

Variations in sex ratio studied in a single breeding population of an endangered salamander: a long-term study

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Variations in sex ratio studied in a single breeding population of an endangered salamander: a long-term study. - A small population of a rare, xeric-inhabiting salamander *Salamandra infraimmaculata* Martens, 1885, was studied throughout 25 years at the breeding ponds on Mt. Carmel, Israel. The breeding period extended between October and January but most females visited the ponds during November and December. The number of salamanders fluctuated during the study period not showing any particular pattern. The sex ratio was male-biased during most of this period while female numbers dropped during the last few years. Only such long-term observations can illustrate this point in perspective of time leading to the conclusion that the observed drop in female numbers may eventually effect a decline in the species' presence in this fringe habitat. The subject is discussed and reviewed and a general comparison with variation in sex ratio in other urodele species is presented.

Keyword: Amphibian decline - Endangered species - Long-term study - *Salamandra* - Sex ratio.

INTRODUCTION

The salamander, *Salamandra infraimmaculata* Martens, 1885, is a rare and protected species inhabiting mountainous regions in northern Israel where it is limited in its distribution to three disjunct metapopulations. The main population is located in the mountains of the Western and Central Galilee (Degani & Warburg, 1978). In addition there are two smaller ones at about 50 km distance from, and unconnected to the main area. One is in the north-eastern part of Israel at the foot of Mt. Hermon at Tel Dan (Degani & Mendelssohn, 1982), the other is located southwest of the main area in the northern part of Mt. Carmel Warburg (1986, 1994).

This metapopulation of salamanders on Mt. Carmel comprises the southeastern limit of the species' Palaearctic distribution. Therefore, it inhabits a fringe area where conditions are optimal only part of the time to the animals. It seems possible that salamanders in this area may have to cope, at times, with unsuitable conditions not encountered by other populations inhabiting more favorable environments in the Galilee mountains (Degani & Mendelssohn, 1982; Degani & Warburg, 1978), or by other *Salamandra* species in the center of the species' distribution in Central Europe (Joly, 1968; Feldmann & Klewen, 1981; Klewen, 1985, 1988; Thiesmeier, 2004).

The adult salamander is largely a terrestrial animal returning to water only when mature at the age of 3-4 years, and then only the females for a few hours to breed (Warburg, 2009). Males usually remain out of water even during the breeding period as mating takes place on land. Its aquatic life during the larval period lasts only three to four months. Since as adult, the female enters water only for a few hours, the species' aquatic life totals about 1.25% of its lifetime.

The uniqueness of this species is because of two main of reasons:

1. It occupies a fringe habitat at the edge of its Palaearctic distribution.
2. It has to survive the weather in a xeric Mediterranean region characterized by a rather short rainy season unpredictable in its duration and magnitude between October and January when about 66% of the average annual rain falls. On Mt. Carmel the average annual rainfall ranged between 440-1160 mm during the 25 years of study (averaging 690 mm annually). Since the rainy season is followed by eight months of hot-dry weather, breeding has to take place by January at the latest or the metamorphosing larvae will die (Cohen *et al.*, 2005, 2006). In these studies it was shown that through both differential growth and cannibalism, half-sib larval cohorts facilitate spacing-out the timing of metamorphosis resulting in spacing-out of both temporal and spatial dispersal in juvenile *S. inframaculata* (in preparation). This is an important mechanism for survival eventually enabling colonization of new breeding ponds (Degani *et al.*, 2007).

This long-term study was not planned as such but started as a family project during which the salamanders were observed in their breeding rock-pools on Mt. Carmel, on cold-rainy nights. It developed into this long-term study as ever-more questions arose regarding different aspects of their life history.

The original objective of this long-term study was to learn about the life history and phenology of *S. inframaculata* by monitoring adult salamanders during the breeding season in a single breeding metapopulation. It later evolved into a study on breeding pond tenacity (Warburg, 2006), longevity (Warburg, 2007a), phenology (Warburg, 2007b), recapture rates (Warburg, 2008a), dimensions (Warburg, 2008b), growth (Warburg, 2008c), and reproduction (Warburg, 2009), as these salamanders were observed over a long period (25 years). Consequently new questions arose: does the sex ratio studied in this single population show changes over the years? When can a drop in the number of females be interpreted as a decline?

MATERIALS AND METHODS

The study area was located 12 km south of Haifa on the top of Mt. Carmel towards its western slopes. The study site (about 60x100 m) contains four shallow rock-pools which are one of the main breeding sites for the salamanders in this area. There are a few other far apart breeding ponds that are used by the Mt. Carmel *Salamandra* metapopulation. The average annual rainfall based on 25 years of meteorological observations is 690 mm. Since the breeding season when adult salamanders emerge from their aestivation sites starts earliest in September (generally October) and lasts till January, I used data only for these months. The study period lasted from 1974 to 1998 with the exception of one breeding season (1990/91) altogether 24 years of observations.

Adult salamanders were observed 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), continuing until mid-January.

The animals were identified individually by their typical yellow patterns on a black background on the dorsal side of the salamander. These hardly ever change throughout its lifetime (Warburg, 2006 see Fig.1, 2007a, b, 2008a). Consequently the salamanders could easily be identified individually by their photographs throughout the entire study period. Marking animals by toe clipping or subcutaneous insertion of PIT tags were not necessary especially since the first method is only adequate for short-term monitoring due to the high rate of regeneration in amphibians especially in urodeles, and both techniques involve rough handling and molesting this rare, endangered species.

The sex was determined by cloacal examination (see Degani & Warburg, 1978). In this study I have used three different ways to express sex ratio:

1. Male/female ratio when male is always one therefore females may be either larger or smaller than one.
2. I have also used percentage (%) to express the ratio between the genders.
3. For comparing with other data I have also used the male/female ratio where male numbers are divided by the females'.

