

Age and fecundity in *Salamandra algira* (Caudata: Salamandridae)

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Manuscript received: 22 February 2014

Accepted: 29 April 2014 by STEFAN LÖTTERS

Abstract. Amphibians are characterised by potentially indefinite growth. Their body size reflects a trade-off between growth and reproduction. Consequently, growth decreases or even ceases after maturation. Furthermore, the sexes often mature at different ages (sexual bimaturity). We examined fecundity patterns of the terrestrial salamander *Salamandra algira* (Salamandridae) and tested if age, body size and the fecundity of both sexes are connected and how these reproductive traits interact. We revealed positive correlations for female size, age and fecundity traits, i.e., egg number and volume. The male number of testes lobes was also positively correlated with age. Our study provides basic data on a rarely studied terrestrial salamandrid. Further collection-based research is needed to obtain additional data aiding the understanding of life history evolution of the Salamandridae.

Key words. Fecundity, salamanders, Urodela, *Salamandra*, skeletochronology.

Introduction

Amphibians are potentially capable of indefinite growth (HALLIDAY & VERRELL 1988, VERRELL & FRANCILLON 1986, KUPFER 2007). However, growth rate is often low in the early stages, increases with advanced development, and finally ceases completely or even decreases due to several limiting factors of intrinsic and extrinsic nature. Decreasing growth often coincides with sexual maturity, when resources are either split between reproduction and growth, or only invested in reproduction (HALLIDAY & VERRELL 1988, MIAUD et al. 2000, MIAUD et al. 2001, MARZONA et al. 2004). Sexual maturity in amphibians is sex-specific (the phenomenon of sexual bimaturity) and does not only affect the general growth pattern, but also the degree of sexual size dimorphism (SSD). Ecological factors, such as climate and altitude, also play important roles in maturation (HALLIDAY & VERRELL 1988). Several studies have shown that animals grow more slowly at high altitude and that they can become larger, older and even delay sexual maturity (e.g., CAETANO & LECLAIR 1996, MIAUD et al. 2000, MARU-NOUCHI et al. 2000, MIAUD et al. 2001, AMAT et al. 2010). Within species, activity phases in high altitude populations are restricted due to a cooler and rougher climate, compared to those of lowland populations (ARNTZEN 2000). This leads to delayed metamorphosis and maturation, giv-

ing individuals a chance to invest in more resources into growth before arriving at the point of growth–reproduction trade-off. Early metamorphosis and maturation reduce body size and could affect female fecundity, because these traits are linked. Larger females are able to produce more offspring and thus enhance their reproductive success (FAIRBAIRN 2007). To which extent age influences male fecundity is quite unclear, but BRUCE et al. (2002) found that the differentiation and the number of testes lobes increases with age in *Desmognathus ocoee*, *D. monticola* and *D. quadramaculatus* and DOLMEN (1982) detected the same to be true for *Triturus cristatus*.

The North African fire salamander (*Salamandra algira*, BEDRIAGA 1883) inhabits Mediterranean regions of Morocco, Algeria and Spain (Ceuta). The high-altitude populations of the Rif- and Middle-Atlas Mountains were recently described as new subspecies, *S. a. splendens* (BEUKEMA et al. 2013), and are particularly interesting for fecundity studies, as altitude was often reported to influence the reproduction of salamanders (e.g., TILLEY 1973). *Salamandra algira* is viviparous and gives birth to aquatic larvae (lecithotrophic viviparity) or even fully developed juveniles (matrotrophic viviparity) in *S. a. tingitana* (DONAIRE-BARROSO & BOGAERTS 2001, DONAIRE-BARROSO et al. 2001). Viviparous species have a reduced fecundity (clutch size) as an effect of egg retention (DUELLMAN & TRUEB 1994,

WELLS 2007), but their offspring benefit from higher probability of survival, because development of eggs outside the female's body is circumvented. We examined *S. algira* specimens for fecundity patterns of both sexes, identified their age using skeletochronology, and measured body size in order to study the influence of age and size on fecundity in both males and females. It might be predicted that females could compensate their lower fecundity with larger clutch volumes, especially in high-altitude populations, where growth and maturation might be slowed and thus larger body sizes could be reached (as a precondition for having larger clutch volumes). How far male fecundity increases with age will be examined in the following as well.

