DISEASE ECOLOGY

Highly competent native snake hosts extend the range of an introduced parasite beyond its invasive Burmese python host

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Abstract. Invasive Burmese pythons (*Python bivittatus*) have introduced a nonnative pentastomid parasite (*Raillietiella orientalis*) to southern Florida that has spilled over to infect native snakes. However, the extent of spillover, regarding prevalence and intensity, is unknown. We examined native snakes (*n* = 523) and invasive pythons (*n* = 1003) collected from Florida to determine the degree to which parasite spillover is occurring. We found *R. orientalis* has infected 13 species of native snakes collected from areas of sympatry with pythons. Prevalence and infection intensity of *R. orientalis* were significantly higher among native snakes compared with pythons. Moreover, adult female pentastomes achieved larger sizes and represented a greater proportion of the overall parasite population in native snakes vs. pythons, indicating native snakes are more competent hosts of *R. orientalis* than pythons. We also examined native snakes from regions of allopatry with pythons to determine how far *R. orientalis* has spread. We found an infected native snake 348 km north of the northernmost infected python. Our data show that native snakes are highly competent hosts of *R. orientalis* and have facilitated the rapid spread of this nonnative pentastome beyond the range of its invasive host.

Key words: biological invasion; Burmese python; everglades; parasite spillover; pentastome; *Python bivittatus*; *Raillietiella orientalis*.

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Introduction

Biological invasions can impact native ecosystems by altering host–parasite dynamics (Tompkins and Poulin 2006). Nonnative species often contain half the parasite species richness of conspecifics in their native range (Torchin et al. 2003) due to the low probability of a nonnative parasite successfully establishing in its introduced range (MacLeod et al. 2010). Despite obstacles a parasite

must overcome during the invasion pathway (e.g., low host densities and lack of required intermediate hosts), nonnative parasites have become established and spillover of these parasites to native taxa has been widely documented for both terrestrial and marine systems (Daszak et al. 2000, Tompkins and Poulin 2006, Goedknegt et al. 2016, Chalkowski et al. 2018).

When parasite spillover occurs, adverse effects of introduced parasites and pathogens may be exacerbated as native taxa do not share a coevolutionary history with the nonnative parasite (i.e., they are naïve) and therefore often lack adaptations to effectively mitigate or deter infection (Dogiel et al. 1961, Anderson et al. 1986, Holdrich and Reeve 1991, Daszak et al. 2000, Mastitsky et al. 2010). In 85% of cases in which an introduced parasite infects native taxa, the parasite is more virulent in the native host compared with the nonnative host from which the parasite was introduced (Lymbery et al. 2014). For example, the swim bladder nematode (*Anguillicola crassus*), introduced to Europe by the Japanese eel (*Anguilla japonica*), now infects the native European eel (*A. Anguilla*; Kirk 2003); while the effect of the nematode in the Japanese eel is negligible, nematode infection in the European eel yields large worm burdens and causes severe damage to swim bladder function, which may prevent spawning migrations (Kirk 2003). Effects of spillover can have sublethal or lethal impacts on infected native taxa, and mass mortalities have been observed (Goedknegt et al. 2016).

Competent hosts are those in which a parasite can undergo stages of development and reproduction. Nonnative parasites within immunologically naïve hosts can occur at higher intensity, increased prevalence, and larger size relative to nonnative hosts (Kirk 2003). For female parasites, an increase in body length is strongly and positively correlated with the number of eggs produced, the size of the eggs, and total reproductive effort (Timi et al. 2005). Therefore, when native taxa are highly competent hosts of nonnative parasites, they may function to increase parasite transmission among susceptible hosts. With increased transmission, the introduced parasite may spread quickly among novel hosts within its invaded range, allowing the parasite to spread beyond the distribution of the nonnative host. Spread of an introduced parasite beyond the range of its nonnative host has been shown in a nematode (*Camallanus cotti*) that was introduced to Hawaii by nonnative swordtail and guppy fishes. Since its introduction, the nematode has infected the native Hawaiian goby (*Awaous stamineus*) and this nonnative nematode can now be found in river catchments lacking nonnative fish (Gagne et al. 2015).