The animals were then photographed and finally released back to their habitat either during the same night or on the following one.

For the partial review on the subject of changes in sex ratio in urodeles, I was limited in the number of papers I could use since many of the papers describing population structure or dynamics did not provide the original data in the form of Tables but rather in Figures. The urodelan species cited in the text and Tables are listed in the Appendix.

It is of interest to note here that the earliest paper on this subject providing quantitative data was published in this journal (*Revue suisse de Zoologie* 1952) by Fritz Ernst of Zurich Anatomical Institute.

For statistical analysis I have used standard regression analyses since the number of salamanders sampled was rather small.

RESULTS

One hundred and thirty salamanders were captured and about 50% of them were recaptured during the 25 years of study. This paper is based on both captured and recaptured (more than once up to 40 times in males, see Warburg 2006, 2007b, 2008) salamanders.

The number of both males and females did not show significant relation with either years (1974-1998 Fig. 1 A) or rain (Fig.1 B). Nor was there a significant relation between years and rainfall (Fig.1 C).

During the long study the sex ratio (%) fluctuated (Fig. 2 A). Thus, during the first three years (1974-76) there was an increase in the relative number of females which became greater than that of males in the 3rd year (1976). After this, the numbers of males was always greater than those of females. In all but three years (1976, 1980,

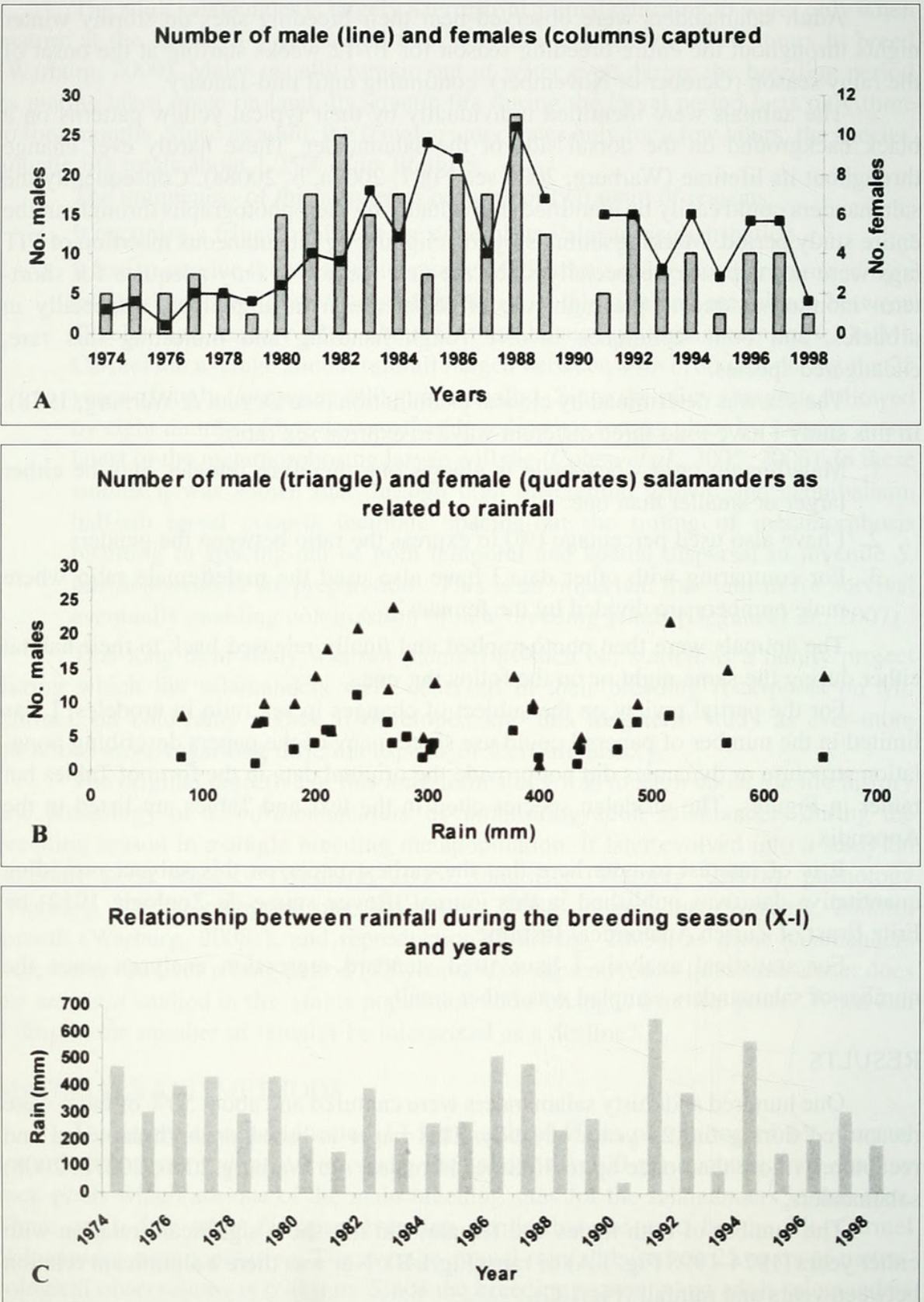


FIG.1

Number of male and female salamanders captured over the years (A) and in relation to rain (B), and between rain and years (C).

1982) males comprised more than half the population and in most years there were more than 70% males (Fig. 2 A). Sex ratio (M:F ratio) did not relate significantly to years (Fig. 2. C). Sex ratio ranged from 1:0.12 (in 1985) to 1:2 (in 1976) averaging 1:0.4 in 24 years of observations (Table 1). There was no significant relationship between number of males and females (Fig. 2 B).

