Canadian Journal of Zoology

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Journal:	<i>Canadian Journal of Zoology</i>
Manuscript ID	cjz-2018-0228.R2
Manuscript Type:	Article
Date Submitted by the Author:	04-Oct-2018
Complete List of Authors:	Venable, Cameron; Pennsylvania State University, Biology; Langkilde, Tracy; The Pennsylvania State University
Is your manuscript invited for consideration in a Special Issue?:	Not applicable (regular submission)
Keyword:	Invasive Prey, Pyramid Ant, <i>Dorymyrmex bureni</i> , Red Imported Fire Ant, <i>Solenopsis invicta</i> , Eastern Fence Lizard, <i>Sceloporus undulatus</i>

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Lizards display an ontogenetic shift in relative consumption of native and invasive prey

Running header: Consumption of native versus invasive ants

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Manuscript for submission to Canadian Journal of Zoology

Abstract:

Interactions between invasive prey and native predators can provide an opportunity to better understand predator-prey dynamics, and how these may change through ontogeny. Fence lizards (*Sceloporus undulatus* (Bosc and Daudin in Sonnini and Latreille, 1801)) are ant specialist, particularly as juveniles. Invasive fire ants (*Solenopsis invicta* (Buren, 1972)) pose a lethal risk to lizards that eat them, especially smaller-bodied juvenile lizards. We examine ontogenetic shifts in lizard consumption of toxic invasive fire ants versus palatable native pyramid ants (*Dorymyrmex bureni* (Trager, 1988)). We predicted that hatchlings should avoid eating fire ants in favor of native ants, whereas less-vulnerable adults should take advantage of both prey sources. However, when given the choice between fire ants and native ants, hatchlings consumed similar numbers of these species whereas adults consumed nearly three times as many native ants as invasive fire ants. Increased consumption of fire ants in adulthood could be the result of lifetime experience, strategies to safely consume fire ants, ontogenetic shifts in the ability to distinguish between ants, or reduced costs to adults of eating venomous ants. Future research should aim to distinguish these alternative mechanisms, and examine the long-term consequences of native species incorporating toxic invasive prey into their diets.

Keywords: Invasive prey, Pyramid Ant, *Dorymyrmex bureni*, Red Imported Fire Ant, *Solenopsis invicta*, Eastern Fence Lizard, *Sceloporus undulatus*

Invasive species are a growing threat to global biodiversity (Gurevitch and Padilla 2004). They can affect native species in various ways including through their role as predators, competitors, or by acting as a novel prey resource (Vitousek et al. 1996; reviewed in Langkilde et al. 2017). Understanding the effects of invasive prey on native predators, whether positive or negative, will provide important insight into the long-effects of invaders and into the evolution of predator-prey dynamics more generally (reviewed in Strauss et al. 2006 and Pintor and Byer 2015).

In their role as novel prey, invasive species can be noxious or palatable. Native species naturally avoid or consume these prey, respectively, or can acquire the ability to do so over time. Some native species innately avoid eating noxious toxic prey by recognizing them as unpalatable (Lindstrom et al. 1999) or due to their unfamiliarity (Reznick et al. 2009). Other species can adapt to avoid noxious invasive prey. For example, Australian red-bellied black snakes (*Pseudechis porphyriacus* (Shaw, 1794)) have undergone selective pressures for smaller head size, making them physically unable to consume toxic cane toads (*Rhinella marina* (Pramuk 2006); previously *Bufo marinus* (Linnaeus, 1758)) large enough to be lethal (Phillips and Shine 2006a, 2006b, 2006c). Coastal horned-lizards (*Phrynosoma coronatum* (Blainville, 1835)), an ant specialist, have learned to avoid eating toxic invasive Argentine ants (*Linepithema humile* (Mayr, 1868); Suarez et al. 2000). By contrast, some native species instinctively consume palatable invasive prey, such as frugivorous birds of Maine that feed on invasive honeysuckle flowers (Drummond 2005) and Pike (*Esox lucius* (Linnaeus, 1758)) that feed on invasive red swamp crayfish (*Procambarus clarkia* (Girard, 1852); Elvira et

al. 1996)). Others have rapidly adapted to take advantage of novel food resources. For example, Soapberry bugs (*Leptocoris tagalicus* (Kilkaldy, 1908)) have evolved 5-10% longer mouthparts to allow them to feed on invasive balloon vines (*Cardispermum grandiflorum* Sw.; Carroll et al. 2005).