Burmese pythons (*Python bivittatus*), native to Southeast Asia, have been introduced to southern Florida through the pet trade where they have been established for over two decades (Meshaka et al. 2000, Snow et al. 2007). Miller et al. (2018) examined the lung parasites of wild-caught Burmese pythons in southern Florida and found them to be infected with a pentastome parasite, *Raillietiella orientalis*, a lung parasite of Old World origin (Asia and Africa) that is known to infect snakes as the parasite's definitive host. The intermediate hosts involved in the indirect life cycle of this parasite have not been identified within its native distribution and its nonnative range. Within its native range, *R. orientalis* infects a diverse array of snakes including members of the families Pythonidae, Elapidae, Viperidae, and Colubridae (Christoffersen and De Assis 2013). However, raillietiellid pentastomes that infect snakes as their definitive host are not known from North America (Christoffersen and De Assis 2013). Since the introduction of *R. orientalis* to southern Florida, spillover of this parasite from pythons to native snakes has occurred (Miller et al. 2018). However, infection dynamics of *R. orientalis* among native snakes and pythons have not been explored.

We examined infection dynamics of *R. orientalis* in novel snake hosts in Florida. Specifically, we measured parasite prevalence, infection intensity, and size and proportion of adult female pentastomes (as size is a positive correlate with fecundity; Timi et al. 2005) as measures of host competency of *R. orientalis* in native Florida snakes and we compared these metrics to those recovered from Burmese pythons in Florida, the host responsible for the introduction of *R. orientalis* (Miller et al. 2018). In addition, as the intermediate hosts involved in the life cycle of *R. orientalis* are unknown we explore the foraging ecology of native snakes in attempt to elucidate dietary patterns that may identify potential

intermediate hosts involved in the transmission of this parasite.

We also examined a potential for *R. orientalis* to spread beyond the python's invasive range through infected native snakes by comparing the prevalence of *R. orientalis* in native snakes collected from locations in sympatry and allopatry with pythons. Areas of sympatry include the python invasion front (low python abundance) and the core of the python distribution (high python abundance). If the prevalence of *R. orientalis* does not differ between native snakes from the invasion front and native snakes from the core of the pythons' distribution, yet the prevalence within native snakes overall is significantly higher than the prevalence of *R. orientalis* in pythons, this would be consistent with the hypothesis that native snakes, and not pythons, are the primary driver of transmission of *R. orientalis*.

Methods

Burmese pythons were collected from throughout their range in southern Florida (Fig. 1) through road surveys and opportunistic captures. Pythons were also provided through a collaborative python removal effort among the U.S. Geological Survey, National Park Service, and University of Florida Fort Lauderdale Research and Education Center. Native snakes were salvaged as roadkill during road surveys conducted in the core of the python's distribution, within the python invasion front, and in areas of allopatry with pythons (Alabama, Georgia, and northern Florida; Fig. 1). Pythons and native snakes were dissected, and lungs and respiratory passageways were examined for pentastomes. All members of the genus *Raillietiella* were assumed to be *R. orientalis* based on a molecular analysis of a large series of this genus (Miller et al. 2018).

The prevalence (the proportion of infected hosts within a sample; first grouping variable) of *R. orientalis* was quantified for native snake species, which were grouped into six foraging modes (terrestrial ambush predators = *Agkistrodon piscivorus* + *Sisturus miliarius*; terrestrial wide-foraging non-constrictors = *Coluber constrictor* + *C. flagellum* + *Drymarchon couperi*; terrestrial wide-foraging constrictors = *Pantherophis*

guttatus + *P. obsoletus* + *Lampropeltis getula*; aquatic non-constricting frog eaters = *Nerodia clarkii* + *Nerodia fasciata* + *Thamnophis sirtalis*; aquatic non-constricting fish eaters = *Nerodia floridana* + *Nerodia taxispilota*; and aquatic constrictors = pythons). Native snakes were grouped into foraging modes to explore whether foraging patterns may aid identification of potential intermediate hosts of *R. orientalis*, as the intermediate host(s) involved in the life cycle of this parasite are unknown. We included regions that vary in python abundance—python core area (Miami-Dade and Monroe counties, FL; high python abundance) and python invasion front (Broward, Charlotte, Collier, DeSoto, Glades, Hardee, Hendry, Highlands, Lee, Manatee, Martin, Okeechobee, Palm Beach, Sarasota, and Saint Lucie counties, FL; low python abundance)—as a third grouping variable and tested for differences in prevalence among foraging modes and region with a log-linear model (CATMOD of SAS). Regions of allopatry with pythons (north of Hardee, Highlands, Lake, Manatee, Okeechobee, and Saint Lucie counties, FL) represented a third region; however, snakes within this region were not included in this analysis (nor subsequent analyses) due to a low number of infected snakes (*n* = 3 individuals) recovered from this region.