When the 25-year study period was divided into six 4-year periods (excluding the year 1990 when the site could not be visited during the breeding season), no significant relation was noticed in either females ($R^2 = 0.0495$ Fig. 3 A), males ($R^2 = 0.634$ Fig. 3 B) or rainfall ($R^2 = 0.1127$ Fig. 3 C). However, the M:F ratio was related significantly when arranged in 4-year periods ($R^2=0.9527$) becoming increasingly male biased during the last two 4-year periods (1991-1998) (Fig. 4). The M:F ratio drops gradually from 1:0.64 (M:F) during the first eight years of observation (1974-1981), to 1:0.26 in later years (1995-1998) showing a decline in the percentage of females in this breeding population (Table 2).

DISCUSSION

The data presented here where assembled over a long period of time during which profound changes in the sex ratio within a single salamander population were noticeable. Two main points need to be discussed:

1. Are there any similar data on urodelan sex ratio that can be compared?
2. How can these temporal variations in the sex ratio be explained?

Regarding comparable data: Similar studies on sex ratio in the genus *Salamandra* show that the sex ratio ranged between 1:0.29 to 1:1.14 M:F ratio (Table 3). In only three of the 12 studies reviewed, the sex ratio was female-biased. On the other hand, in one 5-year long study of *S. s. terrestris*, there was a significant relation ($R^2=0.7174$) between M:/F ratio and years. The proportion of males continuously increased with years (from 2.31 to 3.52 M:F ratio, see Klewen, 1985).

Reviewing 51 studies on 34 urodele species studying sex ratio (Table 4) the sex ratio in 22 species was about 1:1 (M:F). In eight *Ambystoma* spp. and in five *Plethodon* spp. sex ratio ranged between 1:0.35 to 1:3. In seven *Triturus* spp. sex ratio ranged between 1:0.58 to 1:3.3.

The reason for a higher proportion of males in the populations close to the breeding sites could be because of early maturity in males (Flageole & Leclair, 1992; Leclair & Caetano, 1997). Moreover, their greater activity extending over much of the breeding season arriving at the breeding ponds earlier than females and leaving later, can also contribute to apparent unbalanced sex ratios in adult urodeles (Caetano & Leclair, 1996) thereby explaining some of the spatial and temporal variation in the sex ratio of newts during the season as was suggested by Arntzen (2002). Observations on *S. salamandra* (Linnaeus, 1758) similarly indicated the early activity of males (Warburg, 1994), and Beneski, Zalisko & Larsen (1986) found more males than female *A. macrodactylum* Baird, 1849 at the beginning of the breeding period, the females only being active later on.

Previous studies were concerned with both spatial and temporal changes in sex ratio.

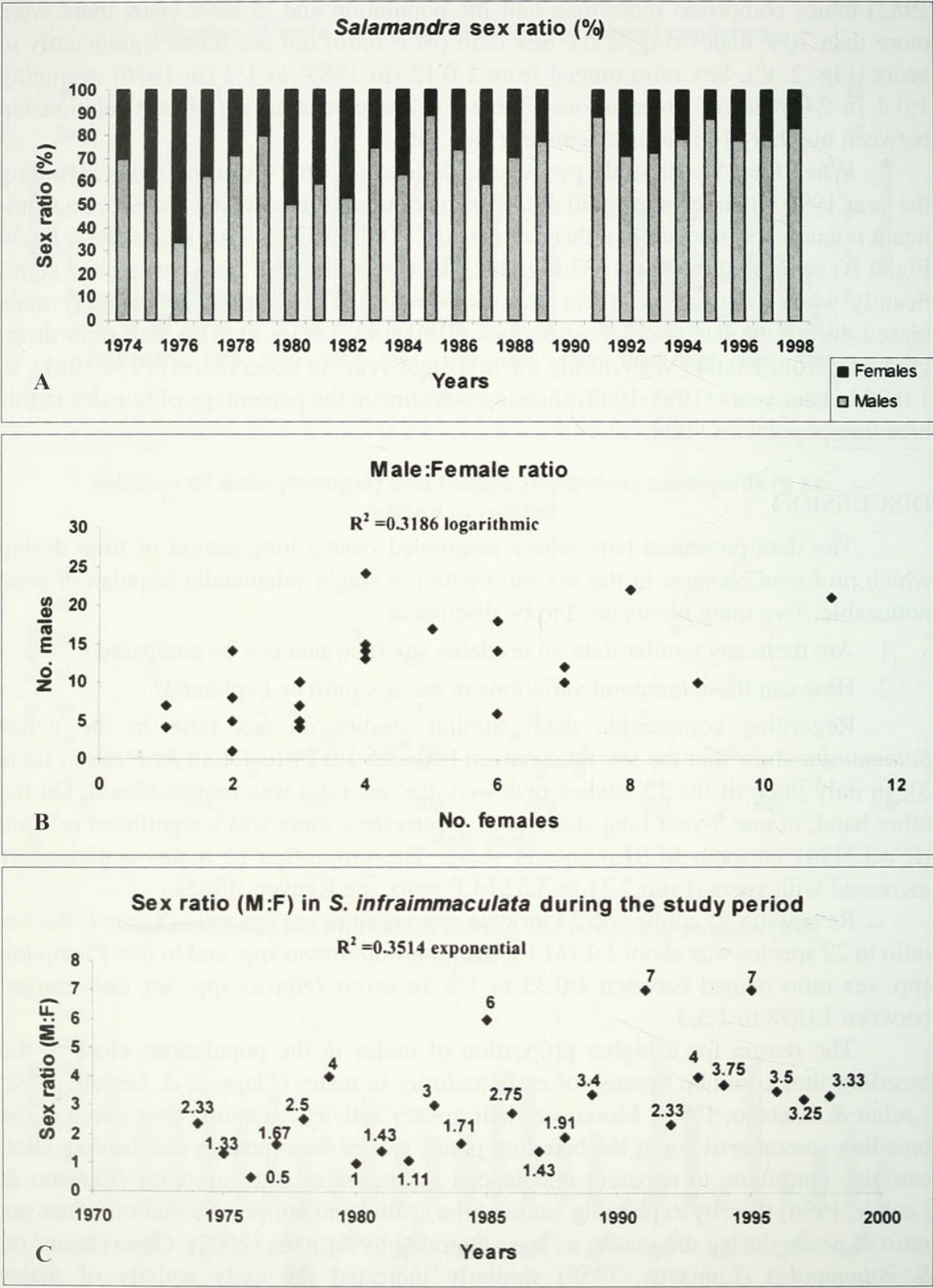


FIG. 2

Sex ratio (M:F) (A), the relationship between the number of males and of females (B) and changes in sex ratio during the study period (C).

