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The phenology of a rare salamander (*Salamandra infra-immaculata*) in a population breeding under unpredictable ambient conditions: a 25 year study

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Abstract. This is a long-term study (1974-1999) on the phenology of the rare, xeric-inhabiting salamander *Salamandra infraimmaculata* in a small isolated population during the breeding season near the breeding ponds on Mt. Carmel. This is a fringe area of the genus' south-easternmost Palaearctic distribution. Salamanders were captured during the 25 year long study. The first years up to the 1980s the total number of salamanders increased but during the last years there seems to have been a decline. Although this could be a phase in normal population cyclic oscillations nevertheless when compared with long-term data on a European *Salamandra* it does not seem so. The interpretation of the species' status is dependent on numbers of salamanders captured as well as on the duration of the study. These subjects are reviewed and discussed in this paper.

Keywords. *Salamandra*, Amphibia, Urodela, phenology, long-term study, unpredictable climate, population decline.

INTRODUCTION

The adult population of *Salamandra infraimmaculata* was studied at the breeding sites on Mt Carmel during 25 years 1974-1998 (except 1990). This relict population inhabits a fringe habitat on Mt Carmel at the south-eastern edge of the genus' range. In Israel this salamander is a rare and protected species and lives in only three disjunct northern areas of the Country. The main population is located in the mountains of the Western and Central Galilee (Degani and Warburg, 1978). In addition, two other smaller populations inhabit two disjunct areas: one about 50 km to the north-east (Degani and Mendelssohn, 1980), and the second about the same distance to the southwest, in the northern portion of Mt Carmel (Warburg, 1986a, 1986b, 1992, 1994). This last population is estimated to be much smaller than that in the Galilee mountains (Warburg, 1992, 1997). There is no apparent reason why salamanders had not extended their distribution into other mountain ranges in the Mediterranean region of central Israel such as Samaria and Judea: they are never found there, although Palaearctic species of animals (and 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 over such a long period. Since it is a fringe population inhabiting an area where conditions are suboptimal to the animals for part of the time, it exhibits special adaptations that are not found in other species in this genus (Sharon et al., 1996; Warburg, 1997).

Adult *S. infraimmaculata* are terrestrial, and only females return to water when mature at the age of 3-4 years, and only for the time needed to lay larvae (see Warburg et al., 1978-1979). Males usually remain outside the ponds.

The objectives of this study were to survey the phenology of a single salamander population over a long period (25 years) in order to assess its status as an endangered species. Since it is extremely difficult to make a definite statement about causes that might endanger a species, long-term studies as this are much better qualified to make any suggestions than a 3-4 year standard length study. Among several long-term studies (43 research papers) 29 of which concerning urodele species, are listed in Appendix 1.

There are several advantages in long-term studies. Firstly, an entirely different outlook emerges as the research unfolds, and secondly, changes in populations can be followed over a long period enabling a different aspect in evaluating oscillations in population cycles of a long-living urodele.

MATERIALS AND METHODS

The study was carried out south to Haifa, at the top of Mt Carmel located towards its western slopes, about 20 km south of the urban area. The area contains four rock-pools which are important breeding sites for the salamanders in this region.

During the 25 years of the study, annual rainfall ranged between 397-1161 mm, being on average 690 mm (Table 1); 460 mm (66.6%) fell during the breeding season, in September-January, while 230 mm during the rest of the rainy season. Rain during the remainder of winter (end of February) is not of great significance to the breeding pattern of the adults, but for the survival of the larvae, since the larvae need at least 6-8 weeks to metamorphose and they might not be able to complete metamorphosis once the pond water warms up (see Cohen et al., 2005, 2006).

Adult salamanders were captured on stormy winter nights throughout the entire breeding season, i.e. about 10-12 weeks from mid-October to the beginning of January. They were collected, sexed by cloacal examination (Warburg et al., 1978, 1979), weighed (Mettler balance at $\pm$ 0.1 g accuracy), measured (to the nearest mm) and photographed, for individual recognition on the basis of dorsal patterns (see Warburg, 2006 for details). They were then released to their original collecting site either during the same or on the following night. The number of salamanders active each year during the breeding season at the study site was rather small (< 30) compared to most of other salamander species as well as to numbers of *Salamandra* spp in Europe (Feldmann, 1987; Klewen, 1985). In order to investigate if the numbers of salamanders varied over years or accordingly with yearly rainfall, we used t-test and regression analyses. In this last case, we performed linear, polynomial, and exponential models and we used that with the higher value of R^2.

