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Arthropod predation in a dendrobatid poison frog: does frog life stage matter?

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ABSTRACT

Frogs in the family Dendrobatidae are well known for their conspicuous colors and variable alkaloid-based chemical defenses. The aposematic coloration in dendrobatid frogs appears to deter predators with color vision, but relatively little is known about how these frogs are protected and their defenses are perceived by non-color vision dominated predators. The neotropical bullet ant *Paraponera clavata* and the red-legged banana spider *Cupiennius coccineus* are predators that avoid adults of the dendrobatid *Oophaga pumilio*, but readily consume non-toxic frogs. Juvenile *O. pumilio* possess the same warning coloration as adult *O. pumilio*, but may be more palatable given that they have lower quantities of defensive chemicals. This may provide juvenile *O. pumilio* protection from color-sighted predators, while leaving them susceptible to predators that use chemoreception. To test this hypothesis, we presented juveniles and adults of both *O. pumilio* and the non-chemically defended frog *Craugastor bransfordii* to bullet ants and banana spiders. Both bullet ants and banana spiders preyed upon *C. bransfordii* significantly more than on *O. pumilio*. Adult and juvenile *C. bransfordii* experienced similar predation rates by both predators. The life stage of *O. pumilio* significantly predicted predation by bullet ants, with juveniles being consumed significantly more often than adults. However, the life stage of *O. pumilio* did not predict predation by banana spiders, as no adults or juveniles were consumed. Our study provides evidence that bullet ants can detect differences in chemical defenses between juvenile and adult *O. pumilio*, resulting in differential predation on the more palatable juvenile frogs. The avoidance of both adults and juveniles by *C. coccineus* suggests the alkaloids in *O. pumilio* act as an effective chemical deterrent to banana spiders, regardless of quantity. Overall, our results suggest that differences in alkaloid defenses among life stages in *O. pumilio* correspond to differences in relative palatability to at least one arthropod predator.

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1. Introduction

The ability to avoid predation is fundamental to the survival of all prey, a characteristic that is evident in the tremendous diversity of defensive adaptations present among organisms. Many defensive adaptations are structural, physically discouraging predators from consuming prey (e.g., spiny palms, caterpillar bristles, porcupine quills), whereas others are based upon behavior, coloration, and/or defensive chemicals (Ruxton et al., 2004; Toledo et al., 2011). Organisms that exhibit coloration similar to their environment are generally considered cryptic, and rely on being undetected by predators for protection (Ruxton et al., 2004; Cooper et al., 2008). Some organisms utilize conspicuous signals (e.g., color, auditory, chemical) as an advertisement of their unpalatability, or toxicity, to potential predators, an evolutionary adaptation known as aposematism (Ruxton et al., 2004; Weldon et al., 2015; Weldon and Burghardt, 2015).

Brightly colored frogs in the family Dendrobatidae (poison frogs) represent a large group of organisms that utilize conspicuous colors/patterns to advertise the presence of their alkaloid-based chemical defenses to natural predators (Summers and Clough, 2001; Saporito et al., 2012). Numerous studies have provided evidence that dendrobatid coloration functions as an effective warning signal and deterrent to avian predators, which use color vision to detect prey (e.g., Darst and Cummings, 2006; Darst et al., 2006; Saporito et al., 2007a; Noonan and Comeault, 2009; Willink et al., 2013; Paluh et al., 2015; however, see Alvarado et al., 2013).

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However, organisms not always considered in the discussion of aposematic prey, such as snakes and arthropods, may also represent important natural predators of dendrobatids (Brodie and Tumbarello, 1978; Fritz et al., 1981; Szelistowski, 1985; Gray et al., 2010; Santos and Cannatella, 2011; Lenger et al., 2014; Stynoski et al., 2014a,b). It is currently unclear how these predators, especially arthropods that use mechano- and chemoreception for prey capture, perceive and respond to chemical defenses of dendrobatids.

Aposematic dendrobatids possess a large diversity of skin alkaloids that are sequestered from a diet of alkaloid-containing arthropods (for review, see Saporito et al., 2009) and are stored in dermal poison glands (Neuwirth et al., 1979; Saporito et al., 2010a). The composition of these defenses is largely dependent on the availability of alkaloid-containing arthropods and has been shown to vary among species, individuals, between sexes, and among life stages (Saporito et al., 2007b, 2012; Stynoski et al., 2014a). In the dendrobatid frog *Oophaga pumilio*, poison gland number and size increases with frog size, and adults contain significantly more and larger-sized glands when compared to juveniles (Saporito et al., 2010a). As a function of differences in diet, and in certain cases gland morphology, individuals of *O. pumilio* differ in the type, number, and quantity of alkaloid defenses (Saporito et al., 2012). In particular, tadpole and juvenile *O. pumilio* contain much smaller quantities of alkaloids than adults (see Daly et al., 2002; Stynoski et al., 2014a), potentially making them more palatable to predators and prone to higher predation. Previous studies on chemically defended anurans that manufacture defenses have demonstrated that differences in ontogenetic stages and gland morphology play an important role in the defense against predators, where some life stages are more protected than others (Formanowicz and Brodie, 1982; Lawler and Hero, 1997; Weldon and Carroll, 2007; Hayes et al., 2009). It is therefore possible that risk of predation will also differ among the life stages of dendrobatid frogs.

