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The effect of altitude, latitude and climatic variables on life-history traits of male *Hyla savignyi* (Audouin, 1827) from Anatolia (Turkey): a skeletochronological study

(Anura: Hylidae)

Der Einfluß von Seehöhe, geographischer Breite und Klima auf Entwicklungsmerkmale männlicher *Hyla savignyi* (Audouin, 1827) aus Anatolien (Türkei): eine skeletochronologische Untersuchung

(Anura: Hylidae)

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KURZFASSUNG

Insgesamt wurden 127 Männchen von *Hyla savignyi* (Audouin, 1827) aus drei Populationen unterschiedlicher Höhenlagen (İskenderun - 10 m, Şanlıurfa - 476 m, Iğdır - 858 m ü. M.) hinsichtlich ihrer Altersstruktur und Körpergröße mit skeletochronologischen Methoden untersucht. Weibchen blieben wegen ihrer geringen Zahl in der Stichprobe unberücksichtigt. In den Populationen von Şanlıurfa und Iğdır waren die ältesten Männchen sechs Jahre, in der Population von İskenderun fünf Jahre alt. Die sexuelle Reife erreichten sie in allen drei Populationen im Alter zwischen einem und zwei Jahren. Männchen aus Populationen von größeren Höhen und geographischer Breite waren im Mittel größer als solche aus tief gelegenen und südlicher gelegenen Populationen.

ABSTRACT

A total of 127 male individuals of *Hyla savignyi* (Audouin, 1827) from three populations of different altitudes (İskenderun - 10 m a.s.l., Şanlıurfa - 476 m, Iğdır - 858 m) were studied for age structure and body size using skeletochronology. Due to the small number of females collected, only males were considered in the analysis. The oldest individuals were six years old, both in Şanlıurfa and Iğdır, compared to five years in the İskenderun population. Age upon attaining sexual maturity ranged from one to two years for all sites. Males from higher altitude and latitude populations were larger than individuals from low altitude and more southern populations.

KEY WORDS

Amphibia: Anura: Hylidae; *Hyla savignyi*, age structure, body size, population ecology, skeletochronology, Anatolia, Turkey

INTRODUCTION

The life-history traits of amphibians are generally subject to geographic variation. Many authors (Miaud et al. 1999; Esteban & Sanchiz 2000; Kutrup et al. 2005; Lu et al. 2006) pointed to the fact that population-specific features such as body size, growth rate, age upon attaining sexual maturity, and longevity are influenced by altitude and geographic latitude. There is a general rule that individuals living at high latitudes or altitudes tend to be larger in size than their conspecifics of low latitudes or altitudes called 'Bergmann's rule' (Bergmann 1847). Among the numerous studies associated with this rule, many supported it, some did not, but over all, there is a broad observational basis on the phenomenon that individuals from higher altitudes tend to be larger in body size than conspecifics from lower altitudes (Lai et al. 2005; Lu et al. 2006; Matthews & Miaud 2007; Olalla-Tárraga & Rodríguez 2007; Ma et al. 2009; Liao & Lu 2010, 2011; Gül et al. 2011; Liao 2011; Liu et al. 2012).

Studies have shown that different environmental temperatures prevailing at diffe-

rent altitudes result in different body sizes within amphibian species (Ashton 2002; Jin et al. 2007). Cold temperatures positively affect amphibian growth and finally size, so that high-altitude and latitude amphibians are generally larger than low-altitude and tropical individuals (Ryser 1996; Miaud et al. 2000). Also, it is argued that limited food availability at higher elevations select for older age at sexual maturity, slower growth and longer longevity (Matthews & Miaud 2007). Increased body size in amphibian populations under the colder conditions of high altitudes and latitudes is explained by lower rates of predation and parasitism than under warmer climate conditions (Schemske et al. 2009).

Age determination is critical for understanding anuran life history traits such as age at sexual maturity, growth rate and longevity (Miaud et al. 1999). Since anuran body size is not consistently correlated with age because of environmental influences (Smirina 1994), the present study applies skeletochronological methods in the determination of individual age.

