SALAMANDRA	**43**	1	21-34	Rheinbach, 20 February 2007	ISSN 0036-3375

Longevity in *Salamandra infraimmaculata* from Israel with a partial review of life expectancy in urodeles

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Abstract. A population of *Salamandra infraimmaculata* was monitored on Mt. Carmel, during 25 annual breeding seasons. A large number of salamanders was recaptured several times (up to 40 times in males) over the years at the same site, i.e. near or at ponds where salamanders transform. Some visited the site for several years (17 years in females, 19 years in males). Since these salamanders visit the breeding ponds only as adults and they become sexually mature only when reaching the age of 3-4 years, their age can be estimated. Consequently, longevity under natural conditions was 22-23 years in males and 20-21 years in females. The various methods used in estimating longevity in amphibians are discussed and a partial listing of longevity in urodeles is provided.

Key Words. Amphibia: Caudata: *Salamandra,* long-term study, longevity, age.

Introduction

Salamandra infraimmaculata Martens, 1885 is a rare and protected species from northern Israel. Three disjunct populations are known only. One is found in the mountains of the Western and Central Galil (Degani & Warburg 1978). In addition there are two smaller areas about 50 km distant from the former mentioned area: at Tel Dan at the foot of Mt. Hermon (Degani & Mendelssohn 1982) and in the northern part of Mt. Carmel (Warburg 1986, 1992, 1994). The latter comprises the south-eastern limit of the genus' mainly Palaearctic distribution. Therefore, it is a "fringe" population inhabiting an area where conditions are only part of the time optimal to the animals. Thus, it seems conceivable that salamanders in this area may have to cope, at times, with unsuitable conditions otherwise not encountered by other populations inhabiting more favourable environments in the Galil mountains (Degani & Warburg 1978, Degani & Mendelssohn 1982), or by their conspecifics in the center of the genus' distribution (Joly 1968, Feldmann & Klewen 1981, Klewen 1985, 1988, Thiesmeier 2004).

Adult *S. infraimmaculata* are largely terrestrial, returning to water only when mature at the age of three to four years, and then only the females for a few hours to give birth to their offspring. Males usually remain out of water. The species' aquatic life during the larval period lasts three to four months only. Since as adults, females enter water only for a few hours, their aquatic life totals about 1.25 % of their lifetime.

The uniqueness of this species is due to two main reasons. (1) It occupies a "fringe" habitat at the edge of the genus' Palaearctic distribution. (2) It has to survive in a xeric Mediterranean region characterized by a rather short rainy season unpredictable in duration and magnitude between November-January when about 66 % of the rain falls (on Mt. Carmel the average annual rainfall ranged 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.

This long-term study was not planned as such but started as a 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.

Various terms are in use for describing the age of an amphibian. Maximal age or its life-span may be synonymous with longevity and life expectancy. None of them can be actually known; the age of a salamander can only be estimated.

The objective of this study was to learn about the longevity of *S. infraimmaculata* by monitoring individually-known salamander specimens during the breeding season in a single breeding population in the field, over a period of 25 years.

Material and methods

The study area was south of Haifa on the top of Mt. Carmel located towards its western slopes. The study 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. The study period lasted from 1974 to 1998 with the exception of one breeding season (1990/1991).

Tab. 1. Known ages in *Salamandra* species. A – age classes based on size (SVL) frequencies in the wild; C – animals kept in captivity; G – age estimation based on yearly growth increments in the wild; M – age estimates based on monitoring individual animals in the wild over the years; S – age estimates based on skeletochronological techniques.