Infection intensity (mean number of individual parasites per infected host) was quantified for infected individuals within three groups: native snakes (all foraging modes pooled together) in the core region (*n* = 95 infected hosts), native snakes in the invasion front (*n* = 22 infected hosts), and pythons from the pooled core (*n* = 119 infected hosts) and invasion front (*n* = 1 infected host) regions. Pythons from the core region and invasion front were combined for analyses due to the low sample size of infected pythons recovered from the invasion front. Data were square-root-transformed to improve fit to a normal distribution and a one-way ANOVA was used to test for differences in mean intensity among groups, followed by a Tukey HSD analysis to determine where any significant differences occurred. Results of statistical analyses were considered significant at $P < 0.05$.

Female pentastome body length was measured (nearest mm) as a proxy for host competency, as female body length in parasites strongly and
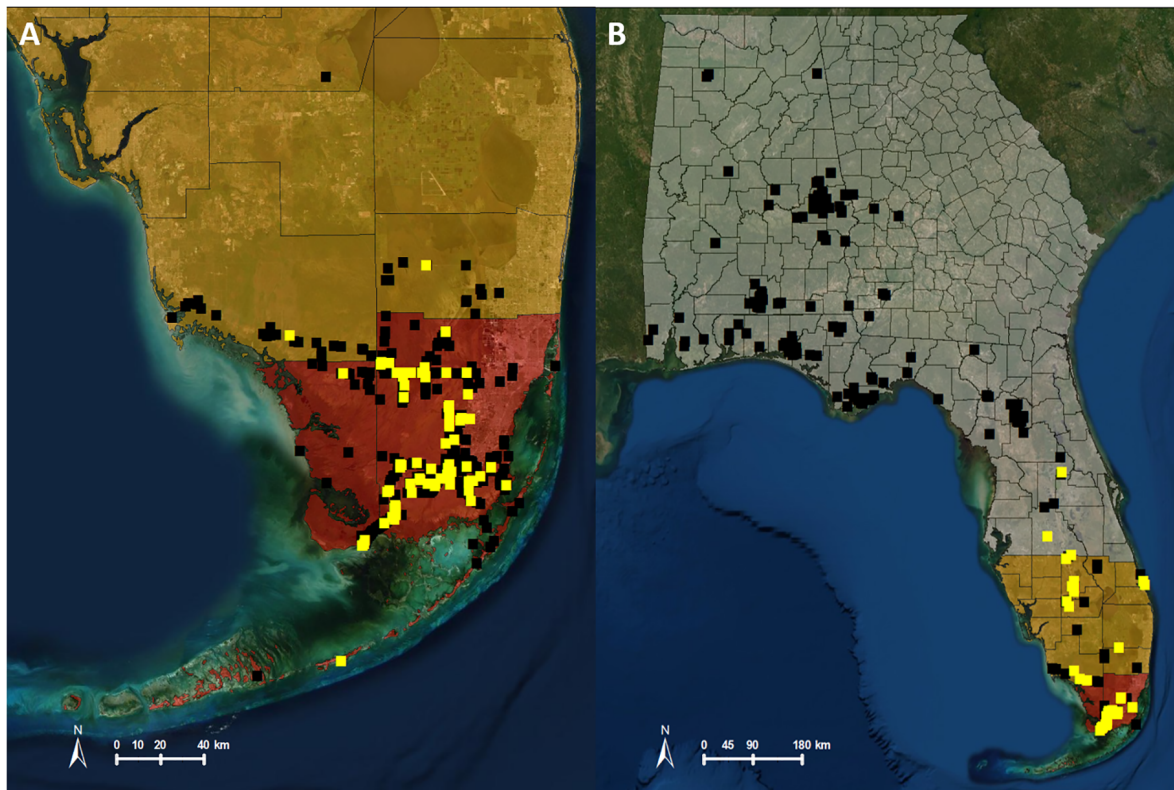
Fig. 1. Map of southeastern United States showing locations where pythons (A) and native snakes (B) were collected within three regions encompassing Florida, Alabama, and Georgia. Regions included the core of the python's distribution (core region, red shading), the expanding edge of the python's distribution (invasion front, orange shading), and a region where pythons are absent (allopatric, gray shading). Snakes infected with *Raillietiella orientalis* are indicated with yellow squares, while those not infected with this parasite are indicated with black squares. Black lines represent counties within each state.

positively correlates with fecundity (e.g., Timi et al. 2005). Female *R. orientalis* ≥ 34 mm in body length can produce eggs, and males never achieve this body size (Hett 1924); therefore, only individuals 34 mm or greater were included. Body length measurements were square-root-transformed to improve normality and pooled into native snakes from the core region, native snakes from the invasion front, and pythons from the core and invasion front combined. ANOVA was used to test for differences in mean body length among these three groups.

