SALAMANDRA 54(3) | 222–228 | 15 August 2018 | ISSN 0036–3375

Carabid predation on *Bombina variegata* metamorphs: size at and timing of metamorphosis matter

Alena Marcella Schäfer, Francesca Schäfer, Thomas Wagner & Ulrich Sinsch

Universität Koblenz – Landau, Institut für Integrierte Naturwissenschaften, Abteilung Biologie, Universitätsstr. 1, 56070 Koblenz, Germany

Corresponding author: Ulrich Sinsch, e-mail: sinsch@uni-koblenz.de

Manuscript received: 8 May 2018
Accepted: 16 July 2018 by Stefan Lötters

Abstract. The potential impact of carabid predation on dispersing *Bombina variegata* metamorphs was studied in the field at the Schmidtenhöhe (Rhineland-Palatinate, Germany) and performing experimental trials in the laboratory. At least four carabid species were demonstrated to feed on metamorphs, with *Carabus violaceus* and *Pterostichus niger* mainly preying on the smallest individuals, and *Abax parallelepipedus* and *Harpalus rufipes* indiscriminately attacking smaller and larger individuals. Predation rates were mostly low (5–15% of metamorphs) despite of high prey densities (83 metamorphs per m²), but hungry beetles consumed up to 60% within five days. Plasticity in the timing of metamorphosis (about two months) and in the size at metamorphosis (11–19 mm) observed in the field seemed to reflect mainly the variability in the spawning date and of aquatic environment during the tadpole development. Still, the tendency of metamorphs to be become larger on average towards the end of the metamorphosis period reduced their risk of being predated because the abundance of potential carabid predators did neither vary among habitat types crossed by dispersing metamorphs nor during the period of metamorphosis. Consequently, informed conservation management of endangered *B. variegata* populations should focus on larval habitats producing large-sized metamorphs to reduce loss of metamorphs by size-assortative carabid predation.

Key words. Amphibia, Anura, Insecta, Coleoptera, *Abax parallelepipedus, Carabus violaceus, Pterostichus niger, Harpalus rufipes*, size-assortative mortality.

Introduction

Amphibians with complex life cycles have evolved life-history strategies to optimize timing of and size at metamorphosis as key adaptations (Wilbur & Collins 1973). A wide range of possible sizes at metamorphosis is expected in species living in variable environments, compared to a narrower range in species inhabiting more stable environments. In fact, environmental heterogeneity favours phenotypic plasticity in morphology and life-history traits of *Rhinella spinulosa* (Márquez-García et al. 2009, 2010). Fast desiccation of ponds triggered accelerated tadpole development resulting in an early metamorphosis and small-sized metamorphs, low desiccation rates caused late metamorphosis and individuals with longer hindlimbs and larger heads (Márquez-García et al. 2009). Thus, plasticity in timing of and size at metamorphosis traits may be adaptive to larval growth environment reflecting the influence of aquatic stressors, and affects fitness in a range of amphibian species (Altwegg & Reyer 2003). Population-level impacts of larval traits on fitness often do not become visible before reaching the terrestrial stage and therefore, represent carryover effects from the aquatic stage (Chelgren et al. 2006).

For example, larval density is negatively correlated with the size of metamorphs in *Epidalea calamita* (Golay & Durrer 1995), *Anaxyrus fowleri* (Yagi & Green 2018), *Pelophylax lessonae* and its hybridogenetic form "*esculentus*" (Altwegg & Reyer 2003). Postmetamorphic growth is uniform among toadlets of any size and does not compensate for size differences at metamorphosis in these species (Golay 1996). Large *Pelophylax* metamorphs enjoy an increased chance of survival to adulthood, faster growth and larger size at maturity as compared with small-sized metamorphs (Altwegg & Reyer 2003). In *Rhinella marina* metamorph size also varies within a wide range and larger individuals show better locomotor performance on land and in water, are more successful in preying and have enhanced survival and growth rate (Cabrera-Guzmán et al. 2013). One of the proximate causes of variability in size and body mass at metamorphosis is the timing of metamorphosis. Plasticity of this trait has been observed in many amphibians, e.g. *Ambystoma talpoideum* (Semlitsch & Wilbur 1988), *Dryophytes versicolor* (Beachy

© 2018 Deutsche Gesellschaft für Herpetologie und Terrarienkunde e.V. (DGHT), Mannheim, Germany
Available at http://www.salamandra-journal.com

et al. 1999), *Rana temporaria* (Merilä et al. 2000), and *R. aurora* (Chelgren et al. 2006). In *Phrynobatrachus guineensis* the increase of mortality rate in drying habitats represents a time constraint that promotes a reduced larval period, also allowing a trade-off between development time and body mass (Rudolf & Rödel 2007).