The West Asian Lemon-yellow Tree Frog *Hyla savignyi* (Audouin, 1827), occupies a wide range of altitudes in the east Mediterranean, including the east and southeast Anatolian regions of Turkey (Stöck et al. 2008; Gvožďík et al. 2008; Gül et al. 2012; Stöck et al. 2012). To compensate for the lack of demographic information regarding this species, the present paper aims to analyze and compare the age structure, body size and growth of male individuals of *H. savignyi* of three populations from different altitudes (10, 476 and 858 m a.s.l.) and ecological conditions in Turkey.

MATERIALS AND METHODS

Sampling and studied populations

Fieldwork was conducted in the east Mediterranean (İskenderun, 10 m a.s.l.), southeastAnatolian (Şanlıurfa, 476 m a.s.l.) and east Anatolian (Iğdır, 858 m a.s.l.) regions of Turkey (Fig. 1; Table 1). A total of 135 (127 male and 8 female) *H. savignyi* adults were collected from the above three localities. In the breeding sites, *H. savignyi* males were more abundant than females, as is frequently reported for anurans with prolonged breeding seasons (Dyson et al. 1992; Bastos & Haddad 1996). Due to few individuals in the sample, females were excluded from the following analyses.

The individuals were caught by hand. Each captured individual was measured for snout-vent length (SVL, to the nearest 0.1 mm) with a digital caliper (Mitutoyo Corp., Kawasaki, Japan), and sexed using the presence of vocal sacs in mature males as a criterion. The distal portion of the longest (4th) toe of the right hind limb was clipped and kept in 96 % alcohol for later skeletochronological analysis of the second phalangeal bone. All the individuals were released after sampling.

The average annual temperature is 18 °C (range: 8.2-27.7 °C) in İskenderun and Şanlıurfa (range: 5.6-31.9 °C), while it is 12 °C (range: -3.3-25.8 °C) in Iğdır. The average annual precipitation rates are 89.83 kg/m^2 (range: 5.1-188.7), 36.04 kg/m^2 (range: 10.7-86.5) and 21.69 kg/m^2 (range: 10.5-47.9) for the localities of İskenderun, Şanlıurfa and Iğdır, respectively, based on monthly average temperature and precipitation data from 1960-2012 (Turkish State Meterological Service 2013). There was no significant difference in the monthly temperatures among the sites; (One-way ANOVA, $F_{2,35} = 1.831$, $P = 0.176$). However, there was a significant difference in the monthly precipitation among the sites (One-way ANOVA, $F_{2,35} = 9.025$, $P < 0.01$); the low altitude site (İskenderun) received much more precipitation than the mid- and high-altitude sites.

Age determination

Standard skeletochronological procedures were applied to determine the age of individuals (Castanet & Smirna 1990). The phalanges were decalcified in 5 % nitric acid for 1.5 h and then washed in tap water. Cross-sections of the diaphyseal part of each phalanx (thickness of slices about 18 μm) were obtained using a freezing micro-

