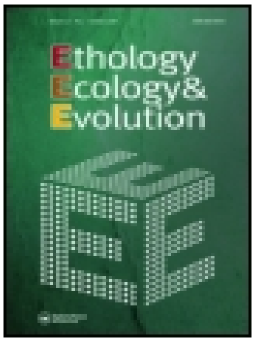

Ethology Ecology & Evolution

ISSN: (Print) (Online) Journal homepage: https://www.tandfonline.com/loi/teee20

Has the indestructible insect met its match? Velvet ants as prey to bufonid toads

Ciara J. Mergler & Brian G. Gall

To cite this article: Ciara J. Mergler & Brian G. Gall (2020): Has the indestructible insect met its match? Velvet ants as prey to bufonid toads, Ethology Ecology & Evolution, DOI: 10.1080/03949370.2020.1789747

To link to this article: https://doi.org/10.1080/03949370.2020.1789747

Ethology Ecology & Evolution, 2020
https://doi.org/10.1080/03949370.2020.1789747

Has the indestructible insect met its match? Velvet ants as prey to bufonid toads

CIARA J. MERGLER and BRIAN G. GALL[*]

Department of Biology, Hanover College, 517 Ball Drive, Hanover, IN 47243, USA

Received 30 January 2020, accepted 26 May 2020

Velvet ants are a group of parasitoid wasps that are well-known for a suite of defensive traits including bright coloration, a thick exoskeleton, and a painful sting. Previous experiments have demonstrated that while virtually all potential predators avoid velvet ants, toads (family Bufonidae) may be able to prey upon them. We conducted a series of trials to determine whether American (*Anaxyrus americanus*) and Fowler's toads (*Anaxyrus fowleri*) prey upon velvet ants. Toad responses toward velvet ants were variable, ranging between complete avoidance, consumption and regurgitation, and consumption and retention. In total, 12 out of 22 trials resulted in the toads consuming a velvet ant. Of these, velvet ants were either regurgitated unharmed (n = 8) or retained (n = 4). In general, there were no significant differences in responses toward velvet ants between American and Fowler's toads. Due to a rapid prey acquisition and their unique foraging behavior, toads present the most likely predator to velvet ants. Our results indicate that toads have the capacity to consume and retain female velvet ants. However, female velvet ants demonstrate the ability to endure upwards of 20 min inside the stomach of a toad and survive.

KEY WORDS: predation, predator-prey, anti-predator, Mutillidae, Bufonidae.

INTRODUCTION

Predation is one of the most powerful forces acting upon species, placing selective pressure on the evolution of organisms' physiology and behavior (Lima & Dill 1990; Brodie et al. 1991). The intense relationship between predator and prey revolves around a dangerous game of life or death, leading to coevolution among some species (Marrow et al. 1992). The selective pressures placed upon prey species by their predators have led to the evolution of a varied assortment of defense mechanisms including toxins (Casewell et al. 2013), physical armaments (Sugiura & Yamazaki 2014), and escape behaviors (Harrold 1982). While these defense mechanisms evolved to prevent predation and therefore increase survivorship, predators face a simultaneous need to eat for the sake of survival (Lima & Dill 1990). This places selective pressures upon predatory species, leading to the evolution of counter-defense

---

[*] Corresponding author: Brian G. Gall, Department of Biology, Hanover College, 517 Ball Drive, Hanover, IN 47243, USA (E-mail: gall@hanover.edu).

mechanisms and behaviors (Brodie & Brodie 1990). Even the most well-defended species of prey are known to have specialized predators that coevolved alongside them and are capable of contending with highly evolved antipredator defenses (Needham & Westfall 1954; Brodie & Brodie 1990; Fathinia et al. 2015).