Timing of and size at metamorphosis does not only affect growth trajectories and fitness of juveniles and even adults, but also may have direct consequences for survival during the dispersal of metamorphs into the terrestrial habitats surrounding the breeding pond. Small-sized metamorphs are more vulnerable to lethal attacks by spiders and carabid beetles than are large-sized ones. Specifically, predation of carabids on temperate-zone amphibians has been reported, but information given is mostly anecdotal (Toledo 2005). Not only anurans (*Bufotes viridis, Hyla savignyi, Pelophylax bedriagae*), but also urodeles (*Triturus vittatus*, *Salamandra infraimmaculata*) are attacked by carabids. Different amphibian life stages are affected, adults as well as metamorphs. Documented cases are reported for *Epomis dejeani* and *E. circumscriptus* in Israel (Wizen & Gasith 2011b), as well as for *Chlaenius darlingensis* in Australia (Robertson 1989). Small specimens were observed to be especially prone to carabid attacks, e.g. *Scaphinotus angusticollis* and *Pterostichus melanarius* prefer small juvenile *Plethodon vehiculum* (Ovaska & Smith 1987). Even the larvae of some carabid species lure their potential prey and show predation behaviour on amphibians. Carabid larvae role-reversal has been reported for *Chlaenius (E.) simba* in South Africa (Scholtz & Ralston 2017), *Epomis dejeani and E. circumscriptus* in Israel (Wizen & Gasith 2011a) as well as for *E. circumscriptus* in Spain (Escoriza et al. 2017). Amphibians are also exposed to carabid attacks outside their activity period, as reported for *Lissotriton vulgaris* while sharing a winter shelter with *Pterostichus niger* in Poland (Bernard & Samolag 2014). However, the risk of predation by arthropods seems to be highest during breeding season when metamorphs are leaving water (Toledo 2005).

In the framework of a demographic study on yellow-bellied toads *Bombina variegata* in the low mountain range of Rhineland-Palatinate (Germany), we found that metamorphs dispersing from the breeding ponds are exposed to a variety of carabid species that forage in the surrounding grassland areas and forests (Taupp et al. 2015). So far, there are no documented cases of carabids preying on *B. variegata*. Aims of our study are to assess (1) timing of and size at metamorphosis of *B. variegata* toadlets in the field, (2) the abundance and diversity of potential carabid predators in three habitat types neighbouring breeding ponds during the period of *B. variegata* metamorphosis, and (3) to determine experimentally the predation rates and prey-size preference of common local carabids. We hypothesize that small-sized metamorphs are more prone to carabid attacks and have greater mortality rates than larger ones, as suggested by Ovaska & Smith (1987).

Materials and methods

Study area

In 2017, metamorphs of *Bombina variegata* were sampled in four clusters of breeding ponds at the former military training area Schmidtenhöhe near Koblenz (area: ca. 700 ha) (Rhineland-Palatinate, Germany; cf. Sinsch et al. 1995). All local waterbodies are manmade, most are remains of tank tracks, others were constructed for the conservation management of yellow-bellied toads. Pond cluster 1 (50.201°N, 7.393°E, 298 m a.s.l.) is located in a former clay pit with a central large quarry pond and about 15 smaller, often temporary ponds. Raw soil areas and developing grassland are surrounded by deciduous woodland. Breeding ponds of *B. variegata* were often located within 10 m of the forest edge. Pond cluster 2 (50.346° N, 7.644° E, 279 m a.s.l.) is located in an area used occasionally for training with heavy vehicle and includes up to 10 permanent and temporary ponds and ditches within an area of bare soil, surrounded with a 30–210 m broad belt of grassland followed by deciduous woodland. Cluster 3 (50.207° N, 7.402° E, 333 m a.s.l.) includes 7 mostly permanent ponds within a grassland and 200–430 m distant from deciduous woodland. The grassland is grazed by Konik horses and Taurus cattle. Cluster 4 (50.209° N, 7.406° E, 338 m a.s.l.) comprises 16 shallow to deep former tank tracks within grassland with shrubs. The forest edge is between 10 and 60 m distant from the ponds. Carabid surveys took place in the vicinity of pond clusters 1 and 3 (for details see below).

Monitoring of recently metamorphosed toadlets

Mid-July of 2017, we observed the first toadlets of *B. variegata* near the breeding ponds and started at July, 21, a roughly weekly survey for metamorphs within a 1-m-belt around the pond shores. All toadlets observed were collected, and snout–vent length (SVL, to the nearest 0.5 mm) and mass (to the nearest mg) were recorded for each individual. We considered all toadlets of a SVL of less than 20 mm as metamorphs because the largest late-metamorphic tadpoles of Gosner stages 44 and 45 with a tail bud remaining had 19 mm SVL. The condition index (studentized residuals of the SVL-mass relationship using a multiplicative model ln(mass) = a + b × ln(SVL), with a = intercept and b = slope; Reading 2007, equivalent to the residual index in Băncilă et al. 2010) is a simple measure describing the state of nutrition following the larval period. Survey dates were July, 21, 28, August, 4, 9, 15, 17, 21, 22, 31, 2017. In September, metamorphosis events were limited to the very few remaining tadpoles in ponds and monitoring was stopped.

