

EGG SIZE VERSUS CLUTCH SIZE: VARIATION AND TRADE-OFF IN REPRODUCTIVE OUTPUT OF *Rana dalmatina* AND *R. temporaria* IN A POND NEAR BONN (GERMANY)

K. Weddeling,¹ G. Bosbach,¹ M. Hachtel,¹
U. Sander,¹ P. Schmidt,¹ and D. Tarkhnishvili¹

Keywords: amphibians, *Rana dalmatina*, *Rana temporaria*, reproduction, egg size, clutch size, fecundity, trade-off, Germany.

INTRODUCTION

The common frog (*R. temporaria*) is a widespread and abundant species of woodland and agricultural landscapes in Europe and north-west Asia. In contrast, the distribution of the agile frog (*R. dalmatina*) is rather scattered and restricted mainly to deciduous and mixed forests in western, central and south-eastern Europe. Within their overlapping range, both species often breed in the same ponds. Although ecology of these brown frog species is well known in parts, many aspects of their biology possibly explaining niche differentiation and large and small scale distribution remain uncertain. Interspecific variation in reproductive output may be one key factor explaining local differences in their abundance and dispersal ability. Our study compares the reproductive output of both species in a single pond near Bonn (Germany) using data on egg size (diameter, egg mass), clutch size, body size, age, and body condition.

METHODS

The study pond is situated near Bonn (Germany) in an agricultural landscape with a distance of 200 m from a mixed forest. In spring 2001 and 2002 an overall sample of 29 females of the agile frog and 34 females of the common frog spawned under field conditions in plastic cages placed inside their breeding pond. For each female snout-vent length (SVL), weight before and after spawning, clutch size, and egg diameter were measured. Skeletochronology of finger bones was used to determine the age of the frogs (Kleinenberg and Smirina, 1969). Somatic condition (computed after Hemmer and Kadel, 1971), egg mass and relative investment in reproduction (clutch mass

spent/weight of spent females) were calculated from these data and used mainly for parametric linear regression analysis. Egg size parameter “egg mass” and “egg diameter” are only weakly correlated ($r^2 = 0.32$, $p < 0.001$); several correlations of egg size with other parameters are only significant with one of these measures, probably indicating a considerable error in measurement of egg diameter.

RESULTS

Clutch size differs significantly between species (Fig. 1, mean \pm standard deviation (S.D.): *R. temporaria*, 1766 ± 529 eggs; *R. dalmatina*, 950 ± 246 eggs) but egg diameter and egg mass do not (*R. temporaria*: egg diameter 2.08 ± 0.160 mm, egg mass 12.70 ± 5.123 mg; *R. dalmatina*: egg diameter 2.14 ± 0.141 mm, egg mass $12.70 \pm$

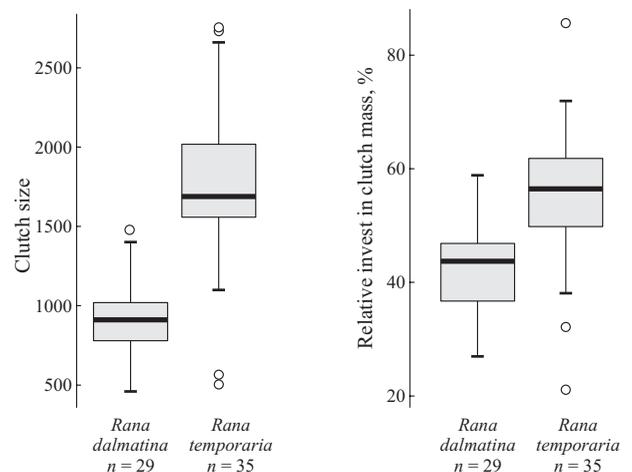


Fig. 1. Clutch size and relative investment in clutch mass ($100 \times$ clutch mass/weight of spent female); clutch size ($t = -8.364$, $p < 0.001$) and relative investment (arcsine transformed data, $t = -4.619$, $p < 0.001$) differ between species. Student's t -test.

¹ Zoologisches Forschungsinstitut und Museum Alexander Koenig, Sektion Herpetologie, Adenauerallee 160, D-53113 Bonn, Germany; E-mail: weddeling@web.de; www.amphibien-projekt.de.

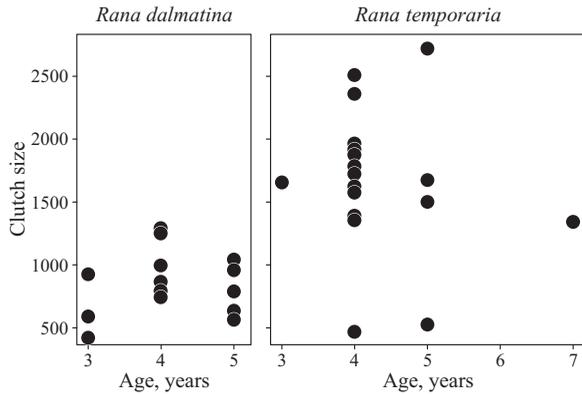


Fig. 2. Age and clutch size of females show no correlation (Spearman correlation, *R. dalmatina*: $r^2 = 0.02$, $p > 0.05$; *R. temporaria*: $r^2 = 0.04$, $p > 0.05$).