One organism that is notorious for its efficient and well-developed suite of antipredator defenses is the velvet ant (Hymenoptera Mutillidae). Velvet ants are a family of solitary parasitoid wasps in which the females are apterous and spend much of their time foraging for bee and wasp host nests in which to deposit their eggs (Mickel 1928). Given their flightlessness, bright coloration, and active diurnal behavior, female velvet ants are likely to be the prime targets for predators. However, these organisms have evolved an entire suite of highly effective antipredator defense mechanisms (Schmidt & Blum 1977; Vitt & Cooper 1988; Gall et al. 2018). For example, female velvet ants are armed with a venomous sting that delivers a notoriously painful venom (Schmidt & Blum 1977), thus earning them common names such as “cow killer”. Paired with this extremely potent sting are a plethora of other defenses, including striking aposematic coloration (red, orange, yellow, or white), high-pitched stridulatory sounds which are produced by the contraction of abdominal segments, the release of chemical alarm cues from the mandibular glands, and an extremely hard and slippery exoskeleton (Mickel 1928; Schmidt & Blum 1977). The combination of so many defense mechanisms indicates that historical selective pressure has been intense upon velvet ants, and yet little is known about the relationship between velvet ants and potential predators.

Few studies have previously examined interactions between velvet ants and various insectivorous predators (Vitt & Cooper 1988; Manley & Sherbrooke 2001; Gall et al. 2018). Although the species tested were predominantly insect predators and known for consuming prey of similar size as velvet ants, virtually all interactions resulted in a lack of consumption and even outright avoidance of the velvet ants (Manley & Sherbrooke 2001; Gall et al. 2018). For example, skinks, with stout jaws and a voracious nature, only managed to consume velvet ants after multiple failed attempts in which the velvet ant would likely escape in the wild (Vitt & Cooper 1988). Similarly, horned lizards avoided three aposematic velvet ant species, and consumed only the drab *Dasymutilla dilucida* which is a small species that mimics ants (Manley & Sherbrooke 2001). The only predator to successfully retain an aposematic velvet ant in a single interaction was an American toad (Gall et al. 2018).

Many toad species (family Bufonidae) are known for eating a wide diversity of insects of varying sizes (Kirkland 1904; Caldwell & Vitt 1999; Quiroga et al. 2009), and are even reported consuming venomous and potentially dangerous prey items such as scorpions (Jared et al. 2020). Toads are predominately nocturnal, yet it is not uncommon for toads to be found active during the day (Hamilton 1955; Carey 1978; Smits 1984). While toads often prefer habitats consisting of denser foliage (Griffin & Case 2001), they are also often found among the loose sandy soil that is favored by velvet ants (Griffin & Case 2001; Boehme et al. 2012). Furthermore, we routinely observe all species used in this study active together during field excursions in the early morning during May and June (B.G. Gall personal observation). This overlap in habitat use indicates a potential for interaction between velvet ants and toads, yet this interaction may not occur frequently enough to place pressure on the evolution of toad-specific antipredator defense mechanisms within velvet ants. Given this potential for interaction and preliminary results indicating a potential of toads preying upon velvet ants (Gall et al. 2018), toads were selected to conduct further predation trials. These trials tested the toad as a potential predator by observing facilitated interactions between the species, focusing on how toads responded when exposed to velvet ants and how toad predation behavior functions against velvet ant antipredator mechanisms.

METHODS

Animal collection and housing

American and Fowler's toads were collected on rainy nights between 22:00 and 03:00 hr from roads around Hanover, Indiana. Toads were housed individually in 2.5 gal aquaria with a layer of damp *Sphagnum* sp. moss (Hummert International, Earth City, MO) that was misted with dechlorinated water every other day. Toads were fed 2–3 commercially available crickets approximately 2–3 times for 1 week. The tanks were maintained at 18 °C on a 12 hr day/night cycle. Female velvet ants (*Dasymutilla occidentalis*) were collected from a privately owned manicured garden in Hanover, Indiana. Velvet ants were housed individually in plastic containers (21 × 13 × 8 cm) with a layer of fine sand and various rocks and leaves to provide shelter. Velvet ants were fed pieces of fresh fruit every other day. The tanks were maintained at 25 °C on a 12 hr day/night cycle. Seven days prior to trials, food was withheld from the toads.