Finally, we generated a contingency table enumerating the number of individual pentastomes that were adult females vs. a pooled category for juveniles and adult males for native snakes from the core region, native snakes from the invasion

front, and pythons from the core region and invasion front. We used a chi-square test to determine whether the proportion of adult female parasites in a population of parasites differed among the three host groups.

RESULTS

We examined 523 native snakes (Table 1) encompassing three families, 17 genera, and 26 species, of which 13 species were native to the core python region and were captured frequently enough to include in our statistical analyses. All 13 native snake species were infected with *R. orientalis*. A total of 1083 *R. orientalis* were recovered from native snakes, six from allopatry with pythons, 304 from the python invasion front, and

Table 1. The sample size, prevalence, and infection intensity of each snake species examined for *Raillietiella orientalis* are presented by region (C = core of python distribution; IF = python invasion front; and A = regions of allopatry with pythons).

Species	Sample size			Prevalence			Infection intensity		
	C	IF	A	C	IF	A	C	IF	A
Agkistrodon contortrix	-	-	6	-	-	0	-	-	-
Agkistrodon piscivorus	43	8	80	67	25	0	7.6	5.6	-
Cemophora coccinea	3	0	2	0	-	0	-	-	-
Coluber constrictor	13	8	19	56	55	0	8.7	1.6	-
Coluber flagellum	0	2	9	-	100	0	-	42.0	-
Crotalus adamanteus	6	0	31	0	-	0	-	-	-
Crotalus horridus	-	-	16	-	-	0	-	-	-
Drymarchon couperi	0	2	2	-	50	50	-	1.0	2.0
Farancia abacura	0	1	8	-	0	0	-	-	-
Heterodon platirhinos	0	1	8	-	0	0	-	-	-
Lampropeltis getula	11	0	3	18	-	0	0.5	-	-
Liodytes alleni	4	0	1	0	-	0	-	-	-
Micrurus fulvius	0	0	2	-	-	0	-	-	-
Nerodia clarkii	10	5	1	50	40	0	5.0	10.6	-
Nerodia erythrogaster	0	0	6	-	-	0	-	-	-
Nerodia fasciata	30	7	6	67	50	18	5.4	13.9	0.2
Nerodia floridana	19	3	0	16	0	-	0.2	-	-
Nerodia taxispilota	17	1	0	6	0	-	0.1	-	-
Opheodrys aestivus	1	1	3	0	0	0	-	-	-
Pantherophis guttatus	9	11	8	44	18	13	1.9	0.3	0.1
Pantherophis obsoletus	5	3	20	20	67	0	4.0	2.3	-
Pituophis melanoleucus	0	0	11	-	-	0	-	-	-
Python bivittatus†	960	43	-	13	2	-	0.3	0.1	-
Sistrurus miliarius	2	0	4	50	-	0	2.5	-	-
Storeria dekayi	1	0	1	0	-	0	-	-	-
Thamnophis sauritus	4	2	3	0	0	0	-	-	-
Thamnophis sirtalis	31	0	9	58	-	0	2.2	-	-

Notes: Prevalence (%) and infection intensity (mean number of parasites per host) of *R. orientalis* are provided per region. Dash (-) represents not applicable to species due to a species not present within a region (sample size column), lack of specimens collected from a region (prevalence column), or species within a region was not infected with *R. orientalis,* thus preventing the calculation of infection intensity (infection intensity column).
† Denotes nonnative species.

773 from the core python region. Three native snake species (*D. couperi*, *N. fasciata*, and *P. guttatus*) collected from regions of allopatry with pythons were infected with *R. orientalis*. The northernmost native snake (*P. guttatus*) infected with *R. orientalis* was collected in Lake County, 348 km north of the northernmost infected python (Fig. 1). We examined 1003 pythons to determine the prevalence and intensity of *R. orientalis*, 43 of which were from the invasion front. A total of 255 *R. orientalis* was recovered from 120 infected pythons. All but two of these parasites were from the core region of the python invasion.