Table 1. Average annual rainfall and number of salamanders captured during the breeding season: September to January.

Year	Rainfall (Av. Ann.)	(%)	Total	Captured	no. visits	Capts/Visits
1974	586	72.5	808	10	5	2
1975	383	59.0	649	7	5	1.4
1976	550	63.1	872	3	3	1
1977	600	**82.8**	724	8	10	0.8
1978	398	74.2	536	7	21	**0.33**
1979	642	69.5	923	5	13	0.38
1980	439	70.5	623	11	6	1.83
1981	**211**	47.8	441	17	14	1.21
1982	600	68.8	872	21	23	0.91
1983	317	61.8	513	21	**33**	0.63
1984	342	56.1	609	19	17	1.12
1985	369	63.0	586	26	17	1.53
1986	622	79.4	783	29	22	1.32
1987	654	68.8	951	16	9	1.78
1988	339	71.1	477	**33**	13	**2.54**
1989	444	60.2	737	21	18	1.17
1990	216	**43.6**	495	(*)	(*)	(*)
1991	**843**	72.6	**1161**	14	9	1.56
1992	533	72.1	739	10	12	0.83
1993	310	51.5	602	10	4	2.5
1994	611	75.3	811	19	26	0.73
1995	412	66.4	620	8	6	1.33
1996	295	47.9	616	18	8	2.25
1997	477	64.0	745	17	8	2.12
1998	303	76.3	397	13	8	1.62
Av	460	66.6%	690			1.23
Total				363		

(*) courtesy of the Israel Meteorological Services Beth Dagan. In bold: highest and lowest values

RESULTS

A total of 363 different individual salamanders were hand-captured during 310 visits to the breeding ponds over a period of 25 years, when one year (1990) was not studied

(Table 1). The average number of visits to the pond in one year (excluding 1990) is 13.4, ranging between 3 and 33 (there was no correlation between the number of visits and the number of salamanders collected: R^2 = 0.34 best fit polynomial regression), and salamanders were captured in 160 visits (51.4 %). Altogether the mean number of salamanders captured per visit was 1.23 (Table 1). Most salamanders were captured between 1983 and 1989, and following 1989 there has been a gradual decline (though non significant R^2 = 0.34) in the numbers of salamanders captured (Table 1). The highest number of salamanders captured in one visit was 32 specimens in 1988.

The captures of salamanders were then calculated for 4-year periods (Table 2). The reason for this was in order to compare with the extent of the usual research projects which last up to four years (Alford and Richards, 1999) although some lasted longer. Six such periods fit into the 24 years studied (Fig. 1a), most of them differing significantly from each other (Table 2). During the first four years (1974-1977), 29 salamanders were captured, while the next four years (1978-1981) 58 salamanders followed by 147 salamanders in the next four years (1982-1985). The last four years of study (1994-1998) 95 salamanders were captured (Fig. 1a). After grouping, there appears to be a definite and statistically significant (R^2 = 0.85 best fit polynomial regression) decline in numbers of salamanders frequenting this breeding site on Mt Carmel (Fig. 1a). No such difference could be seen in the rainfall pattern when this was arranged for 4-year periods (R^2 = 0.04 best fit power regression).

If the study would have lasted four years (which is longer than a 3-year average funded research project) e.g. from 1974 to 1976 it could be concluded that the population of adult salamanders is small and declining (Table 1). A fourth year did show an increase but the population size never reached its 1974 peak until six years later (1980). From that year onwards the population size increased, reaching a maximum of 32 in 1988 (Table 1). In the next 4-year period (1978-1981) the population reached a plateau thereafter starting to increase almost continuously till 1986 when it peaked. If we would have studied this population for a period of three years between 1980-1986 we would conclude that the population is increasing. Nevertheless, there does not seem to be a statistically significant relationship between the duration of study and the number of salamanders captured (R^2 = 0.34) nor in the rainfall pattern over the study period (R^2 = 0.04 best fit power regression).

There is no indication that there was indeed any change in the rainfall pattern (Table 1), in the hydro period of the ponds, the quality of air, water or soil. Moreover, there was no significant relationship between rain and the number of salamanders captured (R^2 = 0.0038 best fit power regression).

Table 2. Differences between 4-year periods (t-tests with 6 df) in captures.