TABLE 1. Sex ratio.

Year	Males	Females	M : F
1974	7	3	1 : 0.43
1975	4	3	1 : 0.75
1976	1	2	1 : 2
1977	5	3	1 : 0.6
1978	5	2	1 : 0.4
1979	4	1	1 : 0.25
1980	6	6	1 : 1
1981	10	7	1 : 0.7
1982	9	10	1 : 1.1
1983	18	6	1 : 0.33
1984	12	7	1 : 0.58
1985	24	3	1 : 0.12
1986	22	8	1 : 0.36
1987	10	7	1 : 0.7
1988	26	11	1 : 0.42
1989	17	5	1 : 0.29
====	the site was not visited		
1991	15	2	1 : 0.13
1992	15	6	1 : 0.4
1993	8	3	1 : 0.37
1994	15	4	1 : 0.27
1995	7	1	1 : 0.14
1996	14	4	1 : 0.28
1997	14	4	1 : 0.28
1998	4	1	1 : 0.25
272			109
			1 : 0.4

TABLE 2. Sex ratio calculated in 4-year periods.

Years	Nos. captured		M : F
	M	F	
1974-77	17	11	1 : 0.65
1978-81	25	16	1 : 0.64
1982-85	63	26	1 : 0.41
1986-89	75	31	1 : 0.41
=====			
1991-94	53	15	1 : 0.28
1995-98	39	10	1 : 0.26
Total	272	109	1 : 0.4

SPATIAL CHANGES

The sex ratio in salamanders varied between localities. In *Salamandra atra* Laurenti, 1768 it ranged between 1:0.49 and 1:0.84 M:F ratio (Klewen, 1986), in *Batrachoseps attenuatus* (Eschscholtz, 1833) M:F sex ratio ranged between 0.17-1.78, and in *Aneides lugubris* between 0.73-1 depending on the locality (Anderson, 1960). Likewise, in *Notophthalmus viridescens* (Rafinesque, 1820), differences in the sex ratio were found in populations from different localities ranging from 1:0.6 to 1:2 M:F