The prevalence of *R. orientalis* differed among the snake foraging modes (χ^2 = 37.93; df = 5; $P < 0.001$; Fig. 2). The prevalence in terrestrial wide-foraging constrictors was significantly greater than in pythons and aquatic non-constricting fish eaters (χ^2 = 10.17; df = 2; $P < 0.01$) and significantly less than in aquatic non-constricting frog eaters, terrestrial wide-foraging non-constrictors, and terrestrial ambush predators (χ^2 = 9.39; df = 3; $P < 0.05$). None of the three-way interactions (foraging mode × area × infection) were significant, indicating that prevalence patterns were similar between core and invasion front areas.

Mean infection intensity of *R. orientalis* differed significantly among groups (F = 25.56; df = 2; $P < 0.001$; Fig. 3) with intensity in pythons significantly less than intensity in native
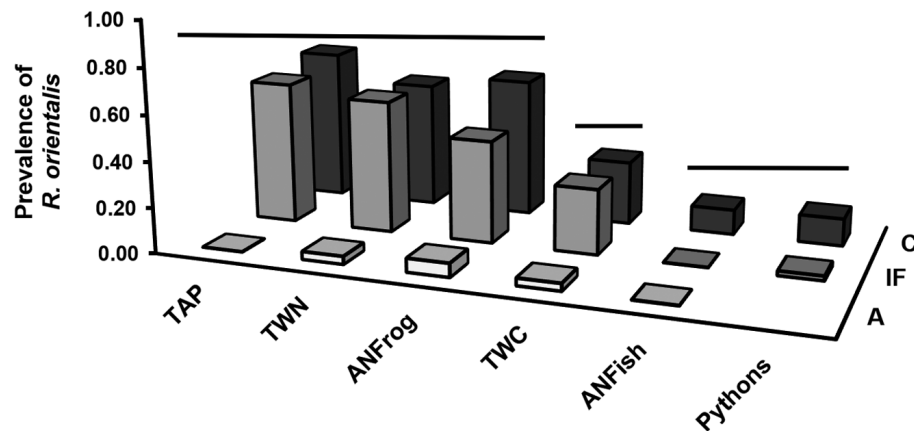
Fig. 2. Prevalence of *Raillietiella orientalis* infection for thirteen native snake species and pythons. Snakes were grouped into the following foraging modes: terrestrial ambush predator (TAP), terrestrial wide-foraging non-constrictors (TWN), terrestrial wide-foraging constrictors (TWC), aquatic non-constricting frog eaters (ANFrog), aquatic non-constricting fish eaters (ANFish), and aquatic constrictors (Pythons). Prevalence of each group was quantified for three geographic regions (C, core of python distribution, black bars; IF, python invasion front, gray bars; and A, region of allopatry with pythons, light gray bars). Black lines unite groups that do not differ significantly when geographic regions are pooled.

Fig. 3. Mean infection intensity of *Raillietiella orientalis* for native snakes collected from two regions (Native C, the core of python distribution; and Native IF, the python invasion front) and pythons from both regions (Python C + IF). Black lines unite groups that do not differ significantly. Horizontal line within boxplot represents median value.
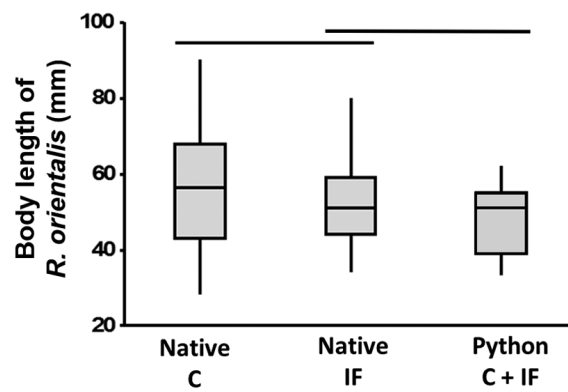

Fig. 4. Mean body length of adult female *Raillietiella orientalis* for native snakes collected from two regions (Native C, the core of python distribution; and Native IF, the python invasion front) and pythons from both regions (Python C + IF). Black lines unite groups that do not differ significantly. Horizontal line within boxplot represents median value.

snakes in the core but not distinguishable from native snakes in the invasion front. The intensity of parasites within native snakes did not differ between these two regions. Infection intensity ranged from 1 to 77 *R. orientalis* for native snakes and 1 to 15 for pythons.