Experimental set-up

Experimental trials were conducted in a plastic chamber identical to the velvet ants' housing containers. Each experimental trial consisted of exposing a toad to a female velvet ant followed by a control cricket. The velvet ant and cricket exposure were separated by a 2 hr between-treatment period. The inside of the chamber was empty and was rinsed thoroughly with deionized water before every trial. A toad was then randomly selected and placed in the center of the test chamber. A 60 sec acclimation period was then initiated. A velvet ant was randomly selected and was removed from its container by gently corralling it into an empty plastic cup; this method prevented exposing the velvet ant to a simulated predation event. The velvet ant was then weighed using a digital scale (Mettler Toledo B204-S) and was placed in the test chamber approximately on the opposite side of the container from the toad. A 30 min trial then commenced, during which interactions between the toad and velvet ant were recorded by an observer and a video camcorder (Cannon Vixia HF G20). In addition to general observations, we recorded potential predation or avoidance behaviors exhibited by the toads. Predation behaviors included the tendency to orientate in the direction of and to strike at the velvet ant. Avoidance behaviors included any instance in which a toad would back away or turn away from the velvet ant. An orientation was recorded if the toad exhibited a recognition of the velvet ant, most commonly by physically turning to face the potential prey item and preparing to lunge. In order for a movement to be considered a strike, the toad had to display a lunge in the immediate direction of the velvet ant. At the conclusion of the trial, the velvet ant was returned to its home container (if not consumed). The toad was then weighed and returned to its home container. After a 2 hr acclimation period in their home tank, the toad was tested again with a control cricket of similar size to the velvet ant. If the toad had struck or consumed a velvet ant, they were monitored frequently for the following 4 days for signs of regurgitation or distress. Toads were never reused in experimental trials. Due to limited availability, velvet ants that were not struck at or consumed in a trial may have been retested > 24 hr following experimentation. With one exception, velvet ants that had been eaten and regurgitated were allotted a 7-day period before being re-tested.

Following experimental trials, the toads were toe-clipped to ensure they would not be reused in trials and were then released at the site of capture. The velvet ants were released

Table 1.

Compiled results regarding the consumption of velvet ants and crickets by both American (*Anaxyrus americanus*) and Fowler's (*A. fowleri*) toads.

Toad sp.	Prey sp.	# Consumed	# Not consumed	% Consumed	% Not consumed
American	Velvet ant	3	8	27	73
	Cricket	9	2	82	18
Fowler's	Velvet ant	1	10	9	91
	Cricket	11	0	100	0

back into the manicured garden from which they were collected. Toads that consumed neither a velvet ant nor a cricket were excluded from final analyses. Two American toads failed to consume the cricket during control trials, however these two specimens previously consumed velvet ants; as such, these data were included within analysis (Table 1).

Statistical analysis

We compared the number of orientations on velvet ants between American and Fowler's toads using a repeated-measures two-way ANOVA with species (American or Fowler's) and prey type (velvet ant or cricket) as the two main effect factors. When a significant interaction term was identified, Tukey's post-hoc comparisons were conducted. We also compared the number of strikes on velvet ants between American and Fowler's toads using a repeated-measures two-way ANOVA with species (American or Fowler's) and prey type (velvet ant or cricket) as the two main effect factors. Three 2 × 2 contingency tables were conducted with toad species and each stage of the predation event (swallow, regurgitate, or consume) as the categories to evaluate the relationship between the likelihood of each toad species to perform each of these events with velvet ants. Finally, a *t*-test compared the latency to regurgitate a velvet ant between American and Fowler's toads.

RESULTS

Out of 22 total interactions, nearly all toads ($n = 21$) displayed an orientation in a velvet ant's direction and over half of the trials ($n = 12$) resulted in a toad striking at and attempting to consume a velvet ant (Table 1). Every toad that attempted to strike a velvet ant also ultimately swallowed a velvet ant. After initially swallowing a velvet ant, toads exhibited an array of behaviors indicative of distress, such as scratching at their stomach and mouth, sporadically extending and retracting their limbs, or attempting to regurgitate the velvet ant. Of the toads that swallowed a velvet ant, four successfully retained and fully consumed a velvet ant; the remaining toads ($n = 8$) regurgitated their velvet ants (Table 2). Velvet ants that were swallowed spent an average of 15 min within the stomachs of the toads, with the longest time being just under 21 min (Table 3). When regurgitated, the velvet ants were encased in a film of mucous and curled in upon themselves. While immobile immediately after regurgitation, each velvet ant was actively extending and retracting their sting, indicating envenomation is likely continuous while in the stomach of the toad. All velvet ants

Table 2.

