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Long-term study on the reproductive strategy of *Salamandra infraimmaculata* MARTENS, 1855 females in a single, isolated population breeding under precarious ambient conditions
(Amphibia: Caudata: Salamandridae)

Langzeituntersuchung zur Fortpflanzungsstrategie der Weibchen von *Salamandra infraimmaculata* MARTENS, 1855 einer isolierten Population unter widrigen Umweltbedingungen
(Amphibia: Caudata: Salamandridae)

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KURZFASSUNG

Fünfundzwanzig Jahre hindurch (1974-1998/99) wurde das Vorkommen von *Salamandra infraimmaculata* MARTENS, 1855 an einem Fundort im Karmel-Gebirge (Israel) beobachtet. Eine Anzahl von Weibchen besuchte die Laichgewässer mehrmals, einige von diesen taten das in aufeinanderfolgenden Jahren, andere in mehrjährigen Abständen. Dies deutet auf folgendes hin: 1. Die weiblichen Salamander müssen Samen nicht speichern, sie können sich jedes Jahr paaren. 2. Weibchen dürften auch benachbarte Laichgewässer aufsuchen, sodaß Jahre zwischen den Besuchen an den untersuchten Laichgewässern vergehen können. Die Salamander erscheinen nur bei Regenwetter an den Laichgewässern. Gewöhnlich tritt eine Regenpause nach dem Einsetzen der feuchten Jahreszeit in der Mitte des Herbstes auf. Larven, die zu Beginn der Fortpflanzungszeit (Oktober) abgelegt werden, sind dadurch einem erhöhten Austrocknungsrisiko der Gewässer ausgesetzt, die sich erst später wieder mit Wasser füllen (Larven können bis zu drei Wochen im feuchten Schlamm überleben). Diese früh geborenen Larven können überleben und ernähren sich dann von später abgelegten Larven der eigenen Art. Einige der wiederholt zum Laichgewässer gewanderten Weibchen bringen die Larven immer zu einem frühen, andere ausschließlich zu einem späten Termin zur Welt und wieder andere verhalten sich in dieser Hinsicht nicht konstant. Anzahl und Masse der abgesetzten Larven stehen in keinem klar erkennbaren Zusammenhang mit frühem oder spätem Geburtstermin bzw. mit Masse oder Alter der Mutter.

ABSTRACT

Female *Salamandra infraimmaculata* MARTENS, 1855 were monitored for 25 years (1974-1998/99) at a single site on Mt. Carmel (Israel). Some of the females visited the breeding ponds on several occasions, some of them visited on consecutive years while others at intervals of several years. This indicates two points: 1. salamander females do not need to store sperm since they can mate every year. 2. they may be visiting nearby breeding ponds therefore years may elapse between their visits to the breeding site under study. The salamanders only appear near the ponds in stormy weather. Since there is usually an intermission in the rains after the onset of the rainy season in mid-autumn, larvae that are released early in the breeding season (October) face the risk of ponds drying before they refill (larvae can survive for up to three weeks on wet mud). These early-born larvae may survive and prey on conspecifics, that are born later. Some of the females that returned several times always breed early in the season, others only late and some varied their timing. The number of larvae or their mass is not correlated with either timing of their birth, nor with their mother's age or mass.

KEY WORDS

Amphibia: Caudata: Salamandridae: *Salamandra infraimmaculata*; population ecology, amphibian reproduction, consecutive breeding, pond duration, sperm storage, unpredictable weather, Israel

INTRODUCTION

The adult population of *Salamandra infraimmaculata* MARTENS, 1855, was studied at a single breeding site on Mt. Carmel during 25 years 1974-1998/99 (except for one year 1990). This is a rare and protected species found solely in three disjunct populations in northern Israel. The main population is located in the mountain ranges of the Western and Central Galilee (DEGANI & WARBURG 1978; DEGANI et al. 2007). In addition they are found in two smaller areas separated from the main one: the first about 50 km to the northeast (DEGANI & MENDELSSOHN 1982), and the other about the same distance to the southwest. The southwestern habitat is confined to the northern part of Mt. Carmel (WARBURG 1986a, 1986b, 1992, 1994, 2007b).

This relic metapopulation on Mt. Carmel, inhabits a fringe habitat in the southeasternmost area of the genus' Palaearctic distribution. Part of the time conditions are suboptimal for this urodele as it has a rather short breeding season and there is a limited time period suitable for dispersal of postmetamorphs. As a result, this species developed special adaptations in this genus (such as readiness of mature oocytes see SHARON et al. 1997; WARBURG 1997) that are not found in other species.

The adult salamander is largely a terrestrial animal. After spending its first 6-7 weeks as larvae in water, only mature females, 3-4 years old, return to the water and then only for a few hours to breed releasing their larvae. Juveniles are very rarely found near the ponds. Courtship, spermatophore deposition, and subsequent insemination of the female, all take place on land (REBELO & LECLAIR 2003). Since their longevity is at least 20 years it means that they are hardly aquatic as adults.

There are several advantages in long-term studies. Foremost among them is the fact that an entirely different outlook emerges as the research unfolds. Changes in populations can be followed over long periods enabling a different perspective in evaluating oscillations in population cycles (WARBURG 2007b, 2008a).

The objective of this study was to follow changes in the reproductive strategy of this salamander breeding population over a long period (25 years) in order to try to assess its status as an endangered species.

MATERIALS AND METHODS

The study area was south of Haifa located at the top of Mt. Carmel towards its western slopes. The site, about 60 m x 100 m, surrounds four shallow rock-pools which are one of the main breeding sites for the salamanders in this area.

Annual rainfall ranged between 397-1160 mm averaging 690 mm over the last 25 years. Of this 443.8 mm (64.3 %) rain fell during the breeding season October-January and the remaining 246.2 mm (35.7 %) during the rest of the rainy season (until the end of February). The later rains are of no significance to the breeding pattern of the adult female but are of the utmost importance to the larvae which need at least 6-8 weeks to metamorphose. They might not be able to complete metamorphosis once the pond water warms up and/or dries out, sometimes as early as late winter (see WARBURG 1992; COHEN et al. 2005, 2006).

The adult salamanders were observed for a few hours near their breeding sites on stormy winter nights throughout the entire breeding season for 10-12 weeks starting at the onset of the rainy season (October or November) and continuing until mid-January. Because of the limited time spent at the site it is possible that some females may have visited the ponds either before I arrived there or after I had left. As a result, this report is at its best a conservative estimate of the female's reproductive pattern. (Because of various reasons no trapping method was applied at this particular site).

The salamanders were collected, brought to the laboratory and were then identified by their photographs, using the yellow patterns on the dark background of their backs, as markers. As the unique pattern of each salamander does not change throughout its lifetime, each individual could be identified during this long study period (see WARBURG 2006). They were then weighed on a Mettler® balance at ±0.1 g and measured on millimeter paper or slide rule to ±1.0 mm. The sex was determined by cloacal examination (see DEGANI & WARBURG 1978; WARBURG et al. 1978/79). Finally the salamanders were released back to their habitat either during the same night or the following one.

The number of salamanders active during the breeding season at the study site

Table 1. Dates of visits to breeding ponds by individual female salamanders *Salamandra infraimmaculata* MARTENS, 1855 that visited more than once.

Tab. 1: Daten von Laichgewässer-Besuchen für einzelne Weibchen von *Salamandra infraimmaculata* MARTENS, 1855, die das Laichgewässer mehr als einmal aufsuchten.