Carabid diversity and abundance

Carabids were captured in wet and dry pitfall traps, i.e. glass container (7 cm diameter, 9 cm deep) sunk into the soil so that the mouth is level with the soil surface (Barber 1931). Wet pitfall traps were filled with saturated NaCl-solution plus detergent to kill and conserve the beetles, and to estimate carabid diversity and abundance. Each of the five trapping period lasted two weeks, starting at July, 4, when the first *B. variegata* tadpoles had reached metamorphic stages. At the end of each trapping period traps were emptied, carabids washed with water and conserved in 70% Ethanol until species determination (keys in Freude et al. 1976). Traps with fresh salt solution were put in place again to start the next trapping period. Dry pitfall traps with some soil and leaf litter on the ground were used to capture carabids for predation trials. Trapping started at July, 4, as well, but traps were checked for carabids twice per week. Carabids of at least 11 mm body length were transported to the lab facilities, kept in temperature-controlled chambers at 20 ± 2°C and LD 12:12, and fed with small arthropods until predation trials started.

In pond cluster 1, a row of 5 wet and 2 dry traps (4 m distant from the next neighbour) were placed in the grassland (GS) between a breeding pond and the 10 m distant edge of the adjacent woodland. A parallel second row of 5 wet and 3 dry traps was located within the woodland (F) about 10 m distant from the edge. An array of 15 traps (10 wet, 5 dry; three rows, each trap 4 m distant from each other) was placed between pond cluster 3 and the forest edge within the grassland (P). An electric fence around the trap array kept horses and cattle off. The abundance of each carabid species was defined as the number of individuals captured in wet pitfall traps per 10 traps and 10 weeks.

Predation trials

Predation trials followed a standardized procedure in the temperature-controlled chambers at 20 ± 2°C and LD 12:12. Three to five trials were performed simultaneously in plastic containers (40 × 60 × 20 cm) filled with wet sand, cobbles and grass to a height of 5 cm to provide moisture and shelter. Each box was covered with a narrow mesh to allow for air circulation, but to prevent metamorphs and carabids from escape. At the beginning of a one-week trial each box was equipped with one carabid beetle originating from the dry pitfall traps and 20 metamorphs captured in the vicinity of the clay pit ponds (Cluster 1). Thus, initial prey density was 83 metamorphs per m^2. SVL (to the nearest mm) of each metamorph was measured before starting the trial. At the end of each trial, number and SVL of the surviving metamorphs were assessed again. Carabid specimens tested were *Abax parallelepipedus* (n = 4), *Carabus violaceus* (n = 1), *Harpalus rufipes* (n = 1), and *Pterostichus niger* (n = 7). Trials were performed during the peak period of metamorphosis in the field, at July 21–28 (5 trials), July 28–August 4 (3 trials), and August 4–11, 2017 (5 trials).

Statistical analyses

Data distributions were tested for normality determining standardized kurtosis and skewness. Since SVL distributions often deviated from normality, medians were compared by the non-parametric Mann-Whitney-Wilcoxon W-test and shapes by the two-sided Kolmogorov-Smirnov test. The time course of SVL and CI were fitted to a polynomial regression using the date July 21, 2017 as day 1. Statistical significance was set at alpha = 0.05. Statistical analyses were conducted using the software package StatGraphics 18.

Results

Temporal variation of size and condition of metamorphs

Recently metamorphosed toadlets were observed in low number in early July, but massive metamorphosis did not occur before mid-July. SVL of 291 juveniles collected in the shore region of breeding ponds and considered as metamorphs varied between 11 and 19mm (median: 16 mm), whereas SVL of 62 late-metamorphic Gosner (1960) stages collected in the shallow water and about to leave the pond varied between 14 and 19 mm (median: 16 mm). SVL medians of metamorphs and late Gosner stages did not differ significantly (Mann-Whitney-Wilcoxon W-test; W = 9354.0, p = 0.505), but shapes of size distributions did (two-sided Kolmogorov-Smirnov test; p = 0.009). Metamorph SVL distribution varied significantly in time ($F_{2,351} = 81.8$; $p < 0.0001$), with variation being largest in July (polynomial regression model: $R^2 = 31.9\%$; SVL [mm] = 14.1946 + 0.2313 × day-0.0046 × day^2). Very small-sized metamorphs (11–13 mm SVL) were more frequent at the beginning of the metamorphic period, but absent during the later season (Fig. 1A). Interestingly, large metamorphs were observed at any time, dominating the size-distribution in the mid-part of the metamorphosis period. At the end of the metamorphosis period the proportion of small-sized metamorphs (14–15 mm SVL) increased again. The condition index (CI) of metamorphs without remains of the tail did not correlate with SVL (linear regression model, $R^2 = 0.0002$; $F_{1,289} = 0$; $p = 0.9685$). In contrast, CI varied slightly, but significantly in time ($F_{2,289} = 6.83$; $p = 0.0013$), again with variation being largest in July (polynomial regression model: $R^2 = 4.5\%$; CI = -0.0389-0.0247 × day+0.0009 × day^2; Fig. 1B).

Carabid diversity and abundance

A total of 24 carabid species was collected within the three trapping areas, 14 in pasture area of cattle and horses (P), 13 in the grassland (GS) of the clay pit and 9 in the forest (F; Table 1). Fourteen were considered as potential predators of *B. variegata* metamorphs because they are known to be carnivorous (Zahradnik 1985, Paoletti 1999) and had a body length of 11 mm or more which is in the SVL range of metamorphs. In all trapping areas these species were among the most abundant. Log10-normalized carabid abundance (individuals in 10 traps per two weeks) did not differ significantly among the three trapping areas (ANCOVA, $F_{2,14}$ =

Table 1. Diversity, size and abundance of carabid species collected in the study area. Literature data on body length refer to Freude et al. (1976), empiric measurements are given as average and range, if there was a variation. Wet pitfall traps were located near pond cluster 1 in the grassland area (GS) and within the forest (F) and near pond cluster 3 within the pasture area (P). Abundance is given as number of individuals per 10 traps and per 10 weeks' capture period. Species considered as potential predators (body length equal that of smallest metamorphs; i.e. 11 mm) are indicated with an asterisk, those captured in the dry pitfall traps and tested in predation trials are marked in grey.

Carabid species	**Body length [mm]** Literature data	**Body length [mm]** Study site	**P** Standardized abundance	**GS** Standardized abundance	**F** Standardized abundance
*Abax parallelepipedus**	16–21	18 (17–19)	0	4	8
*Abax parallelus**	13–17	15	0	0	2
*Amara aulica**	10.5–15	13 (12–14)	9	0	0
Amara equestris	8.5–13	9	3	0	0
Amara lunicollis	6.5–8.5	7	1	0	0
Anchomenus dorsalis	5.8–7.5	6	2	0	0
Badister bullatus	5–6	6	0	2	0
*Calathus fuscipes**	11–14	12.6 (12–13)	42	2	0
Calistus lunatus	4.2–7	7	1	0	0
*Carabus granulatus**	17–23	20.7 (19–22)	0	12	0
*Carabus monilis**	17–32	25.5 (25–26)	0	0	4
*Carabus violaceus**	22–35	29 (28–30)	4	2	0
Chlaenius nigricornis	9.5–12.5	10	1	0	0
Harpalus affinis	9–12	9.7 (9–10)	3	2	0
Harpalus latus	8–11	10	0	2	0
*Harpalus rufipes**	11–16	13.3 (12–15)	3	16	0
*Limodromus assimilis**	10–12	10.7 (10–11)	0	0	30
*Nebria brevicollis**	10–13	12.3 (12–13)	0	4	8
*Ophonus ardosiacus**	10–13	11.3 (11–12)	0	4	4
Ophonus schaubergerianus	7.5–10	7.3 (7–8)	4	0	0
*Poecilus versicolor**	8–11.5	11 (9–12)	8	8	2
*Pterostichus madidus**	13–18	14.2 (13–15)	0	0	16
*Pterostichus niger**	15–21	19.8 (17–22)	2	38	20
Pterostichus vernalis	6–7.3	6.5 (6–7)	2	2	0
Total number of species			14	13	9

