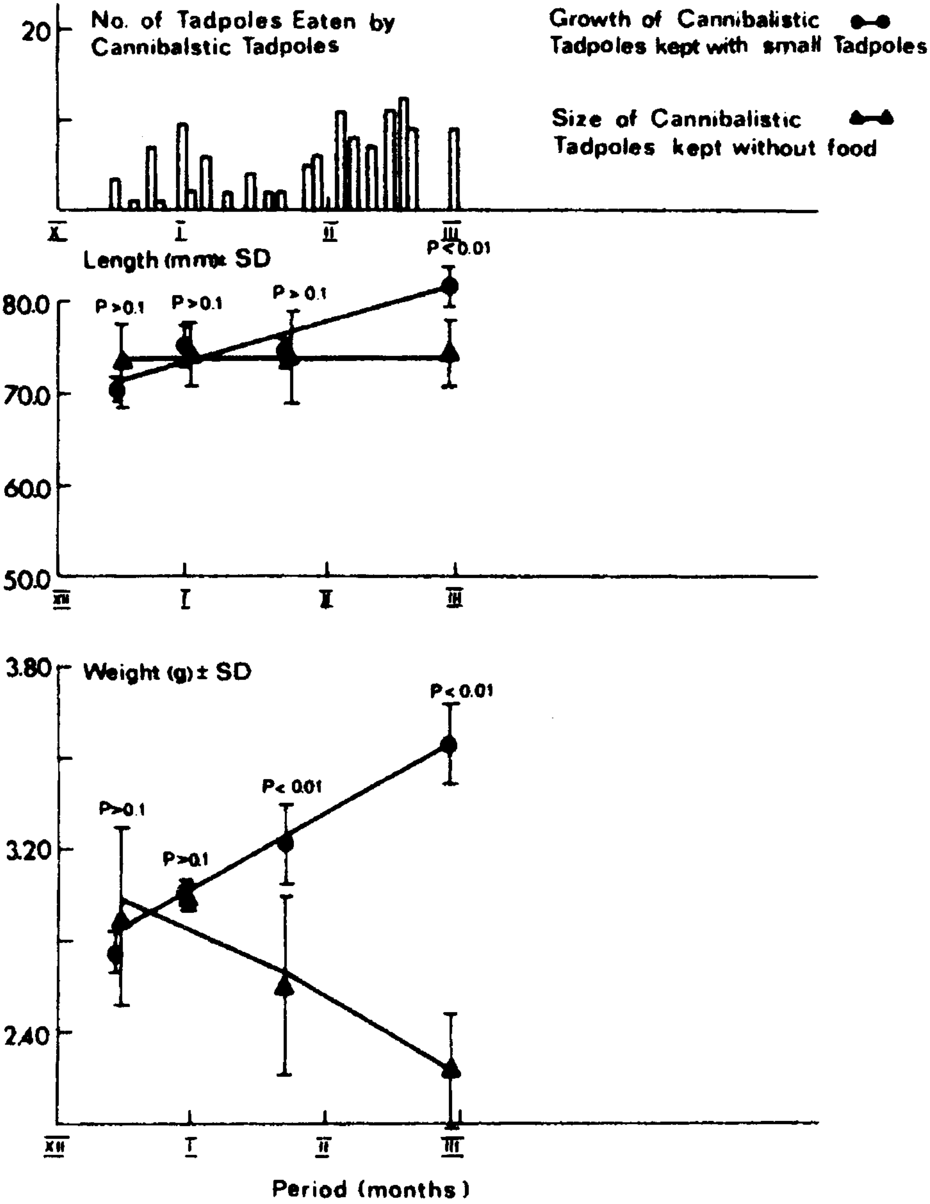


Figure 9.5. Rate of growth and degree of cannibalism in larvae (Degani, 1993).

EXPERIMENT 7

In addition to determining the effect of food shortage on the rate of growth and on cannibalism, this experiment also tested the ability of larvae to withstand the absence of food. Fifty larvae, from a single Galilee brood, were divided into groups. The first group (20 larvae) was maintained in an aquarium measuring 40 × 20 × 10 cm, and was fed invertebrates throughout the duration of the experiment. The second group (also 20 larvae) was placed in a similar aquarium, but was fed only after 4 months. The remaining 10 larvae were put into individual 25-ml Erlenmeyer flasks and were not fed at all.

The results of these experiment showed that neonatal larvae are able to survive up to 4 months, in temperatures of 10–15°C; if they are then supplied with food, they grow and undergo metamorphosis, although they remain small (Fig. 9.6).

EXPERIMENT 8

In an experiment to examine the effect of population density on the growth rate, 60 larvae from a single Galilee brood were divided into three equal groups. The first group was placed in an aquarium, measuring 60 × 25 × 32 cm, the second into an aquarium of 30 × 25 × 35 cm, and the third into an aquarium of 15 × 10 × 15 cm, and maintained at ambient temperature. All three groups were fed *ad libitum* with equal quantities on invertebrate food. The larvae were weighed and measured once a month.

The experiment demonstrated how larvae can survive, develop rapidly and undergo rapid metamorphosis in such densely populated winter pools as the one at Gush Halav. It was found that density of population had no significant effect on the rate of growth, nor on the degree of cannibalism: the availability of food and, to a lesser extent, the temperature, were the determining factors in both cases (Fig. 9.7). Indeed, where food was plentiful, no signs of cannibalism were found.

EXPERIMENT 9

The influence of water composition on the growth rate of larvae was examined. Forty larvae, from a single brood at Hammama, were divided into two equal groups, the first of which was kept in an aquarium filled with distilled water, the second in an aquarium of identical size, filled with water brought from the Hammama spring. This spring water is the richest in ions of all the water bodies studied in Israel, with a conductivity of 1.2–2.6 mmho (Degani, 1976). The larvae in this experiment were weighed and measured once a month. Only the rate of growth was examined: once the larvae in the ion-rich water began to show signs of metamorphosis, the experiment was terminated.

No difference was found between the two groups (Fig. 9.8).

EXPERIMENT 10

The aim of this experiment was to compare rates of growth of larvae from Galilee

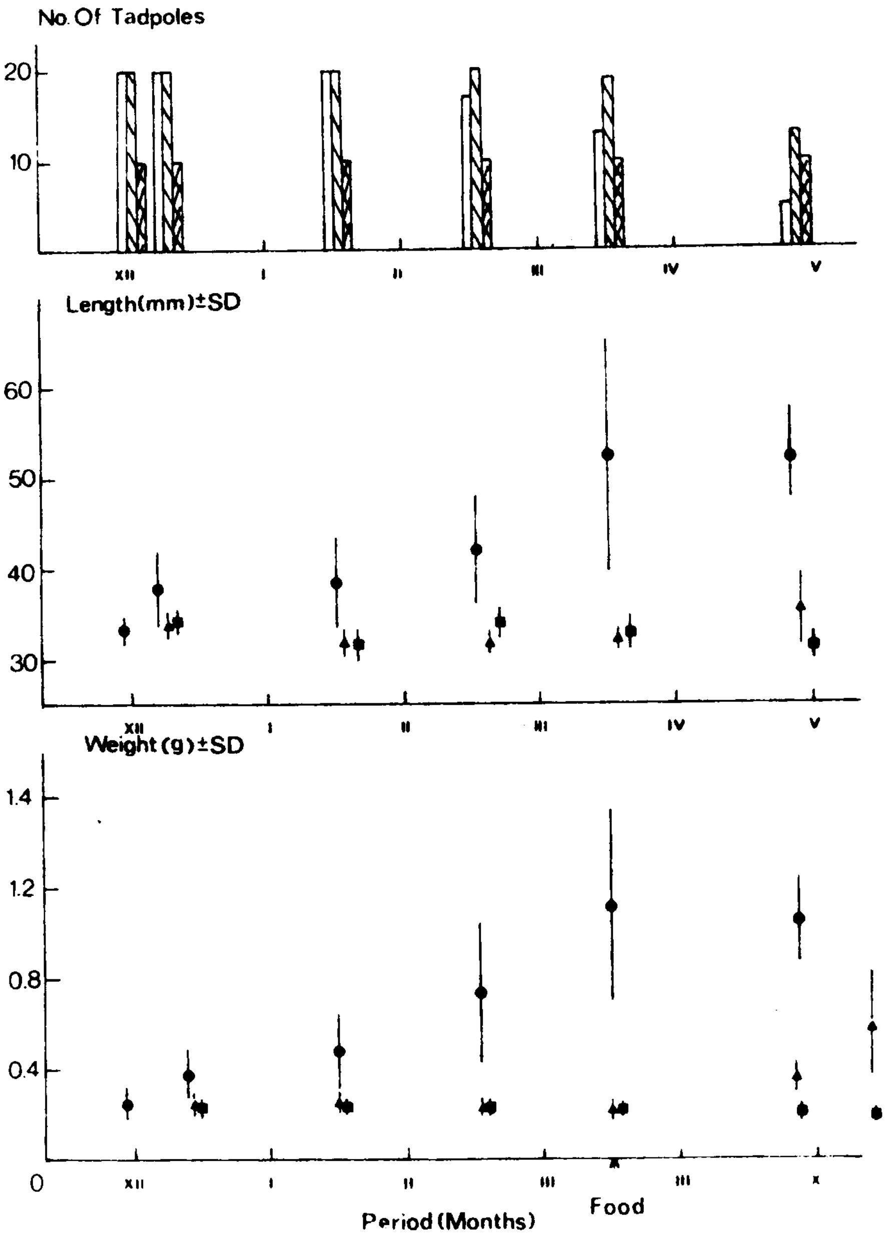


Figure 9.6. Rate of growth and degree of cannibalism of larvae feeding only by cannibalism. ● = with limited food; ▲ = group without food; ■ = individuals without food (Degani, 1993).

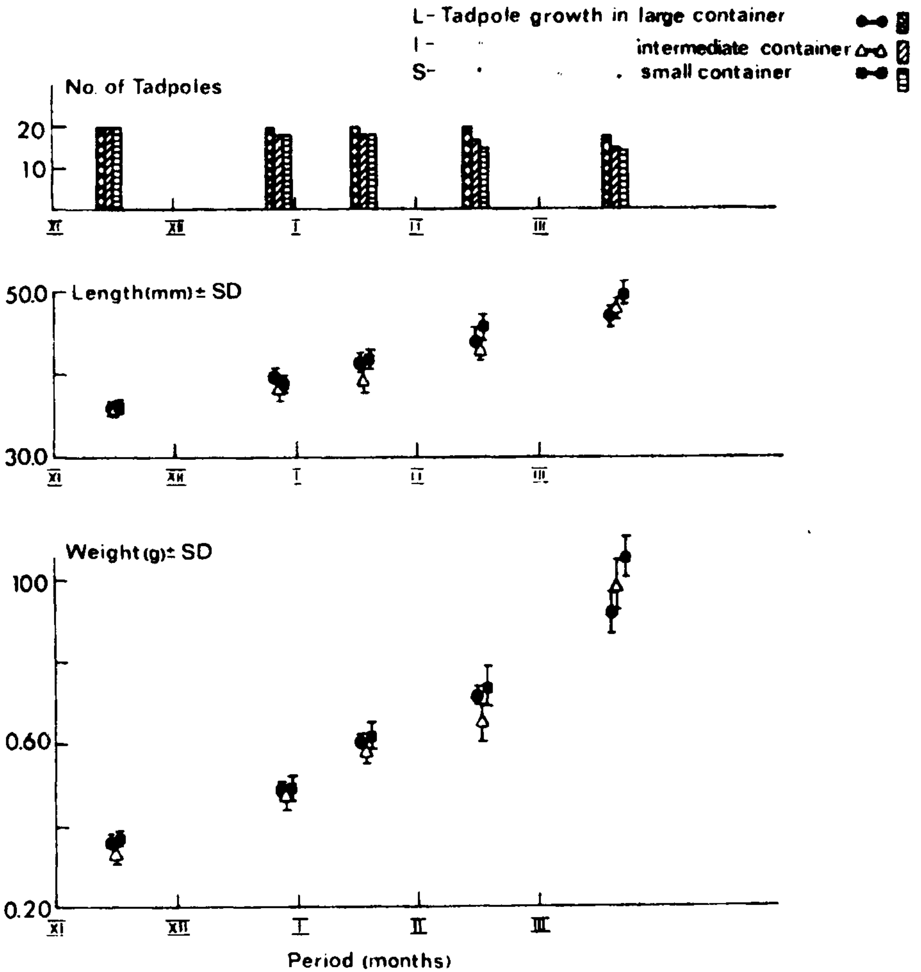


Figure 9.7. Influence of population density on growth and cannibalism (Degani, 1993).

with those of larvae from Tel Dan. Sixteen larvae of a single brood from Galilee were placed in a 40 × 20 × 10-cm aquarium, and 16 of a brood from Tel Dan in another. The broods were contemporaneous. Food was distributed equally to the two containers. The larvae were weighed and measured monthly.

A higher rate of cannibalism was observed among the larvae from Galilee than among those from Tel Dan (Fig. 9.3).

Summing up, we can conclude that salamanders are able to overcome lack of food through cannibalism. The availability of food and the temperature of the water

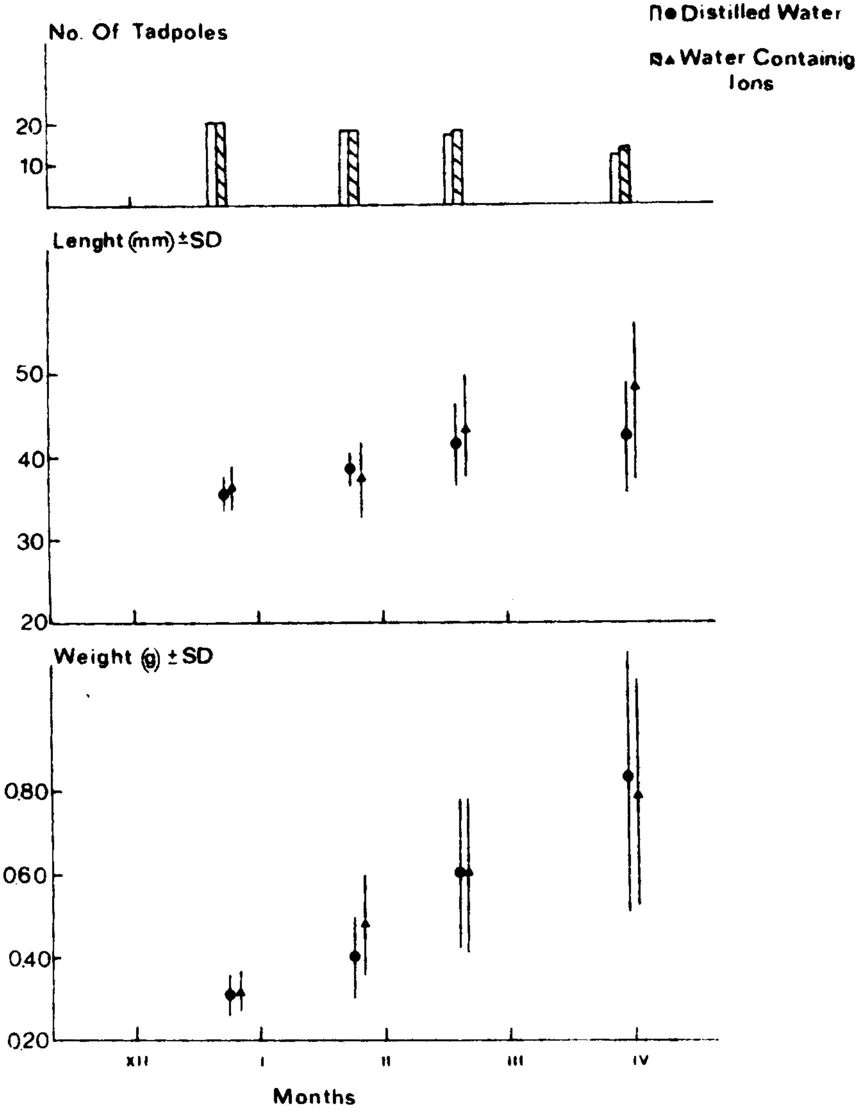


Figure 9.8. Rate of growth in distilled water and water containing ions (Degani, 1980).

are the major influences on their rate of growth, but the species shows its high degree of adaptability by developing under wide ranges of these conditions. The general agreement among researchers, that environmental factors are dominant in the growth and metamorphosis of Urodela (Shoop, 1974; Bell and Lawton, 1975, Eagleson, 1976) was further suported in the case of *S. salamandra*, in the areas studied in the experiments described above.

A wide variety of sources of food, temperatures and water qualities is to be found in the water bodies containing salamander larvae that were studied in our research. However, the studies described here are among very few that examined the influence of food, temperature and water quality on growth, growth rate and completion of metamorphosis under controlled laboratory conditions, with each factor isolated.

Species of amphibians do not grow in temperatures of 5°C or less (Wilbur and Collins, 1973). Eagleson (1976) showed that variations in water temperature affect the rate of growth and metamorphosis in *Ambystoma gracile*. The same phenomenon has been demonstrated in *Triturus vulgaris*, whose rate of growth varies in different pools, and, as we now see, in *S. salamandra* growing in different water bodies. The considerable influence of temperature on growth rate that has been demonstrated for other varieties of Urodela serves to confirm the reliability of our results.

In temperatures of 15–20°C, and with an abundance of food, consisting mainly of *Daphnia*, salamander larvae from Galilee take some 35 days from birth to complete metamorphosis. Prof. Mendelssohn (personal communication) found that, where the principal food consists of *Tubifex*, *Antrisot* and *Enchytraeus*, the process can be completed in as little as 3 weeks. When the food supply is limited, the growth rate is slower and partial cannibalism develops, with larvae supplementing their invertebrate food by preying on each other.

The finding that salamander larvae can survive for 4 months without food at these temperatures, and still complete metamorphosis if food becomes available after this period, has not been examined in other varieties of Urodela. Consequently, any conclusions drawn can be applied only to *S. salamandra*. It appears that the larvae survive over this long period on nutritive materials stored in the body. In caves and other dark water bodies, little food is available in winter, so larvae which can survive for a long period without food are at an advantage. As we have seen, the main breeding period of hill populations is at the beginning of winter, apparently because conditions for adult activity are optimal. On the other hand, the optimal conditions for the growth of larvae prevail in late winter and early spring, when temperatures begin to rise and food grows abundant. Salamander larvae are capable of bridging this gap without food and, therefore, have an improved chance of survival.

In the work on *A. gracile* by Eagleson (1976), mentioned above, on differences in growth rates and metamorphosis, in similar temperatures (21°C), he found that the development of larvae from an environment at 1200 m was faster that of larvae whose origin was at 100 m. His conclusion was that the difference between these two populations was genetic, and that the rapider growth rate found at greater heights was an adaptation to the short summer that obtains at these heights, in caves in the mountains of British Columbia. The shortness of the summer obliges the larvae to complete metamorphosis more rapidly.

A parallel phenomenon was found in our research on *S. salamandra*, though evidently as a result of different climatic conditions. The rate of growth of larvae from Galilee was higher than that of larvae from Tel Dan, with significant differences at most stages of growth, whereas no significant difference was found between the growth rate of larvae from Galilee with those from Carmel. These findings, however, point to adaptation to the availability of water rather than to temperature: in Galilee and Carmel, the habitats of the salamander are mostly seasonal water bodies, such as winter pools or the summer stream, whereas in Tel Dan water is reliably available throughout the year. Although there are differences in seasonal temperatures between these habitats, they are by no means as marked as in Eaglesonís work, and hence it is unlikely that temperature limitation is the main factor in the genetic adaptation of salamanders in Israel, though it is certainly one factor in genetic variations, as we shall see.

Cannibalism has been described in a number of amphibian species (Heatwole and Test, 1961; Heusser, 1970). In some populations of *A. tigrinum*, cannibalism is likely to occur, whereas in others the main food consists of invertebrates (Rose and Armentrout, 1975). In this case, the cannibals are bigger than their prey and exhibit certain other morphological differences from them.

Joly (1968) described intra-uterine cannibalism among *S. salamandra* found in the mountains of Europe. This form of cannibalism enables the predator to develop to an advanced stage within the uterus, or even to attain metamorphosis and leave the uterus as a fully formed salamander. In the areas studied in our research, the southern limit of the salamanderís distribution, cannibalism in nature was found only in Hammama in Galilee, where food is short, and in a Carmel spring. However, in our laboratory work, we found that cannibalism can also develop among larvae which originate in populations in which no cannibalism is found in nature. Attempts at cannibalism feature constantly among salamander larvae, but as we mentioned above, succeed only where there is a significant difference in size between predator and prey.

Two forms of cannibalism were observed in the laboratory. The first form is partial cannibalism, in which the source of nutrition is a mixture of invertebrates and other salamander larvae: this form was found when food was limited. The second form is full cannibalism, in which large larvae subsist solely on smaller ones.

The illustration below (Fig. 9.9) presents a model of larval growth, under the influence of various conditions of nutrition, which allows the prediction of whether cannibalism will occur under given conditions in nature, in what form and at which stage of development.

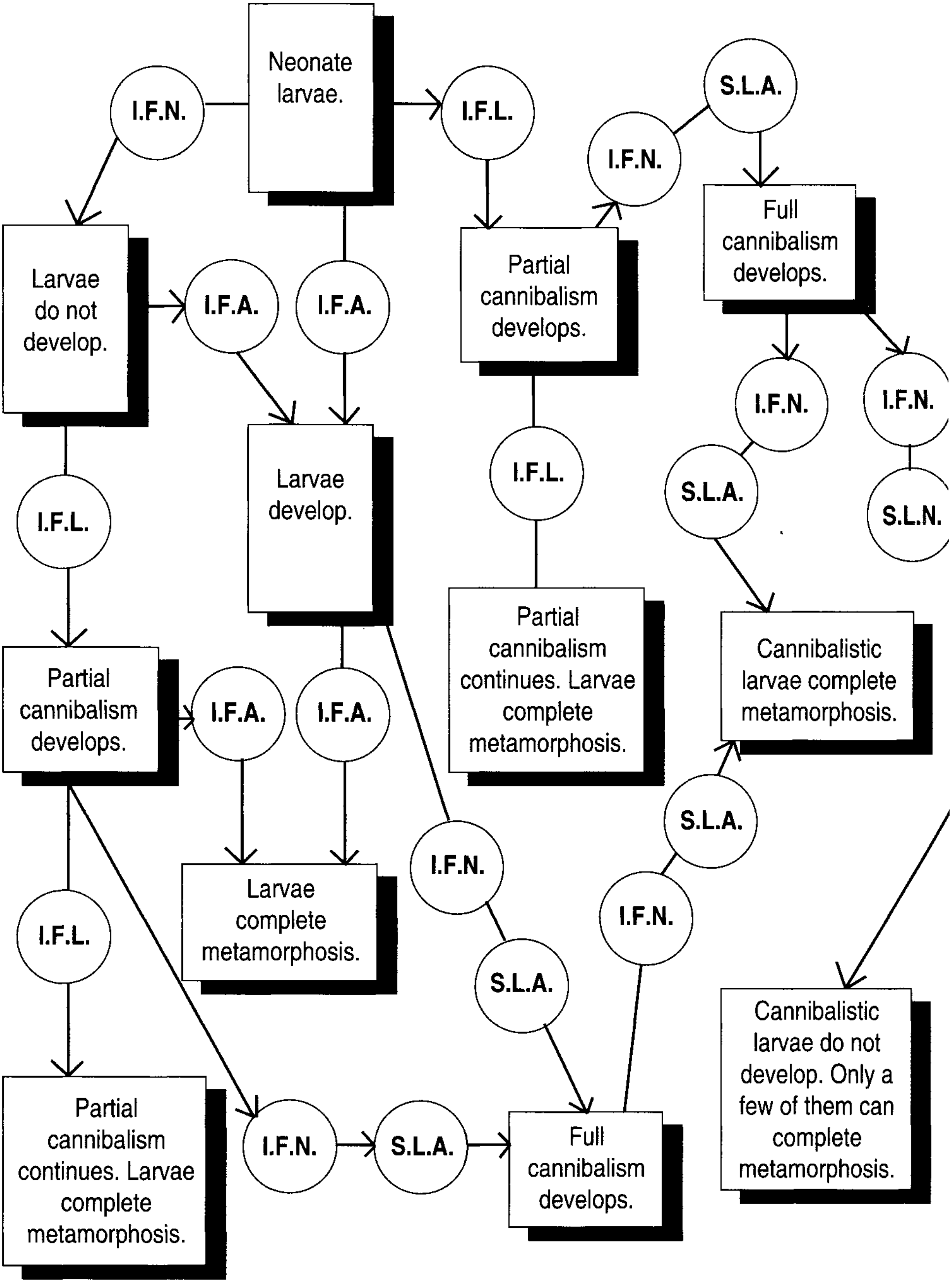


Figure 9.9. Model of the influence of food on development (Degani and Mendelssohn, 1978). IFA = Invertebrate food available; IFN = Invertebrate food not available; IFL = Invertebrate food limited; SLA = Small larvae available; SLN = Small larvae not available.

PART III:

BEHAVIORAL ADAPTATION TO ENVIRONMENT

CHAPTER TEN

CHOICE OF SHELTER

The availability of water is one of the major factors that influence the behavior of the terrestrial Urodela. Activity on the ground and migration to the breeding ground are influenced mainly by rainfall and relative humidity (see Chapter 2). Urodela prefer moist soil (Rosenthal, 1957; Batson, 1965; Joly, 1968), but there are variations in the degree of soil moisture selected by water-loving species subject to dehydration (Anderson, 1972; Marangio and Anderson, 1977).

In the case of *S. salamandra* at its southern limit, populations which inhabit seasonal pools and streams undergo metamorphosis just at the time when these water bodies are beginning to dry up, with the result that the young come under the threat of dehydration, to which the they are more subject than the adults, because of their higher ratio of body surface area to body weight. Their response is to seek shelter. The populations in the hilly regions are exposed to harder conditions in this respect than salamanders in Tel Dan, and furthermore it is more difficult for them to find shelters with moist soil than in areas where water is plentiful. This chapter considers the principal factors that influence the choice of shelter, and the influence of soil moisture on behavior. The behavior of young *S. salamandra* will be compared with that of adults and of adult salamanders from different habitats. The way the species finds shelter forms a very important component of its adaptation to extreme conditions. Relevant papers were published by Degani and Mendelssohn (1980; 1982) and Degani and Warburg (1980).

SOIL MOISTURE SELECTION

The first experiment in our study of the influence of soil types and soil moisture involved wooden boxes (45 × 35 × 45 cm), each holding four containers of soil or sand at different degrees of moisture: the former was heavy soil, taken from Sasa, and the latter was dune sand, from near the sea shore. The depth of the substrate, in all cases, was 10 cm (Fig. 10.2).

The salamanders were caught as described in Chapter 2. Young specimens were taken as larvae from the hilly areas of Galilee and Carmel, in March and April, and maintained in the laboratory under the same conditions as those for adults: 16°C; 12 h light: 12 h darkness. Experiments on the young animals were carried out within a year or two of their metamorphosis.

The water capacity of the various substrates was determined as follows: a glass was half filled with the substrate and topped up with water. After an hour, the glass was emptied and the substrate allowed to drain of all excess water for a further hour, leaving only that held by the soil. The substrate was weighed, then oven dried at 105°C until its weight remained constant. The percentage of water in the soil at saturation point was then calculated by deducting the weight of the dry soil from that of the saturated soil. The percentage of water in saturated sand was 24.6% and that in heavy soil, 35.8%. The figure of 24.6% was taken as the 100% base level in examining behavior with various percentages of water: 13, 38, 63 and 88%. For example, in order to examine behavior on 88%-saturated sand, the amount of water (g) added to W g of sand was

$$\frac{24.6}{100} \times \frac{88W}{100}$$

The following experiments were conducted:

EXPERIMENT 1

To examine behavior at different degrees of moisture, adult and juvenile salamanders were placed in containers which offered a choice of sand at 3.08, 9.23, 15.38 and 21.53% moisture (Fig. 10.2), and the number on each was counted after 10 h in each case. The experiment was conducted between 1700 and 0800 at a constant temperature of 16°C.

The experiment demonstrated that the salamanders showed a clear preference for the moist sand. There were significant differences among the numbers choosing the various degrees of moisture, random distribution and those choosing the various controls, all at 21.53%. Among the juvenile salamanders, 89.7% chose either 21.53 or 15.38% saturation, whereas only 75.9% of the adults chose either of these. This represents a significant difference between juvenile and adult specimens ($p<0.05$) significance of differences was tested in all these experiments by the (χ^2 test) (Fig. 10.1).

EXPERIMENT 2

To examine the effect of moisture in different substrates on behavior, young and adult salamanders from Galilee were placed in separate containers containing, respectively, dry sand, saturated sand, dry soil and saturated soil. The animals were counted after 12 hours.

The results (Fig. 10.3) showed that moisture, not the type of substrate, is the more important factor in the choice of shelter. All the adult salamanders and 97.6% of the juveniles chose a saturated substrate, with both age groups preferring soil to sand.

EXPERIMENT 3

To examine the effect of water loss on behavior, an experiment similar to Experiment 1 was conducted, except that the substrates used were soil, at moisture contents of 4.65, 13.6, 22.55 and 31.5%. Juvenile salamanders from Galilee were tested after 15–20% dehydration, and the specimens were counted after 0.5, 1, 2 and 24 hours.

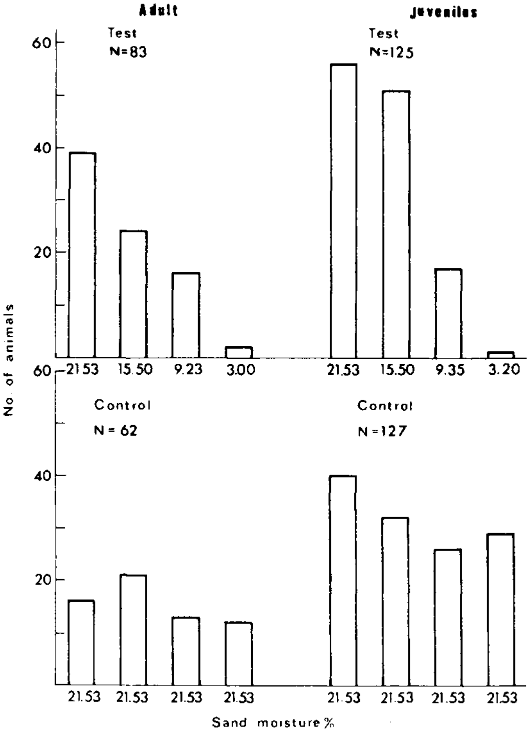


Figure 10.1. Response of adult & juvenile salamanders to substrate moisture (Degani, 1980).

Figure 10.2. Boxes in which behaviour was observed and recorded (Degani and Warburg, 1980).

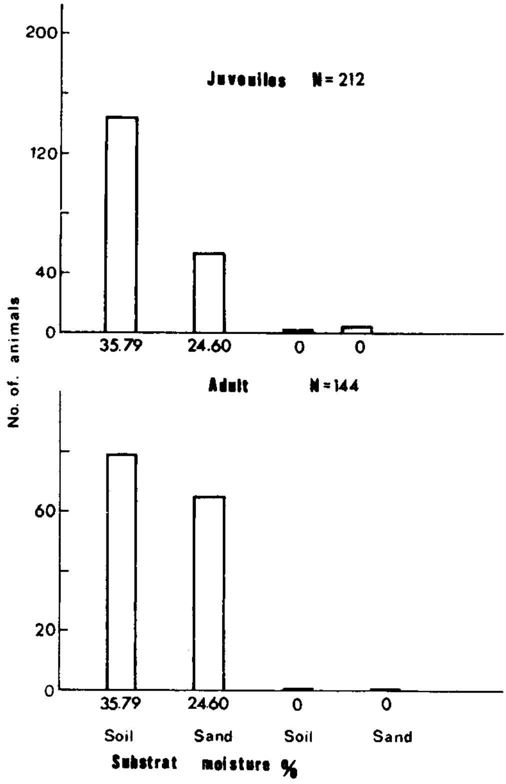


Figure 10.3. Response of adults and juveniles to sand vs. soil moisture (Degani and Warburg, 1980).

A clear preference for saturated soil was already evident after half an hour, and was maintained throughout the experiment (Fig. 10.4). A significant difference was found between the choice among various soil moisture levels and that among controls all of which were at 31.5% ($p>0.001$). Although no significant change in the salamanders' pattern of choice was found between half an hour and an hour, there were significant differences ($p<0.01$) among the proportions that chose various degrees of moisture at each time.

EXPERIMENT 4

This was the same as Experiment 3, except that the specimens examined were juvenile salamanders from Carmel.

There was a clear preference for moist soil over dry soil, with 92.9% of the salamanders choosing the two wetter soils (22.55 and 31.5%). As in the case of juvenile salamanders from Galilee, a high proportion (67.97%) of the Carmel

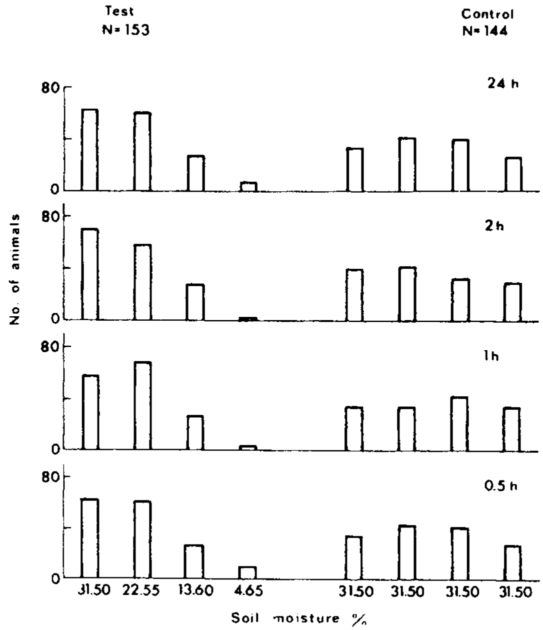


Figure 10.4. Response of dehydrated Galilee juveniles to soil moisture (Degani and Mendelssohn, 1982).

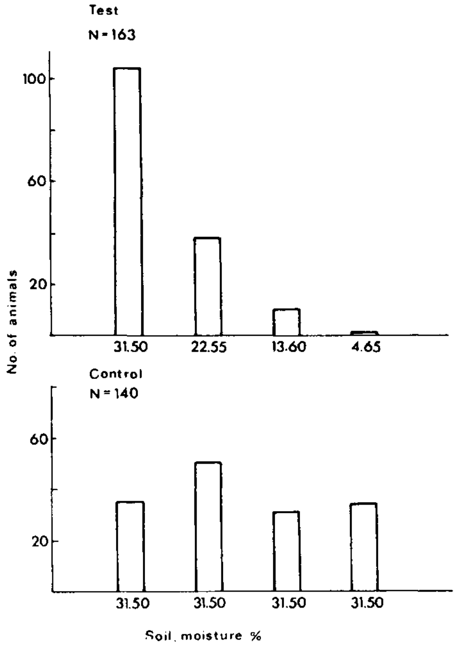


Figure 10.5. Response of Carmel juveniles to soil moisture (Degani and Mendelssohn, 1980).

specimens preferred the wettest soil. There was a significant difference ($p<0.001$) between the distribution of percentages choosing the various moisture levels and the random or control distribution (Fig. 10.5).

EXPERIMENT 5

The aim of this experiment was to determine whether groups of salamanders from different populations differed in their selection behavior. As in Experiment 3, the specimens were partially dehydrated (15–20%), but in this case they were drawn from Galilee, Carmel and Tel Dan populations. The soil water percentages used were tested were 11.6, 23.2, 38.8 and 46.4% (20, 40, 60, and 80% filled capacity), with the last also being used in a control experiment, because this was the upper limit determined in the previous experiments. The number of specimens that selected each soil was counted at 4, 6 and 8 hours.

The specimens from hill populations (Galilee and Carmel) already showed a

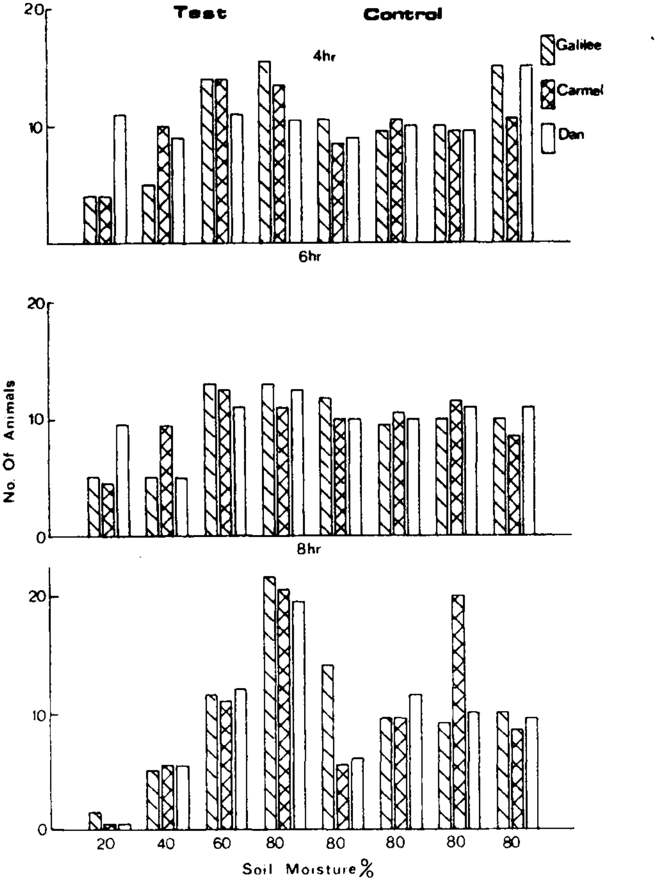


Figure 10.6. Response to soil moisture of salamanders from different localities (Degani, 1980).

significant preference for moist soil after 4 hours, compared with 6 hours for the Tel Dan specimens, but by 8 hours there was no significant difference among the three populations (Fig. 10.6). A significant difference ($p<0.01$) between test and control was exhibited by the Galilee population after 4 hours, by the Carmel salamanders after 6 hours, and by the Tel Dan salamanders only after 8 hours.

INFLUENCE OF MOISTURE AND HOLE SIZE IN SELECTION OF SHELTER

The basic equipment in these experiments was a wooden board (100 × 100 cm), on which an enclosing wall measuring 80 × 80 cm, with rounded corners, was built of clay, to a height of 6.5 cm and thickness of 1.5 cm, and baked at 100°C. Equidistant from each corner, two circular chambers, 8 cm in diameter and the height of the wall, were built of the same material, connected to the enclosure by rectangular openings, that reached from the base to a height of 5.5 cm (Figs. 10.7, 10.8). The entire enclosure was covered with glass and the chambers were covered with black cardboard to darken them. For the purpose of calculations, the results from pairs of chambers were combined.

The salamanders used in these experiments were juveniles, immediately after metamorphosis, measuring 4–7 cm in length and with a maximum width of 1 cm, from a pool at Gush Halav. The animals were placed into the enclosure in the evening and taken out in the morning, after 10 hours. Some 15 specimens were used in each experiment.

EXPERIMENT 6

To examine how the size of the opening to the chamber affected choice of shelter in dry conditions, two of the openings were 0.5 cm wide, two 1.0 cm, two 1.5 cm and two 2.0 cm. The different sizes were located at random. A plastic bag of dry soil, with the opening at the top, was placed in each chamber.

Few salamanders were found in the chambers of 0.5 cm and 1.0 cm. Instead, all of them gathered together in chambers of 1.5 cm and 2.0 cm (Fig. 10.9).

EXPERIMENT 7

To examine how the size of the opening to the chamber affected choice of shelter in moist conditions, an enclosure, with the same variety of openings to the chambers as in Experiment 6, was used. The sole difference was that the soil put into the chambers was saturated with water. As a control, this experiment was repeated in an enclosure in which the openings were all 1 cm wide, as in Experiment 8, below.

All salamanders entered chambers when the soil was wet, with 60% choosing the widest opening, 27.5% choosing the 1.5-cm opening and 12.9% the 1-cm opening. None entered the chambers with 0.5-cm openings. This represents a significant difference ($p<0.001$) between the experimental results and random or control figures. There was also a significant difference between random and control ($p<0.5$) (Fig. 10.10).

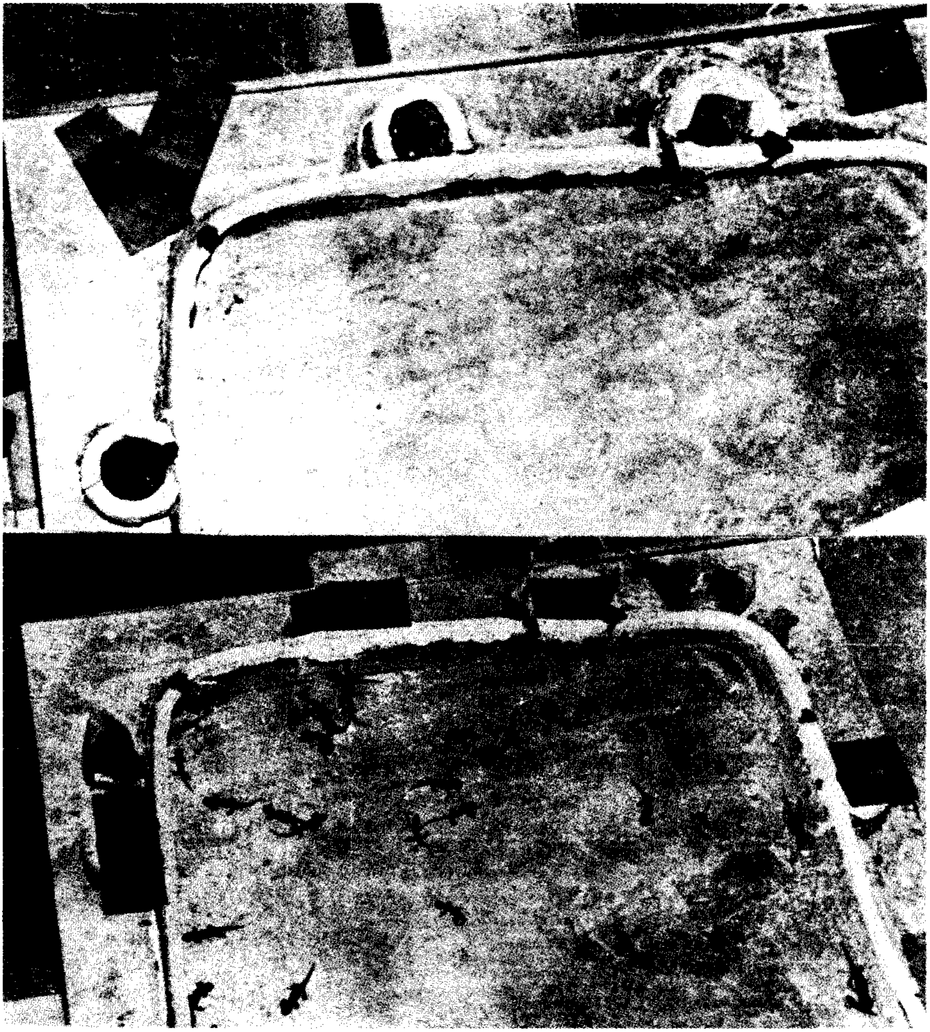


Figure 10.7. Enclosure used to examine shelter choice by salamanders (Degani and Mendelssohn, 1980).

EXPERIMENT 8

To examine the influence of moisture on the choice of shelter, the enclosure was modified, so that the openings to the chambers were all 1 cm wide. Saturated soil was placed in four chambers and dry soil in the remaining four, the dry weight of the soil being identical in all cases. In repetitions of the experiment, the order of placement of the soils was changed at random, and the entire enclosure was turned clockwise by one room, each time.

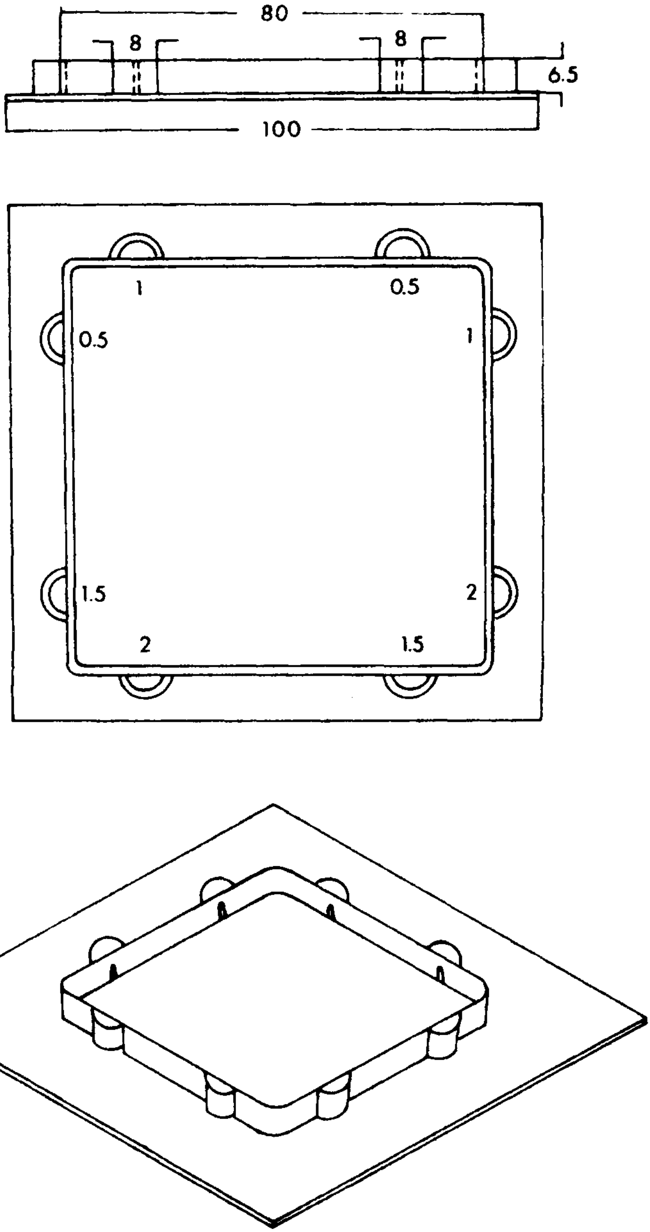


Figure 10.8. Measurements of enclosure used to examine shelter choice (Degani and Mendelssohn, 1980).

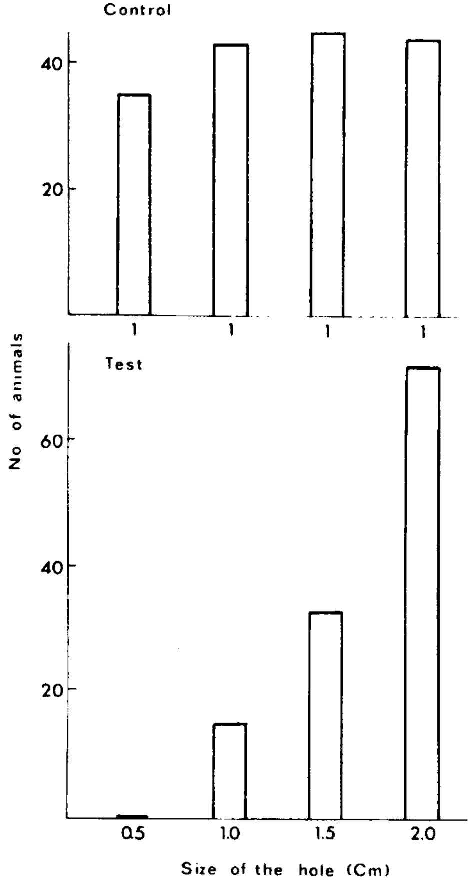


Figure 10.9. Influence of size of opening to shelter on choice by juvenile salamanders under dry conditions (Degani and Mendelssohn, 1980).

A significant majority (87%) of the salamanders used in this experiment chose chambers with wet soil, the remaining 13% choosing chambers with dry soil (Fig. 10.11).

EXPERIMENT 9

To determine the salamanders' preference among soil moisture percentages, soil with each of four moisture contents (4.65, 13.6, 22.55 and 31.5%, representing 20, 40, 60 and 80% of saturation) was placed in two chambers, located at random. The highest percentage was used as a control.

The salamanders used showed a clear preference for chambers with a high degree

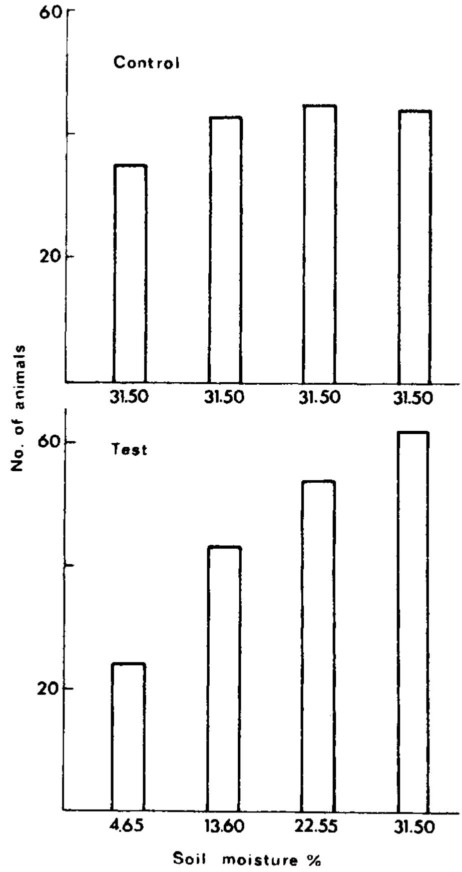


Figure 10.10. Influence of size of opening to shelter on choice by juvenile salamanders under moist conditions (Degani and Mendelssohn, 1980).

of moisture. Thus, 34.6% of the specimens chose the wettest shelter, and only 13% chose the least wet.

INFLUENCE OF MOISTURE AND DEPTH ON CHOICE OF SHELTER

To examine the influence of depth and moisture on the choice of shelter, two glass aquariums, measuring 90 × 35 × 40 cm, were divided lengthwise into two with plywood, filled with soil, and covered with black cloth to keep out the light. Holes were bored in the soil, to depths of 5, 10, 15, 20, 25 and 30 cm, on both sides of the partition (Figure 10.12). In Experiment 10, the holes at 5, 10 and 15 cm were wetted to saturation with water, while in Experiment 11, the other sets of three holes were

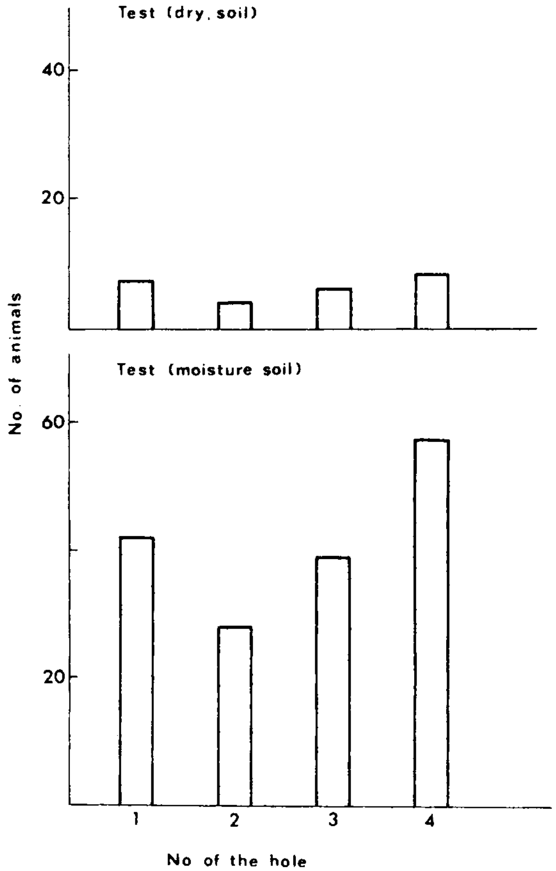


Figure 10.11. Choice of dry and moist soils for shelter by juveniles (Degani and Mendelssohn, 1980).

left dry. In a second experiment, all the holes on one side of the aquarium were wetted to saturation, and those on the other side left dry. In each experiment, eight young salamanders from Galilee were placed in the aquarium. After 24 h, the number of holes containing salamanders was counted. The experiments took several weeks, with altogether 30 salamanders taking part.

Even where the wetted holes were shallower, the salamanders showed clear preference for them over moist holes (Fig. 10.13). The second of these two experiments confirmed this finding. The depth of the holes did not influence choice to any significant effect.

This series of experiments gave the unambiguous results that both juvenile and adult salamanders prefer moist substrates, as reported by Batson (1965) for other species of Plethodontidae — *Eurycea bislineata*, *Desmogthanus fuscus* and *Pseudotriton montanus* — among which 57% preferred wetter substrates, as against 34% which preferred less wet ones. Jeager (1971) reported similar findings for *Plethodon cinereus* and *P. richmondi.*

Juvenile salamanders exhibited a stronger preference than adults for high moisture. This is because they are in greater danger of dehydration, as noted above. The influence of water loss on the choice of substrate was tested in *Ambysloma opacum*, after partial dehydration; it showed a clear preference for soil that had been wetted to 98% of saturation. The preference for soil over sand, with both saturated, is due to the greater availability of the water.

Partial dehydration led to rapid choice of wet soil by juvenile salamanders: significant results were observed after only half an hour. Marangio and Anderson (1977) reported the same phenomenon in *Ambystoma opacum*, in a study which

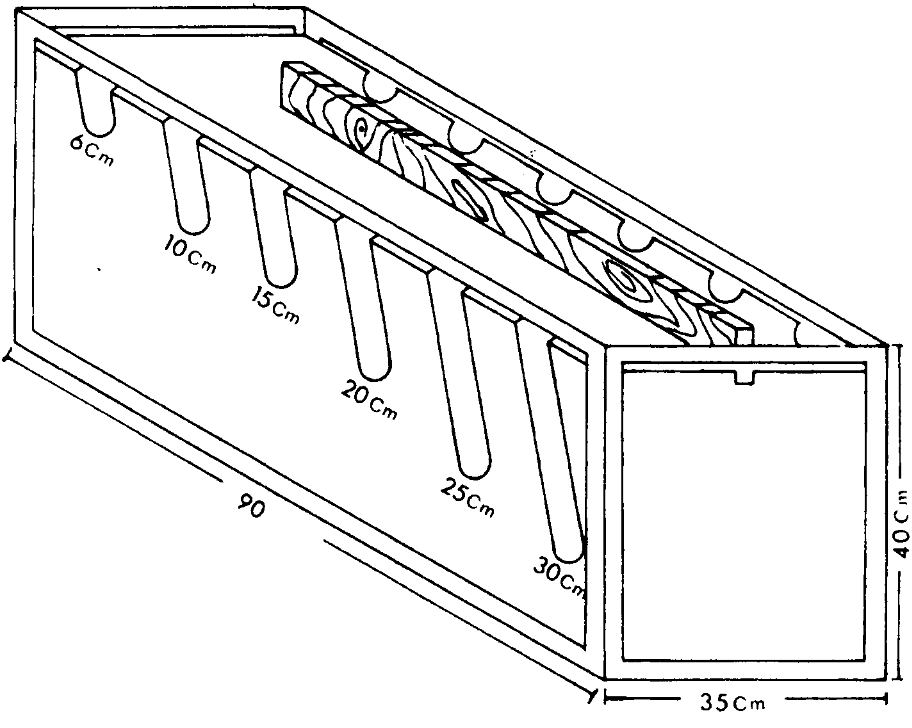


Figure 10.12. Soil-filled aquarium with holes bored to test salamanders' preferences in hole depth and moisture level, in choosing a shelter (Degani, 1980).

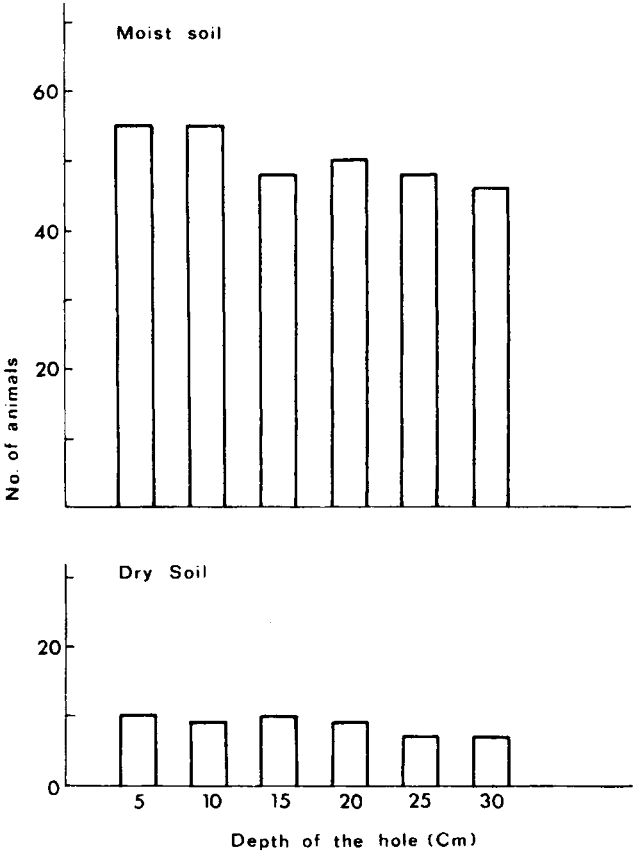


Figure 10.13. Response of shelter-seeking juvenile salamanders to different depths and degrees of moisture (Degani, 1980).

showed that dehydrated specimens preferred high moisture (89%), compared with normal specimens, which showed no significant preference, though in our study, normal salamanders also preferred wet substrate.

In our studies, the salamanders showed a preference for a combination of optimal moisture and easy access, by remaining in such chambers, but no parallel studies have been made in other species of Urodela, to enable any general conclusions to be drawn.

CHAPTER ELEVEN

REGULATION OF BODY TEMPERATURE

Behavior is the main mechanism used by exothermic amphibians to control body temperature, and has consequently been of great interest to research workers who deal with these animals. Working on the larvae of *Ambystoma tigrinum*, Prosser (1911) found that they move to the warmer areas of their pool. Mullaly (1953), Brattstrom and Warren (1955) and Brattstrom (1962) reported the same findings in other species of Anura, for larvae of *Bufo canorus, B. boreas, Hyla regilla* and *H. crucifer*. These studies show that it can be reasonably considered that temperature selection has a considerable influence on the movement of larvae in nature. However, this factor should not be treated separately from the many other factors that evidently govern the behavior of amphibian larvae, such as shelter location (Licht and Brown, 1967), oxygen concentration (Whitford and Massey, 1970) and food (Lillywhite, 1971).

Attempts in the laboratory to examine the influence of a temperature gradient on behavior failed to produce a single model to fit all species of amphibians. It is evident that the selection of temperature varies from species to species, and results are influenced by experimental methods, as well as by the age larvae and the temperature, climate and habitat. There is even some disagreement as to whether each species selects its own specific ambient temperature range, or whether the tendency is simply to avoid extremes of temperature. A range of approximately 3–36°C appears to cover the behavior of all amphibians (Licht and Brown, 1967; Lucas and Reynolds, 1967; Keen and Shroeder, 1975) and is the range that was adopted in the work described in this chapter.

Although less work has been done on temperature selection by amphibians after metamorphosis, there is evidence of some differences between larvae and post-metamorphosis animals, though in their behavior patterns again no single model fits all species. The most extreme range of temperatures in which *S. salamandra* exists is to be found in Israel, and Degani (1984) conducted a study to see whether the behavior of larvae and juvenile *S. salamandra* in the region differs in different populations, to adapt to the temperature range of that specific habitat.

For these experiments, samples of adult salamanders were captured from the Galilee, Carmel and Tel Dan populations, and placed in containers with water, to allow them to breed. The Galilee and Tel Dan salamanders bred in the same week, so their larvae were of the same age. These were maintained in the laboratory, at room temperature, and fed identical diets of invertebrates, caught in water bodies at Sasa. Since these two groups were maintained under identical conditions, a valid comparison could be made between them. The specimens form Carmel could not be induced to breed at the same time, with the result that, in the end, only a few specimens could be studied for comparison with Galilee larvae that were bred in the same week.

A special apparatus (Fig. 11.1), resembling that of Lucas and Reynolds (1967) was constructed to determine selected temperature. This apparatus consisted of a glass aquarium, measuring 140 × 20 cm and 13 cm deep. The floor was covered with tin, to ensure high conductivity of heat. The depth of water in the aquarium was 5 cm during experiments with larvae, and 2 cm for juveniles who had lost their gills. These depths were determined on the basis of preliminary trials, which aimed to establish the maximum temperature gradient, on the one hand, and to enable the larvae to move freely in the water, on the other. Ice was placed at one end of the aquarium, and a heater, in a glass of water, at the other. Both extremes, hot and cold, were blocked off by transparent, water-permeable screens, to prevent the larvae reaching them. The aquarium was divided transversely into 10 areas, with a thermometer at the center of each one: the thermometer reading, in each case, was taken as the temperature of that area. The apparatus created a gradient of 5–35°C.

The salamander larvae were put through a "course of trials" in the temperature gradient each month, altogether four times as larvae and once as juveniles, after metamorphosis. Each course consisted of four kinds of tests on behavior in the gradient:

1. Putting them in directly from the environment in which they were growing;
2. Putting them in after three days' acclimation at 10°C;
3. Putting them in after three days' acclimation at 25°C;
4. A control, in which the temperature control apparatus was not in operation, so that the temperature was uniform.

Aside from the control, the temperatures in the apparatus were constant for all experiments. The specimens were spread along the gradient at random.

Thirty minutes was allowed for acclimation, a length of time which preliminary trials established as sufficient to eliminate any effect on behavior resulting from the transfer from one container to another. From that time on records were taken, every five minutes for 55 min, of how many larvae were to be found in each area, and of the temperature in the area. Specimens were acclimated by placing them in a glass container at 10°C or 15°C for three days. Twelve to 15 specimens from each population went through each trial, each population separately. The significance of differences in the results was analyzed by the χ^2-test.

TEMPERATURE SELECTION BY DIFFERENT POPULATIONS

Tel Dan salamanders

A comparison between the larvae that were acclimated at 10°C and those that were acclimated at 25°C shows no clear difference in the temperature choice of the two groups. Thus, for example, 14% of the first group selected temperatures of 25°–30°C, and 15% of the second group also selected this temperature range (Table 11.1).

The highest temperature at which movement of larvae was recorded, and in which they remained only for a short time, was 32°C. Most larvae which had been transferred from ambient temperature moved to the 20°C zone (Fig. 11.2); their distribution along the gradient resembled that of the larvae acclimated at 10°C more than that of those acclimated at 25°C. In the control, the spread was at random along the aquarium, except in a number of instances when they tended to concentrate on the end of the aquarium that was heated in the tests but not in the control experiment itself (Fig. 11.4). In every case, the common characteristic was flight from extreme, especially, high (30°C) temperatures, with cold temperatures exerting less influence. No clear preference for a particular temperature was recorded. Selection was spread over a wide range of temperatures, but most of the specimens were to be found in the 15°–25°C range. This range was chosen by 51.4% of the larvae acclimated at 10°C, some 53.4% of those acclimated at 25°C, and 56.4% of those acclimated at ambient temperature.

Galilee salamanders

The temperatures selected by larvae from Galilee were, on the whole, similar to those chosen by the Tel Dan larvae, but there were some differences. Larvae acclimated at 25°C showed a greater tendency to select warm temperatures than those acclimated at 10°C, a tendency that was clearer in Galilee larvae than in those from Tel Dan. On the other hand, larvae acclimated at 10°C showed a much lower preference for the 25–30°C zone: an average of 6% at all the stages of growth selected this zone, compared with 13% of the larvae acclimated at 25°C. The maximum temperature at which Galilee larvae were found was 28°C. As with the Tel Dan larvae, the behavior of Galilee larvae acclimated at ambient temperatures resembled that of the 10°C larvae more closely than that of the 25°C larvae (Table 11.2, Figs. 11.3, 11.4).

Carmel salamanders

Allowing for minor differences, the larvae from Carmel behaved in a similar way to those from Galilee (Fig. 11.5). A relatively high percentage selected temperatures under 10°C: 22% of those acclimated at 10°C and 20% of those acclimated at 25°C — higher percentages those than found among the Tel Dan population. This difference was especially marked for the two groups of juveniles.

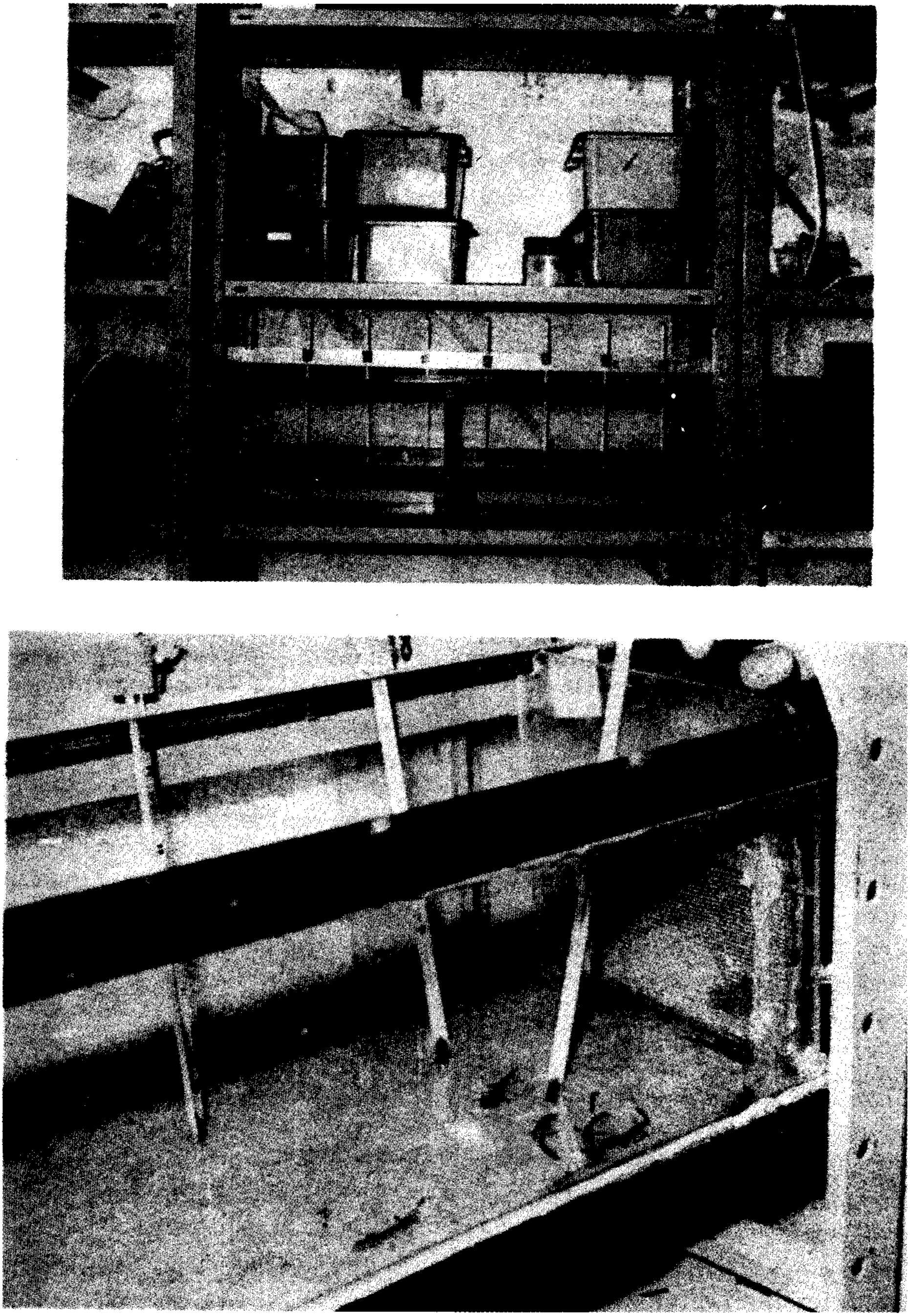


Figure 11.1. Temperature grading apparatus (Degani, 1980).

Table 11.1. Temperature selection by larvae and juveniles from Tel Dan. (Figures represent the percentage selecting the given range) (Degani, 1980).

			Acclimation at 10°C		
Age	5–10°C	10–15°C	15–20°C	20–25°	25–30°C
May	11.11	20.64	23.05	19.84	25.36
June	10.01	15.30	29.12	34.34	11.23
July	2.22	24.59	31.53	29.51	12.22
August	7.73	31.77	36.41	14.79	9.30
Sept.	29.30	21.62	26.89	11.67	11.72
Average	12.05 ± 10	22.72 ± 6	29.40 ± 5	22.03 ± 10	13.97 ± 6

			Acclimation at 25°C		
Age	5–10°C	10–15°C	15–20°C	20–25°C	25–30°C
May	9.80	25.29	26.71	19.97	18.23
June	5.46	20.09	64.46	9.16	0
July	17.81	17.17	45.92	10.81	8.29
August	12.02	14.51	22.39	31.12	19.96
Sept.	17.51	18.86	21.68	14.65	27.38
Average	12.52 ± 5	19.18 ± 4-4	36.23 ± 18	17.14 ± 9	14.76 ± 11

			Acclimation at ambient temp. (18–31°C)		
Age	5–10°C	10–15°C	15–20°C	20–25°C	25–30°C
May	9.25	8.35	33.30	12.64	14.42
June	6.64	45.94	45.62	1.80	0
July	7.91	4.86	47.25	37.87	2.11
August	8.41	12.13	36.04	34.62	8.80
Sept.	14.34	25.52	51.06	9.80	0
Average	9.31 ± 3	19.37 ± 17	47.05 ± 7	19.35 ± 16	5.07 ± 6

As in the case of the Galilee population, the majority of specimens selected temperatures between 10 and 25°C. This range was selected by 71.86% of those acclimated at 10°C, 61.2% of those acclimated at 25°C and no less than 81.45% of those acclimated at ambient temperatures. These figures compare with 59.34% and 69.16%, respectively, for 10°C and 25°C in the larvae brought from Galilee.