Material and methods

Animal dissection and statistics

We analysed specimens of *Salamandra algira* housed in the Bavarian State Collection of Zoology Munich (ZSM, see Appendix 1 for specimen numbers). Because of their colouration and collection locality (Taza, Morocco) we referred to them as *S. a. splendens* (BEUKEMA et al. 2013). Specimens were sexed via externally visible sexual characters (e.g., swollen cloaca), but also by inspecting the gonads via a ventrolateral incision. Sizes of individuals of both sexes were measured as snout–vent lengths (SVL in mm). All salamanders (females $n = 15$, males $n = 21$) were carefully dissected and the following data was collected (see Fig. 1 for dissection situs): in females, the clutch size (number of eggs in each ovary) was counted and egg diameters were measured with digital callipers (ROK International Industry Co., Ltd.) under a stereomicroscope to the nearest 0.01 mm. In males, the number of testes lobes was counted. The egg volume was calculated following DZIMINSKI & ALFORD (2005):

$$v_{\text{egg}} (\text{mm}^3) = \frac{4}{3} \pi (\sqrt{A/\pi})^3 \text{ and } A = \text{egg } \varnothing^2$$

The clutch volume was calculated by multiplying clutch size with egg volume. The correlation of fecundity traits and age or SVL was carried out using Spearman correlation analysis and linear regression. All statistical tests were conducted with Prism 5.01 and Microsoft Excel 2007 for Windows 7.

Histology and skeletochronology

To assess the age of the salamanders, the longest finger (third finger) was clipped off from all *S. algira* specimens. They were embedded in paraffin wax, and cross sections (thickness: 7 μm) were produced using a microtome (HM 360 and a mounted Zeiss Stemi 1000). All cross sections were stained using kresyl-violet (comp. SCHOLZ et al. 2010). The lines of arrested growth (LAGs) were counted three times using an optical microscope (Zeiss Axioskop with a mounted Pixelink PL-B622CF camera).

Results

Female fecundity and age

Female SVL ranged from 86.7 to 109.9 mm (mean 98.0 ± 7.6 mm), and they were on average 11.1 years old (± 3.7 years, range: 5–19 years; see the age distribution histogram in Fig. 2). The mean number of eggs in female ovaries was $12.9 (\pm 4.1, \text{range: } 7\text{--}22 \text{ eggs})$. The mean diameter of eggs was 3.9 ± 0.4 mm (range: 3.1–4.4 mm). The resulting egg volume was $8.4 \pm 2.4 \text{ mm}^3$ (range: 3.9–11.9 mm^3) and clutch volume was $106.9 \pm 40.0 \text{ mm}^3$ (range: 27.3–187.5 mm^3). The egg distribution was asymmetric in the left and right ovaries in 12 of the 15 females (left side of ovary: 3–13 eggs; right side of ovary: 3–11 eggs). A comparison of the fecundity data with age and SVL in female salamanders revealed a significant correlation between egg and clutch volume with age, i.e., the volume of both the eggs ($r^s = 0.5171, p \leq 0.05^*$) and the whole clutch ($r^s = 0.5350, p \leq 0.05^*$) increased with age. This also holds true for the correlation of SVL with egg number ($r^s = 0.6655, p \leq 0.01^{**}$), which increased with increasing body size (Figs. 3A–C). In general, all clutch characteristics were positively correlated with age and SVL, except for the SVL–egg volume correlation. A linear regression analysis confirmed these results.