Female No.	Number of visit / Zahl des Besuches								
Weibchen Nr.	1st	2nd	3rd	4th	5th	6th	7th	8th	9th
2	Nov '74	Dec '79	Dec '80	Nov '81					
14	Dec '75	Nov '76							
18	Nov '76	Dec '77							
19	Dec '76	Dec '77							
21	Dec '77	Dec '80	Dec '82	Nov '86					
22	Dec '77	Nov '78							
63	Dec '80	Nov '81	Nov '82	Dec '83	Nov '84				
65	Dec '80	Nov '81	Nov '82	Nov '84	Oct '87	Nov '88	Nov '89	Jan '94	Oct '96
69	Nov '81	Dec '85	Nov '86	Dec '88	Dec '96	Dec '97			
70	Nov '8l	Nov '82	Nov '84	Nov '85					
81	Nov '82	Nov '83	Oct '87	Nov '89	Nov '92	Nov '94			
82	Nov '82	Dec '84	Jan '94	Dec '96	Nov '97				
83	Nov '82	Nov '83	Dec '85	Nov '86	Nov '87	Dec '88	Oct '96		
84	Dec '82	Nov '84	Dec '91						
86	Dec '82	Nov '83	Dec '83	Dec '84	Nov '86				
98	Dec '83	Nov '88	Oct '89						
102	Jan '84	Dec '84	Nov '94	Dec '98					
111	Dec '85	Dec '88							
114	Nov '86	Oct '87	Nov '88	Oct '89	Nov '92				
119	Nov '86	Dec '87							
121	Dec '86	Jan '94							
131	Dec '88	Nov '97							
132	Dec '88	Nov '95							
157	Dec '91	Nov '94							

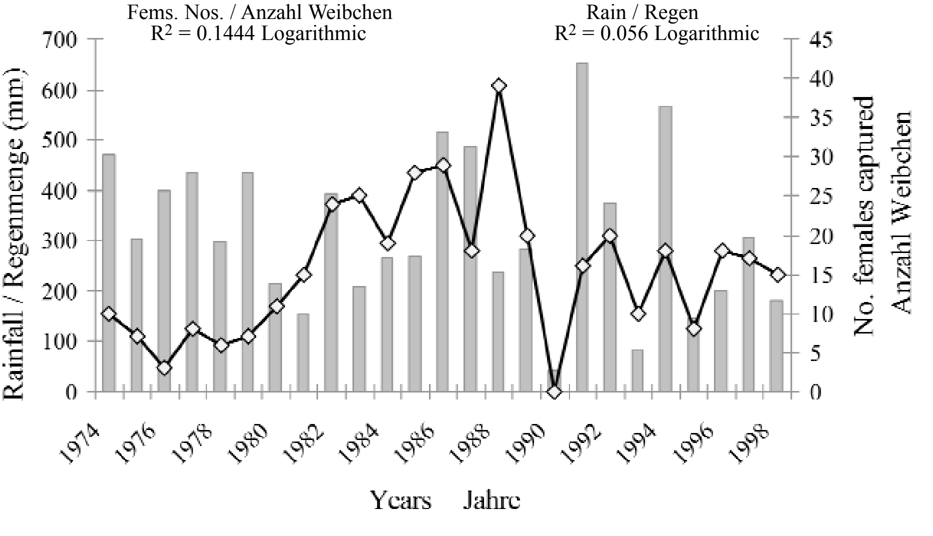

Fig. 1: Number of female *Salamandra infraimmaculata* MARTENS, 1855 captured during the breeding season throughout the study (line) as related to rainfall from September to January (columns). Study site: Mt. Carmel, Israel.

Abb. 1: Anzahl der Weibchen von *Salamandra infraimmaculata* MARTENS, 1855, die im Untersuchungsgebiet (Karmel-Gebirge, Israel) in den einzelnen Untersuchungsjahren zur Laichzeit gefangen wurden (Linie) in bezug zur Regenmennge von September bis Jänner (Säulen).

was rather small compared to other salamander species. Consequently, the small yearly sample size did not enable any elaborate statistical treatment except t-test and regression analysis.

The data obtained in this 25-year long term study were previously used to describe changes in the phenology (WARBURG 2007b), recapture rate (WARBURG 2008a), dimensions (WARBURG 2008b), and sex ratio in this species. The extent of their site tenacity was described in WARBURG (2006), and it was possible to estimate their longevity (WARBURG 2007a). All these studies have indicated a decline of this populations and its aging. However, since the female's reproductive potential (in view of its life span) and average brood size are both high, the possibility of a recovery of this population can not be ruled out.

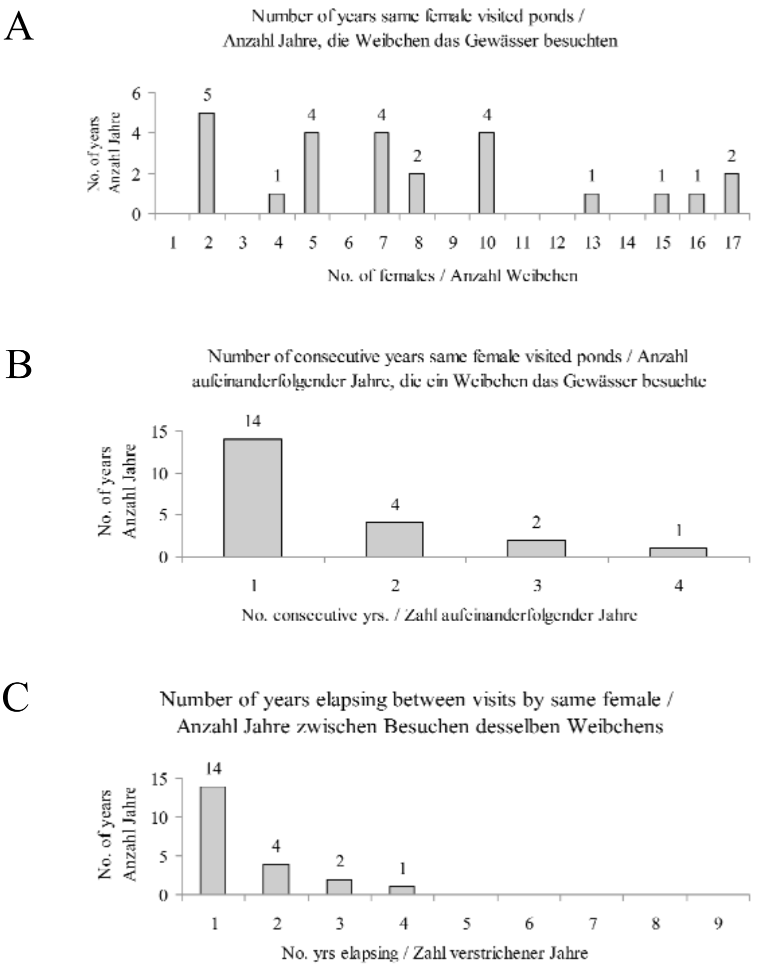

Fig. 2: A - Number of years the same female visited the breeding site ; B - Number of consecutive years the same female visited the breeding site; C - Number of years elapsing between visits of the breeding site by the same female.

Abb. 2: A - Anzahl der Jahre, die Weibchen das Laichgewässer besuchten; B - Anzahl aufeinanderfolgender Jahre, die ein Weibchen das Laichgewässer besuchte; C - Anzahl der Jahre zwischen den Besuchen einunddesselben Weibchens am Laichgewässer.