species	years	method	source
Salamandra atra	15-17	M	Fachbach 1978
Salamandra atra	10	C	Freytag 1955
Salamandra atra	10 (males)	G	Kalezić et al. 2000
Salamandra atra	11 (females)	G	Kalezić et al. 2000
Salamandra gallaica	19 (males)	S	Rebelo & Caetano 1995
Salamandra gallaica	15 (females)	S	Rebelo & Caetano 1995
Salamandra infraimmaculata	11	G, M	Warburg 1986
Salamandra infraimmaculata	14	S, G, M	Warburg 1992
Salamandra infraimmaculata	18	S, G, M	Warburg 1994
Salamandra infraimmaculata	21	M	present paper
Salamandra lanzai	24	S	Miaud et al. 2001
Salamandra maculosa	6	C	Flower 1925
Salamandra salamandra	33	C	Gäbler 1935
Salamandra salamandra	24	C	Senning 1940
Salamandra salamandra	25	C	Freytag 1955
Salamandra salamandra	> 20	M	Joly 1968
Salamandra salamandra	13 (males)	A	Kalezić et al. 2000
Salamandra salamandra	14 (females)	A	Kalezić et al. 2000
Salamandra salamandra	13	N	Feldmann 1978
Salamandra salamandra	> 50	C	Böhme 1979
Salamandra salamandra	17	M	Feldmann & Klewen 1981
Salamandra salamandra	5	M	Klewen 1985
Salamandra salamandra	25	M	Rebelo & Leclair 2003
Salamandra s. quadrivirgata	> 20	M	Joly 1968
Salamandra s. quadrivirgata	43	C	Schmidtler & Schmidtler 1969

Tab. 2. Dimensions of juveniles and of young adults (see text).

specimens	weight (g)	total length (cm)
61 juveniles of known age	14.5-63.4 (average 33.4 ± 11.5)	12-22 (average 15.9 ± 2.3)
Dimensions of four smallest young adults captured (age unknown)	18.5	16.5 (male)
	24	15.5. (male)
	29	17 (female)
	44	21.5 (female)
Dimension of a three-year-old male recaptured	36	18.5

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 till mid-January.

Animals were identified individually by their yellow patterns on black background on the dorsal side which hardly change throughout lifetime

Thereby, the salamanders could be easily identified individually by their photographs throughout the entire study period. Marking animals by toe clipping was not necessary, especially as it is adequate only for short-term monitoring due to the high rate of regeneration in certain amphibians.

Sex was determined by cloacal examination (see Degani & Warburg 1978, Warburg et al. 1978/79), salamanders were weighed, measured, photographed and finally released back to their habitat either during the same night or on the following one.

In the present study in order to estimate longevity of the salamanders I used three techniques:

(1) monitoring the population over 25 years and recapturing the same animals several times in following years.

(2) applying the skeletochronological technique modified from Leclair & Castanet (1987).

A phalange was cut and fixed in 10 % formalin. After fixation the phalange was transferred to 70 % ethanol, decalcified in 3 % nitric acid, and sectioned (15 µm) on a Bright's cryostat. Alternatively, it was processed histologically and paraffin sections were obtained (Warburg 1986). The sections were then stained with haematoxylin-eosin and mounted in aquamount. The haematoxylinophilic lines, considered to indicate lines of arrested growth (non-active periods of the animal), could be estimated (Francillon-Vieillot et al. 1990, Warburg 1992; see also review in Miaud et al. 2001). It is possible that in such long-lived animals growth during advanced age is minimal and thus, the most recent arrested growth rings become indistinguishable.

(3) estimating the age based on increments of annual growth in individual ani-

Tab. 3. Examples of lab-raised specimens recaptured and their growths.

specimen	year	age	weight (g)	length (cm)
male # 87 (born 1979)				
Released	1982	3	36	18.5
Recaptured	1983	4	58	21.5
Recaptured	1985	6	61	23
Recaptured	1986	7	60	23.5
Recaptured	1987	8	71	24
Recaptured	1988	9	64	25
female # 163 (born 1989)				
Released	1992	3	28.7	15
Recaptured	1997	8	93.9	22
male # 169 (born 1989)				
Released	1992	3	24	12
Recaptured	1997	5	68	22

mals (Hagström 1977, Warburg 1986, Caetano & Leclair 1996). As each time the same salamanders were recaptured during different breeding seasons, it was possible to obtain their weights and dimensions and calculate the increase in both.

Thus, the average annual weight increase was calculated for each weight class of adult salamanders except for the heavy weight classes where weight increase is negligible since the percentage of weight increase declined with the weight (= age) of the salamander. As an example: salamanders weighing between 40-50 g, weighed on average at the beginning of the year 41.1 g and a year later 60.1 g increasing in weight by 46.2 %. In the weight class between 80-90 g there was only 1 % weight increase during one year (see Table 5).

