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Influence of the Aquarium Volume on Egg-Laying of the Alpine Newt (*Ichthyosaura alpestris*)

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Abstract: Characteristics of reproduction habitat can influence egg-laying in amphibians. Egg-laying variables are studied in experiments focused on reproduction. However, the potential influence of the facility where the animals are housed during experiments is unknown. Therefore, I performed an experiment with a caudate species widely used in behavioural experiments – the Alpine newt (*Ichthyosaura alpestris*). Sixty-four females were captured in the Czech Republic and divided into two groups after controlled mating. Females from the first group were reared individually in small tanks (volume of 6 dm^{-3}), females from the other - in large tanks (volume of 20 dm^{-3}) and differences in egg-laying variables (the overall number of laid eggs, duration of the egg-laying period and the rate of egg-laying) between these groups were compared. The proportion of females that laid at least one egg (63%) did not differ between the groups. The average number of laid eggs per female was 77 (range 3-176), the mean duration of the egg-laying period (from first to last laid egg) was 15.35 days (range 3-34) and the mean rate of egg-laying was 4.73 eggs laid per day (range 0.40 - 12.40). The volume of tank did not influence these variables; however, the body length of the female (SVL), but not weight, was positively associated with the total number of laid eggs and the rate of egg-laying. We can conclude that an aquarium volume of 6 dm^{-3} of water is sufficient for individual housing of Alpine newt females and it does not represent any limitation in their reproduction outcomes.

Key words: Amphibians, breeding, Caudata, housing, reproduction

Introduction

The number of offspring produced by females of amphibians during a single reproductive cycle is influenced by external (climate, weather, competition, risk of predation, availability of sexual partners etc.) and internal (age, body size, condition, hormonal status etc.) factors (Berven 1988, Morrison & Hero 2003, Lüdtke & Forster 2019). In the case of experiments performed in a controlled laboratory environment, we can very effectively manipulate the external and, recently, also a variety of internal, factors.

Age and body length are the main internal factors associated with reproduction that cannot be manipulated. It is widely accepted that in amphibians, older females are larger and larger females produce more offspring (Bell 1977, Kaplan & Salthe 1979, Castellano et al. 2004). The number of eggs that a fe-

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male can lay in one reproductive cycle is determined early in the season by the number of egg germs released to the ovaries during ovulation; this number cannot increase and is based on the accumulated energy reserves (Jorgensen 1992). However, the size of eggs and the content of yolk are influenced by the actual nutrition state of the female (Kaplan & King 1997). In other words, the difference in the number of eggs laid by females of the same body length is caused by the loss of oocytes of poorly fed females rather than by the increase in the number of oocytes in well-fed females (Kaplan & King 1997).

A widespread European caudate species, the Alpine newt *Ichthyosaura alpestris* (Laurenti, 1768), is among the most widely used amphibians in reproduction experiments. Newts are protected by law in most countries of their occurrence due to the decline in their population (De Troyer et al. 2020). In their natural environment, Alpine newts commonly reproduce in habitats of small ruts on muddy forest roads (Babik & Rafinski 2001, Denoël & Demars 2008). It was confirmed that in such habitats, more newts were in ruts with a higher volume and depth, probably because both these characteristics of ruts were directly related to their potential to dry out (Kopecký & Vojar 2007). Until metamorphosis, eggs and larvae are completely dependent on water, therefore, an improperly selected small volume rut may lead to the loss of offspring, which makes this external factor (depth and volume of the reproductive pool) of utmost importance for the fitness of newts. When several ruts are close to one another and available for newts, females usually move among them (Kopecký et al. 2010, Kopecký et al. 2012). A relatively higher proportion of females in the population move among the ruts during drier years (Kopecký et al. 2012). Therefore, it seems that these movements might be motivated by reducing the risk of losing all offspring caused by a particular rut drying out and, simultaneously, by the female's effort to reduce the competition for her larvae. Woodward (1982) have proven that when females of the spotted salamander *Ambystoma maculatum* (Shaw, 1802) breed in stable pools, they tend to lay more eggs than females breeding in vernal pools. Similar conclusions were reported in the study of invasive populations of the African clawed frog *Xenopus laevis* (Daudin, 1802) where the depth of the pool where frogs breed was one of the factors positively influencing the number of eggs laid by females (Green 2002). However, whether or not the Alpine newt females in deeper ruts (with higher volumes) lay more eggs, remains unknown so far.