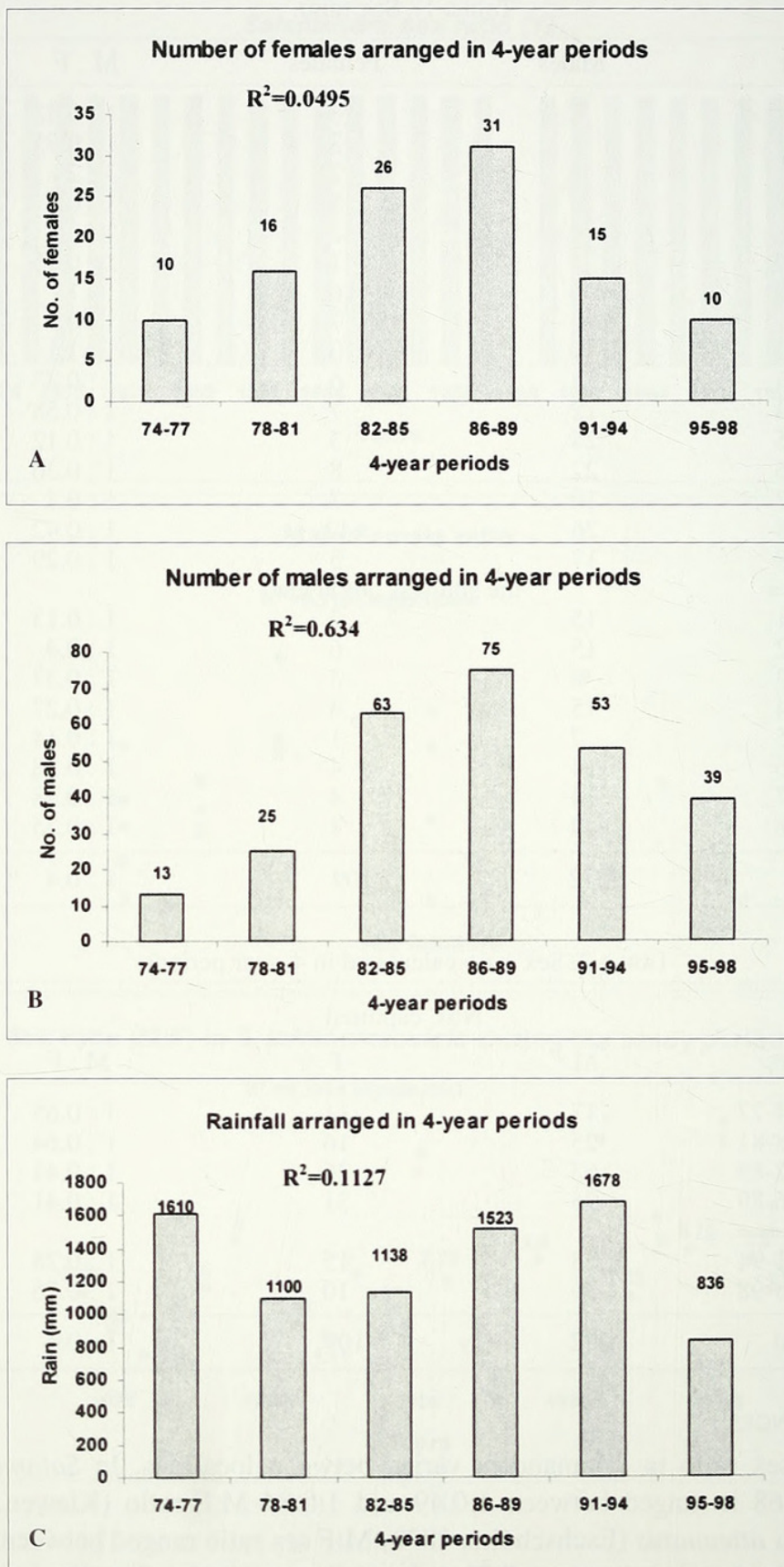


FIG. 3
Number of males, females and rainfall arranged in 4-year periods.

TABLE 3. Sex ratios in *Salamandra*.

Species	M:F	Source
<i>Salamandra salamandra</i>	1:0.55	Geiler, 1974
<i>S. salamandra</i>	1:1	Degani & Warburg, 1978
<i>S. salamandra</i>	1:0.6	Degani & Mendelssohn, 1982
<i>S. salamandra</i>	1:0.29	Warburg, 1994
<i>S. salamandra</i>	1:1.08	Rebelo & Leclair, 2003
<i>S. s. terrestris</i>	1:0.55	Feldmann & Klewen, 1981
<i>S. s. terrestris</i>	1:0.38	Klewen, 1985
<i>S. s. terrestris</i>	1:0.81	Seifert (see Thiesmeier, 2004)
<i>S. s. gallaica</i>	1:1.04	Rebelo & Caetano, 1995
<i>S. salamandra</i>	1:1.14	Catenazzi, 1998 (see Thiesmeier, 2004)
<i>S. infraimmaculata</i>	1:0.41	This study
<i>S. atra</i>	1:0.67	Klewen, 1986
<i>S. atra atra</i>	1:1	Luiselli <i>et al.</i> , 2001

ratio Gill (1978, a,b) and 1:0.53 to 1:1.7 M:F ratio (Leclair & Caetano, 1997). Similar differences in sex ratios among populations of this species were also described by Hurlbert (1969).

In the eastern Galilee population of *S. salamandra*, Degani (1980) found 161 specimens 54.4% of them were males, and in a later study 55% were males (Degani & Mendelssohn, 1982).

Sex ratio in *Desmognathus ochrophaeus* Cope, 1859 changed with altitude: at high elevation it was 1:0.59 M:F ratio and at low elevation 1:0.74 M:F ratio (Tilley, 1973).

SEASONAL CHANGES

Seasonal changes in the sex ratio in a population of *Desmognathus fuscus* (Green, 1818) were studied by Danstedt (1975). He stressed that they may be a consequence of a decline in the frequency of females in the area he studied. Similar seasonal differences in sex ratio of *Triturus vulgaris* (Linnaeus, 1758) were described: in autumn and winter it was 1:2 M:F, in spring and summer 1:0.77 M:F. The terrestrial phase of the newt showed a 1:3.3 M:F averaging 1:1.26 (Griffiths, 1984). In breeding newts Harrison *et al.* (1983) found a sex ratio of 1:1.1 in *Triturus helveticus* Razumowski, 1789 and 1:2.6 in *T. vulgaris*. The sex ratio in outward migrating newts from the ponds was 1:1.4 M:F in *T. helveticus* and 1:0.7 in *T. vulgaris*. In *N. viridescens* the sex ratio was biased towards males inside the ponds (1:0.8 M:F), and towards females outside the ponds 1:1.2. During the spring migration it ranged from 1:0.88 to 1:2 M:F ratio; during the fall migration it ranged between 1:1.37 to 1:0 M:F ratio (Hurlbert, 1969). Finally, the sex ratio in *Ambystoma texanum* (Matthes, 1855) was different in migrating salamanders (1.5 males to 1 female), and in breeding ones (2.2 males to one female) (Petranka, 1984).

ANNUAL CHANGES

Not only spatial and seasonal variations in sex ratios were described in several urodeles, but sex ratio also appears to vary from year to year and in some cases this variability is rather high.