By adding this series of curves into one single curve, a theoretical, cumulative growth curve that is based on the average annual growth increments of individual salamanders arranged in different weight classes, could be constructed under natural conditions of recaptured salamanders.

Longevity was studied in 58 urodele species (for partial list see Table 6). Some species were studied by different authors resulting in even more information about these particular species.

All five techniques were applied in these studies. Thus, 34 salamander species have captive longevity records, 35 species were studied skeletochronologically, nine species were monitored, in seven species estimates are based on growth, and in eight species estimates are based on size-frequencies or age classes. Some studies employed more than one technique (Warburg 1986, 1992, 1994, Castanet et al. 1996, Caetano & Leclair 1996, Trenham et al. 2000, Perret et al. 2003, Maletzky et al. 2004). The present study is an analysis based on these long-term observations on the activities of individual adult salamanders.

Snout-vent length is abbreviated SVL throughout.

Results

A total of 315 visits to the breeding ponds took place over a period of 25 years (excluding one breeding season in 1990-91). During that period 160 days were successful in the sense that salamanders were found (51.4 % success). A total of 128 salamanders were captured. The study is based on 245 salamanders recaptures. Altogether 5.3 new salamanders were captured per year, 0.78 salamanders per visit. During the study period, 23 females and 43 males reappeared consistently. Several males appeared up to seven times, some even 22 or 40 times indicating their greater activity during the breeding season compared to the females ($p < 0.01$ see Warburg 1986, 2006). Several females appeared up to five times; one was captured nine times. Two individual females were captured over 17 years and three males over 19 years.

The data on longevity in *Salamandra* species is given in Table 1. Some of the females gave birth in the lab to larvae that were raised and metamorphosed in the lab. These young post-metamorphs weighed between 1.14-1.92 g (Degani et al. 1980). These juveniles were raised for 2-3 years, and were eventually released (having reached at least 30 g) back to the ponds whence their mother had originated (Table 2). A few of these juveniles were later recaptured (Table 3), thereby providing a measure to estimate the age of young adults captured. The smallest adult salamanders captured near the ponds weighed between 18-44 g (Table 2). Most adult female salamanders weighed over 50 g whereas most males were in the 25-75 g weight class (Table 4).

Tab. 4. Dimensions of salamanders (52 females, 97 males) when first captured.

weight (g)	females n (%)		males n (%)	
	n	%	n	%
< 26	0	0	2	2.1
26-50	4	7.7	27	27.8
>50-75	10	19.2	47	48.4
>75-100	19	36.5	18	18.6
> 100-125	19	36.5	3	3.1

The main problem encountered when attempts to age salamanders are based on size-frequencies in a population (weight or SVL classes), is to match the age to a weight class.

Thus, based on the known size of three-year old juveniles, we are able to say that small salamanders captured were not less than three years old.

The next problem is to estimate annual growth and match it to weight. In this study we could follow the annual growth of individual salamanders, for several years (Table 3). The gain in weight dropped as the salamander grew older reaching 1 % growth in its 8th year (Table 5). The main weight gain (145 %) was in the weight class between 25-60 g. It can be seen that this method is of limited use in older salamanders.

Discussion

Five main methods are used for estimating age in amphibians: (1) monitoring individual salamanders in the wild; (2) keeping animals captive; (3) estimating age by constructing size-frequency classes of recaptured individual animals in field population studies; (4) estimating age by constructing growth curves by adding up annual growth increments of individual animals (5) estimating age using the skeletochronology technique and counting annual arrested growth rings.

Halliday & Verrell (1988) reviewed the literature on 34 amphibian species. Their finding was that 20 used skeletochronology, 17 used mark-recapture and 13 used size-frequency histograms to estimate age. According to Halliday & Verrell (1988), of these methods, two are reliable only, i.e. skeletochronological and mark-recapture of known individuals which is the most reliable way to provide data on age-size relationship. Each of these techniques has its advantages but also drawbacks.

