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Review

A critical review of freshwater crayfish as amphibian predators: Capable consumers of toxic prey?

Natasha J. Wilson, Craig R. Williams*

Sansom Institute for Health Research, University of South Australia, Adelaide, Australia

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ABSTRACT

Consumption of amphibian eggs and larvae by crayfish has been widely reported despite many amphibians being unpalatable and/or toxic to other predators. The aim of this review was to gather information regarding the consumption and/or avoidance of toxic amphibians by these omnivores. We then appraised the extent of toxin consumptive ability in terms of crayfish phylogenetic history so as to speculate as to the evolutionary history of this trait. Reports indicating an ability to tolerate amphibian toxins were collected and reviewed for 12 freshwater crayfish species. In reviewing these, we have established that freshwater crayfish appear to be tolerant of a range of toxic amphibians, often consuming large numbers of eggs and larvae without lethal or apparent sublethal effects. Toxin tolerance was evident within both superfamilies (Astacoidea and Parastacoidea) suggesting that tolerance may be a primitive trait in freshwater crayfish.

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1. Introduction

Although often thought of as detritivores and herbivores (Momot, 1995), freshwater crayfish (Crustacea: Decapoda, also known as crawfish, crawdads) are polytrophic omnivores and will prey upon macroinvertebrates, fishes and amphibians (Dorn and Wojdak, 2004; Gutierrez-Yurrita et al., 1998; Hobbs, 1993; Momot, 1995). The predatory behaviour of freshwater crayfish can play an important role in regulating trophic chains and as such crayfish are considered one of the largest invertebrates to act as keystone species in many ecosystems, influencing energy flow and community structure (Ficetola et al., 2012; Momot, 1995; Nyström et al., 1996). There have been numerous reports of predation of amphibians by crayfish (e.g. Adams et al., 2011; Gamradt and Kats, 1996; Renai and Gherardi, 2004). This indicates that although algae, aquatic vascular macrophytes and detritus make up a considerable amount of the typical crayfish diet (Dorn and Wojdak, 2004; Gutierrez-Yurrita et al., 1998) these crustaceans can also play important roles as predators.

Predation has been repeatedly shown to be an important regulator of larval amphibian communities (e.g. Brockelman, 1969; Heyer, 1976; Heyer and Muedeking, 1976; Smith, 1983). Predators were found to be the key factor influencing the composition of tadpole assemblages in a Brazilian field survey that included an extensive number of sampling sites (Azevedo-Ramos et al., 1999). Crayfish appear to be important predators of larval amphibians in aquatic habitats, reducing larval survivorship and influencing the distribution of amphibians within the water column (Cruz and Rebelo, 2005; Fauth, 1990). The tadpoles of many species adjust microhabitat use in the presence of crayfish by swimming higher in the water column and avoiding the floor space to reduce predation risk (Cruz and Rebelo, 2005; Davis et al., 2012; Fauth, 1990).

This predation by crayfish on amphibians is despite the prolific production of toxic chemicals by the latter.

* Corresponding author. Sansom Institute for Health Research, School of Pharmacy and Medical Sciences, University of South Australia, GPO Box 2471, Adelaide, South Australia 5001, Australia. Tel.: +61 8 830 21906.

E-mail addresses: natasha.wilson@mymail.unisa.edu.au (N.J. Wilson), craig.williams@unisa.edu.au (C.R. Williams).

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Amphibians can produce a range of bioactive compounds including biogenic amines, alkaloids, bufadienolides and peptides (Erspamer, 1993). Chemicals found in the eggs, larvae (tadpoles and efts) and skin of some adult frogs and toads (anurans) and newts (caudates) have been shown to have powerful defensive action (e.g. Brodie, 1968; Daly et al., 1987) yet there have been numerous reports of crayfish consuming these toxic/unpalatable prey.

Freshwater crayfish are a monophyletic group that date back to the Triassic (Crandall and Buhay, 2008). With the splitting of Pangaea (185 mya) came the separation of two superfamilies, the Astacoidea (Cambaridae and Astacidae) in the northern hemisphere and the Parastacoidea (Parastacidae) in the southern hemisphere (Crandall and Buhay, 2008). Totalling more than 600 species, freshwater crayfish are common, widespread animals native to all continents except Africa (Crandall and Buhay, 2008; Hobbs, 1988).