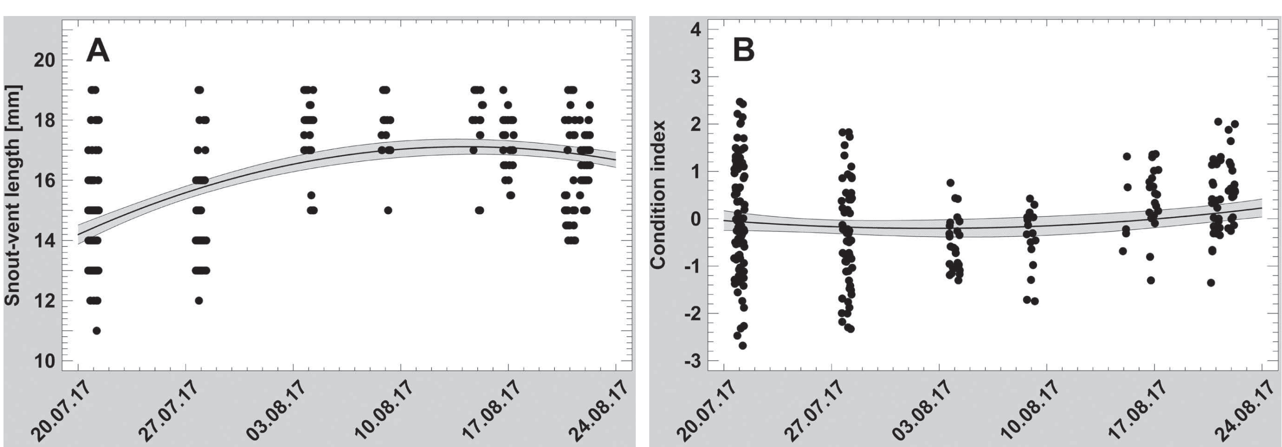

Figure 1. Temporal variation of size (A) and condition index (B) of *Bombina variegata* metamorphs. Each dot represents an individual, the central line the polynomial regression line fitting data distribution and the grey area the 95% confidence interval. Statistical details in the text.

Table 2. Survival rates of 20 *Bombina variegata* metamorphs following a one-week exposure to a carabid beetle. Data are given as arithmetic means and the minimum-maximum range.

Predator species	Average survival rate of metamorphs (range)
Abax parallelepipedus (4 trials)	0.81 (0.65–0.95)
Carabus violaceus (1 trial)	0.45
Harpalus rufipes (1 trial)	0.58
Pterostichus niger (7 trials)	0.71 (0.40–0.85)

1.73, P = 0.222) or show a temporal trend during the 10 weeks of trapping (ANCOVA, $F_{1,14}$ = 0.64, P = 0.442). Individuals of four potential predator species were captured in the dry pitfall traps permitting to test their potential in standardized predation trials: *Carabus violaceus* and *Harpalus rufipes* (abundant in P and GS), *Abax parallelepipedus* and *Pterostichus niger* (abundant in GS and F).

Predation trials

Survival rates of toadlets varied between 40% and 95% among the carabid species tested (Table 2). Replicated trials with *Abax parallelepipedus* and *Pterostichus niger* yielded a wide range of survival rates, i.e. individuals of same predator species differed considerably in the consumption of toadlets. Analysing exclusively the trials with the lowest survival rates of toadlets for each predator species (Fig. 2), size-assortative preference of prey was evidenced by a significant increase in median SVL of surviving toadlets in *C. violaceus* (SVL medians: 13.5 mm (n = 20) vs. 15 mm (n = 9); W-test, p = 0.035) and *P. niger* (SVL medians: 13 mm (n = 20) vs. 15 mm (n = 8); W-test, p = 0.035), but not in *A. parallelepipedus* (SVL medians: 14 mm (n = 20) vs. 16 mm (n = 13); W-test, p = 0.469) and in *H. rufipes* (SVL medians: 13 mm (n = 19) vs. 15 mm (n = 11); W-test,