Alpine newts are often used as a model organism in ethological experiments where the number of eggs laid by females is one of the parameters suitable for observation (Garner & Schmidt 2003, Osikowski 2007, Lüdtke & Foster 2019). The plasticity of behavioural reactions of the Alpine newt is great and the response to the changes in the environment may be rapid as demonstrated in experiments with a reduced light regime (Denoël & Doellen, 2010), different densities of sexual partners (Denoël et al. 2001, Denoël et al. 2005) or with presence of predators (Winandy & Denoël 2013, Winandy et al. 2017). It is possible that an inappropriately chosen aquarium or tank for the breeding of newts in artificial conditions carried out during conservation activities may reduce the efficiency of such actions. The main goal of the presented study was to test whether the number of eggs laid by Alpine newt females affected by the size of the aquarium (volume, water depth) where they are kept. We hypothesised that in artificial conditions, females of the Alpine newt will react to a smaller aquarium or tank by laying a lower number of eggs.

Materials and Methods

Site

Newts were caught at a drift fence from the Čachnov site (N 49°44´31.3´´, E 16°3´55.4´´), which lies in the Pardubice Region, Czech Republic, at the altitude of 745 m a.s.l. The site consists of a reservoir with stone walls (8 × 6 × 1.5 m) built as a little dam on a stream that has been historically used as a reservoir for fire protection. The drift fence around the reservoir was installed on the site during the spring migration (15th - 23rd of April) of the newts to their reproduction site. Each morning during this period, traps were inspected and the caught newts were kept in flat plastic boxes (faunabox Hagen Exo Terra 46 – 23 l) lined with moss and leaves. These boxes were placed outside, near the reservoir, until the transfer of the newts to the Batrachological Laboratory at the Czech University of Life Sciences in Prague, which took place on the 23rd of April. In total, 85 males and 66 females of the Alpine newt were caught during this period.

Housing of newts and experimental design

All newts were caught by the drift fence before entering the water where they reproduce; therefore, it was sure that the captured newts had not mated during the sampled season. In the laboratory, they were classified on the basis of sex. Two groups of males were created (43 and 42 individuals) and also two groups of females (33 and 33 individuals), each of these groups was separately placed into an aquarium

(100 × 60 × 60 cm, water depth 58 cm) with tap water. In the aquariums, newts were fed ad libitum by frozen larvae of Chironomidae, no other intervention was performed. This acclimatisation to the laboratory conditions lasted until 26th of April, the main purpose of this period was to, at least partially, adjust the newts' body conditions to be as inter-individually balanced as possible. Two females died for no apparent reason during this acclimatisation period.

On 26th April, the snout-vent length to the nearest 0.1 mm (from the tip of the nose to the end of the cloaca) of all newts was measured using calliper and each newt was also weighted to the nearest 0.01 g using a digital scale. After that, the females were randomly separated into four groups (two groups of 16 and two groups of 17 individuals) and placed in four aquariums (100 × 60 × 60 cm, water depth 58 cm). Soon after, males were added to each of the four aquariums (three groups of 21 individuals and one group of 22 individuals). In these mixed groups, newts had a chance to mate until 30th of April. Then, we randomly assigned each female to one of two types of plastic tanks: large (faunabox Hagen Exo Terra 37 – volume 20 dm^{-3}, 37 × 23 × 25 cm) or small (faunabox Hagen Exo Terra 23 – volume 6 dm^{-3}, 23 × 16 × 17 cm). Regardless of the type, all tanks were equipped with pieces of polystyrene (approx. 6 × 6 cm) floating on the surface, where newts could rest outside the water, a plastic tube (diameter 3 cm, length 10 cm) attached to the bottom of the tank with silicone, where newts can hide, a stone to facilitate old skin removal, which also served as a weight for a piece of transparent eurofoil (12 × 6 cm), which was cut partially into thin strips. This eurofoil resembles submerged vegetation and, hence, it was used by females for egg-laying. Tanks were filled with tap water, resulting into a depth of depth 23 cm (large) or 15 cm (small).

Subsequently, the conditions in the tanks and the number of laid eggs were inspected every third day. Some females stayed mainly on the floating polystyrene and did not enter the water. Such females were probably not physiologically ready to lay eggs, therefore, were excluded them from further observations as well as females entering water but not laying eggs. Females were fed with frozen larvae of Chironomidae during every other check-up. The tanks were cleaned and water changed during every fourth check-up.

If necessary, eurofoils were also changed to prevent limiting the females of laying egg owing to lack of space. Eurofoils with laid eggs were, after counting, placed together into aquariums, where larvae were allowed to hatch. If eggs were laid elsewhere in the tank (i.e., not on the eurofoil) they were, after counting, also carefully transferred to other separate aquariums.