RESULTS

The number of female salamanders captured annually during the breeding seasons throughout this 25-year long study, did not correlate with either the particular years or with the amount of average annual rainfall during that period (Fig. 1 - Number of females: R^2 = 0.1444 logarithmic; rainfall (mm): R^2 = 0.056 logarithmic). Dates when 24 females have been collected more than once are given in Table 1. Many (14 out of 44) of these females visited the ponds three or more times, one was collected nine times. From these data two main facts emerge: 1. Some females visited the ponds on consecutive years. 2. For other female salamanders, years elapsed between two visits. These facts are shown in Fig. 2 A-C illustrating the number of years elapsing and consecutive years when females visited the breeding ponds. Thus, two females visited the study site for a total of 17 years (Fig. 2 A), one female visited the ponds on five consecutive years (Fig. 2 B) and in two females 10 years elapsed between consecutive visits (Fig. 2 C).

Not all females visit the ponds during the same month. Some come earlier in the breeding season (during autumn October-November) and some later during winter (Table 2). Ten females out of the 38 females shown here, divided their visits equally arriving half of their breeding during autumn and half during winter. Five females always visited the ponds in autumn and 14 females only in winter. The risks involved in the timing of breeding will be discussed later.

The average annual amount of rainfall early in the rainy season (September to November) is 136 mm (30.3%), whereas 313.2 mm (69.7%) rain falls later in the season during early winter (December-January) (see Table 3; Fig. 3). Rainfall continues February-April but is of no consequence to the adult female since although the ponds may be full of water, the female is unlikely to breed as the larvae will not be able to metamorphose in time before ponds either dehydrate or warm up. There is no significant relationship between either early or late rains and number of breeding females. Nor is there a significant relationship between early- or late-breeding females and years (Fig. 4).

Table 2: Early (E - autumn, October-November) and late (L - winter, December-January) breeding in 24 female *Salamandra infraimmaculata* MARTENS, 1855 salamanders that were captured during different years. Ten females divided their visits equally: 50% E & 50% L; five females visited only early (E), and 13 females only late (L); three females came more times early (E), and four females came more times late (L).

Tab. 2: Frühe (E - Herbst Monate X-XI) und späte (L - Winter, Monate XII-I) Ablagen bei 24 Weibchen von *Salamandra infraimmaculata* MARTENS, 1855 aus Beobachtungen verschiedener Jahre. Bei zehn Weibchen waren die Besuche gleich verteilt (50% E & 50& L; fünf Weibchen erschienen nur früh (E), 13 nur spät (L); drei Weibchen kamen häufiger früh, und vier kamen häufiger spät.

Female No. Weibchen Nr.	Breeding period Laichperiode	E : L (%)
2	ELLE	50 E : 50 L
8	L	100 L
14	LE	50 E : 50 L
15	L	100 L
16	L	100 L
18	EL	50 E : 50 L
19	LL	100 L
21	LLLE	25 E : 75 L
22	LE	50 E : 50 L
57	L	100 L
63	LEELE	60 E : 40 L
64	L	100 L
65	LEEEEEELE	77.8 E : 22.2 L
69	ELLELLL	28.6 E : 71.4 L
70	EELEE	80 E : 20 L
73	L	100 L
81	EEEEEEE	100 E
82	ELLLE	40 E : 60 L
83	EELEELE	71.4 E : 28.6 L
84	LEEL	50 E : 50 L
86	LELLE	40 E : 60 L
98	LELE	50 E : 50 L
102	LLEL	25 E : 75 L
111	LL	100 L
114	EEEEE	100 E
115	E	100 E
119	EL	50 E : 50 L
121	LL	100 L
122	E	100 E
123	E	100 E
125	L	100 L
130	L	100 L
131	LE	50 E : 50 L
132	LE	50 E : 50 L
137	L	100 L
157	LE	50 E : 50 L
174	L	100 L
233	L	100 L
Average/Mittel		31.8 E : 68.2 L

Table 3: Average annual rainfall (in mm, courtesy of the Israel Meteorological Service Beit Dagan) during the early (IX-XI) and late (XII-I) breeding season of *Salamandra infraimmaculata* MARTENS, 1855 near Damun, Mt. Carmel, Israel. Bold letters - successful breeding in those years since ponds sustained sufficient water to enable larvae to metamorphose.

Tab. 3: Mittlere jährliche Regenmenge (in mm, Quelle: Israel Meteorological Service Beit Dagan) während der frühen (IX-XI) und späten (XII-I) Laichzeit von *Salamandra infraimmaculata* MARTENS, 1855 nahe Damun, Karmel-Gebirge, Israel. In Fettschrift - Bruterfolg der Jahre, in denen die Gewässer bis zur Metamorphose der Larven ausreichend Wasser enthielten.

Year Jahr	Early / früh (IX-XI)	Late / spät XII-I
1973/74	171.0	345.0
1974/75	67.0	**519.0**
1975/76	72.0	**311.0**
1976/77	238.0	312.0
1977/78	82.0	518.0
1978/79	74.0	324.0
1979/80	164.0	478.0
1980/81	34.0	**405.0**
1981/82	**129.0**	82.0
1982/83	174.0	426.0
1983/84	**180.0**	137.0
1984/85	142.0	200.0
1985/86	98.0	271.0
1986/87	**319.0**	303.0
1988/89	73.0	166.0
1989/90	195.0	249.2
1990/91	21.0	**195.0**
1991/92	268.0	575.3
1992/93	98.0	435.0
1993/94	68.8	**241.4**
1994/95	**335.7**	275.4
1995/96	102.5	279.9
1996/97	99.6	195.8
1997/98	160.0	317.0
1998/99	35.0	**268.0**
Average / Mittel (mm)	136	313.2
Average / Mittel (%)	30.3	69.7

Total average rain during the breeding season (September - January) = 449.2 mm. / Mittlere Gesamtregenmenge (mm) während der Laichzeit (September - Jänner) = 449.2 mm.

Table 4 summarizes the ambient conditions that prevailed near the breeding ponds during the breeding season. During 25 years of this study only four Novembers were wetter than December (Table 3). However, this does not indicate that in other years conditions were not favorable for the larvae born early in the season, since 13 Novembers were wet enough to enable successful metamorphosis (Table 4). Successful breeding depends on whether November larvae can survive the intermission between rainfalls before the ponds dry out. Indeed, more females (50.9 % versus 49.1 %) released their larvae early in the breeding season (Table 6). Consequently, 62.7% of these larvae are likely to survive until metamorphosing compared to 77.5% of the late-born larvae (Table 6).

Table 5 compares the breeding success in early and late breeding females. A total of 24 salamanders (out of 44 females) came to the pond more than once during the 25 years of study. Out of 91 breeding occasions 51 females bred early and 40 late. Based on the rainfall pattern (whether in October and November rains were sufficient to keep the ponds with water until the main rainfall in December-January fills the ponds) successful breeding could be evaluated. Eight salamanders were always successful in their breeding. Seven salamanders were successful in most of their breeding. Out of the 51 early-breeders, 32 were successful, and 31 of the 40 late-breeders. On the whole, 62.7% of the early-breeders were successful as compared to 77.5% of the late-breeders. An average of 70.9% was successful breeding.