The length of adult female *R. orientalis* differed significantly among groups ($F = 6.47$; df = 2; $P < 0.01$; Fig. 4). Female *R. orientalis* reached significantly longer body lengths in native snakes ($\overline{x} = 56.1 \pm 0.91$ SE) collected from the core region than in pythons ($\overline{x} = 47.9 \pm 1.59$ SE) but
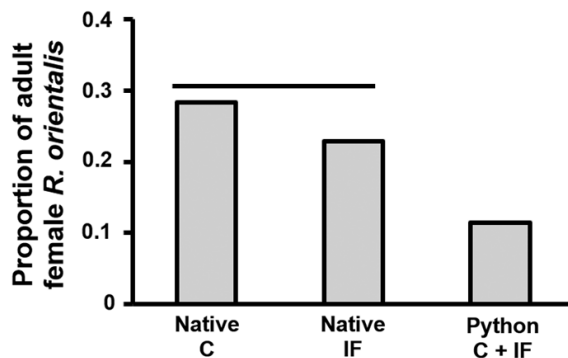
Fig. 5. Proportion of *Raillietiella orientalis* that are adult females for native snakes collected from two regions (Native C, the core of python distribution; and Native IF, the python invasion front) and pythons from both regions (Python C + IF). Black lines indicate groups that do not differ significantly.

did not differ from native snakes ($\overline{x}$ = 52.3 ± 1.37 SE) from the invasion front. There was no difference in female body length of *R. orientalis* between pythons and native snakes collected from the invasion front.

The proportion of adult female *R. orientalis* differed among native snakes from the core region and pythons (χ^2 = 19.10; df = 1; P < 0.001; Fig 5). Native snakes from the invasion front also varied significantly (χ^2 = 8.32; df = 1; P < 0.05) from pythons, but not from native snakes from the core region (χ^2 = 1.76; df = 1; P = 0.185).

DISCUSSION

Burmese pythons have introduced a nonnative pentastome, *R. orientalis*, to southern Florida where this parasite has infected native snakes (Miller et al. 2018). The diversity of native snakes infected (13 species) represents 50% of the snake fauna that we sampled and is at least 29% of the 45 species known from Florida (Bartlett and Bartlett 2003). Four families of snakes are infected by *R. orientalis* within its native range (Christoffersen and De Assis 2013), three of which (viperids, elapids, and colubrids) are native to North America, and two of which (viperids and colubrids) we found to be infected by *R. orientalis* in this study. Within its native range, *R. orientalis* exhibits an exceptionally broad geographic distribution, which likely

emerges from the use of a diverse assemblage of intermediate and definitive hosts. The relatively large portion of snakes in Florida that are susceptible to *R. orientalis*, in concert with the diverse assemblage of available hosts in North America, suggests that the parasite may continue to expand both to new areas and new snake species.

Aside from this parasite's ability to infect many snake species, our study shows that certain species in the parasite's introduced range are more competent hosts than are pythons. We observed higher prevalence, higher intensity, larger female body size, and greater proportion of adult female *R. orientalis* in populations of native snakes than in pythons. This has enabled native snakes to spread *R. orientalis* outside the known range of pythons and approximately 350 km farther north than the northernmost infected python observed in this study. The prevalence of *R. orientalis* among native snakes collected from the python invasion front did not differ from that of native snakes collected from the core of the python's distribution. Yet, the prevalence in native snakes from both these regions was significantly higher than in pythons, again suggesting that *R. orientalis* is spread more effectively through native snake hosts, which may present a risk to native species well beyond the physiological/climatic restraints potentially limiting the northward expansion of pythons (Rodda et al. 2011). Farrell et al. (2019) recently observed *R. orientalis* in a sample of three pygmy rattlesnakes (*Sistrurus miliarius*) in Volusia County, Florida, and their observation extends the range of *R. orientalis* approximately 33 km northeast from the northernmost native snake infected with *R. orientalis* observed in this study. These observations support that *R. orientalis* can expand its range independent of the presence of pythons. We did not recover *R. orientalis* during extensive sampling of native snakes from Alachua County northward, indicating that the invasion front of this nonnative parasite may reside between Alachua County south to Lake and Volusia counties.

Our data suggest that native snakes within certain foraging modes (e.g., terrestrial ambush predators, terrestrial wide-foraging non-constrictors, aquatic non-constricting frog eaters) are more competent hosts of *R. orientalis* than native snakes within other foraging modes (e.g., aquatic non-constricting fish eaters) and pythons.