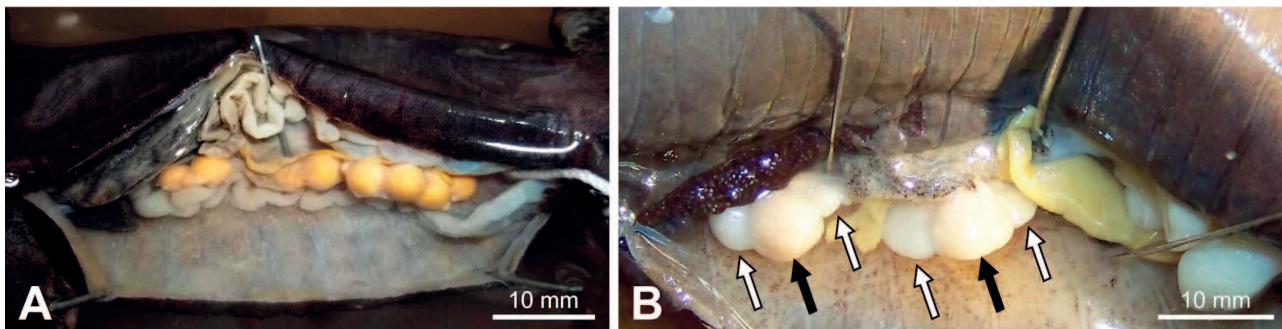


Figure 1. Viscera of *Salamandra algira*. A) Situs of an adult female with fully yolked ova in one ovary; B) situs of an adult male. Two testes segments are shown: segments that are in the retention phase are marked with black arrows; anterior and posterior lobes, which are in regeneration and active for the coming breeding season are marked with white arrows.

Male testes lobes and age

Male SVL ranged from 81.8 to 112.2 mm (mean 96.0 ± 8.0 mm), and males were on average 12.8 years old (± 4.9 years, range: 4–20 years; see the age distribution histogram in Fig. 2). Counting the testes lobes revealed a mean number of lobes of 5.2 ± 1.8 for both sides combined, (range: 2–8 lobes; 0–4 on left and right side, respectively). Twelve males had the same number of lobes on each side,

but the remaining nine individuals showed an asymmetric distribution pattern, e.g., two lobes on one side and one on the other or even four lobes on one side and none on the other. Age was significantly positively correlated with the number of testes lobes ($r^s = 0.5459$, $p \leq 0.05^*$, Fig. 4). Although the correlation of SVL with the number of testes lobes was not significant, a tendency towards a positive relation was found ($r^s = 0.1535$), which was confirmed by a linear regression analysis.

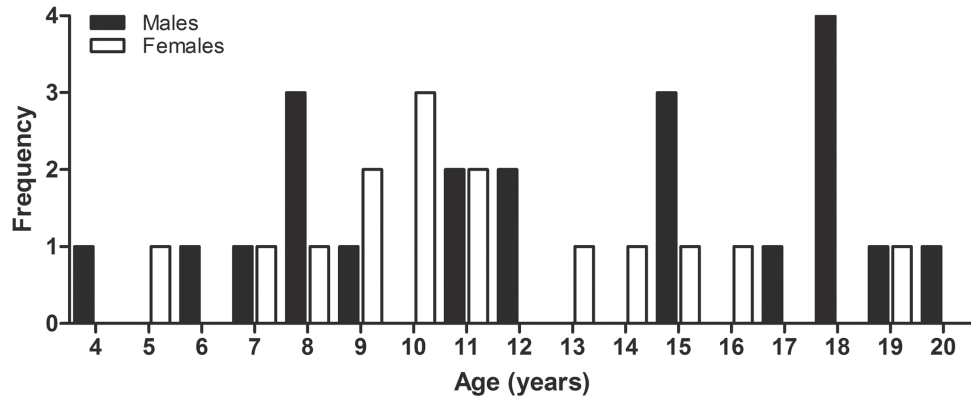


Figure 2. Age frequency histogram for male ($n = 21$) and female ($n = 15$) *Salamandra algira*.

