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Nonlethal injury caused by an invasive alien predator and its consequences for an anuran tadpole

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Abstract

Nonlethal tail injury resulting from unsuccessful predation attempts is common in anuran larvae and can potentially induce significant fitness costs in terms of survival and growth. We tested the hypotheses that the alien red swamp crayfish, *Procambarus clarkii*, is an important inducer of tail injury in tadpoles of the Iberian spadefoot toad, *Pelobates cultripes*, and that tail damage can have important consequences for the tadpoles' life history and morphology. This was investigated by first estimating frequencies of caudal injury in *P. cultripes* tadpoles in temporary ponds, with and without crayfish. Secondly, we performed a laboratory experiment in which four levels of tail injury frequency were combined with two levels of food availability.

The frequency of tadpoles with damaged tails was higher in ponds with crayfish and the presence of this predator was the strongest predictor of tail injury frequency in a pond. Induced tail loss decreased larval survivorship and affected tail morphology, with injured tadpoles developing deeper tail muscles and shallower tail fins. The magnitude of these effects depended on injury frequency, as well as on food availability. The results suggest that *P. clarkii* is inflicting tail injuries at much higher levels than those occurring before its introduction; these injuries affect tadpole morphology and may induce delayed fitness costs.

Zusammenfassung

Verletzungen des Schwanzes als Folge von erfolglosen Prädationsversuchen, die nicht lethal sind, sind bei Larven der Anuren weit verbreitet und können potenziell zu signifikanten Fitnesskosten in Bezug auf die Überlebensrate und das Wachstum führen. Wir untersuchten die Hypothese, dass der eingewanderte Nordamerikanische Flusskrebs, *Procambrus clarkii*, ein wichtiger Verursacher dieser Schwanzverletzungen bei Kaulquappen des iberischen Messerfußes, *Pelobates cultripes*, ist und dass die Beschädigung des Schwanzes wichtige Konsequenzen für die weitere Entwicklung und die Morphologie der Kaulquappen hat. Dieses untersuchten wir, indem wir als erstes die Häufigkeit der Schwanzverletzungen bei *P. cultripes*, Kaulquappen in ephemeren Teichen mit und ohne Flusskrebs ermittelten. Als zweites führten wir ein Laborexperiment durch, in welchem vier verschiedene Häufigkeiten der Schwanzverletzungen mit zwei verschiedenen Verfügbarkeiten von Nahrung kombiniert wurden.

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Die Häufigkeit von Kaulquappen mit beschädigten Schwänzen war in den Teichen größer, in denen Flusskrebse vorhanden waren, und die Anwesenheit dieser Räuber erlaubte die beste Vorhersage für die Häufigkeit von Schwanzverletzungen in dem jeweiligen Teich. Induzierter Schwanzverlust verminderte die Überlebensrate der Larven und beeinflusste die Morphologie des Schwanzes, da verletzte Kaulquappen tiefere Schwanzmuskeln und flachere Schwanzsäume ausbildeten. Die Größenordnung dieser Effekte hing sowohl von der Häufigkeit der Verletzungen als auch von der Nahrungsverfügbarkeit ab. Die Ergebnisse lassen vermuten, dass *P. clarkii* einen wesentlich höheren Level von Schwanzverletzungen verursacht als vor seiner Einführung gegeben war und dass diese Verletzungen die Kaulquappen in der Morphologie beeinflussen und im weiteren Verlauf zu Fitnesskosten führen können.

Keywords: Unsuccessful predation; Alien crayfish; Tail injury; Tadpoles; Costs

Introduction

Invasions of exotic species are one of the major factors contributing to worldwide amphibian decline (Kats & Ferrer 2003). Freshwater ecosystems are particularly vulnerable to nonindigenous predators, such as crayfish (Hobbs, Jass, & Huner 1989). Crayfish, often successful invaders, can impact native communities across multiple trophic levels and readily prey upon amphibians (Nyström, Svensson, Lardner, Brönmark, & Granéli 2001). Crayfish introductions can then have important ecological consequences for amphibians, since predation is one of the major biotic factors structuring amphibian larval communities (Wilbur 1980).