Air temperature in the laboratory was maintained at 19°C throughout the whole experiment by an air-conditioning unit. The light regime was natural (approx. 14 hours of light and 10 hours of darkness). The experiment was terminated when no eggs were laid by any of the females for two consecutive controls, i.e., on 14th June 2013.

Statistical analysis

Differences in the proportion of egg-laying females between groups in large and small tanks were evaluated using frequency tables. The total number of eggs laid by each female was monitored during the experiment as well as the duration of the egg-laying period (the number of days from the first to the last laid egg). The accuracy of these data was four days (the interval between inspections). The rate of egg-laying, represented by the total number of eggs divided by the duration of the egg-laying period, was the last evaluated value.

Evaluation of the influence of the type of tank on the total number of eggs, duration of egg-laying period, rate of egg-laying (independent variables) was performed by general (rate of egg-laying) or by generalised linear models with Poisson distribution (total number of eggs, duration of egg-laying period). In samples of the total number of eggs, the duration of egg-laying overdispersion was detected, therefore quasi-Poisson distribution was used in tests. I used a process of model simplifying with a comparison of models by the "LRT" command. The basic model for simplification contained three factors (x ~ SVL + weight + type of tank), while the last compared model was a model without any factors (x ~ 1). The level of statistical significance of all tests was set to 0.05. All analyses were performed using R Statistical Software version 4.1.2 (R Core Team 2021).

Results

Out of 64 females included in the experiment, 40 (63%) laid eggs. Neither the number of females that avoided water (spent most of the time on the floating polystyrene), nor the number of females that laid no eggs, differed between groups (overall 11 females in large tanks vs. 13 females in small tanks) (frequency table: chi-square = 0.27, P = 0.61). Nineteen females in small tanks and 21 females in large ones, respectively, laid eggs. The proportion of egg-laying females (n = 40) did not differ between both types of

Table 1. Descriptive statistics of monitored variables related to egg-laying by females of the Alpine newt reared in small and large tanks.

		range	mean	SD
number of laid eggs (N)	small tank	5 - 176	73.05	58.15
	large tank	3 - 171	80.90	61.66
	overall	3 - 176	77.18	59.38
duration of egg-laying period (days)	small tank	3 - 34	14.37	8.52
	large tank	3 - 28	16.24	8.01
	overall	3 - 34	15.35	8.20
rate of eggs laying (N/day)	small tank	0.75 – 12.40	4.78	3.05
	large tank	0.40 – 11.08	4.69	3.06
	overall	0.40 – 12.40	4.73	3.01

Table 2. Statistical significance of factors related to egg-laying (number of laid eggs, duration of egg-laying period, rate of egg-laying) by females of the Alpine newt.

		P
number of laid eggs (N)	SVL	< 0.05
	weight	0.772
	type of tank	0.545
duration of egg-laying period (days)	SVL	0.086
	weight	0.880
	type of tank	0.971
rate of eggs laying (N/day)	SVL	< 0.05
	weight	0.928
	type of tank	0.307

tanks, nor did the females differ in SVL (t-test: t = 0.12, P = 0.67) and weight (t-test: t = 0.64, P = 0.49).

Only 2.71% of all eggs were not laid on eurofoil strips. The ratio of eggs laid on the bottom of the tank did not differ between the large and small tanks (frequency table: chi-square = 0.17, P = 0.68). Females from small tanks laid on average 4.16% (range 0 – 44%) of eggs on the bottom of the tank, while females from large tanks laid on average 7.40% (range 0 – 100%) of eggs on the bottom of the tank, respectively. Laying of eggs on the bottom occurred only at the beginning of the experiment, none of the females laid eggs on the bottom after the 12th of May 2013.

The groups of females bred in large and small tanks did not differ in terms of egg laying (Tab. 1). The type of the tank influenced neither the total number of eggs laid by females, the duration of the egg-laying period nor the rate of egg-laying (Tab. 2). only SVL had a significant effect on two of the independent variables (the number of laid eggs and the rate of egg-laying) (Tab. 2, Fig. 1).

Discussion

Results clearly show that the type (volume) of tank in which the females were placed has no significant effect on any of the number of eggs, duration of egg-laying period and rate of laying eggs. The evaluation concerning two basic morphometric characteristics (SVL, weight) showed the effect of SVL on the number of laid eggs and the rate of egg-laying.