Both avoidance and targeted consumption of novel invasive prey relies on the ability of native species to distinguish these invaders from native prey. Some invasive prey are ecologically, visually, and chemically similar to native prey. Such similarities may make it difficult for native predators to distinguishing prey, thus imposing fitness relevant costs in what is referred to as an evolutionary trap (Schlaepfer et al. 2005). For example, female monarch butterflies (*Danaus plexippus* (Linnaeus, 1758)) will oviposit 25% of their eggs on invasive black swallowwort (*Vincetoxicum nigrum* L.), which is visually similar to their native host plant, the common milkweed (*Asclepias syriaca* L.), even though their larvae are unable to develop on the black swallowwort (Tewksbury et al. 2002). Australian snakes are evolutionarily naïve to toxic toads and some will readily eat toxic cane toads (e.g., Phillips and Shine 2006a). Similarly, native predators that acquire the ability to avoid noxious invasive prey may unintentionally avoid consuming the similar native prey species, thereby incurring costs associated with loss of food resources.

The propensity to consume or avoid prey can change across an individual's lifetime due shifts in dietary composition or risk imposed by the prey. Many such ontogenetic shifts in diet are size-dependent. For example, many taxa increase diversity and size of their prey as they grow larger and are no longer gape-limited (tiger sharks,

Galeocerdo cuvier (Péron and Leseur, 1822; Lowe et al. 1996), water snakes, *Nerodia* spp. (Baird and Girard, 1853; Mushinsky et al. 1982), Yellow-finned tuna, *Thunnus albacares* (Bonnaterre, 1788; Graham et al. 2007), European hedgehog, *Erinaceus europaeus* (Linnaeus, 1758; Dickman 1988)). Ontogenetic shifts in prey consumption could also be related to changes in vulnerability to prey species. For example, larger (presumably older) snakes are less vulnerable to lethal effects of consuming cane toads than smaller (younger) snakes (Phillips and Shine 2006b). The ontogeny of consumption of invasive prey species, or ability to distinguish invasive from non-native prey could be important for determining the potential effects of invasive species on native predators (see Phillips and Shine 2006c; Robbins and Langkilde 2012).

Here we test differential consumption of a toxic invasive and non-toxic native ant prey species by a native lizard predator at two life stages (hatchling and adult). Although invasion status and toxicity are confounded in this instance, we only use Eastern fence lizards (*Sceloporus undulatus* (Bosc and Daudin in Sonnini and Latreille, 1801) from fire ant invaded populations that have been exposed to both ant species since the 1930s (~40 generations; Langkilde 2009). Previous research has focused on invasive fire ants (*Solenopsis invicta*; Buren, 1972) as novel toxic predators of these lizards, demonstrating morphological and behavioral adaptations of fence lizards within fire ant invaded areas (Langkilde 2009, 2010). Lizards will also eat fire ants, but this can prove lethal, particularly for juvenile lizards (Langkilde and Freidenfelds 2010). It is currently unclear whether the lethal effects of consuming fire ants is from ingestion of the venom or from being stung inside the mouth by fire ants during consumption;

therefore we refer to fire ants as a toxic prey (Langkilde and Freidenfelds 2010). Lizards originating from fire ant-invaded sites but raised in the absence of fire ants avoided consuming fire ants compared to their counterparts originating from fire ant-free sites (Robbins et al. 2012). This innate avoidance suggests selective pressure to avoid eating these toxic ants. However, sub-adult fence lizards increased consumption of fire ants with increased exposure across multiple contexts (multigenerational, distant past, and recent exposure; Robbins et al. 2013; Herr et al. 2016). In all of these experiments, lizards were presented with fire ants as their only prey option, meaning their ability to distinguish fire ants from native ants, a key assumption, has not been tested. Here we investigate 1) whether lizards from fire ant-invaded sites differentially consume toxic invasive fire ants versus non-toxic native ants when simultaneously presented with both prey options and 2) if this relative consumption differs between life stages (i.e. hatchlings and adults). We hypothesize 1) hatchling lizards will preferentially consume native ants over invasive fire ants, as these native ants are not harmful and hatchlings can be killed by eating fire ants (Langkilde and Freidenfelds 2010) and 2) adults will show no difference in consumption of these two species as their larger size makes them less vulnerable to envenomation by fire ants during consumption (Robbins and Langkilde 2012).