No significant difference in the female's mass between either early- or late-breeders could be detected over the years (Fig. 5). Since generally most research projects do not last longer than four years, I decided to arrange both data on captures of females and on their mass into 4-year periods (Fig. 6). The number of late-breeding females captured dropped (though not significantly), and the early-breeding females' average mass increased significantly (R^2 = 0.8523 linear) meaning that during recent 4-year periods only larger females arrived at the ponds.

Examining the number of larvae in a cohort produced by early- and late-breeding females (Fig. 7) showed no significant difference between them. Moreover, there was no significant relationship between early- or later-born larvae and their mother's mass (Fig. 8).

The number of larvae produced by the same female is shown for five females that have bred in the laboratory for four times or more (Fig. 9). Except for the marked increase in larval numbers produced by F-86

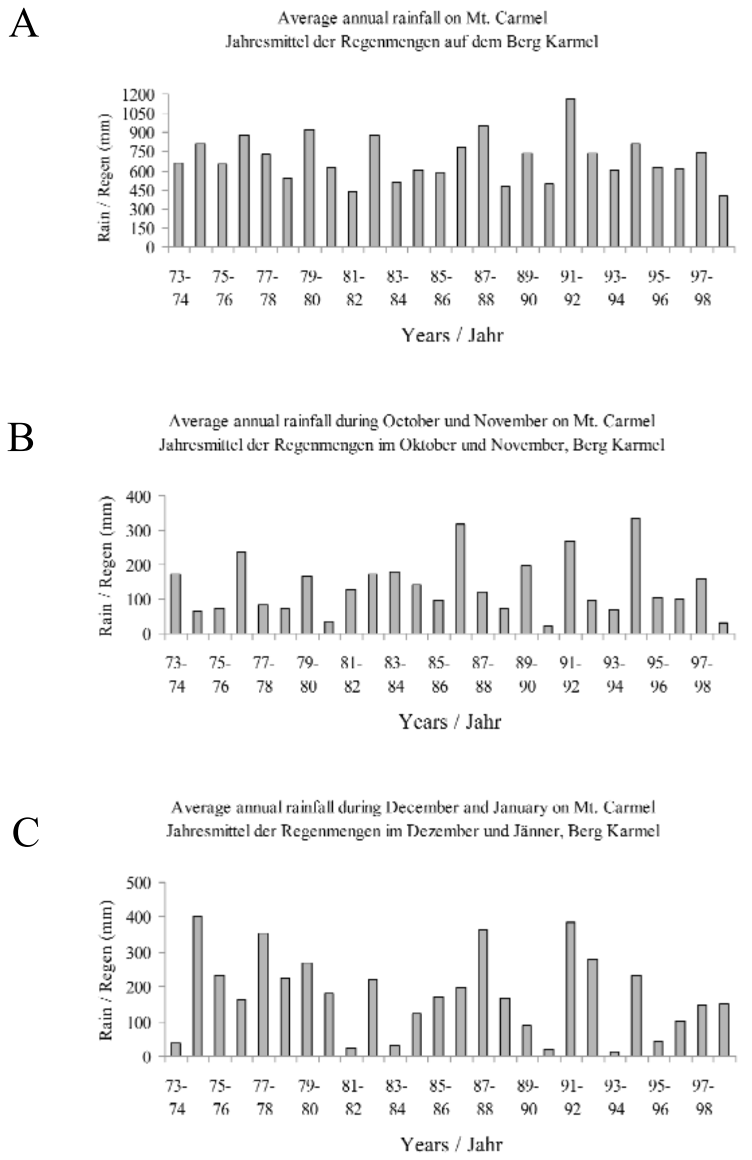

Fig. 3: Average annual rainfall during the years 1974 - 1998 on Mt. Carmel (Israel).
A - Average annual rainfall; B - Average annual rainfall during October and November;
C - Average annual rainfall during December and January.

Abb. 3: Jahresmittel der Niederschläge von 1974 bis 1998 im Karmel-Gebirge (Israel).
A - Jahresmittel der Regenmengen; B - Jahresmittel der Regenmengen im Oktober und November;
C - Jahresmittel der Regenmengen im Dezember und Jänner.

that correlated significantly ($R^2 = 0.9342$) with the mother's estimated age, all other females did not show a significant difference in numbers related to age.

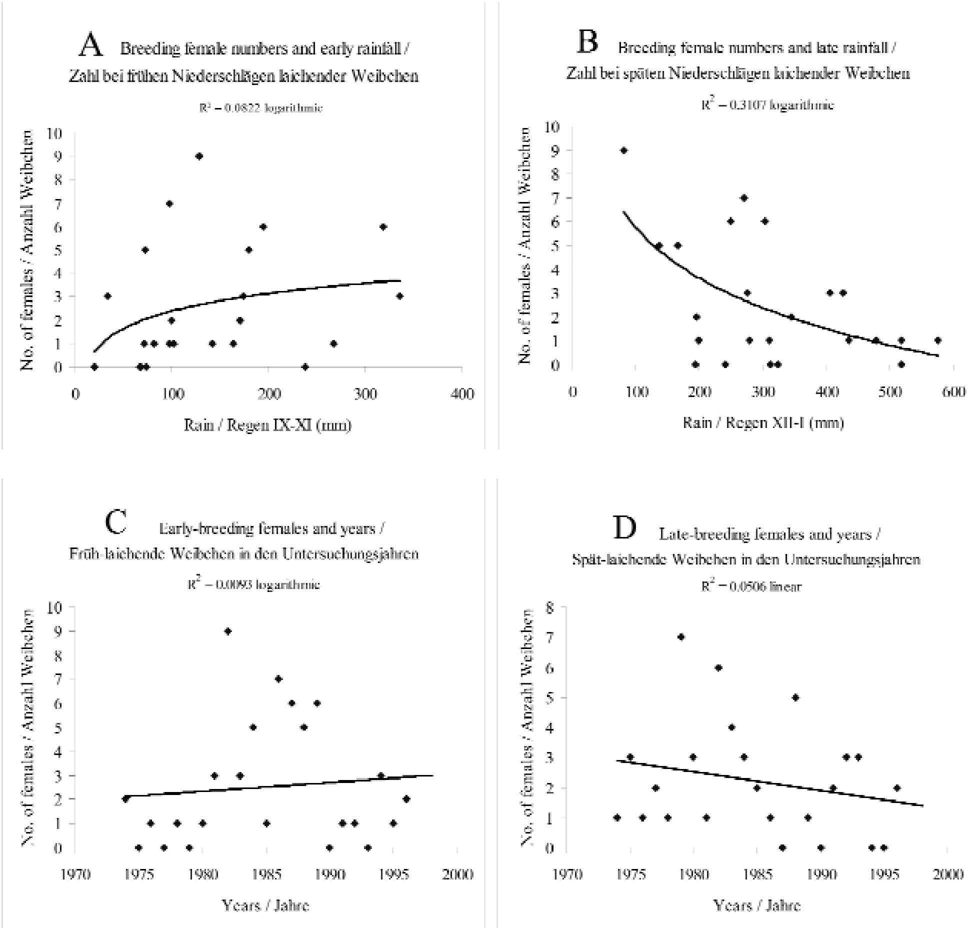

Fig. 4: Relationship between number of females captured and both years and rainfall. A - Early breeding female numbers versus early rainfall (September - November); B - Late breeding female numbers versus late rainfall (December - January); C - Early (September - November) breeding female numbers versus year of observation; D - Late (December - January) breeding female numbers versus year of observation.