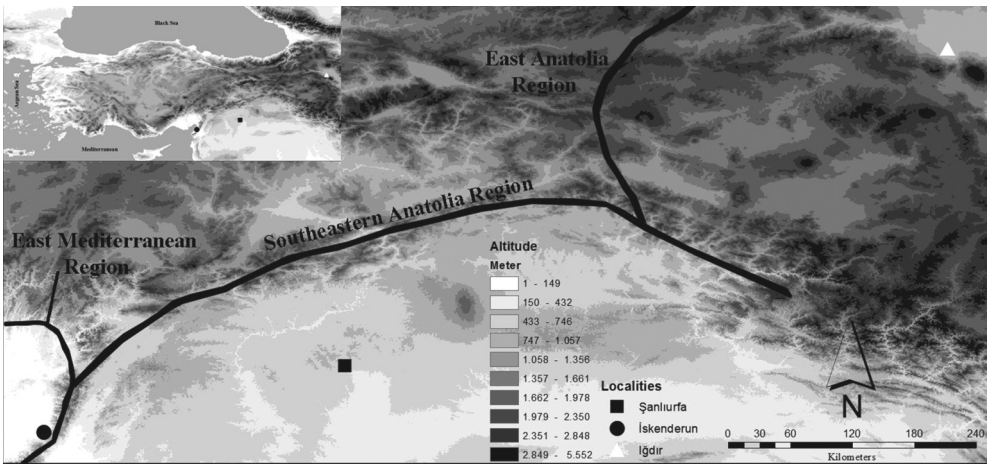

Fig. 1: The geographic position of İskenderun (●), Şanlıurfa (■) and Iğdır (△), the Anatolian sampling sites of *Hyla savignyi* (AUDOUIN, 1827) in this study.

Abb 1: Die geographische age von İskenderun (●), Şanlıurfa (■) and Iğdır (△), der anatolischen Untersuchungsstandorte von *Hyla savignyi* (AUDOUIN, 1827).

tome and stained in Ehrlich's haematoxylin. The phalanges having the smallest medullar cavity were selected and mounted in aqueous synthetic resin for observation.

On each section, the number of LAGs (Lines of Arrested Growth) was assessed by two observers (T. ERGÜL and A. ALTUNIŞIK), independently, then the results were compared. Double lines and endosteal resorption did not cause any serious interpretation problems as concerns age estimation, and full agreement between the observers was achieved for all samples. The distance between two adjoining LAGs is a good indicator of individual growth in a given year (KLEINENBERG & SMIRINA 1969). Consequently, situations where an obvious decrease in spacing between two subsequent LAGs was observed to begin were taken to mark the age when growth decelerated, i. e. sexual maturity was achieved (RYSER 1988).

Statistical analysis

One-way ANOVA and post hoc multiple comparisons (Tukey's test) were used for comparing differences in average body size and age between populations. ANCOVAs with age as covariate were performed to reveal differences among populations in terms of body size. Partial correlation analysis was done to consider the relationship between body size and age after correcting for altitude. Correlation between climatic

Table 1: Geographic and climate characteristics of the three Anatolian study localities of *Hyla savignyi* (AUDOUIN, 1827).

Tab.1: Geographische und klimatische Charakteristika der drei anatolischen Untersuchungsstandorte von *Hyla savignyi* (AUDOUIN, 1827).

Population	Altitude (m a.s.l.) Seehöhe (m ü. M.)	Geographic Latitude geographische Breite	Geographic Longitude geographische Länge	Mean Annual Precipitation (kg/m^2) mittlere Jahresniederschlagsmenge (kg/m^2)	Mean Annual Temperature (°C) mittlere Jahrestemperatur (°C)
İskenderun	10 m	36.586863	36.172571	89.83	18
Şanlıurfa	476 m	37.159149	38.796909	36.04	18
Iğdır	858 m	39.921765	44.046679	21.69	12

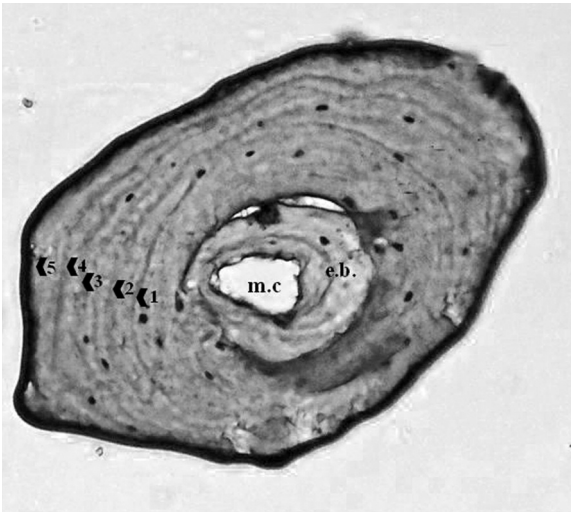

Fig. 2: The cross-section (18 µm thick) at the diaphysis level of a toe phalanx of a male *Hyla savignyi* (AUDOUIN, 1827) from the İskenderun population shows 5 LAGs and numerous osteocytes in the osseous matrix. m.c. - marrow cavity, e.b. - endosteal bone.