	1974-77	1978-81	1982-85	1986-89	1991-94
1978-81	0.329				
1982-85	0.001	0.011			
1986-89	0.003	0.014	0.531		
1991-94	0.014	0.014	0.091	0.072	
1995-99	0.041	0.328	0.003	0.036	0.512

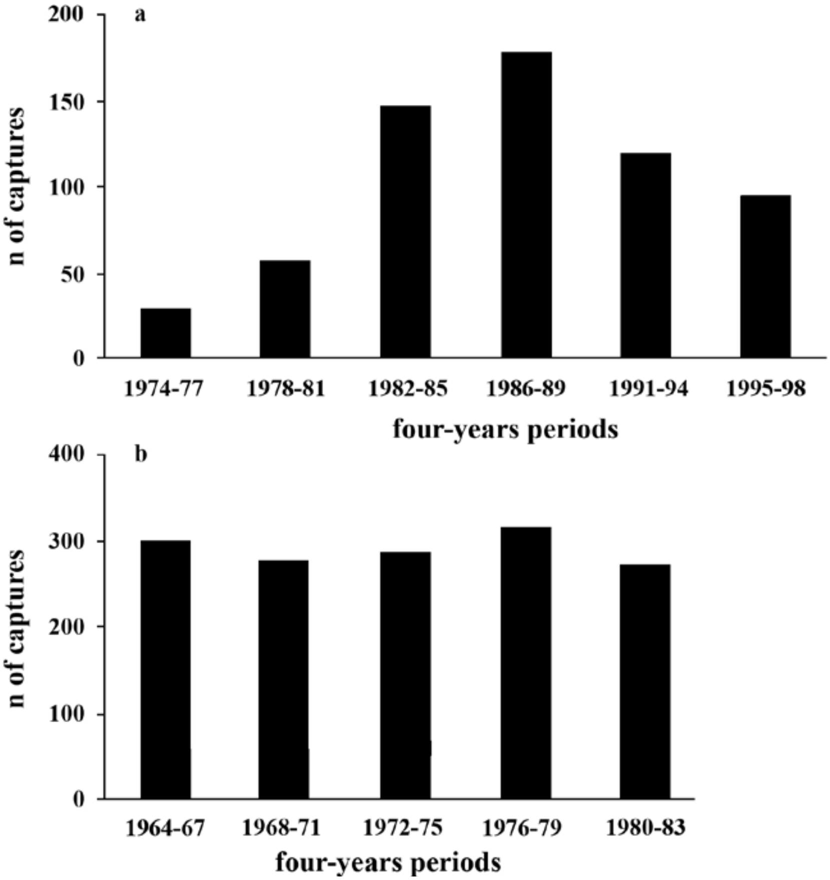

Fig. 1. Phenology of (a) *S. infraimmaculata* arranged in 4-year periods, and (b) *S. terrestris* over 21 years study and arranged in 4-year periods; data from Feldmann (1987) by permission.

It would not have been possible to reach the conclusion that there are natural population oscillations unrelated to the amount of annual rainfall unless these long-term observations became available in spite of the fact that no statistically significant relationship could be demonstrated between the duration of the research and the number of salamanders captured.

DISCUSSION

The chances of capturing salamanders increase greatly with the duration of the study period since salamanders are known to return to the breeding sites even after long intervals (Warburg, 2006). The reasons why both capture and duration are important for such study are: (i) a specimen may be missed by a few minutes consequently it is not certain that the salamander did not visit; (ii) if the study would have been shorter, there was the risk to miss salamanders that do not visit the pond every year. *S. salamandra* in particular seems to be a favorite object for these studies (14 studies see Appendix 1). Perhaps because they are remarkable in their site fidelity both to the breeding ponds as well as to their winter or summer refuges (Feldmann, 1987; Warburg, 1996, 2006) and because they are such long-lived animals (see Warburg, 2007). Thus, many salamanders (50% Feldmann, 1971, 63.1% in Feldmann, 1978, 70% in the present study and 84% in Feldmann and Klewen, 1981) returned to their winter refuges for at least six years.

The most important point in this study is how to interpret the apparent decline in number of salamanders visiting the ponds on Mt Carmel. Although of statistical significance when analyzed for 4-year periods, this decline could also indicate a low point in long-term population oscillation. Similar long-term phenological studies on other urodeles show a variety of patterns: Thus, a 6-year study on *Notophthalmus perstriatus* (Dodd, 1993), a 7-year study on *Triturus cristatus* (Kupfer and Kneitz, 2000), and a 16-year study on *Ambystoma tigrinum*, all show a decline in numbers. Nevertheless, all these studies may have in fact described a phase in normal population oscillations taking place in urodeles. However, long-term data (21 years) on a *S. terrestris* population in Central Europe did not reveal a significant change over the years (Feldmann's data, see Fig. 1b). So, we are left with one possibility: a definite decline in numbers of *S. infraimmaculata*.