For host species (*A. piscivorus*, *C. constrictor*, *N. clarkii*, *N. fasciata*, and *T. sirtalis*) with a sample size greater than 10 individuals examined from the core region, we observed the prevalence of *R. orientalis* to be 50% or greater indicating that these species may be drivers of parasite infection patterns observed in this study. These highly competent native hosts, which are already at increased risk of infection, heighten the likelihood of *R. orientalis* transmission compared with less competent native snake hosts. We infer that the reservoir of intermediate hosts used by *R. orientalis* in Florida explains differences in competency among infected native snake species. Dietary patterns of native snakes suggest that fish are unlikely to be an important intermediate host but that frogs are likely to serve this role. Kelehear et al. (2014) reached a similar conclusion regarding the role of anurans in transmitting *R. orientalis* to snakes native to Australia. Miller et al. (2018) first documented *R. orientalis* larvae collected from mammals, which may serve as critical intermediate hosts that promoted the establishment of this parasite within the founding population of pythons. However, both correlative and experimental studies strongly suggest that mammal populations have been reduced or eliminated within the core range of pythons in Florida due to predation by this invasive snake (Dorcas et al. 2012, McCleery et al. 2015, Sovie et al. 2016). Therefore, the low prevalence of *R. orientalis* in pythons, as well as within mammal-eating native snakes (terrestrial wide-foraging constrictors), may result from the reduction in mammal populations that serve as intermediate hosts. If this is true, *R. orientalis* eventually should become more prevalent in terrestrial wide-foraging constricting snakes as the parasite expansion outpaces the effect of pythons on native mammals. Regardless, the pool of intermediate hosts used by *R. orientalis* appears to be diverse and crucial to its rapid range expansion in native snakes.

Our results indicate that several native snake species are unlikely to be infected by *R. orientalis*. Many of these will require additional samples to eliminate the possibility that the parasite is present in the species but not detected in current samples. For example, *R. orientalis* was not detected in our sample of six *Crotalus adamanteus*, a large mammal-consuming ambush predator. However, Metcalf et al. (2019) recently documented several *R. orientalis* collected from *C. adamanteus* in southwest Florida (Lee County), increasing the total number of native snake species infected with *R. orientalis* to 14. Yet, it seems unlikely that the prevalence will be as high in *C. adamanteus* as it is in other sympatric ambush predators with broader diets. An absence of *R. orientalis* in samples of *Liodytes* and *Storeria* suggests that native invertebrates are unlikely to serve as intermediate hosts. Similarly, our failure to detect the parasite in *Farancia abacura* suggests that aquatic salamanders also are unlikely to serve as intermediate hosts.

When an immunologically naïve host is infected with a nonnative parasite, virulence is predicted to increase, leading to a reduction in host fitness (Combes 2001, Matitsky et al. 2010). Over time, as the nonnative parasite and naïve host coevolve, the host may adapt to either resist infection or to develop tolerance toward infection, allowing the host to mitigate harmful effects (Best et al. 2008, Svensson and Raberg 2010). Effects of pentastome infection on coevolved hosts may include scarring of lung tissue, hemorrhage, infection, pneumonia, reduced reproductive output, adverse effects on metabolic rate, and blockage of respiratory passageways (Pence and Selcer 1988, Riley 1986, Paré 2008, Caballero et al. 2015). These effects may be augmented in naïve hosts, leading to lethal or sublethal effects that result in reduced host fitness and ultimately host population declines, particularly when parasite prevalence and intensity are high within a naïve host. The snake hosts representing the highest prevalence, intensity, proportion of adult females, and female body size of *R. orientalis* are among the most ubiquitous and widely dispersed snakes in the United States (e.g., *A. piscivorus*, *N. fasciata*, and *T. sirtalis*). If *R. orientalis* continues to spread northward independent of pythons, it has the potential to adversely affect snakes throughout North America and possibly beyond. Farrell et al. (2019) suspected three pygmy rattlesnakes (*S. miliarius*) they observed infected with *R. orientalis* died as a result of infection by this parasite, and the authors extrapolate that *R. orientalis* may be responsible for purported declines in pygmy rattlesnake populations in southern Florida. Additional studies

examining the cost of infection to host fitness are needed to fully understand the impact this non-native pentastome may have on native snake populations.

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