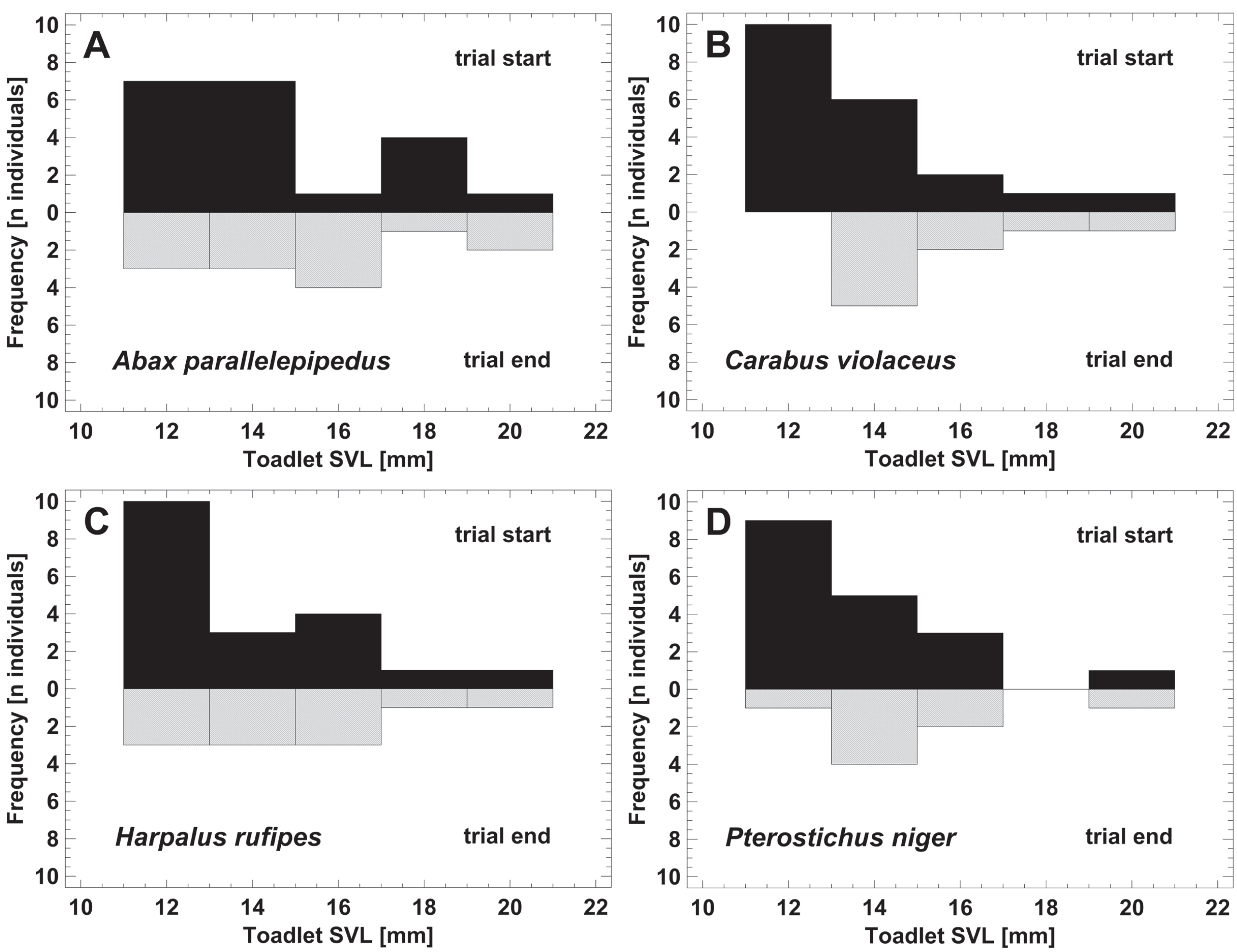

Figure 2. Pre- and post-trial SVL distributions of *Bombina variegata* toadlets in those trials in which exposure to the predator yielded the lowest survival rate of toadlets.

p = 0.346). In fact, almost all toadlets of SVL 11–12 mm were consumed by *C. violaceus* and *P. niger* (Fig. 2B, D), whereas the loss of this size group was lower when exposed to *A. parallelepipedus* and *H. rufipes* (Fig. 2A, C).

Discussion

Our study provides evidence that many carabid beetle species inhabiting the same areas as *B. variegata* do pose a predation risk to metamorphs. Successful carabid attacks usually end with the death of the toadlet, as previously observed by Robertson (1989) and Scholtz & Ralston (2017), and in our predatory trials. The potential impact on the toads´ local population dynamics depends on the magnitude of metamorph mortality caused by foraging carabids. Predation risk is a function of the local number of carabid species large enough to successfully attack metamorphs and of the abundance of beetles at the period of metamorphosis. We focus discussion first at the possible adaptive timing of metamorphosis to occur mainly at periods with low predator species abundance. Then we explore the interactions among metamorph size, timing of metamorphosis and predation rates to evaluate the assumed overall loss of metamorphs during dispersal.

Timing of metamorphosis and the abundance of carabids

As a pioneer species, *B. variegata* breeds in shallow and often temporary ponds, whenever they are available in the area inhabited. Reproduction is prolonged ranging from the late April to early August in Germany yielding metamorphs from July to September (Nöllert & Günther 1996), a feature shared by the population studied at the Schmidtenhöhe. The variability in timing of metamorphosis reflects mainly the plasticity in the date of spawning, whereas an adaptive timing in response to pond drying as in *Rhinella spinulosa* and *Pelophylax* spp. (Altwegg & Reyer 2003, Márquez-García et al. 2009, 2010) seems to be absent in *B. variegata* (Böll 2002). Adaptive avoidance of periods of high carabid abundance is unlikely, as beetles large enough to prey on metamorphs are present during the entire reproduction period (Taupp et al. 2015), and the abundance of these carabids did not vary in time (this study). In conclusion, plasticity of metamorphosis timing seems rather to be a by-product of the prolonged breeding.