Like frogs, chemically defended invertebrates that sequester chemical defenses from dietary sources also exhibit variation in defense (Bowers, 1993; Opitz and Müller, 2009; Savitzky et al., 2012). In some cases, this variation can result in a 'palatability spectrum' of prey, whereby individuals exhibit differences in palatability that are perceived by natural predators (Brower et al., 1968). In these cases, predators are able to detect differences in palatability and preferentially consume prey with fewer chemical defenses (Brower et al., 1968; Bowers, 1993; Saporito et al., 2012). Arthropod predators that largely use chemoreception in prey detection may be especially sensitive to variation in alkaloid defenses, which could result in differential predation upon life stages of *O. pumilio*.

The neotropical bullet ant, *Paraponera clavata* (Formicidae), and the red-legged banana spider, *Cupiennius coccineus* (Ctenidae), have both been experimentally shown to reject most adult *O. pumilio*, despite consuming other non-toxic leaf-litter frogs as prey (Fritz et al., 1981; Szelistowski, 1985). Recently, these same predators have also been shown to avoid alkaloid-containing tadpoles of *O. pumilio*, but to a much lesser extent when compared to adults (Stynoski et al., 2014a,b). Fritz et al. (1981) and Szelistowski (1985) suggested that bullet ants and banana spiders, respectively, might use contact chemoreception to determine the palatability of prey. Although bullet ants and banana spiders appear to exhibit differences in the degree of predation between tadpole and adult *O. pumilio* (Fritz et al., 1981; Szelistowski, 1985; Stynoski et al., 2014a,b), it is not known how they respond to juveniles of *O. pumilio*, which have lower levels of chemical defenses when compared to the adult life stage (Stynoski et al., 2014a).

Therefore, in the present study, we examined differences in predation upon juveniles and adults of the dendrobatid frog *O. pumilio* as compared to the non-chemically defended leaf-litter frog *Craugastor bransfordii* by two different arthropod predators, the bullet ant, *P. clavata* and the red-legged banana spider, *C. coccineus*. If chemical defenses in *O. pumilio* effectively deter arthropod predation, we expect to see lower predation rates on *O. pumilio* when compared to *C. bransfordii*. Furthermore, if bullet ants and banana spiders are able to detect differences in chemical defenses (i.e., differences in palatability) between juvenile and adult *O. pumilio*, then we expect juveniles to experience higher predation rates when compared to adults.

2. Materials and methods

2.1. Sample and data collection

The present study was conducted at La Selva Biological Research Station in north-eastern Costa Rica (10° 26′ N, 83° 59′ W) during two different time periods, representing two independent experiments. We conducted the first experiment from 22 June 2011 to 20 July 2011 and the second experiment from 06 June 2015 to 01 July 2015.

O. pumilio is a conspicuously colored, chemically defended, diurnal frog species, whereas *C. bransfordii* is a cryptically colored, non-chemically defended, diurnal frog. Both species are similar in size and are commonly found in the same leaf litter habitats at La Selva (Guyer and Donnelly, 2005).

2.2. Experiment 1: red-legged banana spider predation

We collected 40 *O. pumilio* and 40 *C. bransfordii* from the leaf litter throughout the main trail system at La Selva. For each species, half of the frogs were juveniles (snout–vent length (SVL) < 18.0 mm; although 19 mm SVL is the cut-off size between juveniles and adults of *O. pumilio*, we chose to only consider frogs as juveniles if they were < 18 mm and did not use any frogs that were between 18 and 19 mm) and the other half were adults (SVL > 19.0 mm). Equal numbers of male and female adult *O. pumilio* were used to control for potential differences in defenses between sexes (see Saporito et al., 2010b). Male frogs were identified by the presence of a darkened throat patch (Donnelly, 1989). We collected frogs during the day and housed them individually in plastic bags with a small amount of leaf litter at ambient temperature for no more than three days prior to an experiment.

The red-legged banana spider *C. coccineus* actively hunts at night on vegetation, and retreats during the day to hiding places in the same vegetation (Barth et al., 1988a). We conducted predation trials with 80 individual spiders found along the Camino Experimental Sur Trail between 0 m and 550 m and between 1900 h and 0000 h. We located the spiders on tree trunks or leaves, and identified the species and sex of each individual (Barth et al., 1988a). Female *C. coccineus* were more commonly encountered, and therefore we conducted the majority of the trials with female spiders ($n = 79$), and only one trial with a male spider. We did not perform trials in rainy conditions to avoid the potential confounding effects on spider behavior (Barth et al., 1988b). *C. coccineus* often remain in the same location over time, and therefore we flagged the location of each spider following each trial and did not use the same individual in more than one experimental trial.

For each trial, we presented a randomly chosen frog to a single spider while holding the base of a back leg of the frog with a pair of 26 cm long forceps (similar to the methods of Fritz et al., 1981). To avoid the possibility of alkaloid contamination during trials with *C. bransfordii*, we used one pair of forceps for presenting *O. pumilio* and a different pair for *C. bransfordii*. Once secured by the forceps, each frog was positioned upright, facing the spider, and was slowly moved toward the spider until about 1 cm of distance remained between the frog and the spider. If the spider did

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