Average mass (± SD) of all toad specimens used in trials. Predation events in which the velvet ant (VA) were initially struck at and swallowed by the toad were recorded. After being swallowed, the velvet ant was either regurgitated or consumed and retained by the toad.

Toad species	Toad mass (± SD)	# VA Swallow	# VA Regurgitate	# VA Consume
American	49.35 ± 2.87	8	5	3
Fowler's	30.54 ± 12.41	4	3	1

Table 3.

Data from all trials (n = 22) detailing the number of trials a velvet ant were tested in as well as the resulting conclusion of the predation event.

Velvet ant ID	# Trials tested	# Trials ignored	# Trials eaten	Mean time in predator (sec)	Total time in predator (sec)	Regurgitated [Retained]
DOF-1	1	0	1	consumed	consumed	0 [1]
DOF-4	3	0	3	784 ± 337	2452	3 [0]
DOF-5	5	4	1	754	754	1 [0]
DOF-6	4	2	2	850 ± 578	1700	2 [0]
DOF-7	3	1	2	978	978	1 [1]
DOF-8	4	2	2	1148	1148	1 [1]
DOF-9	2	1	1	consumed	consumed	0 [1]

that were regurgitated survived unharmed and appeared to return to normal activities between 3 and 24 hr after regurgitation.

We found no significant difference between the number of orientations on velvet ants between *A. americanus* and *A. fowleri* ($F_{[1,43]} = 0.31$, $P = 0.58$, Fig. 1). There was a significant main effect of prey type on the tendency of toads to orient ($F_{[1,43]} = 4.3$, $P = 0.052$), with toads performing more orientation behaviors when a velvet ant was provided as compared to a cricket (Fig. 1). There was no interaction effect between toad species and prey type ($P = 0.88$). A repeated-measures two-way ANOVA found no significant main effect of species ($P = 0.33$), but did find a significant main effect of prey type ($P = 0.01$) on the number of strikes exhibited by toads. However, there was also a significant interaction between species (American vs Fowler's) and prey type (velvet ant vs cricket) on the number of strikes ($F_{[1,43]} = 5.33$, $P = 0.032$, Fig. 2). In this case, American toads responded similarly to both prey types (Fig. 2). However, Fowler's toads exhibited more strikes on crickets compared to American toads ($P = 0.02$, Fig. 2). Fowler's toads were also more likely to strike at a cricket compared to a velvet ant ($P = 0.002$, Fig. 2). We found no significant difference in the tendency to swallow velvet ants between American and Fowler's toads (df = 1, $\chi^2 = 2.93$, $P = 0.08$). There was no significant difference in the tendency of American or Fowler's toads to regurgitate velvet ants (df = 1, $\chi^2 = 1.22$, $P = 0.26$) or to consume velvet ants (df = 1, $\chi^2 = 0.79$, $P = 0.38$). Finally, we found no significant difference in latency to regurgitate