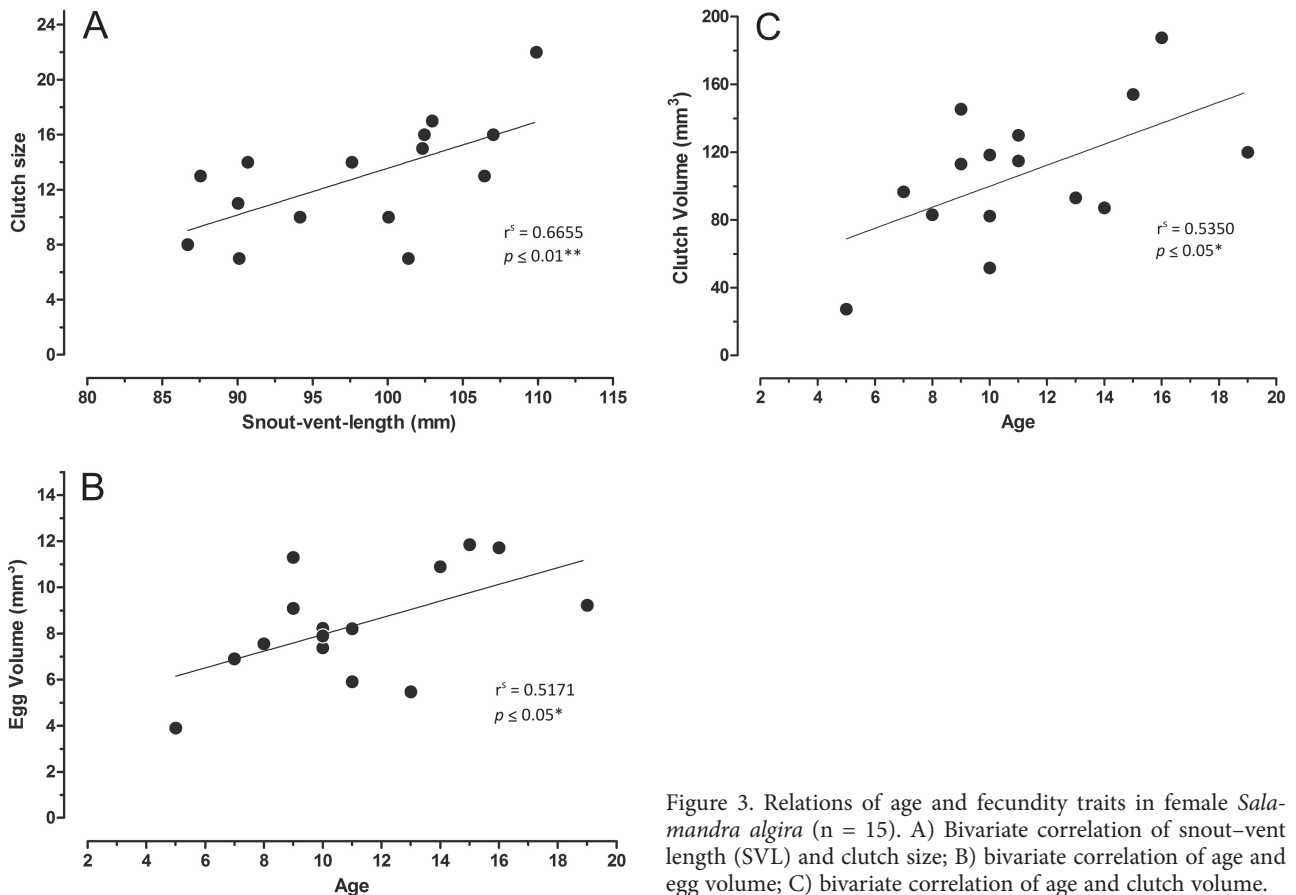


Figure 3. Relations of age and fecundity traits in female *Salamandra algira* ($n = 15$). A) Bivariate correlation of snout-vent length (SVL) and clutch size; B) bivariate correlation of age and egg volume; C) bivariate correlation of age and clutch volume.