Metamorph size and predation risk

More successful predation on small-sized salamander juveniles than on larger individuals has been observed in two carabid species tested in laboratory encounters (Ovaska & Smith 1987). Size-assortative predation on *Bombina* metamorphs was evident in *C. violaceus* and *P. niger* as well as only the smallest metamorphs were consumed. In contrast, *A. parallelepipedus* and *H. rufipes* did not show any size preference among the prey offered. *P. niger* seems to be an opportunistic predator on amphibians which is known to feed also on *Lissotriton vulgaris* (Bernard & Samolag 2014). The individual variation of predation rate in *Pterostichus* and *Abax* specimens tested was probably due to different nutritional states affecting the motivation to attack. The overall risk of a *Bombina* metamorph to face a lethal encounter with a hungry carabid is probably low because the metamorph density in the experimental predation trials may be occasionally found at the shores of breeding ponds during the metamorphosis peak, but is much less than one individual per square meter during dispersal. Even under the trial conditions favouring predator–prey encounters, metamorph mortality was low in nine out of 13 trials indicating predation the result of random encounters rather than active hunt. We never observed patrolling carabids at the shores of breeding ponds during periods of metamorphosis as reported for *Chlaenius darlingensis* in Australia (Robertson 1989).

The chance to reduce predation risk by large metamorph size seems to be limited to some, but not all potential carabid species. Therefore, it seems unlikely to assume that there is a selection towards large-sized metamorphs in response to predation by carabids. The observed considerable plasticity of size at metamorphosis most probably reflects different environmental conditions in the larval habitats (Böll 2002), as in several other anuran species (Altwegg & Reyer 2003, Chelgren et al. 2006). This is in agreement with life-history theory which predicts a wide range of possible sizes at metamorphosis in species living in uncertain environments (Wilbur & Collins 1973, Semlitsch & Wilbur 1988).

Still, metamorphosis at smaller sizes and lower body mass caused by the larval development in warm, fast-drying temporary ponds (Böll 2002, Rudolf & Rödel 2007) implies that these metamorphs are more prone to die due to carabid attacks during dispersal (this study). Development in permanent ponds resulting in larger metamorphs (Böll 2002) with an increased chance of survival (Márquez-García et al. 2009, Cabrera-Guzmán et al. 2013) improves the survival during the early terrestrial life stage by reducing the risk of being predated by a carabid. Implications for the informed management of *B. variegata* sites are obvious; the creation of potential breeding ponds should not be limited to very shallow and temporary ponds. Management of localities harbouring *B. variegata* populations should consequently focus on larval habitats producing large-sized metamorphs, e.g. ponds with a longer hydroperiod than just a few weeks.

Acknowledgements

We thank the Struktur- und Genehmigungsdirektion Nord in Koblenz for the support and providing the permits for field study and laboratory experiments, as well as the Heinrich Böll Stiftung for financial commitment.

References

Altwegg, R. & H.-U. Reyer (2003): Patterns of natural selection on size at metamorphosis in water frogs. – Evolution, **57**: 872–882.

Băncilă, R. I., T. Hartel, R. Plaiasu, J. Smets & D. Cogalniceanu (2010): Comparing three body condition indices in amphibians: a case study of yellow-bellied toad *Bombina variegata*. – Amphibia-Reptilia, **31**: 558–562.

Barber, H. S. (1931): Traps for cave-inhabiting Insects. – Journal Elisha Mitchell Science, **46**: 259–266.

Beachy, C. K., T. H. Surges & M. Reyes (1999): Effects of developmental and growth history on metamorphosis in the gray treefrog, *Hyla versicolor* (Amphibia, Anura). – Journal of Experimental Zoology, **283**: 522–530.

Bernard, R. & J. Samolag (2014): An event of underground predation on a wintering caudate amphibian by a carabid beetle. – Entomologica Fennica, **25**: 157–160.

Böll, S. (2002): Ephemere Laichgewässer: Anpassungsstrategien und physiologische Zwänge der Gelbbauchunke (*Bombina variegata*) in einem Lebensraum mit unvorhersehbarem Austrocknungsrisiko. – PhD-thesis, Bayerischen Julius-Maximilians-Universität Würzburg.

Cabrera-Guzmán, E., M. R. Crossland, G. P. Brown & R. Shine (2013) Larger body size at metamorphosis enhances survival, growth and performance of young cane toads (*Rhinella marina*). – PLoS ONE, **8**: e70121. doi:10.1371/journal.pone.0070121.

Chelgren, N. D., D. K. Rosenberg, S. S. Heppell & A. I. Gitelman (2006): Carryover aquatic effects on survival of metamorphic frogs during pond emigration. – Ecological Applications, **16**: 250–261.

Escoriza, D., L. Mestre, G. Pascual & J. Buse (2017): First case of attack of an adult *Bufo spinosus* (Daudin, 1803) by a carabid beetle larva of *Epomis circumscriptus* (Duftschmid, 1812). – Boletín de la Asociación Herpetológica Española, **28**: 51–52.