Abb. 4: Die Beziehung zwischen der Anzahl der festgestellten Weibchen und dem Kalenderjahr bzw. der Regenmenge. A - Anzahl früh laichender Weibchen in Abhängigkeit zur Regenmenge (September - November); B - Anzahl spät laichender Weibchen in Abhängigkeit zur Regenmenge (Dezember - Jänner); C - Anzahl früh (September - November) laichender Weibchen in Abhängigkeit vom Beobachtungsjahr; D - Anzahl spät (Dezember - Jänner) laichender Weibchen in Abhängigkeit vom Beobachtungsjahr.

DISCUSSION

There are guesses about age at maturation in salamanders, but no quantitative data are available. In another study, recapturing 4-year old salamanders (born and raised in the laboratory from larvae) indicated that they mature at the age of 3-4 years, perhaps even sooner.

The reproductive strategy of female *S. infraimmaculata* is depicted in a scheme (Fig. 10). In this scheme I recognize two main processes in the reproductive strategy of the female: 1. the oocyte cycle. 2. the female's mating, fertilization and parturition. Process 1. the oocyte cycle of vitello-

Table 4: Ambient conditions of temperatures and rainfall on Mt. Carmel (Israel) during the breeding season of *Salamandra infraimmaculata* MARTENS, 1855 from October to January.

Tab. 4: Temperatur- und Niederschlagsbedingungen im Karmel-Gebirge (Israel) während der Laichzeit von *Salamandra infraimmaculata* MARTENS, 1855 von Oktober bis Jänner.

Temperature / Temperaturen		OCT	NOV	DEC	JAN
Maximum	Range / Spannweite	26.5-31.6	19.6-25.9	14.6-21.2	12.6-17.6
	Mean / Mittel	2 8.6±1.3	23.1±1.3	17.5±1.7	15.6±1.4
Minimum	Range / Spannweite	15.5-20	11.2-15.8	7.9-11.9	6-10.5
	Mean / Mittel	17.5±1.0	13.7±1.3	9.8±1.1	8.2±1.2

	OCT - NOV	DEC - JAN
Average Temperature / Mittlere Temperatur (°C)	15.6±1.1	9.0±1.1
Temperature range / Spannweite der Temperatur (°C)	11.2-28.6	6.0-17.5

Rainfall / Regenmenge	OCT - NOV	DEC - JAN	TOTAL
Rainfall (mm)	136	313.2	449.2
Rainfall (%)	30.3	69.7	
Total Precipitation (IX-V)(mm)			690.4

No. of years Novembers were wetter than Decembers Anzahl Jahre mit Novembern, die feuchter als Dezember waren	4
No. of years Decembers were wetter than Novembers Anzahl Jahre mit Dezembern, die feuchter als November waren	21
No. of years Novembers were wet enough to enable survival of larvae Anzahl Jahre,die feucht genug waren, daß Larven überleben konnten	13
No. of years Novembers were too dry to enable survival of larvae Anzahl Jahre mit Novembern, die für das Überleben von Larven zu trocken waren	12
No. of years Decembers were too dry to enable survival of larvae Anzahl Jahre mit Dezembern, die für das Überleben von Larven zu trocken waren	2

genesis and oogenesis has been described previously (DEGANI et al. 1997; SHARON et al. 1997). The latter study has shown the uniqueness of this species in that it has mature, post-vitellogenic oocytes that increased in number following gestation which lasts about a year [in *Salamandra salamandra terrestris* LACÉPÈDE, 1788 about eight months (FELDMANN & KLEWEN 1981)]. It appears that the mature oocytes are ready for fertilization during the breeding season towards the beginning of spring. Does fertilization trigger ovulation? The rapid process of ovulation in this salamander as well as ova fertilization have been rarely observed. Process 2. some data are presented here and an attempt is made to discuss the timing of parturition.

The dates of oviposition or larval release (i.e. parturition) are significant in order to avoid conspecific larvae in ponds (MARSH & BORRELL 2001), and the likelihood of larval predation (i.e. cannibalism). Timing of the onset of parturition is of great significance for the survival of the larvae**.** The female seems capable of adjusting the onset of parturition. Some breed only early in the season and others only later. However, apparently this does not enable them to predict the risks involved in releasing larvae either early or late in the season, nor guarantee their successful metamorphosis. The chances of success favor early breeding (see Table 5).

Both the number of cohorts and their size (i.e. number of larvae in each) are important factors determining the reproductive potential of a female salamander. What are the relationships between larval numbers and female's age or size (mass, length)? From the present study there does not appear to be a significant relationship between females' mass and larval numbers. However, the recorded number of larvae born in the laboratory does not always indicate the total number of larvae born during the entire breeding season, as the female salamander has been shown to be capable of

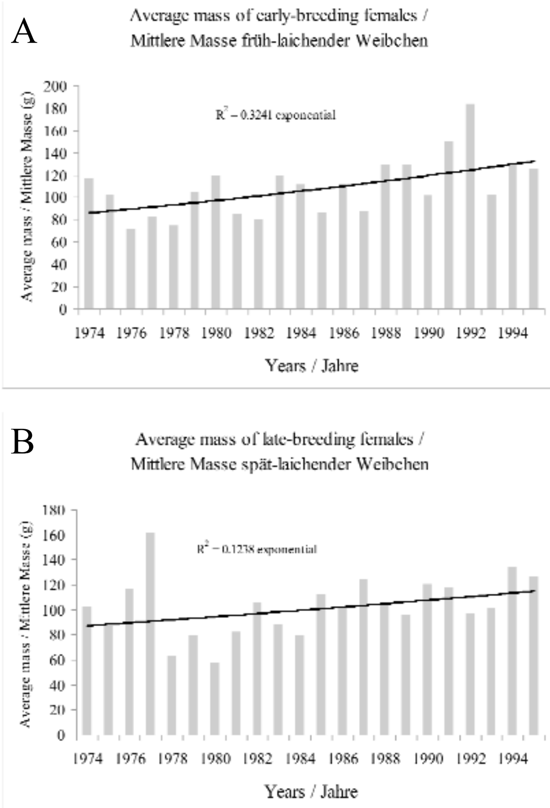

Fig. 5: Average mass (g) of A - early (September-November) and B - late (December-January) breeding female *Salamandra infraimmaculata* MARTENS, 1855 from Mt. Carmel (Israel), over the years.

Abb. 5: Jahreswerte der durchschnittlichen Körpermasse (g) von A - früh (September - November) und B - spät (Dezember - Jänner) laichenden Weibchen von *Salamandra infraimmaculata* MARTENS, 1855 vom Karmel-Gebirge (Israel).

