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Aquatic-terrestrial food web coupling modulated by freshwater snail shell morphology

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Abstract: Terrestrial predators consumed aquatic snails during the dry phase of a ditch. Shell crushing suggests opportunistic predation. Predation rate locally was 30 % for *Valvata cristata*. This species had an almost tenfold higher predation risk when compared to *Anisus leucostoma* (agg.), indicating a strong positive selection of passive defences such as shell thickness (20-25 μm for *Valvata*, 65-75 μm for *Anisus*) and coiling density (predation path 4.5 times longer in *Anisus*). *Valvata* shells were mainly broken along the base, that is, the shortest predation path, whereas the completely flat-shelled *Anisus* displayed no preferred side of the shell.

Keywords: biotic interaction, Carabidae, Coleoptera, prey handling, temporal waters, trophic chain, shell traits

Zusammenfassung: Während der Trockenheitsphase eines Grabens wurden Wasserschnecken durch terrestrische Prädatoren aufgebrochen. Die Schalenaufbrüche suggerieren opportunistische Räuber. Die Prädationsrate lag für *Valvata cristata* stellenweise bei 30 %. Die Art hatte im Vergleich zu *Anisus leucostoma* (agg.) ein gut zehnfach höheres Prädationsrisiko, was eine starke positive Selektion passiver Abwehrmechanismen wie Schalendicke (20-25 μm bei *Valvata*, 65-75 μm bei *Anisus*) und Windungsdichte (Prädationsweg bei *Anisus* 4,5-fach länger) suggeriert. *Valvata*-Gehäuse wurden überwiegend entlang der Schalenbasis, also entlang des kürzesten Weges, aufgebrochen, wohingegen für die ganz flachen *Anisus* keine präferierte Schalenseite nachgewiesen wurde.

Introduction

Ditches play an important role for regional diversity (e. g. DRAKE 1998, PAINTER 1999, ARMITAGE & al. 2003, WATSON & ORMEROD 2004, HERZON & HELENIUS 2008). Yet, because many ditches are facing dry phases, they tend to harbour a comparatively low alpha diversity of aquatic taxa (WILLIAMS & al. 2003). Aquatic snails usually are detritivorous or phytophagous generalist grazers that, because they function as basal trophic guild, can reach high densities (e. g. HEITKAMP 1982). When a ditch dries out, this standing stock of biomass can suddenly become available for terrestrial consumers. As this is an unpredictable event from the terrestrial predator's point of view, it might be assumed that the predators are opportunistic rather than specialized snail feeders. An example of such opportunistic predators are the numerous passerine species that feed on aquatic invertebrates from wet habitats in an agricultural matrix (BRADBURY & KIRBY 2006). The following small study highlights the extent to which larger-sized terrestrial invertebrate predators can utilize aquatic snails as temporally available resources in the field, and hence the degree of aquatic-terrestrial food web coupling. It can be hypothesized that the operculum of aquatic prosobranchs is an effective barrier during shell crushing, as this is no defence that terrestrial snail predators usually encounter in temperate Europe. Further, it may be hypothesized that predators minimize handling costs to approach the snail and opt for the shortest way when breaking the shells.

Material and Methods

Two substrate samples were collected from a ditch of the water meadows in the floodplain of the river Queich near Neumühle West of Landau in der Pfalz, Germany. The ditch dried out in the hot and dry summer of 2015 and still was without water during sampling in late October. The two samples covered 50 x 50 cm each and were taken at a distance of about 10 m. Snails were sorted from the sieve-fractionated dry substrate under a magnification lens.

To scrutinize the predation path, shells of *Anisus leucostoma* (agg.) (MILLET 1813) and *Valvata cristata* O. F. MÜLLER 1774 were counted and classified according to whether or not the shells had been broken up and if the functional upper or lower side was affected. Both taxa are comparable, but show slight differences. The umbilicus of both taxa is widely open. *A. leucostoma* is planar, *V. cristata* is almost so. Although *Anisus* is anatomically sinistral, it can be compared to *Valvata* because planorbids have switched the upper side to the functional lower side of the shell, mimicking dextral shells. Chi² tests were run in R (available at <http://cran.r-project.org/>). SEM photographs were taken in an ESEM (Quanta 250, FEI) with detector settings to Large Field Detector (LFD), 10 kV.