Abb. 2: Der Querschnitt (Schnittdicke 18 µm) im Diaphysenbereich eines Zehengliedes einer männlichen *Hyla savignyi* (AUDOUIN, 1827) der İskenderun-Population zeigt fünf Linien verlangsamten Wachstums und zahlreiche Osteozyten in der Knochenmatrix. m.c. - Markhöhle, e.b. - endostaler Knochen.

and demographic data was expressed by Pearson's correlation coefficient. Kolmogorov-Smirnov and Levene tests were used to test for normality of distribution and homogenity of variances. Based on the R^2 values, a simple cubic equation resulted from the regression between age and SVL. Statistical tests were done using the software SPSS version 18.0 (for Windows; SPSS, Chicago).

RESULTS

Both SVL and age showed normal distribution (Kolmogorov-Smirnov test, $P > 0.05$) and homogeneity of variance (Levene test, $P > 0.05$). Descriptive statistics of age and body length are summarized in Table 2. Lines of arrested growth (LAGs) and osteocytes were seen in the sections of all individuals (Fig. 2). Some of the individuals from İskenderun, Şanlıurfa and Iğdır showed double LAGs (23 %, 47 % and 20 %, respectively), recognized by their lighter color than of annual LAGs. Endosteal resorption affected only the first (innermost) LAG, and was observed in 10 %, 13 %, and 30 % of individuals from İskenderun, Şanlıurfa and Iğdır populations, respectively.

The mean age was 3.03, 3.60 and 3.95 years in İskenderun, Şanlıurfa and Iğdır populations, respectively. In terms of age composition, dominant age was three years in İskenderun and Şanlıurfa populations, while it was four years in Iğdır. The oldest individuals were six years old, both in Şanlıurfa and Iğdır, while they were five years in the İskenderun population. The age when entering maturity ranged from one to two years for all locations. The mean SVL was 32.03, 35.95 and 37.01 mm in İskenderun, Şanlıurfa and Iğdır populations, respectively. Age frequency distributions and body size observed are shown separately for the three populations in Fig. 3.

Table 2: Mean snout-vent-length and age of 127 male individuals of *Hyla savignyi* (AUDOUIN, 1827) from populations of the three Anatolian study localities characterized in Table 1.

Tab. 2: Mittlere Kopf-Rumpflänge und mittleres Alter 127 männlicher *Hyla savignyi* (AUDOUIN, 1827) von Populationen der drei in Tabelle 1 charakterisierten anatolischen Untersuchungsstandorte.

Population	Number of male individulas (years) Anzahl Individuen (Alter)	Mean SVL ± SD (mm) mittlere KRL ± SD (mm)	Range SVL Spannweite KRL	Mean age ± SD (years) Mittleres Alter ± SD (Jahre)	Range Age Spannweite Alter	Endosteal resorption Endostale Resorption
İskenderun ∑	57 (2 - 5)	32.03 ± 3.16	26.5 - 39.8	3.03 ± 0.86	2 - 5	10 %
	16 (2)	28.46 ± 1.16	26.49 - 30.64			
	27 (3)	32.14 ± 1.81	28.33 - 36.96			
	10 (4)	35.07 ± 0.95	33.46 - 36.62			
	4 (5)	37.93 ± 1.87	35.64 - 39.84			
Şanlıurfa ∑	50 (2 - 6)	35.95 ± 3.26	28.5 - 43.2	3.60 ± 0.88	2 - 6	13 %
	4 (2)	30.45 ± 1.31	28.50 - 31.26			
	20 (3)	33.98 ± 1.84	30.11 - 36.94			
	19 (4)	37.77 ± 1.84	35.05 - 40.59			
	6 (5)	39.48 ± 2.17	37.17 - 43.24			
	1 (6)	41.54	---			
Iğdır ∑	20 (2 - 6)	37.01 ± 2.38	32.1 - 41.6	3.95 ± 0.94	2 - 6	30 %
	1 (2)	34.63	---			
	5 (3)	34.53 ± 1.65	32.05 - 36.11			
	9 (4)	37.05 ± 1.32	35.02 - 38.76			
	4 (5)	39.47 ± 0.63	38.73 - 40.26			
	1 (6)	41.56	---			

