

Elucidating mechanisms of invasion success: Effects of parasite removal on growth and survival rates of invasive and native frogs

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Funding information

U.S. Environmental Protection Agency, Grant/Award Number: CAREER 83518801; National Science Foundation, Grant/Award Number: EF-1241889; National Institutes of Health, Grant/Award Number: R01GM109499 and R01TW010286; U.S. Department of Agriculture, Grant/Award Number: 2009-35102-0543 and NRI 2006-01370

Handling Editor: Don Driscoll

Abstract

1. Identifying the mechanisms underlying biological invasions can inform the management of invasive species. The enemy release hypothesis (ERH) suggests that invasive species have a competitive advantage in their introduced range because they leave behind many of their predators and parasites from their native range, allowing them to shift resources from defences to growth, reproduction and dispersal. Many studies have demonstrated that invasive species have fewer parasites than their native counterparts, but few studies have tested whether the loss of these natural enemies appears to be a primary driver of the invasion process.
2. To test the ERH, we conducted a mark-recapture study in which we used an anthelmintic drug to successfully reduce parasitic worms in invasive Cuban treefrogs *Osteopilus septentrionalis* and native treefrogs (*Hyla* spp.) at half of 12 wetlands, marking nearly 4,200 frogs. If the ERH is supported, we would expect that treating for parasitic worms would have a greater benefit to native than invasive hosts.
3. Growth and survival rates of invasive and native treefrogs responded similarly to the anthelmintic treatment, suggesting that the Cuban treefrog's release from parasitic worms does not appear to significantly contribute to its invasiveness in established areas. Instead, it appears that the overall faster rates of growth and maturation, higher survival rates and larger body sizes of Cuban treefrogs that we observed may contribute to their expansion and proliferation.
4. *Synthesis and applications.* Although Cuban treefrogs have a lower diversity of parasitic worms in their invasive than native range, this does not appear to significantly contribute to their invasion success in areas where they have been established for more than 20 years. This suggests that any manipulation of parasites in invasive or native hosts would not be an effective method of controlling Cuban treefrogs or reducing their impacts. Further research into other hypotheses is needed to explain the Cuban treefrog's success and help guide management actions to reduce their spread and negative impacts. Our study demonstrates that enemy release may not be a primary driver of invasiveness, highlighting the need for more experimental tests of the enemy release hypothesis to examine its generality.

KEY WORDS

Cuban treefrog, enemy release, growth, host–parasite interactions, introduced species, mark–recapture, parasite removal, survival

1 | INTRODUCTION

Biological invasions alter community structure and threaten biodiversity worldwide (Mack et al., 2000; Sakai et al., 2001; Vilà et al., 2011). Identifying the mechanisms underlying the invasion process can inform management decisions to reduce the abundance and spread of invasive species and their impacts on invaded communities. The enemy release hypothesis (ERH) provides one mechanism of invasion success by suggesting that introduced species can leave behind predators and parasites from their native range, allowing them to invest fewer resources in defences against natural enemies (Mitchell & Power, 2003; Torchin, Lafferty, Dobson, McKenzie, & Kuris, 2003). This allows greater investment into growth, reproduction and other traits that allow them to outcompete native species. Many studies have observed enemy loss by comparing enemies (or their impacts) in invasive and native species in the same habitat (the community approach) or between an invasive species' native and introduced ranges (the biogeographical approach; Colautti, Ricciardi, Grigorovich, & MacIsaac, 2004; Liu & Stiling, 2006; Meijer, Schilthuizen, Beukeboom, & Smit, 2016; Prior, Powell, Joseph, & Hellman, 2015), including several studies on introduced amphibians (Marr, Mautz, & Hara, 2008; Ortega, Price, Campbell, & Rohr, 2015; Schoeman, Kruger, Secondi, & du Preez, 2019). However, few studies on any taxa have tested whether the loss of natural enemies can account for the competitive advantage of invaders by using manipulative experiments to exclude natural enemies and measure effects of their loss. This experimental approach has been largely restricted to terrestrial plants and has yielded mixed results (DeWalt, Denslow, & Ickes, 2004; Genton, Kotanen, