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BREEDING PATTERNS IN A FRINGE POPULATION OF FIRE SALAMANDERS, *SALAMANDRA SALAMANDRA*

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ABSTRACT

The fire salamander, *Salamandra salamandra,* population on Mt. Carmel was studied for 15 years. This is a particularly interesting population as it inhabits the southern-most habitat in which this species is found in Israel, and thus the south-eastern fringe area of its entire palaearctic distribution.

The ovoviviparous female breeds during both November and December. The November cohort is likely to die of desiccation as the ponds dry out due to interrupted rains. Only every third year (on average) is November wet enough to enable the ponds to contain enough water, to give the larvae a chance to survive to metamorphosis. Some of these larvae will have an advantage, due to their cannibalistic traits enabling them to prey on the later larval cohorts of December. These cannibalistic larvae develop rapidly and metamorphose at a greater size than the average larvae.

The survival of this salamander population depends on a balance between two conflicting strategies: early breeding and late breeding. The first is advantageous during years with early winter rains when the larvae can survive long enough to be able to prey upon the later larval cohorts. On the other hand, late breeding is advantageous in dry years when larvae in the early cohorts die of desiccation.

INTRODUCTION

The fire salamander, *Salamandra salamandra*, is found in Israel in three disjunct populations. The main population is located in the mountains of the Western and Central Galil (Degani and Warburg, 1978). In addition there are two smaller areas, separated from the main area: one to the northeast, and the other to the southwest of the main area. The first area is located in the north-eastern part of Israel at Tel Dan at the foot of Mt. Hermon (Degani and Mendelssohn, 1982). The second area is located south of the main one, in the northern part of Mt. Carmel (Warburg, 1986 a,b).

The population of salamanders on Mt. Carmel comprises the southeastern limit of its palaearctic distribution. Therefore, it is a fringe population inhabiting an area where conditions are presumably suboptimal to the animals. Otherwise, this species could just as well have penetrated other mountain ranges in the Mediterranean region of central Israel: Samaria and Judea where they are not found. Other palaearctic species of animals (or plants) have succeeded in colonizing this area (Yom — Tov and Tchernov, 1988).

The fact that the salamanders are not found south of Mt. Carmel is of interest, and provided the main stimulus for studying this isolated population for such a long period. It seems that salamanders in this area may have to cope, at times, with unsuitable conditions otherwise not encountered by their conspecifics inhabiting more favourable environments in the Galil mountains or in the center of the species' distribution (i.e. in Central Europe: Joly, 1968; Klewen, 1985).

MATERIALS AND METHODS

The study area was south of Haifa on the top of Mt. Carmel located towards its western slopes. The area surrounds four rock pools which are one of the main breeding sites for the salamanders in this area. The study started in 1974 and continues to the present day (1990). Animals were captured throughout the breeding season on stormy nights, immediately at the beginning of the rainy season (October or November). This continued for 9-10 weeks throughout the entire breeding season: from mid-October to the beginning of January.

The animals were identified individually by their typical yellow patterns. Their sex was determined by cloacal examination (see Warburg *et al*., 1978/79), they were weighed, measured, photographed and finally released back into their habitat either during the same night or on the following night. As the yellow patterns on a black background on the dorsal side of the salamander hardly change throughout its lifetime, the salamander could be easily recognized throughout the study period by their photographs.

RESULTS

One hundred and twenty salamanders were captured during the 15 years of study. The average sex ratio was 1.5 male to 1 female. The pattern of capture shows that slightly more female salamanders were captured in December as compared to October-November (Fig. 1). Eighteen females were recaptured over the years. The females very rarely appeared more than once during the same breeding season. During the course of the study, only four females appeared twice during the same breeding season.

The females entered the ponds as soon as they arrived at the breeding site. They would then release their ova and the larvae hatched immediately upon contact with the water. The males rest on higher observation posts (stones, logs etc.), surrounding the ponds and will mate with the females upon their emergence from the ponds. The breeding pattern of the females (n = 42), shows an almost even distribution between the two main months of the breeding season: November and December (Table 1).

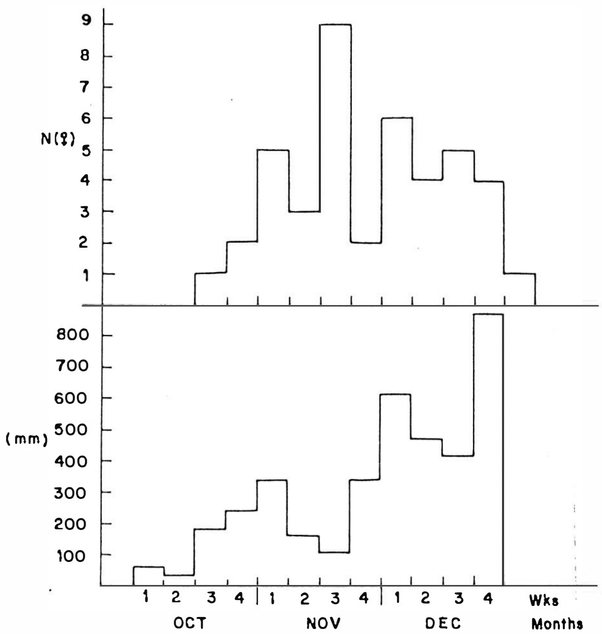

Fig. 1. Breeding patterns (top) of *Salamandra* females. on Mt. Carmel over a period of 15 years. Precipitation is given for the same period (bottom).

Months	OCT.	NOV.	DEC.	JAN.	Total
Weeks					
1		5	6	1	
2		3	4		
3	1	9	5		
4	2	2	4		
Total	3	19	19	1	42
(in %)	7.2	45.2	45.2	2.4	100

TABLE 1: The number of females bearing young and the date they gave birth.

During October-November when the rainy period starts, the dry ground is not yet soaked with water. The soil dries out whenever there is a pause in the rains which happens quite often during this period (Table 2). Thus, there is a rather good chance that the early larvae deposited in October-November will die of desiccation (Fig. 2). If the break in the rains is not longer than 7-10 days, the larvae could survive on the mud under the stones. Throughout the study period, ten Novembers out of fifteen (2/3) were drier than December months (Table 2). December received on average about twice as much rainfall as compared to November (Table 2, Fig. 1). During December the soil is saturated with water, and less likely to dry out especially as December temperatures are lower than those of November. Thus the larvae deposited during December do not die because of desiccation as the ponds remain filled with water.

The survival of *Salamandra* on Mt. Carmel is a result of adaptation to two main factors: food and weather (Table 3). If food is scarce more larvae may become cannibalistic. If rains come early and in sufficient quantity, the early (November) larvae will survive. However, if rains are late, the November larvae will die, and only the late (December) larvae will survive (Table 3).

DISCUSSION

The breeding migration and the appearance of salamanders near the ponds depends on the first heavy rains towards the end of autumn. In *Ambystoma talpoideum*, it seems that the breeding migration is related to the cumulative rainfall during the breeding period (Semlitsch, 1985). Migration during the breeding season in *Ambystoma macrodactylum*, takes place on rainy nights after heavy rains (Anderson, 1967; Beneski, Zalisko and Larsen, 1986) much like here.

Larvae hatch out of the egg envelope immediately upon contact with water, (Warburg, Degani and

(1973/4-1988/9) (in mm)	IX	X	XI	XII	I	II	III	IV	V	Total
1973/4	0	20.0	151.0	36.0	309.0	65.0	40.0	38.0	0	659.0
1974/5	0	0	67.0	403.0	116.0	176.0	46.0	0	0	808.0
1975/6	0	3.0	69.0	231.0	80.0	157.0	62.0	41.0	6.0	649.0
1976/7	0	54.0	184.0	162.0	150.0	55.0	142.0	125.0	0	872.0
1977/8	0	54.0	28.0	354.0	164.0	41.0	73.0	10.0	0	724.0
1978/9	0	38.0	36.0	223.0	101.0	54.0	65.0	16.0	3.0	536.0
1979/80	0	70.0	94.0	270.0	208.0	174.0	59.0	48.0	0	923.0
1980/1	0	32.0	2.0	181.0	224.0	99.0	70.0	15.0	0	623.0
1981/2	0	13.0	116.0	25.0	57.0	156.0	65.0	6.0	3.5	441.0
1982/3	0	1.0	173.0	220.0	206.0	154.0	110.0	3.0	5.0	872.0
1983/4	0	3.0	177.0	30.0	107.0	53.0	84.0	59.0	0	513.0
1984/5	0	45.0	97.0	123.0	77.0	156.0	9.0	102.0	0	609.0
1985/6	0	47.0	51.0	171.0	100.0	141.0	24.0	24.0	28.0	586.0
1986/7	1.0	31.0	287.0	198.0	105.0	46.0	97.0	16.0	2.0	783.0
1987/8	0	104.0	18.0	365.0	167.0	197.0	91.0	9.0	0	951.0
1988/9	0	8.0	65.0	165.0	*	*	*	*	*	*
Average	0	32.7	100.9	197.3	144.7	114.9	69.1	34.1	3.2	703.3
(n)	(16)	(16)	(16)	(15)	(15)	(15)	(15)	(15)	(15)	(15)

TABLE 2: Average Monthly Rainfall in Beit Oren (near Damun) on Mt. Carmel. (Data Courtesy of the Israel Meteorological Service, Beit Dagan.)

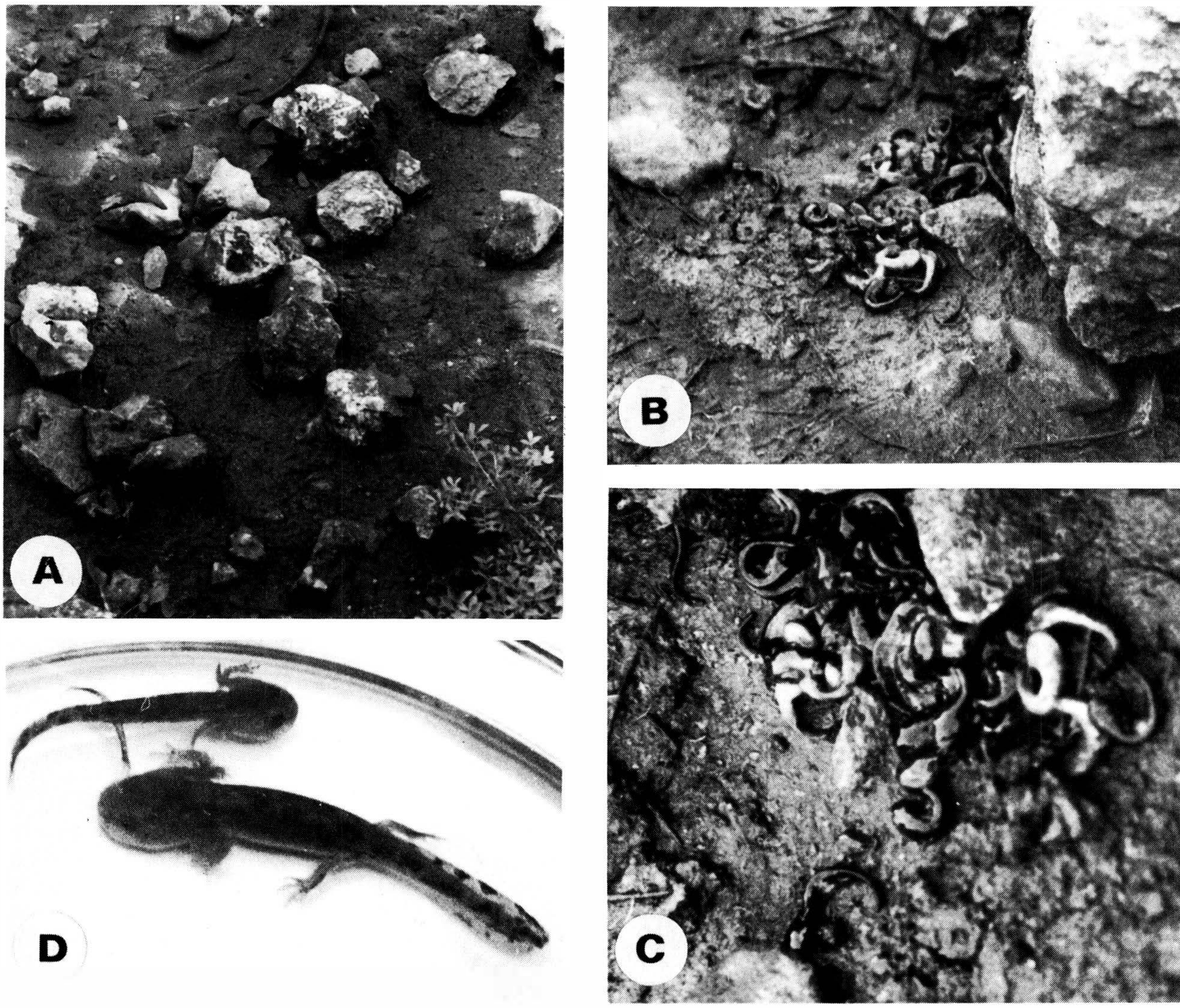

Fig. 2. Photograph of the dry breeding ponds on Mt. Carmel (A). Salamander larvae were found on the mud under a stone in a dry pond. The larvae were still alive and survived later in the lab (B,C). Five-week old larvae belonging to the same batch raised without extra food, one of them cannibalistic (D).

FOOD		WEATHER				
		NOVEMBER BREEDING			DECEMBER BREEDING	
Egg Larvae		Egg Larvae			Egg Larvae	
Food Scarce	Food Abundant	Dry November		Rainy November	Dry November	Rainy November
Development Retarded	Development Rapid (no cannibalism)	Larvae Survive 1 wk, on mud		Increased Cannibalism	Food Abundant (Due to enriched organic matter from dead November larvae)	Larvae Provide Prey for November Larvae
Late Metamorphosis	Early Metamorphosis	Rains	No Rains	Development Rapid	Rapid Development (No cannibalism)	No Survivors
Small Juveniles (except for cannibals)	Normal Juveniles	Larvae Survive	Larvae Perish	Early Metamorphosis	Normal Juveniles	
		Increased Cannibalism		Large Juveniles		
		Late Metamorphosis				
		Few Large Juveniles				

TABLE 3: Factors affecting survival of *Salamandra salamandra* larvae in rock-pools on Mt. Carmel.

Warburg, 1978/79). Duration of larval deposition lasts mostly up to one hour, sometimes longer up to a few hours, and on rare occasions (in the lab), even up to four days (Warburg *et al.*, 1978/79). If the same pattern occurs in nature it could explain why some females visit the pond more than once during the same season possibly releasing larvae on each occasion.

In a permanent water body at Tel Dan in the Upper Galil, the salamanders seem to be active throughout the year (Degani and Mendelssohn, 1982), and thus their breeding season may extend into spring. Similarly, in Europe the breeding season may extend over a period of five months (Zakrzewski, 1970). In the centre of its distribution *Salamandra* larvae metamorphose after 12-16 weeks (Zakrzewsky, 1970), whereas larvae on Mt. Carmel metamorphosed normally after 6-8 weeks.

We have recently attempted to estimate the longevity of the salamanders on Mt. Carmel (Warburg in prep). The estimate is based on the growth rate of a juvenile salamander (a male) born and raised in the lab. After three years it was released into the breeding site from where its mother had originated. This salamander was recaptured several times since, and its growth rate can give an indication of the general growth rate of these salamanders in their natural habitat on Mt. Carmel. Furthermore, a skeletochronological investigation of the same population (currently in progress) indicates a similar pattern (Warburg, in prep).

Based on these techniques of estimating longevity, we can assume that the average age of the salamanders on Mt. Carmel is about 10.5 years (about 6 years old when first captured, and then recaptured for another 4.5 years on average, Warburg, in prep.). We can also assume that the females reach their reproductive stage when they first appear at the ponds (at the age of 6). If so, they probably continue to breed for at least four years (We found females that were captured year after year and bred in the lab each time.) As the average brood is about 100 larvae (Warburg, *et al.*, 1978/79, the latest figure obtained since then, is 98 larvae averaged from 22 batches), a female can produce (at least) a total of about 400 larvae throughout her reproductive life.

From previous studies we have found that in almost every cohort there are a few cannibalistic larvae growing much faster than the other larvae in the same cohort (Degani, Goldenberg and Warburg, 1980 and Figs. 2, 3). Preliminary studies have shown that the cannibalistic larva is found more often in larval cohorts of October-November. On the other hand cannibalism can also be artificially induced by selectively feeding a larva more frequently. This causes the larva to grow faster than other larvae in the same batch and it will become cannibalistic.

As was shown in *Hynobius* larvae (Kusano, Kusano and Myawaki, 1985), cannibalism depends on the difference in size of the larvae. The cannibalistic morphs of *Ambystoma tigrinum* larvae developed faster than the normal larvae (Lannoo and Bachmann, 1984). Survival of *Ambystoma maculatum* larvae depended greatly on their developmental rates (Shoop, 1974). The larger larvae of *Ambystoma tigrinum* metamorphosed at a larger size, and were therefore less vulnerable (Rose and Armentrout, 1976). Moreover, these larvae eventually became larger adults (Semlitsch, Scott and Pechmann, 1988). On the other hand, *Ambystoma talpoideum*