Methods:

Animal Collection and Husbandry

We captured adult male fence lizards ($n = 24$) by hand-held noose from 3 sites in Alabama: 1) Conecuh National Forest and Solon Dixon Forestry Education Center, Andalusia, (2) Geneva State Park, Kinston, and 3) Historic Blakeley State Park, Spanish Fort, in May 2016. Hatchlings ($n=28$) were obtained from eggs from 18 adult females from the same sites and tested at 15-20 days old. Animal collection was permitted by the Alabama Department of Conservation and National Resources; LIC#: 2018095450668680. Lizards were housed in plastic containers (56 x 40 x 30 cm, L x W x H) furnished with a water dish and a basking log placed under a 60 W incandescent light bulb to provide shelter and allow thermoregulation. The room was on a 12:12hr, light: dark schedule (0700-1900 hrs), and the heating lamps provided heat for 8 hours per day (0800-1600 hrs).

We used 2 species of ant in this study: the invasive fire ant, *S. invicta*, and the native pyramid ant, *Dorymyrmex bureni* (Trager, 1988). These species were chosen because they are the two most abundant potential ant prey species at our study sites (approx. one mound of each species is present every 10 meters; Langkilde 2009; Langkilde unpubl. data); the fact that *D. bureni* are not threatening to the lizards (non-venomous and non-attacking ants, Davis 2005); and their visual similarity (both species are small (2-6mm) red/orange colored ants; Buren 1975; Davis 2005). Preliminary trials revealed that adult and hatchling lizards ate both of these ant species during staged trials (Venable, unpubl. data). We collected ants directly from their mounds immediately prior to trials, placed them separately into a small plastic collection container lightly dusted with talc powder to prevent escape, and transported them to the test arenas.

Lizard feeding trials

Test arenas (30 x 20 x 25 cm, $l \times w \times h$) were wrapped in opaque paper to prevent lizards from seeing one another or other stimuli during the trials. Prior to each trial, the walls of each arena were lightly dusted with talc powder (Equate, Bentonville, Arkansas) to prevent ants from escaping. 60-watt incandescent bulbs were suspended above each arena to maintain an ecologically relevant temperature gradient. Four individuals of each ant species were placed into a test arena immediately prior to introducing a lizard to the center of the arena. Trials ran for 30 minutes (hatchlings) or 2 hours (adults). This time difference was due to a higher propensity of juvenile to consume ants. Ants comprise a large part of the juvenile lizard diet (80%) and a substantial but smaller portion of the adult lizard diet (50%; Demarco et al. 1985; Parker 1994). Thus, the longer duration of trials for adults allowed us to capture a reasonable amount of ant consumption. At the completion of a trial, lizards were returned to their respective home containers and the number of ants of each species that were consumed by each lizard was recorded. All lizards were used in two trials conducted 24 hours apart.

This research adheres to the Guidelines for the Use of Animals in Research and the Institutional Guidelines of Penn State University (IACUC #44595).

Statistical analysis

We tested whether hatching or adult lizards differentially consumed fire ants or native ants using mixed-model analysis of variance (ANOVA). The number of ants of each species consumed by a lizard in each of the two trials was log-transformed and included as the dependent variable (for each lizard we had two values for each trial: one for the number of invasive fire ants eaten and one for the number of native ants eaten). The species of ant consumed (whether the dependent variable reported was for fire ants or native ants), age (hatchling or adult), and trial (trial 1 or 2), and interactions between all three, were included as factors. Lizard identity was included as a random effect to control for repeated testing of individuals across the two ant species and the two trials. A Tukey HSD posthoc test was used to interpret causes of significant interactions between factors. All analyses were conducted in JMP (Version 13, SAS Institute Inc) with $\alpha = 0.05$.