Could such a decline endanger *S. infraimmaculata* population on Mt Carmel and cause its extinction? In my opinion it is unlikely since this single population studied here is only one of Mt Carmel's salamanders metapopulation which consists of a few, isolated, patch-like populations. Moreover, since this rather large salamander (up to 30 cm in length with some females weighing well over 100 g) is capable of moving over long distances and withstanding dehydration (Warburg, 1997) it can colonize other ponds (Degani et al., 2007). In addition, the female salamander produces annually an average brood size of 100 larvae during at least 16 years as mature female totaling 1600 larvae whence it needs only 2-3 to reach maturity in order to sustain the population. Given the long life expectance (20 or more years, see Warburg, 2007) and the fact that the female can breed every year (in prep.).

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Appendix 1. Long-term studies on some urodeles (> 5 Yrs)

Species	Years	Source
Cryptobranchus alleganiensis	20	Wheeler et al. (2003)
Ambystoma talpoideum	6	Semlitsch (1987)
A. talpoiderum	8	Semlitsch et al. (1988)
A. talpoideum	9	Pechmann et al. (2001)
A. talpoiderum	12	Semlitsch et al. (1993)
A. talpoideum	16	Semlitsch et al. (1996)
A. opacum	16	Semlitsch et al. (1996)
A. opacum	12	Pechmann et al. (1991)
A. tigrinum	9	Pechmann et al. (2001)
A. tigrinum	16	Semlitsch et al. (1996)
A. maculatum	5	Husting (1965)
A. maculatum	6	Blackwell et al. (2004)
A. maculatum	12	Brodman (2002)
A. jeffersonianum	12	Brodman (2002)
A. californiense	7	Trenham et al. (2000)
Hynobius nebulosus tokyoensis	7	Kusano (1982)
Desmognathus ochrophaeus	7	Tilley (1980)
D. quadramaculatus	6	Dodd and Dorazio (2004)
Plethodon kentucki	7	Marvin (2001)
P. jordani	6	Dodd and Dorazio (2004)
P. jordani	7	Hairston (1983)
P. glutinosus	5	Hairston (1983)
P. ornata	12	Pechmann et al. (1991)
P. cinereus	14	Jaeger (1980)
P. shenandoah	14	Jaeger (1980)
Eurycea quadridigitata	16	Semlitsch et al. (1996)
E. quadridigittata	6	Dodd (1992)
E. quadridigittata	9	Pechmann et al. (2001)
Triturus marmoratus	6	Diaz-Paniagua et al. (1996)
T. marmoratus	5	Martinez-Solano et al. (2003)
T. cristatus	6	Arntzen and Teunis (1993)
T. cristatus	6	Arntzen (2000)
T. cristatus	7	Kupfer and Kneitz (2000)
T. cristatus	20	Beebee (1997)
T. vulgaris	20	Beebee (1997)

Appendix 1. continued

Species	Years	Source
T. vulgaris	11	Gressler et al. (1997)
T. helveticus	20	Beebee (1997)
T. alpestris	5	Martinez-Solano et al. (2003)
T. dobrogicus	11	Gressler et al. (1997)
T. dobrogicus	5	Jehle and Hödl (1998)
Salamandra salamandra	5	Martinez-Solano et al. (2003)
S. salamandra	6	Rebelo and Leclair (2003)
S. salamandra	10	Kästle (1986)
S. salamandra	20	Schmidt et al. (2005)
S. terrestris	7	Feldmann (1971)
S. terrestris	13	Feldmann (1978)
S. terrestris	21	Feldmann (1987)
S. terrestris	17	Feldmann and Klewen (1981)
S. terrestris	5	Klewen (1985)
S. terrestris	6	Klewen (1986)
S. infraimmaculata	10	Warburg (1986a)
S. infraimmaculata	11	Warburg (1986b)
S. infraimmaculata	18	Warburg (1994)
S. infraimmaculata	25	Warburg (present study)
Notophthalmus viridescens	16	Semlitsch et al. (1996)
N. viridescens	9	Pechmann et al. (2001)
N. perstriatus	6	Dodd (1992, 1993); Dodd and Cade (1998)
Taricha rivularis	7	Twitty et al. (1967)