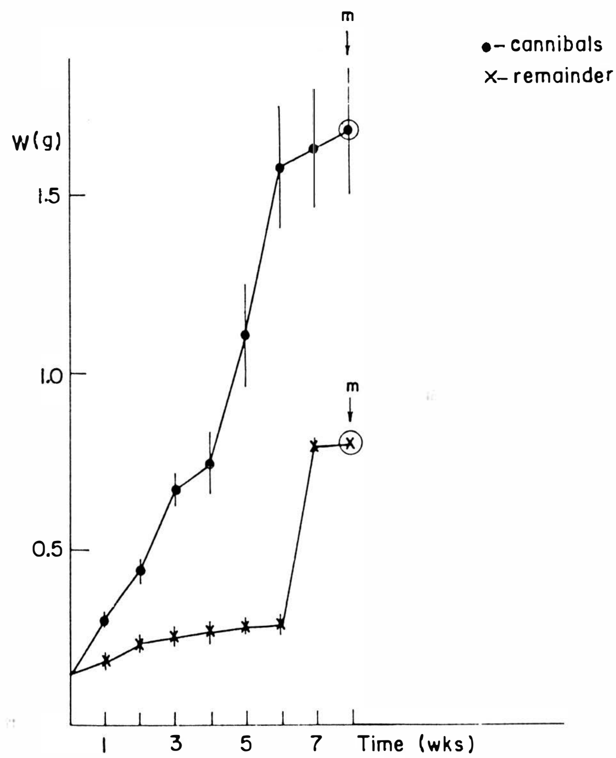

Fig. 3. Growth of *Salamandra* larvae belonging to the same cohort. Cannibalistic larvae grow much faster than the remainder, and metamorphose at a larger size. Cannibalism appears also in the remaining larvae after 6 wks. (± SE).
m — date of metamorphosis.

metamorphosed later in the season (thus larval life is prolonged), but metamorphs were not significantly larger (Semlitsch, 1987; Semlitsch *et al.*, 1988). In anurans (*Scaphiopus couchi*), there is a positive correlation between size at metamorphosis and length of larval period (Travis, 1984; Newman, 1989).

In only about a third of the 15 year period of study was November rainy enough to enable the ponds to contain water during the dry intervals between the rains (Tables 1,2). Therefore, only about 33% of the progeny of females breeding in November would survive. Most of the time (2 out of 3 years), the ponds are likely to dry out before the larvae had a chance to metamorphose. Larvae deposited during these "wet Novembers" will have the best chance to survive as they will become cannibalistic, and will feed largely on the later December cohorts. In such years (of wet Novembers), only few of the December larval cohorts will have a chance to survive (Table 3).

If the female is always an early (November) breeder, and as only every 3rd or 4th year will have a wet November, then one out of four breeding efforts is likely to be successful.

On the other hand if the female is a late December breeder two-thirds of her progeny may have a chance of survival. This is because the "dry" November larval batches will not survive, and thus the ponds are free of a major predator. In that case they may have a shorter period to develop possibly resulting in smaller metamorphs.

In other amphibians leading a precarious life in deserts, longevity is the key factor enabling the survival of the population (e.g. *Bufo punctatus*, Tevis, 1966). In

Scaphiopus couchi, less than 10% of the ponds produced metamorphs, largely because of early desiccation (Newman, 1987). It seems therefore that early breeding is of sufficient selective advantage every third year on average, to maintain this trait in this fringe population of *Salamandra* population on Mt. Carmel.

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SHORT NOTES

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NEW RECORDS OF MOROCCAN HERPETOFAUNA

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Information concerning the distribution of Moroccan amphibians and reptiles was summarized by Bons (1967). Since this date numerous new data have been published describing increases in distribution ranges of many species. This new information has been compiled recently by Mellado and Dakki (1988), although new data is constantly being published (see Schouten and Thevenot, 1988; Destre *et al.*, 1989; Valverde, 1989a, b; Mellado and Olmedo, 1990).

This note presents more new data concerning herpetofaunal distribution in former Morocco (Western Sahara excluded) and describes (1) considerable increases in the distribution of some species, (2) new localities for some species, and (3) the confirmation of the existence of some species in previously poorly surveyed areas. These records have been selected from a considerable amount of new observations made by the authors since 1982, in addition to existing material deposited since 1952 in the collection at the Estacion Biologica de Doñana, Seville. The latter has been recently described by Ignacio de la Riva and the second author of this note (in preparation). In Table I appears a list of 45 new localities for 29 species of Moroccan herps, whose geographic situation is mapped (Fig. 1).