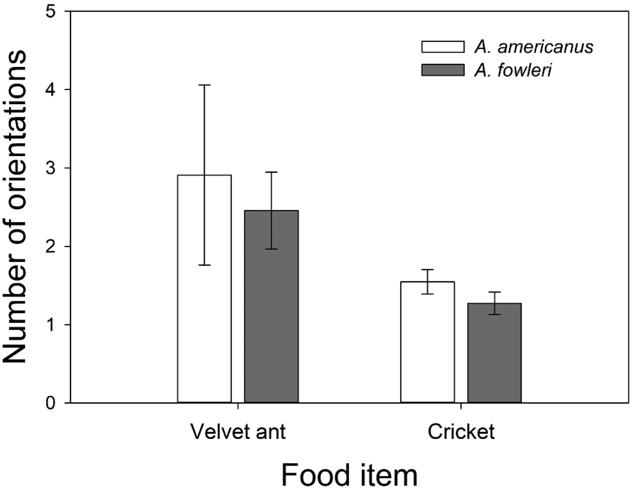

Fig. 1. — Mean (± SE) number of orientation behaviors on velvet ants or crickets by American toads (white bars) and Fowler's toads (gray bars). Toads, regardless of species, performed more orientation behaviors toward velvet ants than toward crickets ($P = 0.052$). There was no effect of toad species on the number orientations ($P = 0.58$) and no significant interaction effect between toad species and prey type ($P = 0.88$).

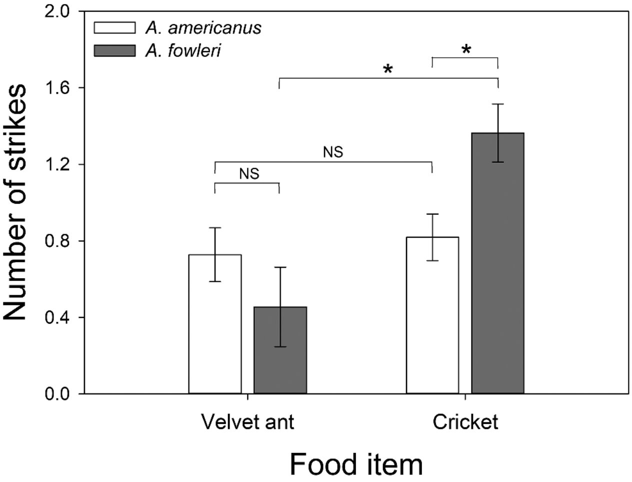

Fig. 2. — Mean (± SE) number of strikes upon velvet ants and crickets by both American toads (white bars) and Fowler's toads (gray bars). A significant interaction ($P = 0.032$) between toad species and prey type indicates that Fowler's toads exhibited more strikes on crickets compared to American toads and struck at velvet ants less often relative to crickets (* indicates $P \leq 0.02$, NS indicates $P > 0.23$).

velvet ants between American ($\bar{x} = 950 \pm 343$) and Fowler's toads ($\bar{x} = 728 \pm 249$) (df = 20, $t = 0.97$, $P = 0.19$).

DISCUSSION

Velvet ants are notorious for a suite of defenses which render them nearly invulnerable to predation (Vitt & Cooper 1988; Gall et al. 2018), and previous studies have demonstrated that these antipredator mechanisms are highly effective against numerous birds, small mammals, and reptiles (Gall et al. 2018). However, the results of our study suggest that carnivorous toads have the potential to be an important predator of velvet ants, with over half of all interactions leading to a toad swallowing the velvet ant and 18% of velvet ants being successfully consumed. Toads present an unexpected but ideal predator against the suite of defenses employed by velvet ants, and appear pre-adapted to avoiding several of the velvet ant's most effective antipredator defenses. First, toads strike at velvet ants with their everted tongue, drawing the velvet ant into the mouth and swallowing it near instantaneously (Wells 2007). This process occurs so rapidly that velvet ants do not appear to be capable of stridulating before being completely swallowed; we never observed a velvet ant stridulate after being struck by a toad. More importantly, this rapid capture and subjugation prevent the female velvet ant from employing the powerful sting as a defense. In contrast with toads, all other potential vertebrate predators (lizards, birds, small mammals) grasp their prey with the jaws/beak which requires the predator to manipulate the velvet ant within the mouth before it is swallowed (Vitt & Cooper 1988; Manley & Sherbrooke 2001; Gall et al. 2018). This delay enables velvet ants to stridulate and sting the predator while in the mouth which invariably leads to their release and escape. Even in the event of a sting, many toad species have demonstrated high levels of resistance to other venomous prey items, including scorpions and bombardier beetles (Dean 1980; Jared et al. 2020), indicating a likelihood for increased success against the velvet ant's notorious sting.