SELECTION ACCORDING TO ACCLIMATION

Acclimation at 10°C

The selection by specimens from Galilee and Tel Dan was very similar, though at various times minor differences were observed. Larvae from Carmel showed a greater tendency to select the cool zone, in the 5–10°C range, than those from

Table 11.2. Temperature selection by larvae and juveniles from Galilee. (Figures represent the percentage selecting the given range) (Degani, 1980).

Acclimation at 10°C

Age	5–10°C	10–15°C	15–20°C	20–25°	25–30°C
May	16.63	16.73	55.27	7.94	3.10
June	9.10	18.10	23.02	41.56	8.12
July	1.67	16.72	19.31	55.14	7.63
August	9.20	31.36	21.57	30.37	7.52
Sept.	49.49	21.65	15.36	10.24	3.27
Average	17.27 ± 19	20.17 ± 6	26.91 ± 16	29.05 ± 24	5.93 ± 3

Acclimation at 25°C

Age	5–10°C	10–15°C	15–20°C	20–25°C	25–30°C
May	4.45	11.00	40.36	9.78	34.81
June	6.64	45.94	45.62	1.80	0
July	7.91	4.86	47.25	37.83	2.09
August	12.02	6.31	30.59	34.10	16.94
Sept.	14.76	18.80	49.00	6.72	10.73
Average	9.16 ± 4	17.38 ± 17	42.56 ± 7	17.97 ± 17	12.92 ± 14

Acclimation at ambient temp. (18-31°C)

Age	5–10°C	10–15°C	15–20°C	20–25°C	25–30°C
May	1.14	6.86	37.19	28.74	25.97
June	7.32	37.75	42.58	12.31	0
July	23.45	41.86	29.81	0.86	4.02
August	8.00	16.69	31.39	17.47	26.45
Sept.	37.68	29.71	14.50	2.90	15.22
Average	15.55 ± 15	26.60 ± 15	31.09 ± 11	12.49 ± 11	14.33 ± 13

Galilee, and both groups showed higher preference for this zone than the Tel Dan population. The mean selected temperature of Galilee larvae was 17°, compared with 12° for the Tel Dan specimens (Tables 11.1, 11.2).

Acclimation at 25°C

Here, too, there was a similarity between the groups from Tel Dan and Galilee. Of the Tel Dan group, 13% chose the 5–10°C zone, compared with 9% for the Galilee group. In the 15–20°C zone, the corresponding figures were 36 and 43%, and in the 20–25°C zone, 17 and 18%, respectively. The maximum temperatures selected were 29°C (Tel Dan) and 3°C (Galilee) (Tables 11.1, 11.2).

In the comparison between larvae from Carmel and Galilee, similar behavior was also observed, with 20% of the Carmel larvae selecting the 5–10°C range, compared

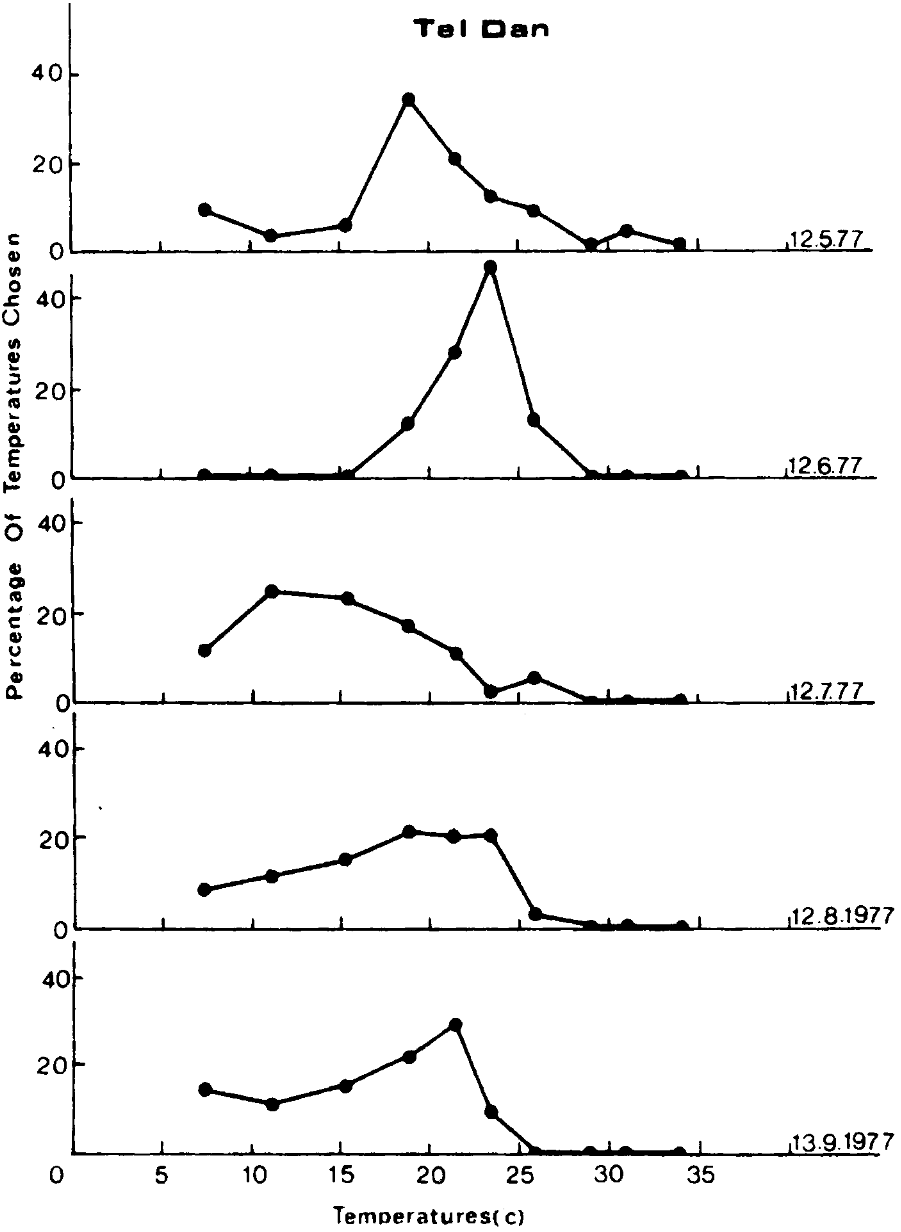


Figure 11.2. Temperature selection by larvae and juveniles from Tel Dan. Acclimated at 10°C, 25°C and room temp. (12–15 animals; N = 150) (Degani, 1984).

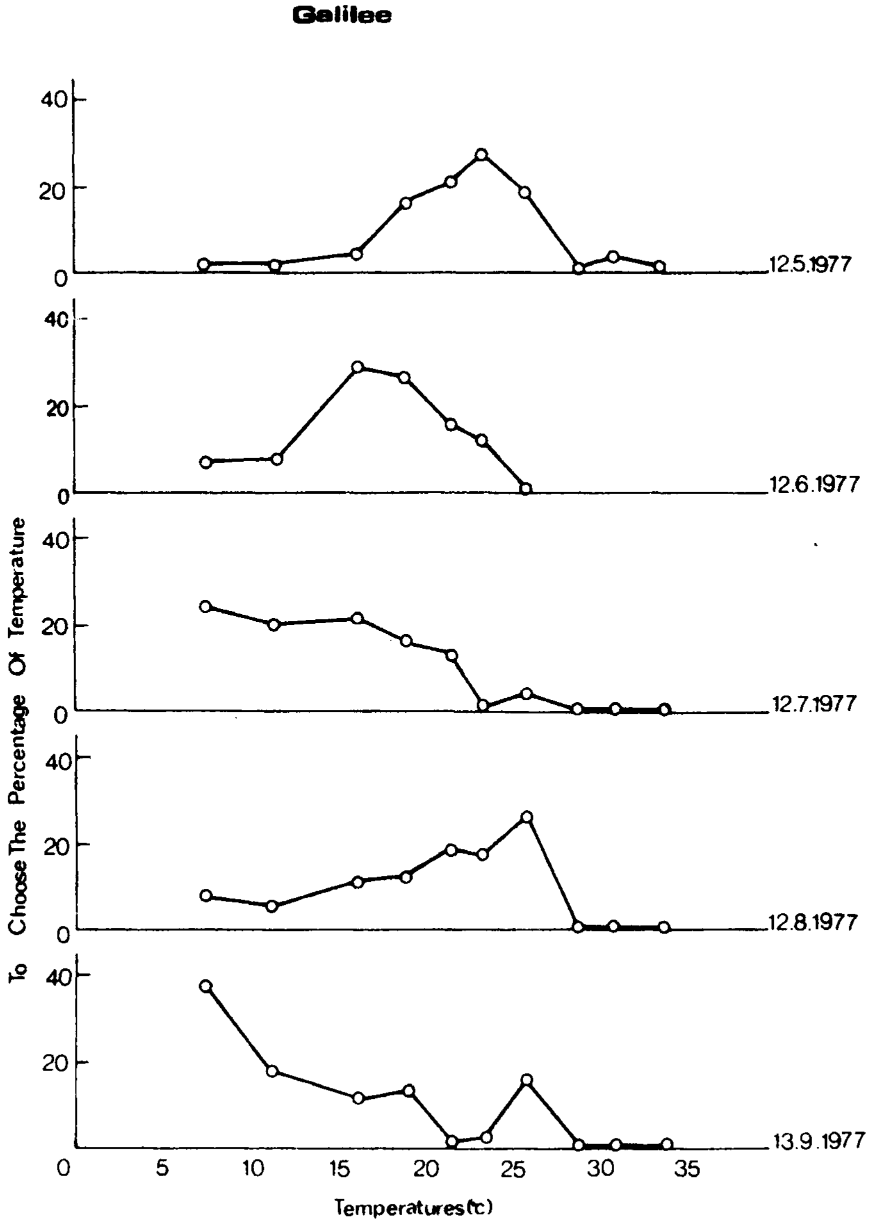


Figure 11.3. Temperature selection by larvae and juveniles from Galilee. Acclimated at 10°C, 25°C and ambient temp. (12–15 animals; N = 150) (Degani, 1984).