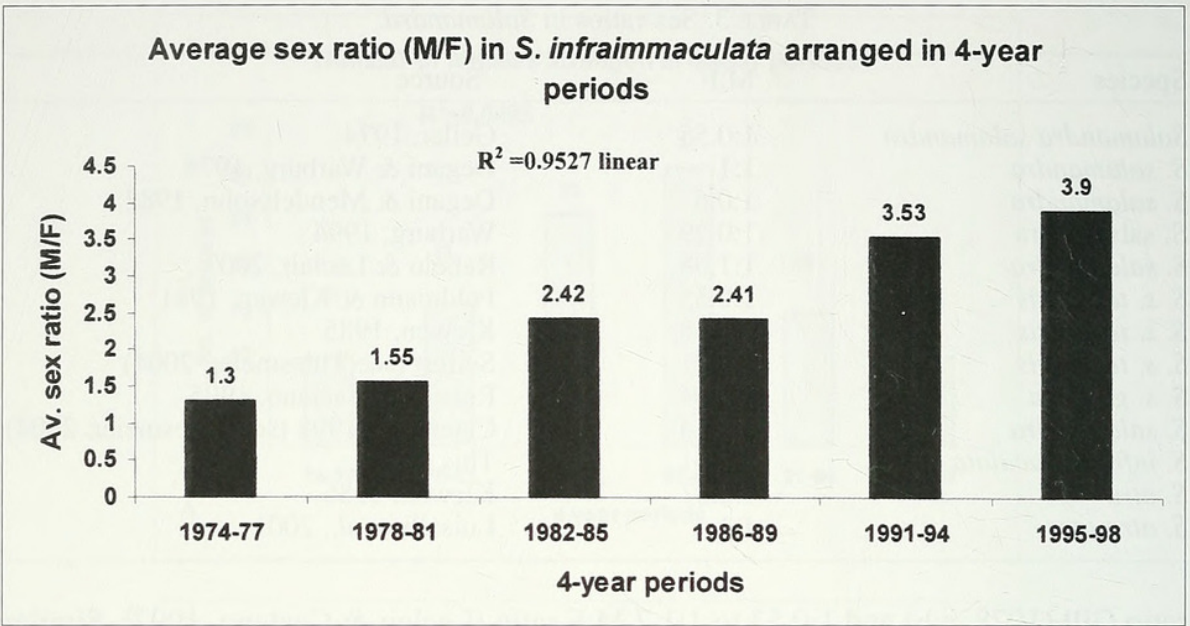


FIG. 4

Average sex ratio (M:F) in *S. inframaculata* arranged in 4-year periods.

TABLE 4. Sex ratios in other urodeles.

Species	M:F	Source
<i>Cryptobranchus allageniensis</i>	1:0.85	Humphries & Pauley, 2005
<i>C. allageniensis</i>	1:0.77 to 1.1.35	Nickerson & Mays, 1972
<i>Ambystoma maculatum</i>	1:0.53	Husting, 1965
<i>A. maculatum</i>	1:1	Blackwell <i>et al.</i> , 2004
<i>A. maculatum</i>	1:0.5	Flageole & Leclair, 1992
<i>A. macrodactylum</i>	1:3	Fukumoto & Herrero, 1998
<i>A. opacum</i>	1:1	Parmelee, 1993 (vide Petranka, 1984)
<i>A. opacum</i>	1:1	Stenhouse, 1987
<i>A. talpoideum</i>	1:1.06	Hardy & Raymond, 1980
<i>A. talpoideum</i>	1:1	Raymond & Hardy, 1990
<i>A. texanum</i>	1:0.45	Petranka, 1984
<i>A. tigrinum</i>	1:0.76	Rose, 1976
<i>A. annulatum</i>	~ 1:1	Briggler <i>et al.</i> , 2004
<i>A. cingulatum</i>	1:0.35	Palis, 1997
<i>Desmognathus fuscus</i>	1:1.27	Orser & Shure, 1975
<i>D. fuscus</i>	1:1	Hall, 1977
<i>D. ochrophaeus</i>	1:0.6	Martof & Rose, 1963
<i>D. ochrophaeus</i>	1:0.68	Tilley, 1973
<i>D. ochrophaeus</i>	1:1	Hall, 1977
<i>Enastina eschscholtzii platensis</i>	1:0.99	Staub <i>et al.</i> , 1995
<i>Plethodon. wehleri</i>	1:0.35 to 1:1.3	Hall & Stafford, 1972
<i>P. websteri</i>	1:1	Semlitsch & West, 1983
<i>P. larselli</i>	~ 1:1	Herrington & Larsen, 1987
<i>P. vehiculum</i>	~ 1:1	Ovaska & Gregory, 1989
<i>P. kentucki</i>	1:0.8	Marvin, 2001
<i>P. cinereus</i>	1:3	Marsh & Goicochea, 2003
<i>Gyrinophilus porphyriticus</i>	1:0.77 to 1:1.19	Bruce, 1978
<i>Eurycea l. longicauda</i>	1:1	Anderson & Martino, 1966

<i>E. quadridigitata</i>	1:1	Semlitsch & McMillan, 1980
<i>Stereochilus marginatus</i>	1:1	Bruce, 1971
<i>Triturus vulgaris</i>	1:0.66	Hagström, 1979
<i>T. vulgaris</i>	1:0.58	Bell, 1977
<i>T. vulgaris</i>	1:2.6	Harrison <i>et al.</i> , 1983
<i>T. vulgaris</i>	1:2-3.3	Griffiths, 1984
<i>T. vulgaris</i>	1:0.92	Verrell & Francillon, 1986
<i>T. vulgaris</i>	~ 1:1	Arntzen, 2002
<i>T. vulgaris meridionalis</i>	1:1	Kleteäki, 1995
<i>T. cristatus</i>	1:0.61	Hagström, 1979
<i>T. cristatus</i>	1:1.03	Arntzen & Teunis, 1993
<i>T. a. alpestris</i>	1: 0.8	Ernst, 1952
<i>T. alpestris</i>	1:1	Kleteäki, 1995
<i>T. alpestris</i>	1:1	Arntzen, 2002
<i>T. helveticus</i>	1:0.93	Gelder, 1973
<i>T. helveticus</i>	~ 1:1	Arntzen, 2002
<i>T. helveticus</i>	1:3	Harrison <i>et al.</i> , 1983
<i>T. marmoratus</i>	~ 1:1	Arntzen, 2002
<i>T. m. pygmaeus</i>	1:1	Diaz-Paniagua, 1998
<i>T. vittatus</i>	1:0.91	Geffen <i>et al.</i> , 1986/87
<i>T. carnifex</i>	1:1	Kleteäki, 1995
<i>Chioglossa lusitanica</i>	1:0.43 to 1: 1.14	Arntzen, 1981
<i>Euproctus platycephalus</i>	1:1	Bovero <i>et al.</i> , 2003
<i>Mertensiella luschani</i>	1:0.78	Tzannetatu-Polymeni <i>et al.</i> , 1977 (Klewen, 1988)
<i>Mertensiella caucasica</i>	1:0.66	Franzen & Nicolai, 1989
<i>Notophthalmus viridescens</i>	1:0.91	Hurlbert, 1969
<i>N. viridescens</i>	1:0.45	Gill, 1978 a
<i>N. viridescens</i>	1:0.52	Gill, 1978 b
<i>N. viridescens</i>	1:1	Healy, 1974
<i>N. viridescens</i>	1:0.9	Healy, 1975
<i>N. viridescens</i>	1:0.7	Leclair & Caetano, 1997

In *S. salamandra* in the eastern part of the Galilee the sex ratio ranged between 1:0.51 to 1:0.8 M:F ratio during three years of study (Degani & Mendelssohn, 1982). Likewise, it ranged between 1:0.83 to 1:1.68 averaging 1:1.08 M:F ratio over a period of five years of study (Rebelo & Leclair, 2003) (see Tables 3, 5). In *S. s. terrestris* Lacepede 1788) the sex ratio ranged from 1:0.28 to 1:0.68 during six years of study (Klewen, 1985, see Table 6).