The first technique of monitoring has the advantage that the age of an individual amphibian can be followed accurately in nature rather than in captivity. This technique has been used in 18 studies (Table 6). The problems of this method include (1) that using mark-recapture techniques may take many years before yielding reliable results; moreover, since it may require that animals be marked by mutilation, it is inappropriate for rare and endangered species (Halliday & Verrell 1988). (2) The age of the amphibian when first captured is not known and can only be estimated. (3) Also, the cause of disappearance does not necessarily have to be death from old age but could be due to a variety of other reasons, among them the time-lapse between visits to the breeding site (Warburg 2006). Consequently, the maxi-

Tab. 5. Calculations of annual growth based on actual measurements of weight gain in free-roaming adult salamanders. W_0: average weight at the beginning of the year; W_1: average weight one year later; ΔW%: percentage of weight increase. (*) Data are based on animals born and raised in the lab for two or three years and weighed; (**) sufficiently reliable data are lacking.

weight class (g)	year class	W_0 ± standard deviation	W_1 ± standard deviation	number	ΔW(%)
< 26(*)	2		14.0 ± 2.0	7	
26-40(*)	3	34.3 ± 7.7		13	145.0
40-50	4	41.1 ± 6.6	60.1 ± 6.0	7	46.2
50-60	5	55.6 ± 3.2	65.0 ± 5.2	6	16.9
60-70	6	66.0 ± 2.1	71.7 ± 6.6	12	8.6
70-80	7	73.7 ± 2.7	79.3 ± 3.5	8	7.6
80-90	8	84.4 ± 3.9	92.9 ± 6.3	6	1.0
> 90(**)					

mal life span can only be guessed.

The second technique has the advantage of keeping an amphibian captive under presumably ideal conditions and actually knowing the time of death. This method has been used in 68 studies (Table 6). It may however not be the actual maximal life span but the cause of death could be due to various reasons other than old age. However, unless the animal is raised from birth the life span can only be guessed.

The third technique (used in 18 studies, see Table 6) is based on the assumption that salamanders grow throughout their life (Kara 1994), and that their growth is highly correlated with age (Leskovar et al. 1998). To follow growth, capture-mark-recapture techniques of population studies are being used in the field trying to construct age groups based on size-frequency histograms (weight or snout-vent-length; see Danstedt 1975, Forester & Lykens 1991, Caetano & Leclair 1996, Trenham et al. 2000, Leclair et al. 2005). The advantage of this technique is providing an idea of the size (= age?) of the majority of animals in a population. Nevertheless, in many cases, correlating size-frequency with age can not be accurate since salamanders stop growing and reach a plateau when about seven to nine years old (Castanet et al. 1996), first in their length then in their weight. According to Halliday & Verrell (1988) extrapolation from size-frequency data is based on the assumption that all sizes have an equal chance of capture. This may not be true in many cases. The main faults are the assumptions that age and size are statistically related and the difficulties in assigning the right age to the smallest or largest size classes. Furthermore, variance in body size within a particular age class can be high especially in the first five years of life ranging between 16 and 22 % (Table 5). Moreover, due to the great inter-individual variability in body size (in both *Salamandra salamandra* & *Triturus vittatus*), although body size does increase with age, this relationship is so weak that size cannot be used to predict age with any confidence (Verrell & Francillon 1986).

The fourth technique tries to construct a growth curve, and was used in 17 studies (Table 6). This technique is based on annual measurements of growth in individual salamanders in the wild adding up the annual growth increments to form one curve (Hagström 1977, Warburg 1986). The advantage is that the data are obtained from animals under natural conditions. From these data it turned out that a large proportion of their growth and increase in weight (from 40 to 90 g) took place during their first 5-10 years of life (Warburg 1986). In addition, the average weights of juvenile salamanders up to three-years old that were raised in the lab is known: two-year old juveniles weigh between 20-30 g, and three-year old between 30 and 40 g. Consequently, it is likely that the youngest salamanders collected near the ponds are three to four years old.

The main disadvantage is that the amphibian growth curve is not exponential but flattens out when growth slows down with the age of the salamander and reaches a plateau (Castanet et al. 1996).