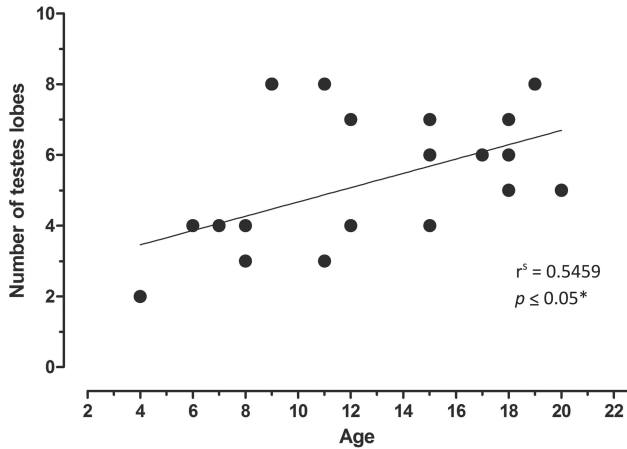


Figure 4. Bivariate correlation of age and testes lobe number of male *Salamandra algira* (n = 21).

Discussion

Reproductive traits, such as egg and clutch sizes, are critical for female reproductive success. Large female size is often correlated with a higher fecundity (e.g., KUPFER 2007, WELLS 2007). The fecundity analysis of female *Salamandra algira* revealed that clutch size would increase with body size. On the other hand, female body mass is not related to reproductive traits such as litter size or total litter mass (KOPP & BAUR 2000). Positive correlations between body size and fecundity were demonstrated to exist in other salamanders, too. For example, larger females with larger eggs as well as a larger clutch sizes have been reported for *Lissotriton vulgaris* (VERRELL & FRANCILLON 1986) and *Triturus carnifex* (CVETKOVIĆ et al. 1996). Further examples of such a relation are also known from plethodontid salamanders, e.g., *Batrachoseps* and *Aneides* (ANDERSON 1960), *Desmognathus ochrophaeus* (MARTOF & ROSE 1963), *Bolitoglossa rostrata* (HOUCK 1977), *Plethodon cinereus* (FRASER 1980) and the ambystomatid *Ambystoma talpoideum* (SEM-LITSCH 1985). Moreover, individual body size and thus fecundity traits are associated with age. The volumes of eggs and the whole clutch of female *S. algira* increase with age. A similar result was obtained for *Hynobius kimurae*, in which egg diameters increase at older age (MISAWA & MATSUI 1999), as well as for *Ambystoma talpoideum* (SEM-LITSCH 1985) and *Lissotriton vulgaris* (VERRELL & FRANCILLON 1986). In general, the tendency of older and larger females carrying larger eggs is well established. Sexual maturity is sex-specific (sexual bimaturity; see KUPFER 2007, WELLS 2007) with females often maturing later than males (comp., e.g., TILLEY 1980). Since age, size and fecundity are interrelated and a larger size and thus more or larger eggs are advantageous to female reproductive success, delayed female maturity compared to males should be of advantage. Females have comparatively high reproductive costs (e.g., MIAUD et al. 2001, SEGLIE et al. 2010), and ear-