In response to velvet ants, both species of toads exhibited more orientation behaviors than on crickets, which may indicate a hesitancy to strike at these dangerous prey or may result from velvet ants being more active and conspicuous. In our experiment, American toads appear more willing to strike at velvet ants in comparison to Fowler's toads (72% vs 36%). Fowler's toads also displayed a tendency to strike at crickets more often than American toads, largely due to Fowler's toads often requiring multiple strikes before successfully swallowing the crickets. This difference in prey acquisition is likely the result of a distinct size difference between the two toad species; Fowler's toads were ~ 40% smaller compared to American toads. Previous research has demonstrated a positive correlation between body mass and prey mass among Bufonidae species (Quiroga et al. 2009), indicating that larger toads are more likely to strike at and consume larger prey (Caldwell & Vitt 1999; Quiroga et al. 2009). Given that the crickets used in control trials were comparable in size to the velvet ants, the apparent hesitancy for Fowler's toads to strike at a common prey item such as a cricket could indicate that a large cricket – or a velvet ant – is in the higher range of acceptable prey mass among Fowler's toads, and therefore a less acceptable prey item for this species.

American toads did not demonstrate a similar hesitancy to strike at velvet ants and, given their larger size, this indicates a higher chance of consumption. Furthermore, preliminary observations also indicate that American toads may be unable to learn to recognize the aposematic coloration of these velvets ants and therefore avoid them. Other major predators that rely heavily on sight, such as birds, are known to react negatively to aposematic coloration on snakes (Brodie 1993; Brodie

& Janzen 1995) as well as aposematic coloration on velvet ants (Gall et al. 2018). While anurans have the retinal cones necessary for color vision and are likely to see color (Jaegar & Hailman 1976a, 1976b), their predation behavior focuses predominantly upon the movement of prey (Hatle & Salazer 2001). It is probable that the toad's lack of regard for coloration ultimately results in predation behavior that is generally apathetic towards aposematic coloration in potentially dangerous prey. In fact, there was no difference in the latency for toads to strike at and swallow velvet ants in comparison to crickets. Pairing the toad's rapid response to prey with its known prey acquisition behaviors seems to indicate that toads are notorious "strike first, ask questions later" predators in regards to potentially dangerous prey.

The velvet ant's utilization of defenses such as aposematic coloration, stridulation, and hard exoskeleton is most effective immediately prior to consumption. Such behaviors are effective against predators that have prolonged handling periods or those that masticate prey (Schmidt & Blum 1977; Vitt & Cooper 1988; Manley & Sherbrooke 2001; Gall et al. 2018). While toads are uniquely situated to avoid these pre-consumption defenses, velvet ants possess other defenses which allow for their escape and ultimate survival after consumption. Velvet ants enter the stomach still alive and continually employ the use of their sting. Of the toads that swallowed a velvet ant, 91% displayed behaviors indicative of distress, including repeated scratching at the facial or abdominal areas, full-body shudders, and attempted regurgitation. Previous trials have demonstrated similar behavior in response to interaction with and attempted consumption of dangerous prey (Dean 1980; Gall et al. 2018). Exposure to the chemical defenses of insects such as bombardier beetles and velvet ants typically lead to heightened distress and aversion in toads (Dean 1980; Gall et al. 2018). Once the velvet ants were fully regurgitated, they were encased in thick layer of viscous mucus. While the legs and body were immobile, the velvet ant was continually extending and retracting the sting. This repetitious behavior coupled with the apparent distress exhibited by the toads indicates the likelihood of multiple envenomations while inside the toad's stomach.

Previous studies have demonstrated how the suite of defense mechanisms possessed by female velvet ants repel virtually all potential predators. These studies have predominantly focused on the phase of the predator–prey interaction occurring prior to consumption. However, toads have a unique capability of subverting the effectiveness of the velvet ant's pre-consumption defense mechanisms, with some also demonstrating tolerance for the velvet ant's post-consumption defenses. While additional research examining the potential for interaction and outcomes of interactions between toads and velvet ants is warranted, this study demonstrated a successful predation rate of nearly 20%, a dramatically higher percentage relative to previous studies. These interactions indicate that some toads are likely capable of preying upon velvet ants, even in field conditions. It seems that the indestructible insect may have finally met its match.