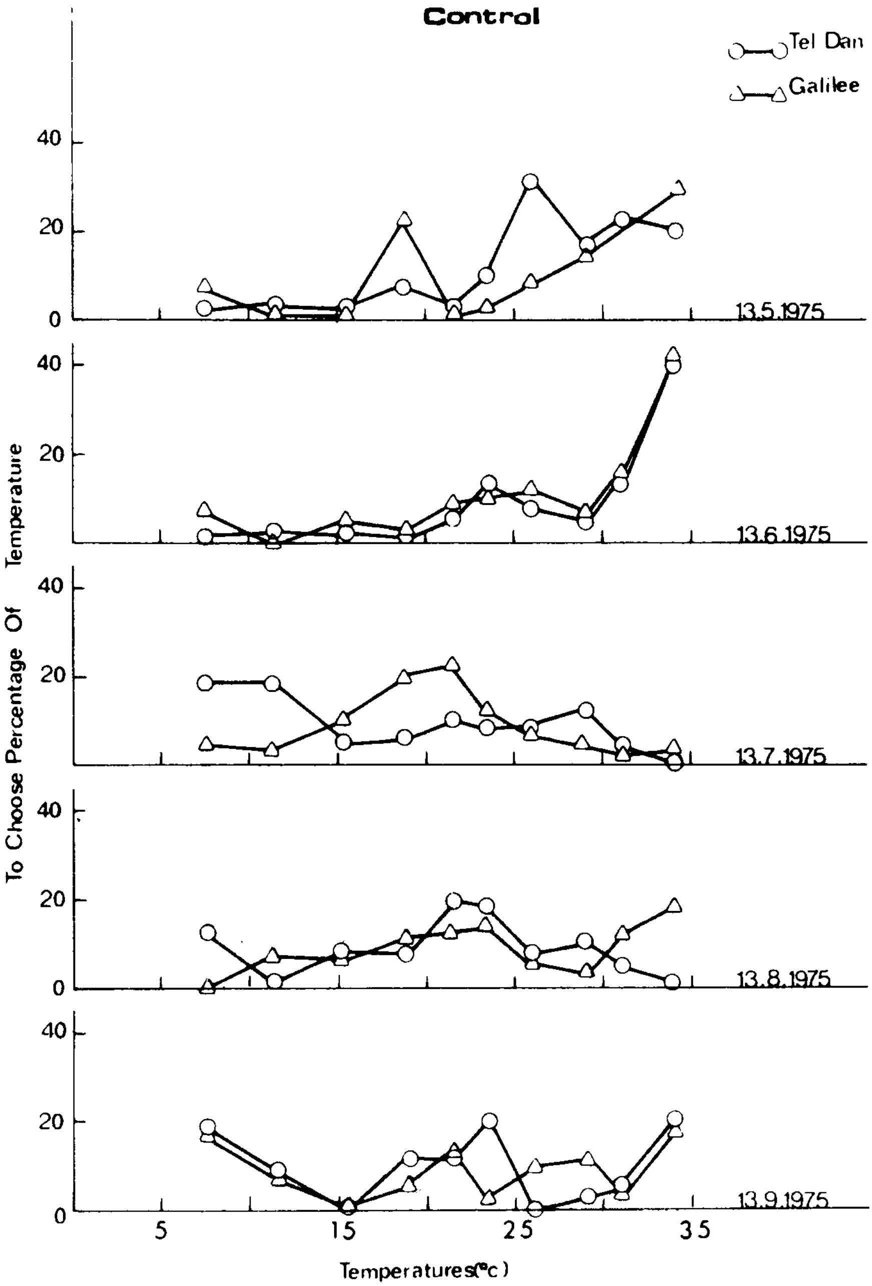


Figure 11.4. Control. Comparison between larvae from Tel Dan and Galilee. (No. animals. 12–15; N = 150) (Degani, 1984).

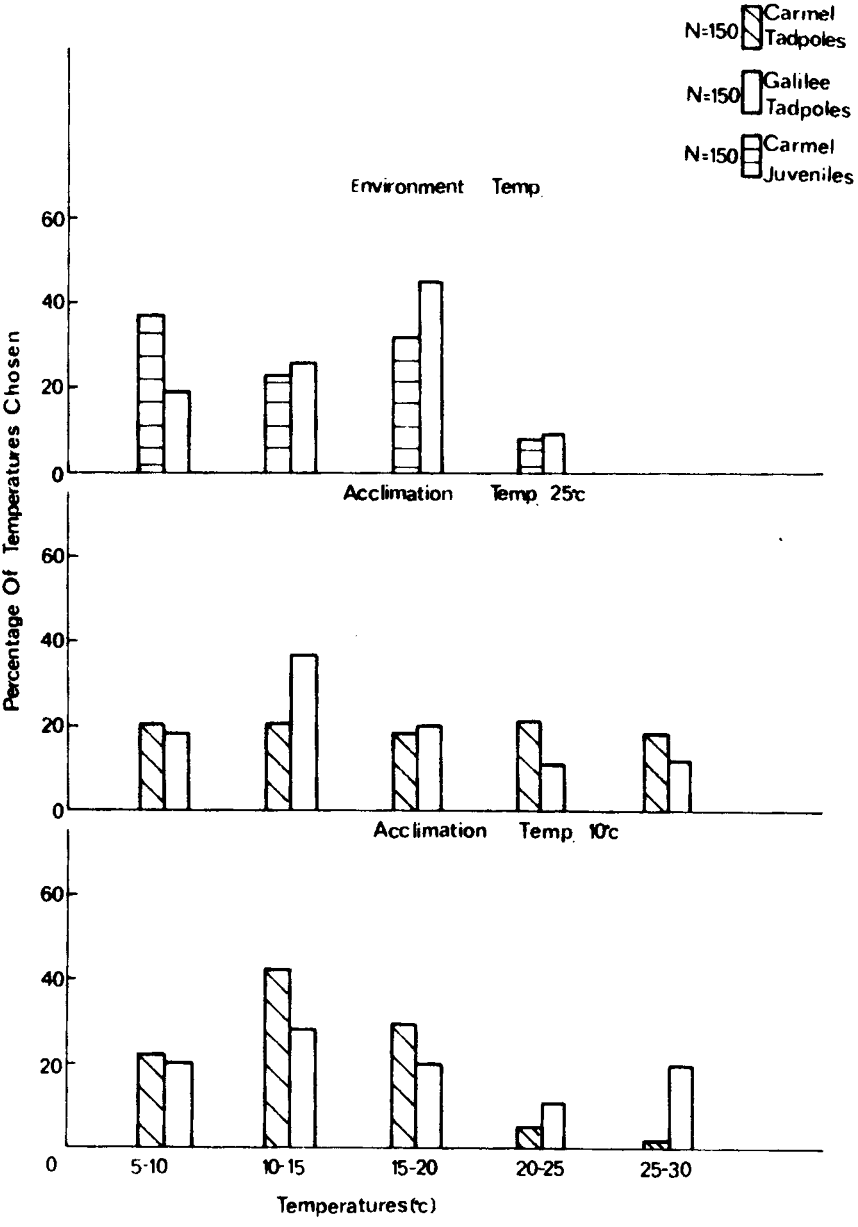


Figure 11.5. Temperature selection by tadpoles and juveniles from Carmel and Galilee at different acclimation temperatures. (No. animals from each source. 12-15; N = 150) (Degani, 1984).

with 19% of the Galilee salamanders. The corresponding figures for the 15–20°C zone were 19% (Carmel) and 20% (Galilee). However, there were greater differences between the groups in the selection of the 10–15°C and 20 –25°C zones.

Acclimation at ambient temperatures

When larvae were acclimated at ambient temperatures (16–30°C), there were few striking differences in behavior among the three populations. Thus, the maximum temperature selected by Galilee specimens was 31°C, compared with 29°C for those from Tel Dan; in both cases the larvae remained in this zone only for a short time. When the results of all the experiments are taken together, more larvae from Galilee chose the 5–10°C zone, on average, than larvae from Tel Dan (16% vs. 9%), while this proportion was reversed in the 20–25°C zone (12% vs. 19%). The corresponding averages for Carmel larvae were 19% for the 5–10°C zone, 26% for 100–15°C, 46% for 15–20°C, and 10% for 20–25°C.

Influence of acclimation in other species

The influence of acclimation temperatures on temperature selection has been studied in many other species, but there is no general agreement on the topic. A number of researchers have concluded that this is not a significant factor, for example in *Taricha rivularis* adults (Licht and Brown, 1967) and *Ascaphus truei* larvae (Vlaming and Burg, 1970), as well as in varieties of Urodela. In *Plethodon c. cinereus*, Feder and Phough (1975) found an inverse relationship between acclimation and selection temperature, as did Lillywhite (1971) in *Rana catesbeiana*, but in most cases the relationship was found to be direct, as in *A. tigrinum*, and in larvae of both *R. catesbeiana* and *R. pipiens* (Lucas and Reynolds, 1967; Lillywhite, 1971),

Table 11.3. Temperature selection of various Urodela.

Species	Temperature selection (°C)	Reference
Ambystoma (larvae)	7–29	Keen & Schroeder (1975)
Rana pipiens (larvae)	13–35 (95%)	Lucas & Reynolds (1967)
R. catesbeiana (larvae)	12–33 (95%)	ditto
A. tigrinum (larvae)	16–31 (95%)	ditto

Table 11.4. Mean selected temperature of various Urodela

Species	Mean selected temperature (°C)	Reference
Salamandra atra	15.00	Knapp (1974)
Rana temporaria	20.16	Reichling (1975)
R. esculenta	20.2–26.4	Ruhmekorf (1958)
Ambystoma (larvae)	30.40	Kauri (1959)
Plethodon c. cinereus	19.3–15.4	Feder & Phough (1975)

and as found in the experiments described in this chapter.

When mean selected temperatures are examined, there are, naturally, differences, but the mean selected temperature has no significance when the range of temperatures is wide. Furthermore, the absence of statistical treatment, to determine the significance of differences unambiguously, makes it difficult to draw meaningful conclusions from the results.

THE INFLUENCE OF AGE AND SEASON

Larvae and juveniles from Tel Dan

The behavior of larvae acclimated at ambient temperatures differed with their age. The later in the year their exposure to the selection experiment, the stronger their tendency to select lower temperatures (Fig. 11.3), and this is particularly marked when the months May and September are compared. In May, when the average temperature of selection was under 20°C, 73% of the specimens concentrated in this zone, while in September, at the end of summer, 91% of them concentrated in it. It should be borne in mind that, by September, the specimens were juveniles, after metamorphosis; and their selection of low temperatures was especially marked, 14% of them selecting the 50–10°C zone. This was the highest percentage in all the experiments to select this zone. It is also noteworthy that no juveniles selected temperatures above 25°C.

Larvae and juveniles from Galilee

There were slight differences between the behavior of Galilee larvae and Tel Dan larvae, the main one being that the former showed an even stronger preference for lower temperatures as they grew older. In May, the majority of these larvae (66%) concentrated in the 15–25°C zones, with few larvae to be found in the cool zones, but in general it was observed that, as they grew older, they tended more and more toward the lower temperatures. Thus, in July, 95% of the larvae were found concentrated in the 5–20°C zones. An exception to this trend was observed in August which, it should be noted, was the month in which they underwent metamorphosis. In September, immediately after metamorphosis, the juveniles showed clear preference for the cool zones, and this was especially noticeable among Galilee specimens, with 38% choosing the 5–10°C zone, compared with 14% of the Tel Dan juveniles. A large majority of the Galilee juveniles (82%) selected temperatures below 20°C (Table 11.2).

Larvae and juveniles from Carmel

A comparison between larvae and juveniles from Carmel reveals a similar pattern to those obtained from the other two groups. Of the larvae from Carmel acclimated at ambient temperatures, 19% selected 5–10°C, a figure which rose to 38% of the juveniles of the same population. A higher percentage of larvae than juveniles chose the warm zone at 20–25°C: 10% vs. 7.5%.

Comparison with other species

A direct link between temperature selection and the age of larvae or time of year has been found in a number of species of Urodela. Lucas and Reynolds (1967) reported a rise in selected temperature with increasing age in *Rana catesbeiana* and *R. pipiens*, while Feder and Phough (1975) reported similar results for *P.c. cinereus*: where the mean temperature of specimens acclimated at 25°C was 16.2°C in June, this figure later rose to 19.1°C. In the same way, larvae of *Ambystoma maculatum* selected high temperatures at the early stages of their development and low temperatures at the later stages (Keen and Schroeder, 1975), as we found for *S. salamandra*.

Larvae of *A. tigrinum* did not show any selection behavior immediately after hatching (Lucas and Reynold, 1967): in the same way, *S. salamandra* were to be found in a wide range of temperatures immediately after birth, especially among the Tel Dan population. Clearer temperature selection was observed only later, as the larvae developed, until after metamorphosis, when the tendency to select cool temperatures was unmistakable, and here the phenomenon was more marked in the hill country populations than in the Tel Dan population. Here, too, the effect of adaptation to the habitat can be inferred, since the stabler temperatures in Tel Dan reduce the need to avoid dehydration. However, a general conclusion for the entire species cannot be drawn, in the absence of comparative behavioral studies elsewhere.

CONCLUSIONS

Avoidance of extreme temperatures can be seen as a general pattern of behavior in the local subspecies of salamander. It was more marked among larvae from hill populations, and the trend increased with the age of the animals: it was most marked after metamorphosis. This phenomenon points to a form of adaptation to specific habitats, since hill-dwelling salamanders are exposed to more extreme temperature differences between summer and winter. Thus, they are exposed to very high temperatures in summer, and must find cooler places, when they leave their water bodies, to escape the danger of dehydration.

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