The female specimens of the Alpine newt captured for this experiment during the spring migration at the breeding site can be considered as unmated because the sperm in the spermatheca of females loses its ability to fertilise eggs after overwintering (Osikowski 2007). I did not control the mating of females during the initial part of the experiment (between the 26th to 30th of April); however, as shown previously, the number of received spermatophores is unrelated to the total number or the subsequent proportion of successfully hatched eggs (Garner & Schmidt 2003). In our experiment, all females came from one population, therefore, the previously clearly demonstrated interpopulation variability in parameters associated with reproduction for amphibians (Morrison & Hero 2003) and, specifically, for newts (Tóth 2015) could not interfere with our results. Females that were physiologically unprepared for reproduction (those which remained on the floating polystyrene most of the time) were not

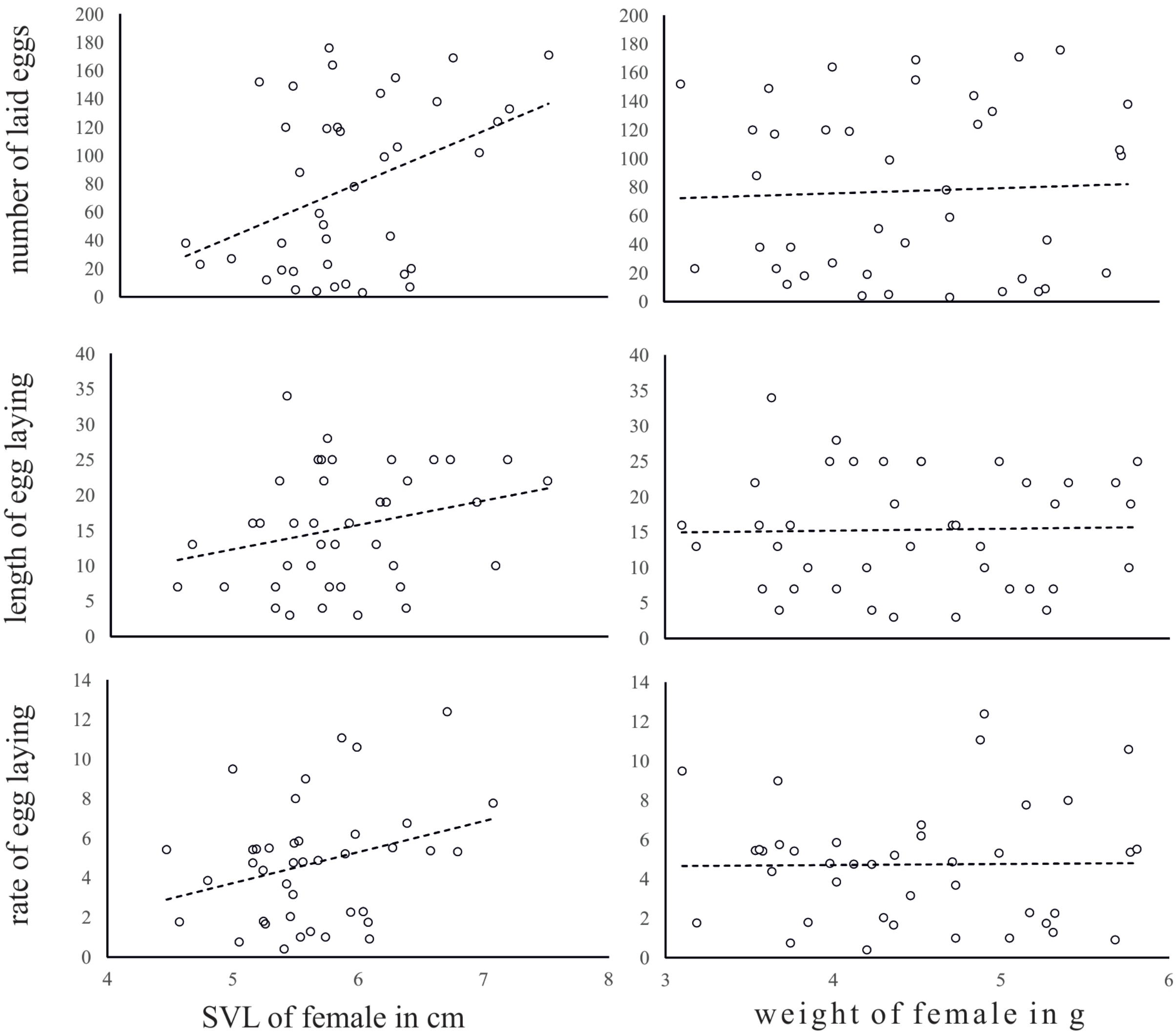

Fig. 1. The influence of female body length (SVL) and weight on egg-laying variables with shown linear trend.

included in the evaluation of the egg-laying parameters and both evaluated groups (small vs. large tank) contained only females ready for reproduction.