In *T. helveticus*, van Gelder (1973) describes differences in the sex ratio during three years: ranging between 1:0.68 to 1:1.47 M:F ratio (Table 6). The sex ratio in *T. vulgaris* ranged from 1:0.47 to 1:1 during a three years study (Hagström, 1979 and Table 5). It changed from 1:0.53 M:F when newts were 8-years old to 1:0.92 M:F at the age of nine years, to 1:1.13 when 10 years, 1:1.6 at 11 years, and when over 12 years old it was 1:3.14 M:F ratio (Bell, 1977). In another study on *T. vulgaris* sex ratio was 1:2 M:F in one year and 1:0.76 in the 2nd year of study averaging 1 M to 0.68 F (Griffiths, 1984). In *T. cristatus* (Laurenti, 1768) it ranged from 1:0.94 to 1:1.22 during a seven years study (Arntzen & Teunis, 1993 and Table 6), and from 1:0.35 to 1:0.82 during a five years study (Hagström, 1979 and Table 6). Finally, in *N. viridescens* (Gill, 1978 b) describes sex ratio ranging between 1:0.35 to 1:1 M:F ratio.

TABLE 5. Yearly changes in sex ratio of some urodeles.

	M:F Species (source)						
	<i>A. talp.</i> (a)	<i>A. macul.</i> (b)	<i>S. sal.</i> (c)	<i>S. sal.</i> (d)	<i>S. s. terrest</i> (e)	<i>N. virid.</i> (f)	<i>N. virid.</i> (g)
Year							
1st	1:1.43	1:0.64	1:0.8	1:1.1	1:0.43	1:0.49	1:0.49
2nd	1:1.64	1:0.35	1:0.5	1:1.68	1:0.48	1:0.82	1:0.77
3rd	1:0.99	1:0.24	1:0.6	1:1.15	1:0.68	1:0.65	1:0.64
4th	1:0.65	1:0.37		1:0.83	1:0.33		
5th	1:0.81	1:0		1:0.93	1:0.32		
6th					1:0.28		

a- Raymond & Hardy, 1990

b- Husting, 1965

c- Degani & Mendelssohn, 1982

d- Rebelo & Leclair, 2003

e- Klewen, 1985

f- Gill, 1978a

g. Gill, 1978b

TABLE 6. Yearly changes in sex ratio in *Triturus*.

	M:F				
Species: Source:	<i>T. cristatus</i> (a)	<i>T. cristatus</i> (b)	<i>T. vulgaris</i> (b)	<i>T. vulgaris</i> (c)	<i>T. helveticus</i> (d)
Year					
1st	1:1.22	1:0.57	1:0.5	1:0.59	1:0.68
2nd	1:1.18	1:0.35	1:1	1:0.34	1:1.47
3rd	1:0.94	1:0.8	1:0.47	1:1	1:0.95
4th	1:1.04	1:0.64	1:0.82		1:0.83
5th	1:1	1:0.82	1:0.78		1:1.18
6th	1:1				1:0.8
7th	1:1.12				

a- Arntzen & Teunis, 1993

b- Hagström, 1979

c- Bell, 1977

d- Van Gelder, 1973

In *Ambystoma talpoideum* (Holbrook, 1838) the sex ratio ranged from 1:0.65 to 1:1.64 during a five years study (Raymond & Hardy, 1990). In *Ambystoma maculatum* (Shaw, 1802) the sex ratio studied during five years (Husting, 1965) varied from 1:0.64 M:F when 1st captured, changing later to 1:0.35 M:F ratio on 1st return; 1:0.24 M:F on 2nd return; 1:0.37 M:F on 3rd return and on 4th return it was 1:0 M:F (Table 6). In *Ambystoma californiense* Gray, 1853 sex ratio was in one year 1:1.25 in the next year it was 1:0.12 M:F ratio (Loredo & VanVuren, 1996) and in *Ambystoma cingulatum* Cope, 1868 sex ratio ranged between 1:1.9 to 1:5.1 M:F ratio during a 2-year study by

Palis (1997). In conclusion, a high variability in female proportions in a population was noted in all these studies.

As regards to the second question: How can these temporal variation in the sex ratio be explained? There are three possible ways to explain the temporal changes in sex ratio described here:

- a. These changes could be an outcome of population oscillations which affect one gender to a greater extent than the other.
- b. The change could be the result of partial population migration aiming at colonizing another pond.
- c. It could be a result of a decline in recruitment of juveniles.

All three possibilities can not be proven.

The first possibility was discussed at length in a previous paper (Warburg, 2007b). In that paper changes in the salamander phenology were observed. It was suggested that a low phase in the population oscillations which is likely to change again, took place.