ly maturation decreases body size as a consequence of the trade-off between growth and reproduction. This might influence the reproductive success negatively, because only large and numerous oocytes maximize offspring numbers and fitness (SHINE 1979, ARNTZEN 2000, MARZONA et al. 2004), which is especially true for viviparous amphibians, as their fecundity is generally lowest compared to species that have aquatic or terrestrial eggs (DUELLMAN & TRUEB 1994, WELLS 2007). Furthermore, a lot of extrinsic factors can influence fecundity. For example, populations from different altitudes are known to differ in reproductive and growth traits, in particular because they have lower metabolic rates and shorter activity seasons and therefore mature only at a more advanced age (e.g., TILLEY 1973, WELLS 2007). The influence of altitude and temperature has even led to a shift from lecithotrophic viviparity to matrotrophic viviparity within different populations of *S. a. tingitana* (BEUKEMA et al. 2010). We examined *S. algira* from higher altitudes. They have to cope with shorter reproductive seasons during comparatively cooler winter months, but as to how far they mature later (compared to other populations) still needs to be tested. Our age data might suggest delayed maturity, as only older males and females (starting at age 4+ and 5+) were present in the sample, which was obtained during the breeding season in December. The absence of younger, immature age groups is common in salamander population studies (THIESMEIER 2004).

For males, the effects of body size on reproductive success are not so clear – their reproductive costs are relatively low, and it might not be mandatory for them to delay sexual maturity to reach a larger body size. Therefore, selection seems to drive body size into different directions in the two sexes, but it is very important to consider the reproductive strategies and mating system of terrestrial salamanders. Males of *Salamandra* spp. have been reported to engage in rivalry fights and do by all means profit from being larger and thus able to outcompete opponents (e.g., KÄSTLE 1986, BOGAERTS & DONAIRE-BARROSO 2005). These reports need to be considered, as well as the fact that rivalry and territoriality are not rare in urodeles (MATHIS et al. 1995). Male *S. algira* also engage in rivalry fights (BOGAERTS & DONAIRE-BARROSO 2005) and a larger size should be an advantage (also during courtship and mating), but the sexes of *S. algira* do not exhibit sexual dimorphism in general body size (REINHARD et al., in press). Selection favours both large males and females in *S. algira*, leading to a lack of sexual size dimorphism, while the evolution of other dimorphic traits, such as enlarged limbs in males, is more important (REINHARD et al., in press).

Age is related to testes lobe number in males. This relation has been demonstrated previously for some newt species such as *L. vulgaris* and *T. cristatus* (DOLMEN 1982, MALMGREN & THOLLESSON 1999) or *Cynops pyrrhogaster* (MARUNOUCHI et al. 2000). As females often prefer larger and older males (for female choice see HALLIDAY 1977), age and size seem to be highly useful fitness indicators. This can be ascribed to both successful survival strategies and courtship success, as well as to an increased individual re-

productive output due to a higher number of testes lobes (and likely sperm number).

In general, it is advisable to consider age, fecundity traits, sexual dimorphism analysis, and also ecological parameters as a whole to obtain a comprehensive insight into the mating systems of amphibians, as many parameters are tightly linked and mutually dependent. Further studies of additional terrestrial salamanders, either collection-based or in the field, would be very useful to proceed with understanding the evolution of life histories and reproductive strategies.

Acknowledgements

We kindly thank LENNART OLSSON for critically reading earlier manuscript versions. We also thank FRANK GLAW and MICHAEL FRANZEN (Zoologische Staatssammlung München, ZSM), who generously provided access to specimens in their care. We also thank BENJAMIN WEISS for his professional and patient help with the histological procedures behind the skeletochronology. SR was financially supported by a doctorate fellowship provided by the Friedrich-Schiller-University Jena Graduate Academy. Previous collection-based research of SR was partly supported by the Wilhelm-Peters-Fund by the German Herpetological Society (DGHT). We kindly thank an anonymous reviewer for constructive suggestions on improving the manuscript.

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Appendix 1

Specimen of *Salamandra atra* examined

ZSM 76/2013, 79/2013, 80/2013, 82/2013–84/2013, 86/2013, 91/2013, 94/2013–96/2013, 98/2013, 99/2013, 102/2013, 104/2013, 106/2013, 109/2013–112/2013, 115/2013–117/2013, 119/2013, 120/2013, 125/2013.