Finally, the fifth method is based on counts of annual growth rings (see Miaud et al. 2001). This method is rather frequently used (in 60 studies) to estimate longevity in amphibians (see Table 6). It is based on the assumption that only one ring is formed per year although the rate of bone deposition remains utterly unknown (Dapson 1980). There remains the technical difficulty in counting annuli. Thus, the growth rings may show either splits or fusions (double resting lines see Hemelaar 1985) as well as resorption of bone-growth layers due to metabolic inactivity (i.e. starvation) in draught years (Smirina 1972, Smirina et al. 1986, Forester & Lykens 1991). Moreover, lines of arrested growth can be difficult to discern especially in later years when growth is much less pronounced.

Nevertheless, this technique is widely used in longevity studies and can supplement the size-class technique by providing comparatively accurate age within and between size classes.

Tab. 6. Known ages in different urodele species. A – age classes based on size (SVL) frequencies in the wild; C – animals kept in captivity; G – age estimation based on yearly growth increments in the wild; M – age estimates based on monitoring individual animals in the wild over the years; S – age estimates based on skeletochronological techniques. For the genus *Salamandra* see Table 1.

species	years	method	source
Siren lacertina	25	C	Flower 1925, Senning 1940, Bourlière 1946
Siren lacertina	14	C	Bowler 1975
Siren intermedia	6	C	Bowler 1975
Hynobius boulengeri	5	C	Bowler 1975
Hynobius kimurae	20 (males)	S	Misawa & Matsui 1999
Hynobius kimurae	27 (females)	S	Misawa & Matsui 1999
Hynobius nebulosus	10 (males)	S	Ento & Matsui 2002
Hynobius nebulosus	6 (females)	S	Ento & Matsui 2002
Onychodactylus fischeri	> 18	S	Smirina 1994
Salamandrella keyserlingii	9	S	Smirina et al. 1994
Andrias japonicus	> 60	C	Nickerson 2003
Andrias japonicus	16	C	Bowler 1975
Andrias davidianus	4	C	Bowler 1975
Megalobatrachus japonicus	62	C	Brodmann 1971 in Feldmann 1974
Megalobatrachus japonicus	> 65	C	Schneider 1932
Megalobatrachus japonicus	55	C	Senning 1940, Bourlière 1946
Megalobatrachus maximus	52	C	Mayenne 1924 in Noble 1954, Flower 1925
Megalobatrachus maximus	70	C	Schneider 1932
Megalobatrachus sligoi	16	C	Senning 1940
Cryptobranchus alleganiensis	55	C	Nigrelli 1954
Cryptobranchus alleganiensis	> 30	G	Taber et al. 1975
Cryptobranchus alleganiensis	29	C	Senning 1940, Bourlière 1946, Bogert 1961
Cryptobranchus alleganiensis	> 30	M	Nickerson 2003
Cryptobranchus alleganiensis bishopi	25	A, G	Peterson et al. 1983
Necturus maculosus	9	C	Bourlière 1946
Necturus maculosus	23	G	Senning 1940
Proteus anguinus	15	C	Senning 1940
Proteus anguinus	100	C	Aljancic 1993
Amphiuma means	26	C	Noble 1954
Amphiuma means	27	C	Flower 1925, Senning 1940, Bourlière 1946
Amphiuma means	11	C	Flower 1925
Amphiuma means	14	C	Bowler 1975
Amphiuma tridactylum	12	C	Bowler 1975
Amphiuma punctatum	25	C	Koch 1952 in Comfort 1979
Chioglossa lusitanica	8	S	Lima et al. 2000
Chioglossa lusitanica	3	C	Thorn 1968, Salvador 1974
Cynops pyrrhogaster	25	C	Wolterstorff 1928 in Noble 1954
Cynops pyrrhogaster	13 (males)	S	Marunochi et al. 2000
Cynops pyrrhogaster	16 (females)	S	Marunochi et al. 2000
Cynops pyrrhogaster	25	C	Senning 1940
Euproctus asper	9-10	S	Montori 1990
Euproctus asper	7	C	Senning 1940
Euproctus asper	> 8	C	Bourlière 1946
Mertensiella luschani	8 (males)	S	Olgun et al. 2001
Mertensiella luschani	10 (females)	S	Olgun et al. 2001
Mertensiella caucasicus	26	A, M	Tarkhnishvili & Gokhelashvili 1994