After successful mating, a female Alpine newt lays between 100 and 500 eggs (Miaud 1993). However, most studies report egg numbers rather at the lower limit of this range, with Griffiths (1996) reporting about 150 eggs, Roček (1992) between 100 and 190. When focusing only on studies from wildlife environments, the number of eggs is higher: an average number of 258 was reported by Thomas et al. (2002) and 293 by von Lindeiner (1992). On the other hand, in laboratory conditions, females lay from 20 to 271 (Thiesmeier & Schulte 2010), from 23 to 451 (Lüdtke & Foster 2019), about 100 eggs (Garner & Schmidt 2003) or even fewer eggs – 69 eggs on average (Oriazola & Braňa 2003). Our results are at the lower end of the range reported for laboratory studies. It should be emphasised that the number of laid eggs is not the only or the most important measure of the reproduction success of the particular female but only its primary premise. Subsequent hatching and larvae survival are also crucial for individual female fitness (Newman 1992, Galloy & Denoël 2010).

The duration of the egg-laying period varies considerably among females, ranging from 6 to 120 days with an average of 62 days (Lüdtke & Foster 2019). In our study, the average egg-laying period lasted only 15 days. The maximal duration of the egg-laying period (34 days) corresponds with the average time that Alpine newts spend in the aquatic environment during their annual life cycle for specific habitat of ruts on muddy forest tracks (Kopecký et al. 2010, Kopecký et al. 2012). Similarly, the data on egg-laying rate (speed) for Alpine newt are scarce. Osikowski (2007) reports 68 – 83 eggs laid per week. These values are in the upper limit of the range found during our experiment, where the females laid 33 eggs per week on average. These differences are probably caused by adaptations to a particular locality or by a direct choice of individual females in a specific situation.

The hypothesis about the body length affecting variables associated with egg-laying has been studied in three studies: Miaud & Merilä (2001) confirmed that SVL affected the number of laid eggs, while Thomas et al. (2002), as well as Lüdtke & Foster (2019), did not confirm those findings. Our results indicated that SVL was a very strong predictor of the total number of laid eggs as well as of the rate of egg-laying. Following previous results (Lüdtke & Foster 2019), the other body measurement – the body weight – did not affect any of the explained variables.

Wrapping eggs in the leaves of aquatic plants is a precaution against egg predation (Miaud 1993, Oriazola & Braňa 2003) and, in addition, serves as a protection of the embryos against UV-B radiation (Marco et al. 2001). Females of the Alpine newt typically "wrap" the majority of the laid eggs in the leaves of aquatic plants (Oriazola & Braňa 2003). According to Miaud (1993), the proportion of wrapped eggs ranges between 75 - 90%, while Oriazola & Braňa (2003) found an even higher proportion of 97%, which is consistent with our observation. The proportion of wrapped/unwrapped eggs can significantly vary among sites. For example, Tóth (2015) found interpopulational differences for the common newt *Lissotrion vulgaris* (Linnaeus, 1758) ranging between 43 – 61% of wrapped eggs. Considering that in his experiment, female newts did not react to the presence of a predator by wrapping a higher proportion of eggs (Tóth 2015), we can assume that the proportion of wrapped eggs was an adaptation rather than a behavioural response of females to the actual situation.

Most amphibians are iteroparous (i.e., they may reproduce repeatedly, several times in their life). Not every female in a particular population participates in reproduction every year. It is assumed that a principle of a trade-off between individual growth and reproductive investment applies. Skipping reproduction means that the female may have a higher SVL in the next breeding period, which is positively associated with the number and/or size of eggs (Lardner & Loman 2003, Harris & Ludwig 2004). The situation is complicated by the fact that females can resorb some or all eggs even during an already started breeding season (Lardner & Loman 2003). This allows the female to retain more energy until the next season, in which the conditions may be more favourable for reproduction. The breeding history of the captured females was not known, nevertheless, the main idea of this study was not affected by this limitation. Besides, it is common in similar studies that the breeding history of females from previous years is generally unknown (Garner & Schmidt 2003, Galloy & Denoël 2010, Lüdtke & Foster 2019).

Conclusion

It was assumed that due to the plasticity of Alpine newts' behaviour, females would react to the lower water volume (a situation similar to unfavourable conditions in nature) in the small tank by resorbing some eggs. However, this assumption was not supported by our results. Therefore, we can conclude that aquariums with volume of 6 $dm^{-3}$of water are sufficient for individual housing of Alpine newt females, do not represent any limitation in terms of their reproduction outcomes in a particular breeding season and, in effect, are sufficient for performing valid experiments on the reproductive behaviour of Alpine newts.

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