Results

Two aquatic snails dominated the assemblages, namely *Anisus leucostoma* (agg.) and *Valvata cristata*. Some *Anisus* shells somewhat resembled *A. spirorbis* (LINNAEUS 1758), but as all snails were already dead at the time of collection, they could not be confirmed anatomically.

A high proportion of shells was spirally broken (Fig. 1, Tab. 1). Predation pressure differed between the two sample locations. At species level, the difference between samples was significant only for *Valvata* (Tab. 1). *Valvata* shells had an about ten times higher probability of being broken up than *Anisus* shells. Shell thickness differs by a factor two to three (in the specimens displayed in Fig. 1 it was ca. 20-25 µm for *Valvata*, 65-75 µm for *Anisus*). Shell handling of the predator differed between the two snail species. The typical path length of predation marks was about 4.5 times longer in *Anisus* than in *Valvata* (compare Fig. 1).

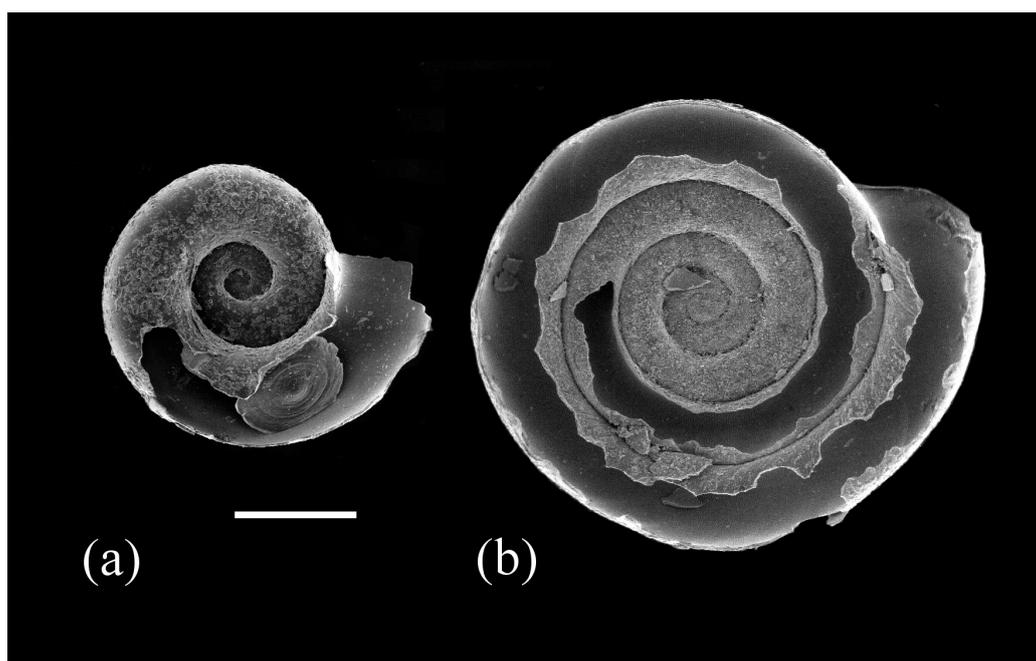


Fig. 1: Typical Predation marks in (a) *Valvata cristata* and (b) *Anisus leucostoma*. Scale bar: 1 mm. (Photos: H. KAPPES).

Tab. 1: Predation rates (total number of shells, of which shells with predation marks, percent with predation marks) of the two snail taxa in the two samples with chi² tests of intact vs. preyed shells (chi²-value, *p*-value).

	0,25m ² - sample a	0,25m ² - sample b	between-sample-chi ² , <i>p</i>
<i>Anisus leucostoma</i> agg.	696, 35 (5.0 %)	154, 3 (1.9 %)	2.1, <i>p</i> = 0.1447
<i>Valvata cristata</i>	437, 132 (30.2 %)	278, 34 (12.2 %)	29.8, <i>p</i> < 0.0001
between-species-chi ² , <i>p</i>	133.4, <i>p</i> < 0.0001	12.1, <i>p</i> = 0.0005	–

The densely coiled *Anisus* shells displayed only small advances of the predator that needed to perform multiple incisions and each time could only remove small parts of the shell. *Anisus* snails seemingly withdraw for one whorl or even slightly more into the shell. In contrast, *Valvata* shell parts were torn off in larger pieces. The predator obviously easily passed the operculum, that remained in several shells and marked the approximate location of the retracted snail (Fig. 1a).

The handling during predation also differed between the two snail species: Of the 166 shells of *Valvata cristata* with predation marks, 147 had been damaged along the functional base, whereas the corresponding figure was 25 of 38 in *Anisus* (between-species- $\chi^2 = 10.5$, $p = 0.0012$). Testing against chance distributions, *V. cristata* was usually broken up along the base ($\chi^2 = 56.2$, $p < 0.0001$), whereas there was no clear preference for the handling of *Anisus* shells ($\chi^2 = 1.3$, $p = 0.2454$). The shell base was the preferred target in *Valvata* shells in both samples (base to other: 119 to 13 in a, 28 to 6 in b; $\chi^2 = 0.9$, $p = 0.3312$). The number of broken shells of *Anisus* in sample b was too low for testing ($n = 3$, Tab. 1).

Discussion

Aquatic snails can reach high densities and provide a substantial food resource for terrestrial predators during drought events. Aquatic snails can hence contribute to aquatic-terrestrial coupling of food webs in a similar way as was suggested for emerging insects (e. g. SCHULZ & al. 2015). As could be shown in this study, the link strength of this coupling is species specific. As up to 30 % of the shells of *V. cristata* were found to be broken (Tab. 1), local populations of that species may face losses up to 30 % by a single type of predation alone during the dry phase of the ditch, adding to the potentially lethal conditions of hot and dry summers. In October 2015, these prolonged climatic conditions likely have led to 100 % mortality of the remaining snails in the samples.

Snails have evolved a number of different passive anti-predator defences, including thickened shells, internal and external shell sculptures, opercula, deep withdrawal or coiling direction (see review by VERMEIJ 2015). While the evolution of defences against predators that occur in the usual habitat of a species seems straightforward because the type of predation is predictable and likely causes directional selection, it is impossible to predict what predator will be encountered when being displaced from the original habitat.

Yet, some investments into antipredator strategies might pay off in both habitat conditions. *Anisus leucostoma*, for example, is a typical inhabitant of ephemeral waters. According to the data *A. leucostoma* seemingly performed better than *V. cristata* in deterring shell crushers. This study showed several adaptations of *A. leucostoma* against predation, including deep retraction into the shell and a comparatively thick shell that is flat and hence needs a long predation path. This study also suggests that the operculum of *V. cristata* plays no significant role in deterring terrestrial shell crushers.

Some predator types are similar in both habitat conditions. Freshwater snails amongst others have to cope with predatory coleopteran larvae that often have special adaptations such as assymmetric mandibles that facilitate shell handling of a specific coiling direction (INODA & al. 2015, and references therein). Predatory beetles also challenge terrestrial snails (e. g. BARKER 2004, BERGAMIN & SMITS 2015). In terrestrial environments, crushed shells are amongst others remains of carabid generalists (DIGWEED 1993), including species of the genera *Pterostichus* and *Calathus* (e. g. DIGWEED 1993, BARKER 2004, and references therein). Indeed, Pterostichinae are common in the water meadows near Landau (SCHIRMEL & al. 2014).

Shell crushing is the most obvious predation mode of larger invertebrate predators. However, additional losses from smaller sized predators with other food access strategies such as some dipteran larvae (e. g. BARKER 2004, and references therein) may have occurred during the dry phase. For the latter type of predator, non-operculate snails might be more accessible. The overall terrestrial predation rate hence might have been substantially higher especially for *Anisus*. The extent to which different, locally acting predators are related to the high beta diversity of ditches remains to be studied.

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