species	years	method	source
Pleurodeles walti	20	C	Flower 1925, Debreuil 1925 in Senning 1940
Pleurodeles walti	10	C	Bowler 1975
Pleurodeles peureti	4-5	S	Francillon & Pascall 1985
Taricha torosa	21	C	Senning 1940, Bourlière 1946
Triturus marmoratus	9 (males)	S, G, M	Diaz-Paniagua et al. 1996
Triturus marmoratus	10 (females)	S, G, M	Diaz-Paniagua et al. 1996
Triturus marmoratus	8-9	A, G	Jakob et al. 2003
Triturus marmoratus	21-24	A, G	Wendt 1934 in Comfort 1979
Triturus marmoratus	14-16	S	Caetano 1990, Francillon-Vieillot et al. 1990
Triturus marmoratus	15	S	Caetano et al. 1985
Triturus marmoratus	9-13 (males)	S	Caetano & Castanet 1993
Triturus marmoratus	9-14 (females)	S	Caetano & Castanet 1993
Triturus marmoratus	9 (males)	S	Danstedt 1975
Triturus marmoratus	10 (females)	S	Danstedt 1975
Triturus marmoratus	9 (males)	S	Diaz-Paniagua et al. 1996
Triturus marmoratus	10 (females)	S	Diaz-Paniagua et al. 1996
Triturus alpestris	> 20	C	Wolterstorff in Krefft 1907
Triturus alpestris	15	C	Senning 1940
Triturus alpestris	9-10	S	Smirina & Roček 1976 in Smirina 1994
Triturus alpestris	6-9	S	Joly & Grolet 1996
Triturus alpestris	> 22	S	Schabetsberger & Goldschmidt 1994
Triturus alpestris	20 (males)	S	Miaud et al. 2000
Triturus alpestris	19 (females)	S	Miaud et al. 2000
Triturus alpestris	6-9 (males)	S, M	Perret et al. 2003
Triturus alpestris	10 (females)	S, M	Perret et al. 2003
Triturus alpestris	10	S, A	Maletzky et al. 2004
Triturus helveticus	12	C	Senning 1940, Bourlière 1946
Triturus vulgaris	10-12	S	Hagström 1977, 1980
Triturus vulgaris	6	S	Verrell & Francillon 1986
Triturus vulgaris	11	S, A	Maletzky et al. 2004
Triturus vulgaris	5-6	S	Cogălniceanu & Miaud 2003
Triturus vulgaris	18	C	Senning 1940, Bourlière 1946
Triturus vulgaris	12 (males)	G	Bell 1977
Triturus vulgaris	13 (females)	G	Bell 1977
Triturus vulgaris	7	S	Marnell 1998
Triturus cristatus	14-16	S	Francillon 1979, Francillon-Vieillot et al. 1990, Hagström 1977, 1980
Triturus cristatus	16 (males)	S	Miaud et al. 1993
Triturus cristatus	14 (males)	S	Miaud et al. 1993
Triturus cristatus	20	S	Miaud et al. 1993
Triturus cristatus	6	C	Flower 1925
Triturus boscai	8	S	Caetano 1990
Triturus dobrogicus	4-5	S	Cogălniceanu & Miaud 2003
Triturus dobrogicus	9	M	Ellinger & Jehle 1997
Triturus carnifex	16	A, S	Maletzky et al. 2004
Triturus carnifex	14 (males)	A	Cvetkovic et al. 1996
Triturus carnifex	13 (females)	A	Cvetkovic et al. 1996
Triturus vittatus ophryticus	10-16	S	Kutrup et al. 2005
Triturus vittatus ophryticus	12 (males)	S	Tarkhnishvili & Gokhelashvili 1999
Triturus vittatus ophryticus	21 (females)	S	Tarkhnishvili & Gokhelashvili 1999