Given that freshwater crayfish are common, widespread and are known to act as predators of amphibians, here we review predator–prey interactions between the two. We begin by reviewing instances of freshwater crayfish predation on potentially toxic amphibians as documented in the literature. Given that many amphibians exhibit varying degrees of unpalatability and/or toxicity, we sought to clarify the abilities of these predators to withstand toxins. Finally, we describe the breadth of amphibian toxin consumptive ability across their phylogenetic diversity and discuss the evolution of this trait. Developing such an understanding may assist in the evidence-based management of introduced crayfish and permit evaluation of the impact on resident amphibian fauna.

2. Methods

2.1. Literature search methodology

We searched the literature for records of crayfish predation on amphibians by performing database searches using Summon®, Google Scholar® and Web of Knowledge® with a particular focus on papers that studied reportedly unpalatable amphibians. Major keywords used included amphibian, crayfish, palatability, predation, tadpoles and toxic. The literature reviewed includes research conducted in Europe, North America and Australia, although this was not an inclusion criterion but rather a happenstance of the available literature.

2.2. Definition of palatability and toxicity

Gunzburger and Travis (2005) reviewed 142 articles on predator-amphibian prey interactions and suggest that despite unpalatability being widely cited as anti-predator defence mechanisms for amphibian eggs and larvae, eggs and tadpoles are rarely found unpalatable. This review included three papers that examined crayfish predators (Formanowicz and Brodie, 1982; Gamradt and Kats, 1996; Ward and Sexton, 1981). Prey was only considered to be unpalatable if it was either always rejected or eaten once and rejected thereafter; this was a very conservative definition of unpalatability (Gunzburger and Travis, 2005). As such, in some instances amphibians were classified as palatable, in contrast to the authors whom conducted the research and themselves concluded that amphibians were unpalatable to certain predators (Gunzburger and Travis, 2005).

The terminology of toxicity and palatability is used inconsistently in the literature, with the terms used interchangeably by some. We defined toxicity as the capacity to cause injury to an organism (Lackie, 2010) and unpalatable as the property of being distasteful and unpleasant and expected this to be reflected in consumption rates. Further, the palatability and toxicity of an amphibian can only really be defined in terms of a single predator species and population.

While some amphibians possess very powerful toxins that are lethal to most predators, others are only mildly or moderately toxic. Though we appreciate that both toxicity and palatability are continuous variables existing on a spectrum, for the purposes of this report palatability was treated as a binomial categorical variable (i.e. palatable or unpalatable). In this review we assessed palatability in terms of the relative rate of consumption because we were particularly interested in predation in terms of potential population regulation. This differs to the approach taken by Gunzburger and Travis (2005), where an amphibian was classified as palatable even if consumed at very low levels. Here, we suggest that, a prey species is significantly palatable to freshwater crayfish if more than 50% of the available prey was consumed, consistent with the definition of a major predator proposed by Portheault et al. (2007) in an assessment of egg and tadpole predators. Evidence of toxicity (i.e. signs of injury or death) has also been described when this was documented in the literature and was treated separately to the assessment of palatability.

We adopted a similar approach to Gunzburger and Travis (2005) in tabulating the research findings with regards to consumption of eggs and tadpoles and have reviewed similar variables. These included predator species, prey species, prey life stages studied, as well as the experimental design which included duration and number of replicates. We also noted the region of study and the status of the crayfish in that region (i.e. native or exotic). Finally, consumption of toxic amphibians was mapped on a phylogenetic tree of crayfish genera to illustrate the potential evolutionary origins of this trait. A phylogenetic tree of freshwater crayfish genera was adapted from a tree constructed by Sinclair et al. (2004) using DNA sequences that were collected from 227 species.

2.3. Statistical analysis – characterising palatability

We conducted a meta-analysis to determine broad influences on palatability. We coded palatability/unpalatability of each published interaction (44 in 17 publications) as '1' and '2' respectively and applied rank-sum tests using STATA data analysis software (version 11) to test a number of hypotheses. We investigated whether the following factors influenced palatability: prey life stage, prey type (anuran or caudate), experimental design (e.g. feeding trial or choice experiment, predator fasting) and the ecological status (native or exotic) of the crayfish predator. A significance level of 0.05 was applied to all statistical tests.

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