Results:

Lizard feeding trials

The number of ants a lizard consumed during a trial was dependent on an interaction between the species of ant and the age of the lizard (species x age: $F_{1, 150} = 7.71$, $p = 0.0062$; species: $F_{1, 150} = 5.96$, $p = 0.0158$; age: $F_{1, 50} = 4.09$, $p = 0.0486$; Figure 1). This interaction results from hatchling lizards consuming native and invasive fire ants at similar rates, but adult lizards consuming significantly more native ants than invasive fire ants (Tukey HSD). This behavior was consistent across both trials (trial $F_{1, 150} = 0.31$, $p = 0.58$; trial x age: $F_{1, 150} = 1.8$, $p = 0.1816$; trial x species: $F_{1, 150} = 1.05$, $p = 0.3069$; trial x age

x species: $F_{1, 150} = 0.0003$, $p = 0.9852$). Omitting trial from the model did not qualitatively change our results on the effects of species and age.

Discussion:

This study revealed that, contrary to our predictions, when simultaneously presented with invasive fire ants and native ants, hatchling lizards consumed these species at similar levels. This is despite native ants being innocuous and the consumption of fire ants being lethal (Langkilde and Freidenfelds 2010). Additionally adult lizards consumed more native ants than fire ants despite being larger and thus less vulnerable to envenomation by fire ants during consumption than hatchlings. It is important to note that the duration of trials differed between adults and hatchlings; hatchling trials were 30 minutes long whereas adult trials were two hours long. This makes our finding that overall juveniles ate more ants than did adults conservative, as juveniles had less opportunity to consume ants. The difference in trial length is unlikely to have affected our results on the differential consumption of the two ant species, as both adults and juveniles were presented with both species simultaneously. Although we find a clear difference between adult and juvenile consumption of native and invasive ants, our conclusions are only the beginning to understanding how invasive prey can change native diets. We cannot effectively differentiate between ontogeny and learning in this study. We thus describe some potential mechanisms underlying these patterns, and future work should aim to better explore these.

It is possible that the differential consumption of native and fire ants by adults but not juveniles is due to differences in lifetime experience. Since adults have been exposed to fire ants for their entire lifetimes (likely frequently over several years) they may have learned that consuming fire ants is noxious or painful and thus learned to avoid them. However, these lizards increase consumption of fire ants with repeated exposure, arguing against learned avoidance (Robbins et al. 2013; Herr et al. 2016). The hatchlings were fire ant naïve and did not have had the opportunity to learn to avoid fire ants. There is evidence that hatchlings can innately avoid consuming fire ants. Robbins et al. (2012) found that naïve hatchlings from fire ant invaded populations were less likely to eat fire ants than those from uninvaded populations. It is important to note that this experiment was conducted using lizards from fire ant invaded populations, but only the adults had been exposed to fire ants. Therefore, we are unable to separate the effect of lifetime experience with fire ants (learning) and ontogenetic stage; this could be tested by raising lizards with different exposure to fire ants and testing consumption at different life stages.

It is possible that lizards could not visually distinguish between these ant species. The two ant species used in this study are visually similar, at least to the human eye. However, the ability to distinguish multiple species of ants has been documented in lizards in the family *Phrynosomatidae*, to which our study species belongs (Cooper 1995). Our results suggest that adult lizards may be able to distinguish these ant species prior to attacking them, either visually or by other means such as chemical cues,

whereas juveniles may not be able to do so. This difference could be due to differences in experience or in the development of optical acuity.

Potentially, lizards did not distinguish between the two ant species but instead captured every ant that they encountered. The native *D. bureni* ants are known to be fast moving (Davis 2005), which may have increased encounter rates between this species and these sit-and-wait predatory lizards within the test arena (Huey and Pianka 1981). Preliminary data showed that, in the absence of a lizard, the native ants moved approx. 15% more often than did the invasive fire ants (Venable and Langkilde unpubl. data). This difference does not explain the observed 3-fold increase in consumption of these native ants by adults, but this would be a fruitful avenue for further research.