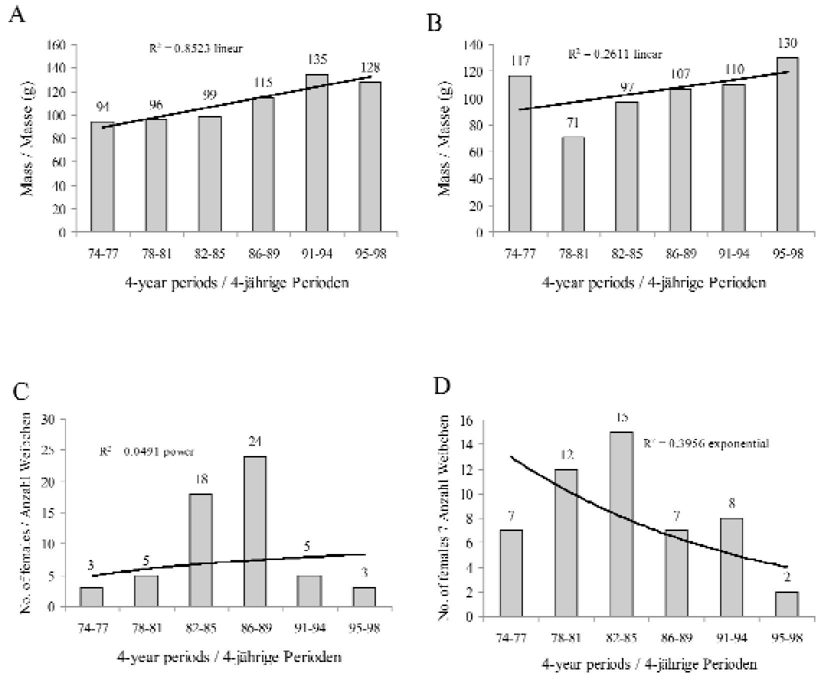

Fig. 6: Number and average body mass (g) of early- and late-breeding females of *Salamandra infraimmaculata* MARTENS, 1855 over the years (arranged in 4-year periods).
A - Mass of early-breeding females; B -Mass of late-breeding females;
C - Number of early-breeding females; D - Number of late-breeding females.

Abb. 6: Anzahl und mittlere Körpermasse (g) früh- und spät ablegender Weibchen von *Salamandra infraimmaculata* MARTENS, 1855 im Verlauf der Jahre (zu 4-jahres-Perioden gruppiert).
A - Masse früh ablegender Weibchen; B - Masse spät ablegender Weibchen;
C - Anzahl früh ablegender Weibchen; D - Anzahl spät ablegender Weibchen.

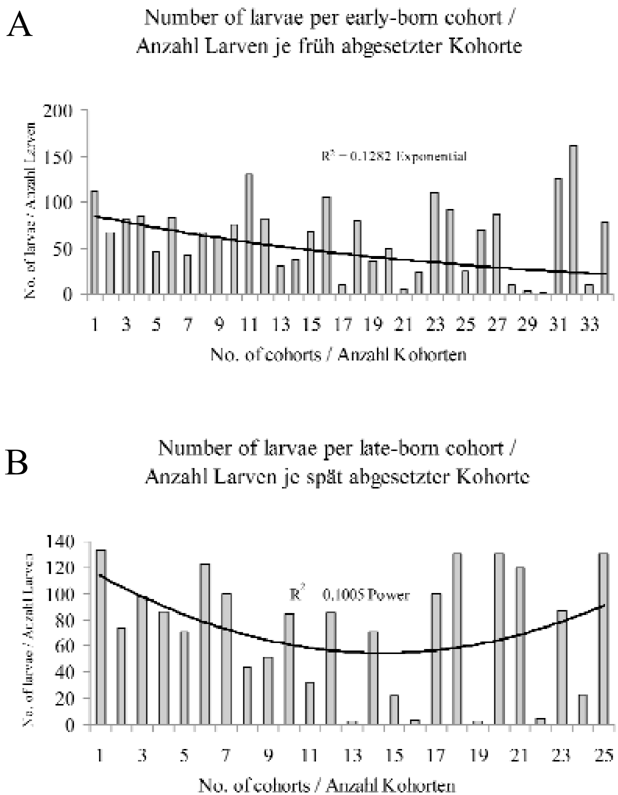

Fig. 7: Number of larvae in early and late born cohorts of *Salamandra infraimmaculata* MARTENS, 1855 from Mt. Carmel (Israel).

Abb. 7: Anzahl der Larven in früh und spät geborenen Kohorten von *Salamandra infraimmaculata* MARTENS, 1855 vom Karmel-Gebirge (Israel).

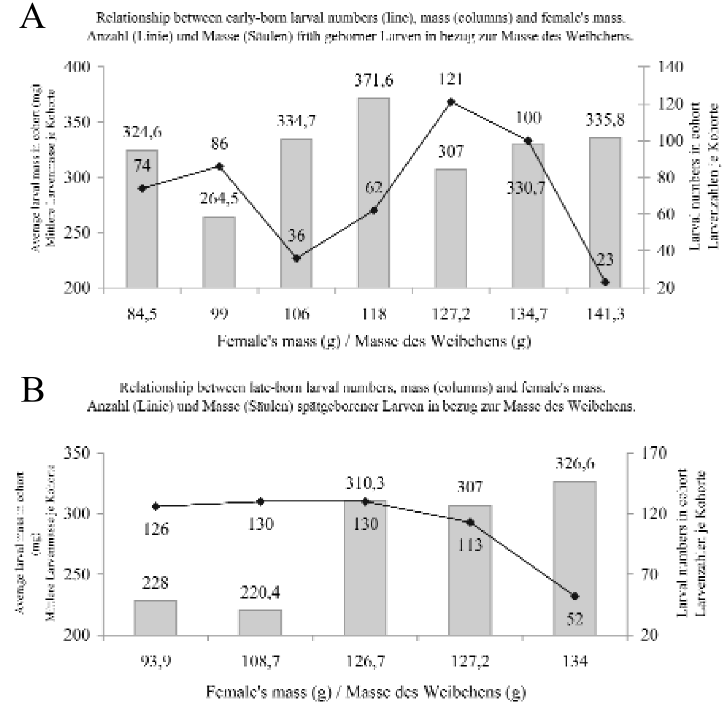

Fig. 8: Relationship between larval numbers and average body mass of larval cohorts, with female's body mass in *Salamandra infraimmaculata* MARTENS, 1855 from Mt. Carmel (Israel). A - in early born larvae, B - in late born larvae.

Abb. 8: Die Beziehung zwischen Larvenanzahl bzw. mittlerer Larvenmasse in den Larvenkohorten und der Körpermasse des Weibchens bei *Salamandra infraimmaculata* MARTENS, 1855 vom Karmel-Gebirge (Israel). A - bei früh geborenen Larven; B - bei spät geborenen Larven.

Table 5: Successful (+) and unsuccessful (-) early (IX-XI) and late (XII-I) breeding by single female *Salamandra infraimmaculata* MARTENS, 1855.

Tab. 5: Erfolgreiche (+) und erfolglose (-) Fortpflanzung (+) bei frühem (IX-XI) und spätem (XII-I) Laichtermin für einzelneWeibchen von *Salamandra infraimmaculata* MARTENS, 1855.

Female's No. Weibchen Nr.	Successful breeding / Fortpflanzungserfolg Early (IX-XI) früh	Late (XII-I) spät	Total success (%) Gesamterfolg
2	++	++	100
14	+	+	100
18	+	+	100
19		-+	50
21	+	-++	75
22	+	+	100
63	++-	+-	60
65	++-+-+-	++	66.7
69	++	-++++	85.7
70	++--	-	40
81	++---+		50
82	+-	+++	80
83	+++--	++	71.4
84	-+	-	33.3
86	++	-+	75
98	--	+-	25
102	+	+++	100
111		++	100
114	++---		40
119	+	+	100
121	-+		50
131	-	+	50
132	+	+	100
157	+	-	50
Total	32 (+); 19 (-)	31 (+); 9 (-)	70.9

colonizing new ponds (i.e. releasing larvae in them) (DEGANI et al. 2007).