A significant difference in age was found between the males of the three populations (One-way ANOVA, $F = 9.79$, $P < 0.01$) and SVL (One-way ANOVA, $F = 32.462$, $P < 0.01$). According to Tukey's test, İskenderun males differed significantly ($P < 0.05$) from Şanlıurfa and Iğdır males in terms of age and SVL, whereas, there was

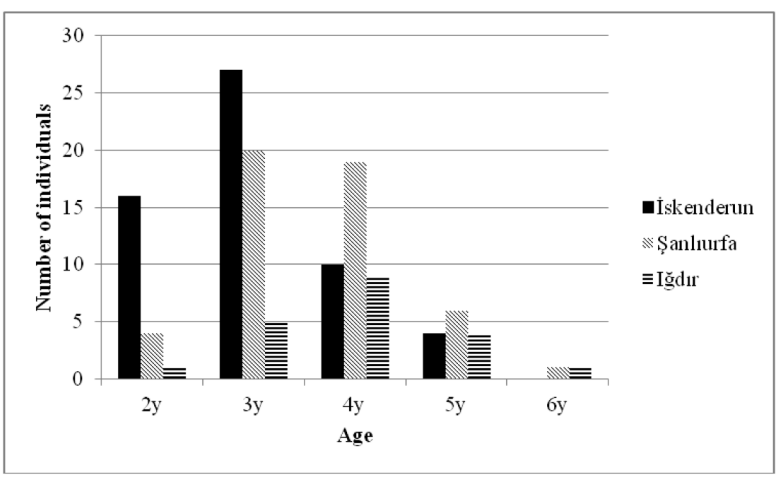

Fig. 3: Frequency distribution of male *Hyla savignyi* (AUDOUIN, 1827) within five age classes (2 y - 6 y) in the studied populations of İskenderun (N = 57), Şanlıurfa (N = 50) and Iğdır (N = 20).

Abb 3: Verteilung männlicher *Hyla savignyi* (AUDOUIN, 1827)auf fünf Altersklassen (2 y - 6 y) in den untersuchten Populationen von İskenderun (N = 57), Şanlıurfa (N = 50) und Iğdır (N = 20).

no such age difference between Şanlıurfa and Iğdır males ($P = 0.342$) and SVL ($P = 0.725$). Body size difference by altitude was significant for males after correction for the effect of age (ANCOVA: males, $F_{2, 123} = 25.316$, $P < 0.001$). After correcting for altitude, a partial correlation analysis revealed a significant positive correlation between body size and age ($r = 0.836$, $df = 124$, $P < 0.001$). The effect of ambient temperature on size and age was not studied since the temperatures at the study sites did not differ significantly. For pooled data of all altitudes, precipitation positively correlated with age and SVL.

As should be expected in a species with lifelong growth, significant positive correlation was found between age and SVL for all populations (İskenderun; $r = 0.880$, $P < 0.01$; Şanlıurfa; $r = 0.822$, $P < 0.01$; Iğdır; $r = 0.846$ $P < 0.01$). Simple cubic regressions fitted the plot of age (years: x-axis) versus body size (mm: y-axis) in all populations (İskenderun: $y = 15.975 + 8.699\ x - 1.439\ x^2 + 0.118\ x^3$, $R^2 = 0.779$, $P < 0.05$) (Şanlıurfa: $y = 23.477 + 2.541\ x + 0.614\ x^2 - 0.0913\ x^3$, $R^2 = 0.698$, $P < 0.05$) (Iğdır: $y = 46.032 - 11.336\ x + 3.274\ x^2 - 0.252\ x^3$, $R^2 = 0.753$, $P < 0.05$).