ACKNOWLEDGEMENTS

Our deepest gratitude and appreciation go to Dr Walter Bruyninckx and Dr Anne-Marie Blancquaert for their careful observance and collection of velvet ants. Without their support, our research on predator–prey interactions involving velvet ants over the past 7 years would not have been possible. We also thank Coach Jim Watts and the Hanover Women's Soccer Team for their assistance in the collection of specimens, and a special thank you to the many friends who were unwillingly dragged from their beds in the middle of the night for the sake of research.

DISCLOSURE STATEMENT

No potential conflict of interest was reported by the authors.

FUNDING

This research was funded by the Hanover College Department of Biology.

ETHICAL STANDARD

Toads were collected according to Indiana's scientific purposes license (permit #19-335). General animal care protocols and limitations of the sample sizes in experiments using vertebrates are based on the "Guide for the Care and Use of Laboratory Animals" published by the National Research Council (2011).

DATA ACCESSIBILITY

All data is available upon request from corresponding author.

AUTHOR CONTRIBUTION

C.J. Mergler and B.G. Gall conceived and designed the experiment. Both authors collected animals and data. C.J. Mergler and B.G. Gall analyzed data. C.J. Mergler wrote the initial draft of the manuscript. Both authors edited and revised the manuscript.

REFERENCES

Boehme NF, Tanner DA, Williams KA, Pitts JP. 2012. Faunal study of velvet ants (Hymenoptera: Mutillidae) and their activity patterns and habitat preference at Ash Meadows National Wildlife Refuge, Nye County, Nevada, USA. Zootaxa. 3587(1):1–45. doi:10.11646/zootaxa.3587.1.1

Brodie ED III. 1993. Differential avoidance of coral snake banded patterns by free-ranging avian predators in Costa Rica. Evolution. 47(1):227–235. doi:10.1111/j.1558-5646.1993.tb01212.x

Brodie ED III, Brodie ED Jr. 1990. Tetrodotoxin resistance in garter snakes: an evolutionary response of predators to dangerous prey. Evolution. 44(3):651–659. doi:10.1111/j.1558-5646.1990.tb05945.x

Brodie ED III, Janzen FJ. 1995. Experimental studies of coral snake mimicry: generalized avoidance of ringed snake patterns by free-ranging avian predators. Funct Ecol. 9 (2):186–190. doi:10.2307/2390563

Brodie ED Jr, Formanowicz DR Jr, Brodie ED III. 1991. Predator avoidance and antipredator mechanisms: distinct pathways to survival. Ethol Ecol Evol. 3(1):73–77. doi:10.1080/08927014.1991.9525390

Caldwell JP, Vitt LJ. 1999. Dietary asymmetry in leaf litter frogs and lizards in a transitional northern Amazonian rain forest. Oikos. 84(3):383–397. doi:10.2307/3546419

Carey C. 1978. Factors affecting body temperatures of toads. Oecologia. 35(2):197–219. doi:10.1007/BF00344732

Casewell NR, Wüster W, Vonk FJ, Harrison RA, Fry BG. 2013. Complex cocktails: the evolutionary novelty of venoms. Trends Ecol Evol. 28(4):219–229. doi:10.1016/j.tree.2012.10.020

Dean J. 1980. Encounters between bombardier beetles and two species of toads (*Bufo americanus, B. marinus*): speed of prey-capture does not determine success. J Comp Physiol A. 135(1):21–50. doi:10.1007/BF00660180

Fathinia B, Rastegar-Pouyani N, Rastegar-Pouyani E, Todehdehghan F, Amiri F. 2015. Avian deception using an elaborate caudal lure in *Pseudocerastes urarachnoides* (Serpentes: Viperidae). Amphibia-Reptilia. 36(3):223–231. doi:10.1163/15685381-00002997