Multi-parenthood

It was previously shown that there is a variability in dimensions of larvae within a half-sib cohort (COHEN et al. 2005, 2006). This can be an outcome of multiple mating resulting in multi-parenthood. Since salamanders are known to be capable of storing sperm in the dorsal roof of the cloacal gland: the spermathecae (SEVER 2002), it is possible that certain sperm-mixing does take place in the uterus. As for sperm-storage, the fact that females arrive near the ponds on consecutive years rules out the need to store sperm in their spermathecae (JOLY et al. 1994) since a salamander gets more than a single chance to mate and can mate every year (WARBURG 2006, and present study). For the female, annual visits to the ponds could enable multiple-mating, spermatophore-storing and insemination resulting perhaps in sperm-mixing. The matter of sperm survival inside the spermatheca needs to be studied and can perhaps provide an answer why a female does arrive near the ponds (and mates to replenish her sperm stock) in spite of its capability to store sperm.

Growth rate of larvae and their size at metamorphosis have been previously described in this species (COHEN et al. 2006). Variability in growth rates is due to differential growth modes identified within the same half-sib cohort as well as due to the presence of cannibalistic larvae which will metamorphose at twice the size of normal larvae (COHEN et al. 2005). Consequently, the age of larvae at metamorphosis could vary between 2-4 months.

Differential dispersion of post-metamorphs

Amphibian post-metamorphs need to disperse and emigrate as soon and as far as possible during the suitable season since they are limited both spatially and temporally. Size of the juveniles is crucial in enabling successful dispersal. Very little is known about dispersal of young urodele post-metamorphs in nature. Dispersal success is dependant on the timing of metamorphosis. The earlier the metamorphosis the better chance for survival of the juveniles. Winter dispersal is much easier, consequently, survival will be better. Spring dispersal is dangerous due to hot spells of high temperatures and low humidity. The rate of water loss of juvenile salamanders is considerably higher that that of adults (WARBURG & DEGANI 1981) although they were shown to be able to survive three days dehydration at low humidity. Nevertheless, it is of great advantage for the juveniles to be able to disperse earlier in the season before the temperature rises and the soil dries out. They can survive 36.5 °C for a few days (WARBURG 1971). Thus, early born larvae will have a better chance in years when November is wetter than December.

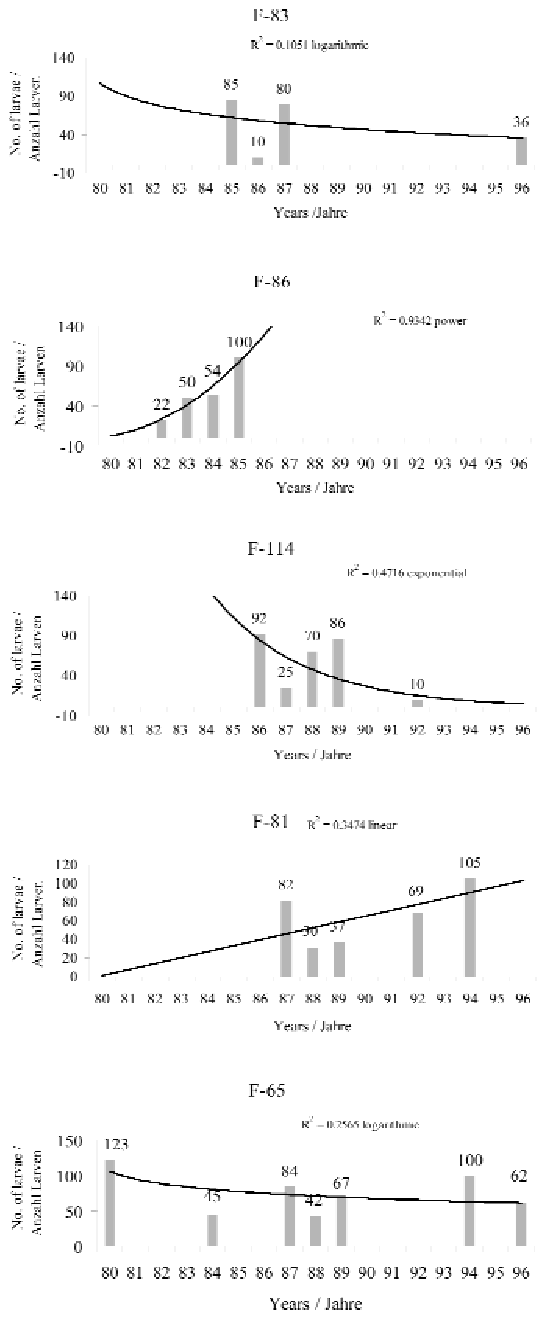

Fig. 9: Number of larvae (in cohorts) born in the laboratory over the years from five females (F-83, F-86, F-114, F-81, F-65).

Abb. 9: Anzahl der Larven (in Kohorten), die von fünf Weibchen (F-83, F-86, F-114, F-81, F-65) über die Jahre hinweg im Labor geboren wurden.

Table 6: Numerical descriptors characterizing a population of early (autumn) and late (winter) breeding females of *Salamandra infraimmaculata* MARTENS, 1855 from Mt. Carmel, Israel.

Tab. 6: Numerische Kenngrößen der Weibchen in einer Population von früh (im Herbst) und spät (im Winter) laichenden *Salamandra infraimmaculata* MARTENS, 1855 des Karmel-Gebirges, Israel.

	Early (IX-XI) früh	Late (XII-I) spät	Total (IX-XI)
Total number of times (and % of time) females bred in the lab .....Anzahl (Prozentsatz) der Weibchen, die im Labor Larven gebaren	36 (58.1)	26 (41.9)	62 (100)
Number of parturitions / Anzahl Larvengeburten	59	57	116
(%) of females / (%) der Weibchen	50.9	49.1	
Female's average body mass (g) / Mittlere Körpermasse (g)	116.2±24.3	101.4±25.9	
Body mass range (g) / Spannweite der Körpermasse (g)	54.5-184.3	29-162	
Female's average total length (cm) / Mittlere Gesamtlänge (cm)	26.5±2.2	25.6±2.5	
Total length range (cm) / Spannweite der Gesamtlänge (cm)	22-29.5	17-29.5	
No. of females captured more than once			24
Av. No. of times female visited ponds			4.1
Maximal no. of times females visited site			9
No. of females that visited ponds more than 3 times			14
No. of females that visited the ponds more than 5 times			5
Four females visited ponds 7 times			
One female visited 9 times			
Av. no. of years during which female visited site			8.1
Maximal no. of years females visited sites			17
No. of times females visited ponds on consecutive years			31
No. of females visited ponds at 10 years intervals between visits			2
No. of times females bred early (X-XI)			52
No. of times females bred late (XII-I)			44
Av. percentage of times females bred early (X-XI)			47.5
Av. percentage of times females bred late (XII-I)			52.5
No. of potentially successful breeding	42	38	80
Mass range (g) of females who gave birth in the lab			58-162
Mass average (g)			109.8±22.1

Both the reproductive potential of a female and the chance of the species' survival depend on three main factors: (1.) longevity. The female's life span in this species has been estimated at 20-21 years (WARBURG 2007a). (2.) size of the cohort (averaging 70 larvae). (3.) the ability to colonize new ponds has been demonstrated by DEGANI et al. (2007). All of these appear to be sufficient to ensure the survival of this species on Mt. Carmel in spite of the significant drop in numbers of females in this population in recent years (WARBURG 2007b, 2008a).

REFERENCES

COHEN, M. & FLAM, R. & SHARON, R. & IFRACH, H. & YEHESKELI, D. & WARBURG, M. R. (2005): The evolutionary significance of intra-cohort cannibalism in larvae of a xeric-inhabiting salamander: an inter-cohort comparison.- Current Herpetology, Kyoto; 24: 55-66.