Freude, H., K. Harde & G. Lohse (1976): Die Käfer Mitteleuropas. Band 2. – Goecke & Evers, Krefeld.

Golay, N. (1996): Die Kreuzkröte (*Bufo calamita* Laur.) als Pionierart. – PhD-thesis, Zoologisches Institut, Universität Basel.

Golay, N. & H. Durrer (1995): Zur Variabilität der Metamorphosegröße bei Kreuzkröten (*Bufo calamita*). – Zeitschrift für Feldherpetologie, **2**: 3–15.

Márquez-García, M., M. Correa-Solis, M. Sallaberry & M. A. Méndez (2009): Effects of pond drying on morphological and life-history traits in the anuran *Rhinella spinulosa* (Anura: Bufonidae). – Evolutionary Ecology Research, **11**: 803–815.

Márquez-García, M., M. Correa-Solis & M. A. Méndez (2010). Life-history trait variation in tadpoles of the warty toad in response to pond drying. – Journal of Zoology, **281**: 105–111.

Merilä, J., A. Laurila, M. Pahkala, K. Räsänen & A. Timenes Laugen (2000): Adaptive phenotypic plasticity in timing of metamorphosis in the common frog *Rana temporaria*. – Eco-Science, **7**: 18–24.

Nöllert, A. & R. Günther (1996). Gelbbauchunke – *Bombina variegata* (Linnaeus, 1758). – pp. 232–252 in: Günther, R. (ed.). Die Amphibien und Reptilien Deutschlands. – Gustav Fischer Verlag, Jena etc.

Ovaska, K. & M. A. Smith (1987): Predatory behavior of two species of ground beetles (Coleoptera: Carabidae) towards juvenile salamanders (*Plethodon vehiculum*). – Canadian Journal of Zoology, **66**: 599–604.

Paoletti, M. (1999): Invertebrate biodiversity as bioindicators of sustainable landscapes. Practical use of Invertebrates to assess sustainable land use. – Elsevier Science, Amsterdam etc.

Reading, C. J. (2007): Linking global warming to amphibian declines through its effects on female body condition and survivorship. – Oecologia, **151**: 125–131.

Robertson, J. G. M. (1989): Predation by a carabid beetle on Australian frogs. – Herpetological Review, **20**: 7–8.

Rudolf, V. H. W. & M.-O. Rödel (2007): Phenotypic plasticity and optimal timing of metamorphosis under uncertain time constraints. – Evolutionary Ecology, **21**: 121–142.

Semlitsch, R. D. & H. M. Wilbur (1988): Effects of pond drying time on metamorphosis and survival in the salamander *Ambystoma talpoideum*. – Copeia, **1988**: 978–983.

Sinsch, U., S. Koch & W. Sommersberg (1995): Sekundärhabitate (Auskiesungen, Standortübungsplätze) als Refugien für die einheimische Herpetofauna. – pp. 47–64 in: Frenzel, B. & C. Servatius (eds): Regionaler Naturhaushalt: Bewertung und Nutzungspotential. – Gustav Fischer Verlag, Jena etc.

Scholtz, C. H. & C. D. Ralston (2017): A beetle (Carabidae: *Chlaenius* (*Epomis*) spp.) that eats frogs. – African Entomology, **25**: 540–543.

Taupp, T., A. Steinebach, A. Karlsson & T. Wagner (2015): Zur Käferfauna (Coleoptera) auf dem ehemaligen Standortübungsplatz Schmidtenhöhe in Koblenz. – Decheniana, **168**: 78–101.

Toledo, L. F. (2005): Predation of juvenile and adult anurans by invertebrates: current knowledge and perspectives. – Herpetological Review, **36**: 395–400.

Wilbur, H. M. & J. P. Collins (1973): Ecological aspects of amphibian metamorphosis. – Science, **182**: 1305–1314.

Wizen, G. & A. Gasith (2011a): An unprecedented role reversal: ground beetle larvae (Coleoptera: Carabidae) lure amphibians and prey upon them. – PLoS ONE, **6**: e25161. DOI: 10.1371/journal.pone.0025161.

Wizen, G. & A. Gasith (2011b): Predation of amphibians by carabid beetles of the genus *Epomis* found in the central coastal plain of Israel. – ZooKeys, **100**: 181–191.

Yagi, K. T. & D. M. Green (2018): Post-metamorphic carry-over effects in a complex life history: behavior and growth at two life stages in an Amphibian, *Anaxyrus fowleri*. – Copeia, **2018**: 77–85.

Zahradnik, J. (1985): Käfer Mittel- und Nordwesteuropas. – Paul Parey Verlag, Hamburg, Berlin.