5.180 mg). Clutch size is not correlated with SVL. Relative investment in clutch mass differs significantly between species, the larger *R. temporaria* (0.557 ± 0.122) invests more than the smaller agile frog (0.421 ± 0.085), but in both species investment is not correlated significantly with SVL (Fig. 1). Mean age does not significantly differ between species (median for females of both species 4 years; Mann – Whitney *U*-test, $U = 153.5$; $p > 0.05$). Age is not correlated significantly with any clutch or egg parameter nor with body condition or relative investment in reproduction (Fig. 2). A significant trade-off between egg mass and clutch size could be shown for both species (log-log-transformed data, $y = \log[\text{egg mass}]$, $x = \log[\text{clutch size}]$: *R. temporaria*, $y = -0.593x + 2.983$, $r^2 = 0.30$, $p < 0.01$; *R. dalmatina*: $y = -0.925x + 3.801$, $r^2 = 0.63$, $p < 0.01$). Trade-off is more pronounced in *R. dalmatina* probably due to the smaller body size compared to *R. temporaria* (Fig. 3). Impact of somatic condition on egg diameter strongly differs between species: In *R. dalmatina* females with better somatic condition produce significantly bigger eggs, in *R. temporaria* in this case eggs are smaller (Fig. 4). Surprisingly condition does not affect clutch size.

DISCUSSION

Differences in clutch size and relative investment in reproduction are mainly due to the marked differences in SVL between species. When clutch size was compared accounting for SVL, mean egg number does not significantly differ between common frog and agile frog. Thus, one main difference in reproductive strategy and fecundity between species is the strongly enhanced growth rate in

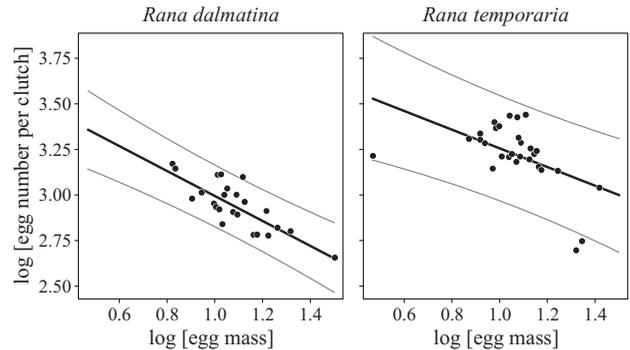


Fig. 3. Both species show a significant trade-off between egg size (measured as mean egg mass) and egg number (linear regression models and 95% confidence intervals, for statistics see the text).

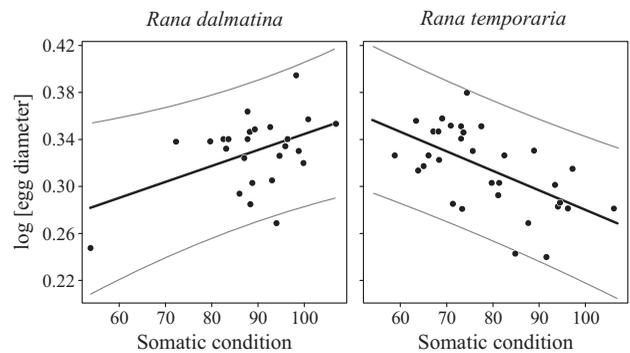


Fig. 4. Egg size response to different somatic conditions of females (linear regression models and 95% confidence intervals): *R. dalmatina* $b_{st} = +0.459$ ($F = 6.141$, $p < 0.05$); *R. temporaria* $b_{st} = -0.562$ ($F = 15.274$, $p < 0.001$).

R. temporaria, resulting in a nearly doubled mean egg number compared to *R. dalmatina*, since both species do not significantly differ in age. These data suggest that pre-suppositions for a high metamorphic output are generally better in *R. temporaria* than in *R. dalmatina*. However, our field census data on juvenile output of the species do not support this hypothesis, since a regular dominance of *R. temporaria* in ponds with *R. dalmatina* cannot be observed. Thus, other factors — probably pond specific survival rates of tadpoles and metamorphs — influence species dominance in the field.

In both species a marked trade-off between egg number and egg size is obvious. This indicates that frogs cannot optimize both, egg size and egg number simultaneously. Assuming that the number of eggs laid in spring is determined by body condition after spawning one year before, egg size is likely to depend on feeding conditions during the following summer and autumn (Kuhn, 1994;

Lüddecke, 2002). Terrestrial habitat quality (including weather conditions) one year before seems to adjust clutch size and egg size in the following season. Thus, maintenance of a considerable variation and a trade-off in reproductive output of *R. temporaria* and *R. dalmatina* in the studied pond might be regarded as a result of recent changes in environmental conditions.

Acknowledgments. This project was financially supported as a ‘testing and development project’ by the Federal Agency for Nature Conservation (BfN) and the Federal Environment Ministry (BMU). Many thanks to our colleagues Regine Damaschek, Anja Dissanayake, Ruth Rottscheidt, Anja Sampels, and Meike Thomas for their work in the field and discussions. Wolfgang Böhme we thank for leading the project.

REFERENCES

- Hemmer H. and Kadel K.** (1971), “Untersuchungen zur Laichgröße nebst Bemerkungen zur Populationsdynamik der Kreuzkröte (*Bufo calamita* Laur.) und der Wechselkröte (*Bufo viridis* Laur.),” *Zool. Beitr.*, **17**, 327 – 336.
- Kleinenberg S. E. and Smirina E. M.** (1969), “A contribution to the method of age determination in amphibians,” *Zool. Zh.*, **48**, 1090 – 1094 [in Russian].
- Kuhn J.** (1994), “Lebensgeschichte und Demographie von Erdkrötenweibchen *Bufo bufo bufo* (L.),” *Zeitsch. Feldherpetol.*, **1**(1/2), 3 – 89.
- Lüddecke H.** (2002), “Variation and trade-off in reproductive output of the Andean frog *Hyla labialis*,” *Oecologia*, **130**, 403 – 410.