Amphibian larvae are often found with damaged tails resulting from unsuccessful predation attempts, which can be caused by a wide variety of vertebrate (turtles, salamanders, and newts) and invertebrate (dragonfly and beetle larvae, crayfish) predators (e.g. Morin 1985; Wilbur & Semlitsch 1990; Tejedo 1993; Nyström et al. 2001). Tadpoles continuously exposed to predators are likely to accumulate several injuries. Injury frequencies in natural populations are influenced by predator densities and often also by factors such as the diversity and complexity of microhabitats (Morin 1985; Figiel & Semlitsch 1991).

The highly fragile tail fin which is easily torn by predators, can help tadpoles escape and survive otherwise lethal attacks (Doherty, Wassersug, & Lee 1998; Van Buskirk, Anderwald, Lupold, Reinhardt, & Schuler 2003). In this aspect, predator-induced tail loss in amphibian larvae resembles autotomy, a widespread antipredator strategy involving self-induced release of a body part, which helps animals escape predator attacks (see Maginnis 2006 for a review). Similarly to autotomy, tail loss has an obvious immediate survival benefit, but its potential costs are substantial and include reduced swimming performance and increased energetic expenditure for regenerating damaged tissue (Wassersug & Sperry 1977; Van Buskirk & McCollum 2000). Swimming performance is not only affected by tail length, but also by tadpole morphology, implying an important role of tadpole shape in predator escape abilities. In the presence of predators, many species develop deeper tails, which increase their survival under predation risk, either due to enhanced swimming performance caused by larger tail muscles (McCollum & Leimberger 1997; Teplitsky et al. 2005; Wilson, Kraft, & Van Damme 2005) or by enabling nonlethal ripping of the deep tail fin (Doherty et al. 1998; Van Buskirk et al. 2003). Regeneration following tail loss may also impose a cost because energy previously used for growth and development is then diverted to repair the damaged tissue (Semlitsch & Reichling 1989). However, the consequences of tail loss seem to depend on injury frequency and severity, as well as on the amount of food available to tadpoles. Injury effects become more pronounced when energy is limited (Parichy & Kaplan 1992).

In the Southwest of the Iberian Peninsula, the Iberian spadefoot toad (*Pelobates cultripes*) often coexists with the invasive red swamp crayfish (*Procambarus clarkii*). This invasive crayfish was introduced in this area, previously devoid of freshwater crayfish, in the early-1970s (Gutiérrez-Yurrita & Montes 1999). It is an active predator of *P. cultripes* tadpoles (Cruz & Rebelo 2005), which can inflict tail injury in mesocosms (Nunes, pers. obs.). Furthermore, it typically consumes and damages aquatic macrophytes, which might reduce periphyton biomass, an important food source for tadpoles (Gutiérrez-Yurrita & Montes 1999; Nyström et al. 2001). *P. cultripes* breeds mostly in temporary ponds that lack fish and other large aquatic predators, but which *P. clarkii* is able to colonize (Cruz & Rebelo 2007). Cruz, Rebelo, & Crespo (2006) showed that, nowadays, the probability of a water body being used as a breeding site by *P. cultripes* is significantly reduced by *P. clarkii*'s presence.

The aim of this study was two-fold. First, we assessed the importance of *P. clarkii* as a tail injury agent on free-living tadpoles, by comparing frequencies of tadpoles with tail damage in ponds with and without *P. clarkii* in south-western Spain. Secondly, we experimentally manipulated frequency of tail injury and food availability in the laboratory, in order to assess survival, growth and development costs of tail damage for *P. cultripes* tadpoles. This integrated approach allowed us to consider a large number of factors that should be addressed in a field study and, at the same time, look into interactions that are often difficult to establish in complex systems but that can easily arise in a controlled laboratory setting.