DISCUSSION

Skeletochronology was successfully conducted in various Old World species of *Hyla* such as *H. intermedia* BOULENGER, 1882, *H. arborea* LINNAEUS, 1758, *H. orientalis* BEDRIAGA, 1890, and *H. annectans* (JERDON, 1870) (e.g., FRIEDL & KLUMP 1997; KYRIAKOPOULOU & GRUMIRO 2002; ROSSO et al. 2004; LIAO & LU 2010; ÖZDEMİR et al. 2012; ALTUNIŞIK & ÖZDEMİR 2013). Among the two hylid species distributed in Anatolia, only *H. orientalis* had been studied in this respect. This first study that applied skeletochronology to estimate the age structure of *H. savignyi* populations in Turkey, observed latitudinal and altitudinal correlations with mean age, longevity and body size. Although they may be related to differences in the ambient temperature and humidity regime, age structure of populations is most likely associated with a variety of ecological factors. Thus, evaluation of the age distribution can be crucial to assess the impact of ecological changes on populations (FRIEDL & KLUMP 1997).

Hyla savignyi males from all regions attained sexual maturity at the age of one or two years, just like the *H. orientalis* males studied (ÖZDEMİR et al. 2012; ALTUNIŞIK & ÖZDEMİR 2013). ÖZDEMİR et al. (2012) observed a maximum age of four years in males of the Antalya population of *Hyla orientalis* BEDRIAGA, 1890 (*Hyla arborea* in their paper), versus five years in males of the Rize and Çanakkale populations. The present study found the maximum observed male lifespan to be six years in the Şanlıurfa and Iğdır populations of *H. savignyi*, while it was five years in the İskenderun population. In both studies, longevity increased in parallel with increasing geographic latitude of the study sites. GVOZDIK et al. (2008) stressed that closely-related species should be expected to react in a similar way to similar environments. In both studies (ÖZDEMİR et al. 2012; this study) the populations of the hottest and wettest but also southernmost locations (Antalya and İskenderun) included the smallest and youngest individuals which is in line with the general observation that ectotherms living at high temperatures mature ealier and at a smaller body size than conspecifics of colder regions. ALTUNIŞIK & ÖZDEMİR (2012) showed that mean body size and age in *H. orientalis* populations increased with increasing altitude of the habitat. The same was observed in *H. savignyi*. Individuals living at higher altitudes (Şanlıurfa - 476 m a.s.l., Iğdır - 858 m a.s.l.) were significantly larger and older than frogs of the lowland population (İskenderun - 10 m a.s.l.). All these observations are consistent with similar studies in other Old World hylid species and in line with Bergmann's rule (BERGMANN 1847) according to which, within a given species, maximum attained body size increases with the latitude/altitude at which the population lives, in other words in parallel with the

declining ambient temperatures. Climate variation and periods of disease or starvation are thought to cause double lines of arrested growth (CASTANET et al. 1993). Amphibian ectotherms exposed to high summer temperatures are forced to reduce their activity. In *H. savignyi*, the proportion of double lines was higher in individuals living at warmer conditions (İskenderun and Şanlıurfa) than in the conspecifics at lower temperatures (Iğdır). Occurrence of double lines was also shown in *H. orientalis* (ÖZDEMİR et al. 2012), in which the higher summer temperatures at Antalya and Çanakkale localities caused more double lines than at the cooler Rize locality.

Although a number of factors other than climate significantly influences bone formation in amphibians (SMIRINA 1972), endosteal bone resorption is more common in animals inhabiting higher altitude habitats (ESTEBAN 1996, 1999). This was confirmed by the tree frogs of Anatolia. In the present study, endosteal resorbtion of individuals from Iğdır (30 %, 800 m a.s.l.) was more frequently found than in frogs of Şanlıurfa (13 %, 400 m a.s.l.) and İskenderun (10 %, 10 m a.s.l.) (Table1). In *H. orientalis*, endosteal resorbtion was found in 78 % of individuals of a highland population at Rize (ALTUNIŞIK & ÖZDEMİR 2013) and in 76 %, 50 % and 28 % of individuals of the lowland populations of Rize, Antalya and Çanakkale, respectively.

In addition to the ambient temperature regime mirrored by altitude and latitude, food availability, moisture, rainfall, predators and interaction with the competing males may essentially influence body size in *H. savignyi*.

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