Could the temporal changes in sex ratio be an outcome of a partial population migration aiming at colonizing another pond? The capability of female urodeles to colonize new breeding ponds could help in maintaining a balanced 1:1 sex ratio. It is well known that animal species are capable of moving from one area to colonize another. Nevertheless, such migration does not necessarily imply that an individual animal belonging to a single species does in fact moves from one area to colonize another. In the case of urodeles it could mean that adult urodeles move in-between ponds. However, this is no proof that they actually breed there. The fact that adult urodeles are capable of moving long distances from where they were previously captured is well documented. This movement can be of short duration during the same breeding season or spread over a longer period (more of migratory in nature). The distance an animal is capable of covering is of great significance when establishing artificial ponds.

S. infraimmaculata is known to be able to colonize new ponds (Degani *et al.*, 2007). It was shown that the same female is capable of moving into another site. However, this second possibility was not proven in the breeding site studies.

Indirect evidence supporting the likelihood of movement is based on the observation that a female can skip a year or more not coming to the breeding ponds. Time elapses between subsequent visits by the same female to the same pond (Warburg, 2006).

Can a pond be re-colonized? I believe that a pond can be re-colonized by salamander larvae even after very long intervals, provided at least one male and one female are successful in metamorphosis, in post-metamorphic dispersion, and in their survival to mature adulthood, it will be sufficient for a single female to maintain the species by producing such viable offspring during one breeding season in her long lifetime. However, it does not seem to be very successful during the 25 year study period on the Mt. Carmel population, since the number of females continually dropped.

Finally, can a decline in recruitment of juveniles result in such changes in sex ratio? Recruitment can be affected by a delay in rains affecting the onset of breeding, delay in the metamorphic cycle, resulting in delayed juvenile dispersal which results in

failure to survive to adulthood. Quantitative data on juvenile recruitment are notoriously hard to obtain and in this particular study site more so because of safety factors involved.

The main questions to be addressed are:

1. How far does the percentage of females in a population have to drop in order to be a threat to the species' existence?
2. Does a sex ratio drop to 1:0.25 M:F endanger survival of *S. infraimmaculata*? How long can a population survive at such low female percentage in the population? I shall try to provide some ideas regarding these points.

There is no doubt that the presence of females in a population is essential for the survival of a population but there is no way telling what the minimal threshold could be. *S. infraimmaculata* female is known to survive in nature to the age of 20 years in the field (Warburg, 2006, 2007, 2008c) and is capable of producing about 70 larvae annually from when it matures at the age of 3-4 years for about 15 years. An easy calculation would show that only 0.2% of the larvae born to a single female need to survive to maturity in order to sustain the population. Thus, a female salamander can skip several years without breeding or alternatively a population can survive through a single female even without new juvenile recruitment which may occur as a result of several years of draught (Warburg, 1992, 1997 a, b, 2008). The matter is more fully discussed in Warburg (2009).

The question of longevity is of great importance for the species survival. Small urodele species that are comparatively short-lived (*Plethodon* spp., *Triturus*) will presumably need a higher female percentage in the population compared to long-lived urodeles (*Ambystoma* spp, *Salamandra* spp. living for 15-25 yrs). Thus, the lowest female percentage in *Plethodon* is 1:0.8 M:F ratio, and in *Triturus* 1:0.6 whereas in *Ambystoma* it is 1:0.35 and *Salamandra* 1:0.25. What is the lowest female percentage that a species can survive? The short-lived newts can survive about 37.5% females in a population (with a sex ratio of 1:0.6); a threefold higher threshold than the long-lived urodeles.

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APPENDIX: List of urodele amphibians in which data on changes on sex ratio were available.

Ambystomatidae

- Ambystoma annulatum* Cope, 1886
Ambystoma californiense (Gray, 1853)
Ambystoma cingulatum Cope, 1868
Ambystoma opacum (Gravenhorst, 1807)
Ambystoma maculatum (Shaw, 1802)
Ambystoma macrodactylum macrodactylum Baird, 1849
Ambystoma talpoideum (Holbrook, 1838)
Ambystoma texanum (Matthes, 1855)
Ambystoma tigrinum tigrinum (Green, 1825)

Cryptobranchidae

- Cryptobranchus alleganiensis alleganiensis* (Daudin, 1803)

Plethodontidae

- Desmognathus fuscus* (Green, 1818)
Desmognathus ochrophaeus Cope, 1859
Plethodon vehiculum (Cooper, 1860)
Plethodon larselli Burns, 1953
Plethodon cinereus (Green, 1818)
Plethodon websteri Highton, 1979
Plethodon wehrlei Fowler & Dunn, 1917
Plethodon kentucki Mittleman, 1951

Aneides lugubris (Hallowell, 1849)
Batrachoseps attenuatus (Eschscholtz, 1833)
Ensatina eschscholtzii Gray, 1850
Eurycea quadridigitata (Holbrook, 1842)
Eurycea longicauda (Green, 1818)
Gyrinophilus porphyriticus (Green, 1827)
Stereochilus marginatus (Hallowell, 1856)
Chioglossa lusitanica Bocage, 1864
Euproctes platycephalus (Gravenhorst, 1829)

Salamandridae

Salamandra salamandra (Linnaeus, 1758)
Salamandra inframaculata Martens, 1885
Salamandra salamandra terrestris (Lacepede, 1788)
Salamandra atra Laurenti, 1768
Salamandra salamandra gallaica Malkmus, 1983
Mertensiella caucasica (Waga, 1876)
Mertensiella luschni (Steindachner, 1891)
Notophthalmus viridescens (Rafinesque, 1820)
Triturus marmoratus marmoratus (Latreille, 1800)
Triturus marmoratus pygmaeus (Wolterstorff, 1905)
Triturus alpestris alpestris (Laurent, 1768)
Triturus cristatus cristatus (Laurenti, 1768)
Triturus vulgaris (Linnaeus, 1758)
Triturus helveticus (Razumowski, 1789)
Triturus boscai (Lataste, 1879)
T. vulgaris meridionalis Boulenger, 1882
Triturus carnifex (Laurent, 1768)



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