Gall BG, Spivey KL, Chapman JR, Delph RJ, Brodie ED Jr, Wilson JS. 2018. The indestructible insect: velvet ants from across the United States avoid predation by representatives from all major tetrapod clades. Ecol Evol. 8(11):5852–5862. doi:10.1002/ece3.4123

Griffin PC, Case TJ. 2001. Terrestrial habitat preferences of adult arroyo southwestern toads. J Wildl Manage. 65(4):633–644. doi:10.2307/3803014

Hamilton WJ. 1955. Notes on the ecology of the oak toad in Florida. Herpetologica. 11:205–210.

Harrold C. 1982. Escape responses and prey availability in a kelp forest predator-prey system. Am Nat. 119(1):132–135. doi:10.1086/283898

Hatle JD, Salazer BA. 2001. Aposematic coloration of gregarious insects can delay predation by an ambush predator. Environ Entomol. 30(1):51–54. doi:10.1603/0046-225X-30.1.51

Jaegar RG, Hailman JP. 1976a. Ontogenetic shift of spectral phototactic preferences in anuran tadpoles. J Comp Physiol Psychol. 90(10):930–945. doi:10.1037/h0077275

Jaegar RG, Hailman JP. 1976b. Phototaxis in anurans: relation between intensity and spectral preferences. Copeia. (1):92–98. doi:10.2307/1443777

Jared C, Alexandre C, Mailho-Fontana PL, Pimenta DC, Brodie ED Jr, Antoniazzi MM. 2020. Toads prey upon scorpions and are resistant to their venom: A biological and ecological approach to scorpionism. Toxicon. 178:4–7. doi:10.1016/j.toxicon.2020.02.013

Kirkland AH. 1904. Usefulness of the American toad. Chicago (IL): US Government Printing Office.

Lima SL, Dill LM. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Can J Zool. 68(4):619–640. doi:10.1139/z90-092

Manley DG, Sherbrooke WC. 2001. Predation on velvet ants (Hymenoptera: Mutillidae) by Texas horned lizards (*Phrynosoma cornutum*). Southwest Nat. 46(2):221–222. doi:10.2307/3672534

Marrow P, Law R, Cannings C. 1992. The coevolution of predator-prey interactions: ESSS and Red Queen dynamics. Proc R Soc Lond B. 250:133–141.

Mickel CE. 1928. Biological and taxonomic investigations on the mutillid wasps. Bull U S Nat Mus. 143:1–135.

National Research Council. 2011. Guide for the care and use of laboratory animals, 8th ed. Washington (DC): National Academies Press.

Needham JG, Westfall MJ Jr. 1954. The manual of the dragonflies of North America (Anisoptera). Los Angeles (CA): University of California Press.

Quiroga L, Sanabria E, Acosta J. 2009. Size- and sex-dependent variation in diet of *Rhinella arenarum* (Anura: Bufonidae) in a wetland of San Juan, Argentina. J Herpetol. 43 (2):311–317. doi:10.1670/07-117R2.1

Schmidt JO, Blum MS. 1977. Adaptations and responses of *Dasymutilla occidentalis* (Hymenoptera: Mutillidae) to predators. Entomol Exp Appl. 21(2):99–111. doi:10.1111/j.1570-7458.1977.tb02663.x

Smits AW. 1984. Activity patterns and thermal biology of the toad *Bufo boreas halophilus*. Copeia. (3):689–696. doi:10.2307/1445150

Sugiura S, Yamazaki K. 2014. Caterpillar hair as a physical barrier against invertebrate predators. Behav Ecol. 25(4):975–983. doi:10.1093/beheco/aru080

Vitt LJ, Cooper WE. 1988. Feeding responses of skinks (*Eumeces laticeps*) to velvet ants (*Dasymutilla occidentalis*). J Herpetol. 22(4):485–488. doi:10.2307/1564347

Wells KD. 2007. The ecology & behavior of amphibians. Chicago (IL): Universtiy of Chicago Press.