COHEN, M. & YEHESKELI-HAYON, D. & WARBURG, M. R. & HALEVI, G. & DAVIDSON, D. & SHARON, R. (2006): Differential growth identified in salamander larvae half-sib cohorts: a survival strategy?- Development, Growth and Differentiation, Carlton South, VIC AU; 48: 537-548.

DEGANI, G. & MENDELSSOHN, H. (1982): Seasonal activity of *Salamandra salamandra* (L.) (Amphibia: Urodela: Salamandridae) in the headwaters of the Jordan river.- Israel Journal of Zoology, Jerusalem; 31: 77-85.

DEGANI, G. & WARBURG, M. R. (1978): Population structure and seasonal activity of the adult *Salamandra salamandra* (L.) (Amphibia, Urodela, Salamandridae) in Israel.- Journal of Herpetology, Marceline MO; 12: 437-444.

DEGANI, G. & SELA, E. & HENKIN, Z. & KOREM, S. & GOLDBERG, T. & WARBURG, M. R. (2007): Movement to rock pool hole breeding sites of *Salamandra infraimmaculata* during colonization of new breeding places in xeric habitats.- Salamandra, Rheinbach; 43: 7-12.

DEGANI, G. & SHARON, R. & WARBURG, M. (1997): Ovarian steroid levels in *Salamandra salamandra infraimmaculata* during the reproductive cycle.- General and Comparative Endocrinology, San Diego CA; 106: 356-360.

/--BREEDING SEASON---/
Laichzeit

Month / Monat	IX	X	XI	XII	I	II	III	IV	V	VI	VII	VIII
Average rainfall Mittlere Regen-menge (mm)	0.24	34.2	106.5	181	155	122	79	30	4.3	0	0	0

Rain / Regen (%) < 29.5% > < 70.5%>

OOCYTE CYCLE / OOZYTENZYKLUS

Ovulation /---------/

Gestation /---/

Vitellogenesis /------------------------/ (34.8%)

Maturation / Eireifung /---------/ (9.4%)

FEMALE / WEIBCHEN

Mating /Paarung /---------------------/

Fertilization (*) /----------------/

Parturition Larvenablage /-------------------------/

Early / früh (50.9%) /--------------/

Late / spät (49.1%) /--------------/

Fig. 10: Summary graph of the reproductive strategy of female salamanders *Salamandra infraimmaculata* MARTENS, 1855 from Mt. Carmel (Israel). /-------/ = Duration.
Data on the oocyte cycle were taken from SHARON et al. (1997), data on parturition from the present study.
It it shown that females need to have mature post-vitellogenic oocytes ready in time for mating and fertilization.

Abb. 10: Übersicht zu den Fortpflanzungsstrategien weiblicher *Salamandra infraimmaculata* MARTENS, 1855 vom Karmel-Gebirge (Israel). /-------/ = Zeitdauer. Die Angaben zum Oozytenzyklus stammen von SHARON et. al. (1997), die Daten zur Larvenablage aus der vorliegenden Studie. Es wird gezeigt, daß Weibchen reife Oozyten mit abgeschlossener Vitellogenese rechtzeitig zur Paarung und Befruchtung bereitstellen müssen.

FELDMANN, R. & KLEWEN, R. (1981): Feuersalamander; pp. 30-161. In: FELDMANN, R. (Ed.): Die Amphibien und Reptilien Westfalens.- Abhandlungen des Landesmuseums für Naturkunde Münster, Münster; Heft 4.

JOLY, J. & CHESNEL, F. & BOUJARD, D. (1994): Biological adaptations and reproductive strategies in the genus *Salamandra*.- Mertensiella, Rheinbach; 4: 255-269.

MARSH, D. M. & BORRELL, B. J. (2001): Flexible oviposition strategies in tungara frogs and their implications for tadpole spatial distributions.- Oikos, Oxford UK; 93: 101-109.

REBELO, R. & LECLAIR, M. H. (2003): Site tenacity in the terrestrial salamandrid *Salamandra salamandra*.- Journal of Herpetology, Marceline MO; 37: 440-445.

SEVER, D. M. (2002): Female sperm storage in amphibians.- Journal of Experimental Zoology, Hoboken NJ; 292: 165-179.

SHARON, R. & DEGANI, G. & WARBURG, M. R. (1997): Oogenesis and the ovarian cycle in *Salamandra salamandra infraimmaculata* MARTENS (Amphibia; Urodela; Salamandridae) in fringe areas of the taxon's distribution.- Journal of Morphology, Hoboken NJ; 231: 149-160.

WARBURG, M. R. (1971): The water economy of Israel amphibians: The urodeles *Triturus vittatus* (JENYNS) and *Salamandra salamandra* (L.).- Comparative Biochemistry and Physiology, New York NY; (A) 40: 1055-1063.

WARBURG, M. R. (1986a): A relic population of *Salamandra salamandra* on Mt. Carmel: a ten-year study.- Herpetologica, Champaign IL; 42: 174-179.

WARBURG, M. R. (1986b): Observations on a relic population of *Salamandra salamandra* on Mt. Carmel during eleven years; pp. 389-394. In: ROČEK, Z. (Ed.): Studies in Herpetology, Prague (Charles University Press).

WARBURG, M. R. (1992): Breeding patterns in a fringe population of fire salamanders, *Salamandra salamandra*.- Herpetological Journal, London; 2: 54-58.

WARBURG, M. R. (1994): Population ecology, breeding activity, longevity and reproductive strategies of *Salamandra salamandra* during an 18-year long study of an isolated population on Mt. Carmel, Israel.- Mertensiella (supplement to Salamandra), Rheinbach; 4: 399-421.

WARBURG, M. R. (1997): Ecophysiology of amphibians inhabiting xeric habitats; Heidelberg (Springer Verlag), pp. 182.

WARBURG, M. R. (2006): Breeding site tenacity during a quarter of a century, in a rare xeric-inhabiting *Salamandra* within an isolated metapopulation.- Bulletin de la Société Herpétologique de France; Paris; 118: 1-18.

WARBURG, M. R. (2007a): Longevity in *Salamandra infraimmaculata* from Israel with a partial review on other salamanders.- Salamandra, Rheinbach; 43: 21-34.

WARBURG, M. R. (2007b): The phenology of a rare salamander in a population breeding under unpredictable ambient conditions: a 25 year study.- Acta Herpetologica, Firenze; 2: 147-157.

WARBURG, M. R. (2008a): Changes in recapture rate of a rare salamander in an isolated metapopulation studied.- Russian Journal of Herpetology, Moskva; 15: 11-18.

WARBURG, M. R. (2008b): Temporal variations in body dimensions followed for 25 years in a breeding population of adult salamanders, with a partial review on other Urodela.- Senckenbergiana Biologica, Stuttgart; 88: 81-105.

WARBURG, M. R & DEGANI, G. (1981): Evaporative water loss and uptake in juvenile and adult *Salamandra salamandra* (L.) (Amphibia: Urodela).- Comparative Biochemistry and Physiology, New York NY; (A) 62: 1071-1075.

WARBURG, M. R. & DEGANI, G. & WARBURG, I. (1978/79): Ovoviviparity in *Salamandra salamandra* (L.) (Amphibia, Urodela) from northern Israel.- Vie et Milieu, Banyuls-sur-Mer; 28/29: 247-257.

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