Hatchling and adult lizards may have different pressures on their ability to distinguish ant prey. Since juveniles rely on ants as prey (comprising 80% of their diet; Demarco et al. 1985; Parker 1994), they may be motivated to consume any ant they can catch. Since fire ants are the predominant ant in invaded areas (only *D. bureni* equal fire ants in mound prevalence at our sites, but fire ants are more individually numerous; Porter and Savignano 1990; Wojcik et al. 2001), avoiding eating fire ants may limit the lizards' prey options. In contrast to hatchlings, adults have a more diverse dietary composition (with ants comprising 50% of their diet; Demarco et al. 1985; Parker 1994) meaning they may be able to afford to avoid consuming fire ants without losing a significant portion of their prey base.

The ability of lizards to distinguish between native and invasive fire ants may be of enormous ecological importance, as it would allow lizards to avoid toxic fire ants

without having to avoid consuming all ants. The coastal horned lizard (*Phrynosoma coronatum*; Blainville, 1835), an ant specialist, specifically avoids eating invasive Argentine ants (*Linepithema humile*; Mayr, 1868; Saurez et al. 2000). This is likely beneficial as these lizards exhibit decreased growth on a prey typical of invaded areas (including these invasive ants) versus un-invaded areas (Saurez and Case 2002). Fence lizards would likely similarly benefit by being able to specifically avoid eating toxic fire ants (as documented for juveniles from fire ant invaded areas; Robbins and Langkilde 2012) while still consuming native ant species. Our data supports the claim that hatchling fence lizards, although from fire ant-invaded areas, do not possess the ability to distinguish between a native and invasive species. Future studies should focus on the mechanism behind this shift in lizards' ability to distinguish between ant species. Broadening this work to include multiple invasive and native ant species would allow for a more generalized interpretation of this pattern. This would also allow us to distinguish between effects of toxicity and invasive status of the ant. These factors are currently confounded in this study, though lizards were from fire ant-invaded areas and so not evolutionarily naïve to either ant species.

Consuming fire ants may seem maladaptive, considering consumption of fire ants can be lethal for these lizards (Langkilde and Freidenfelds 2010). So, why do these lizards continue to consume fire ants? There are several possible explanations for lizard consumption of this aggressive toxic ant. 1) Fire ants are somewhat less active than native ants and thus may be easier to capture. 2) Fire ants may be nutritionally valuable, offsetting the risk of being stung. 3) Lizards may be killing fire ants predominantly as an

anti-predator defense, either consuming them or spitting them out once killed; a strategy employed by Texas horned lizards, *Phrynosoma cornutum* (Harlan, 1825) when attacked by fire ants (Sherbrooke and Mendoza-Quijano 2005). 4) Lizards may consume fire ants to sequester their venom and use this to defend the lizards against potential predators. Sequestration of venom from consumed prey has been documented in several herpetofaunal species including poison dart frogs (ant toxins sequestered in the skin, Daly et al. 1994, Saporito et al. 2009), garter snakes (newt venom sequestered in the liver, Williams et al. 2004), and Asian snakes (toad venom sequestered in specialized nuchal glands, Hutchinson et al. 2007). Future research exploring these alternative explanations for the consumption of these toxic fire ants by fence lizards would be illuminating.

Invasive species are a growing threat to natural ecosystems but can become incorporated into the ecology of native species. Understanding the complexity of interactions between invasive and native species and how this can change across ontogeny is important for determining the long-term effects of invasive species, and for understanding the evolution of predator-prey dynamics. Future work on a range of systems aimed at understanding whether and how native species are able to distinguish invasive and native prey, and the costs and benefits of doing so, will be critical to predicting and managing influences of invasive prey species.

Acknowledgments

The authors thank Dr. Kirsty Macleod, Dustin Owen, David Ensminger, and Nicole Freidenfelds for their assistance in the field, and Joel Martin and the staff of the Solon Dixon Forestry Education Center for logistical support. This research was funded in part by the National Science Foundation (IOS 1456655 to TL).

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Figure caption:

Figure 1. The average number of non-toxic native ants (*Dorymyrmex bureni*) and toxic invasive fire ants (*Solenopsis invicta*) that were consumed by each hatchling and adult fence lizard (*Sceloporus undulatus*) during feeding trials (30 min for hatchlings, 120 minutes for adults). Bars represent means $\pm$ 1 standard error.

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Figure 1.