species	years	method	source
Triturus karelinii	8 (males)	S	Olgun et al. 2005
Triturus karelinii	11 (females)	S	Olgun et al. 2005
Triturus poireti	14	C	Senning 1940, Bourlière 1946
Triturus palustris	28	C	Senning 1940
Tylotriton verrucosus	11	?	Kuzmin et al. in Smirina 1994
Tylotriton verrucosus	5	C	Bowler 1975
Ambystoma mexicanum	25	S	Duellman & Trueb 1986
Ambystoma tigrinum neotenous	25	C	Senning 1940, Bourlière 1946
Ambystoma tigrinum neotenous	10	C	Bowler 1975
Ambystoma californiense	11	M, S	Trenham et al. 2000
Ambystoma macrodactylum krauseei	7-10	S	Russell et al. 1996
Ambystoma maculatum	21 (males)	S	Flageole & Leclair 1992
Ambystoma maculatum	16 (females)	S	Flageole & Leclair 1992
Ambystoma maculatum	22	C	Pope 1937
Ambystoma maculatum	18	C	Senning 1940, Bourlière 1946
Ambystoma opacum	3	C	Bowler 1975
Ambystoma ordinarium	2	C	Bowler 1975
Ambystoma talpoideum	2	C	Bowler 1975
Ambystoma texanum	5	C	Bowler 1975
Rhyacotriton olympicus	2	C	Bowler 1975
Notophthalmus viridescens	13	A, G, S	Caetano & Leclair 1996
Notophthalmus viridescens	13	G	Leclair & Caetano 1997
Notophthalmus viridescens	5	S	Leclair et al. 2005
Notophthalmus viridescens	9	S	Forester & Lykens 1991
Notophthalmus viridescens	15 (males)	?	Gill 1985
Notophthalmus viridescens	12 (females)	?	Gill 1985
Notophthalmus perstriatus	12	C	Bowler 1975
Desmognathus monticola	5-11 (males)	S	Castanet et al. 1996
Desmognathus monticola	5-9 (females)	S	Castanet et al. 1996
Desmognathus aeneus	4	C	Bowler 1975
Desmognathus auriculatus	3	C	Bowler 1975
Desmognathus welteri	5	C	Bowler 1975
Desmognathus ochrophaeus	2-8	S	Tilley 1980
Desmognathus ochrophaeus	3-10 (males)	S, G	Houck & Francillon Vieillot 1988
Desmognathus ochrophaeus	4-7 (females)	S, G	Houck & Francillon Vieillot 1988
Desmognathus quadramaculatus	6-11 (males)	S	Castanet et al. 1996
Desmognathus quadramaculatus	7-13 (females)	S	Castanet et al. 1996
Desmognathus fuscus	8-9 (males)	S	Danstedt 1975
Desmognathus fuscus	9-10 (males)	S	Danstedt 1975
Phaeognathus hubrichti	12 (males)	S	Parham et al. 1996
Phaeognathus hubrichti	11 (females)	S	Parham et al. 1996
Phaeognathus hubrichti	5	C	Bowler 1975
Batrachoseps attenuatus	3-6 (males)	S	Wake & Castnet 1995
Batrachoseps attenuatus	3-7 (females)	S	Wake & Castnet 1995
Batrachoseps attenuatus	> 10	A	Anderson 1960
Enastina eschscholtzii	6-15 (males)	A	Staub et al. 1995
Enastina eschscholtzii	7-8 (females)	A	Staub et al. 1995

species	years	method	source
Eurycea longicauda	5	C	Bowler 1975
Gyrinophilous palleucus	3	C	Bowler 1975
Gyrinophilous porphyriticus	4	C	Bowler 1975
Plethodon kentucki	8-13 (males)	M	Marvin 2001
Plethodon kentucki	7-16 (males)	M	Marvin 2001
Plethodon jordani	5	C	Bowler 1975
Plethodon vehiculum	4	C	Bowler 1975
Plethodon glutinosus	5	C	Bowler 1975
Plethodon elongatus	5	C	Bowler 1975
Plethodon longicrus	5	C	Bowler 1975
Plethodon longicrus	5	C	Bowler 1975

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Manuscript received: 22 December 2005

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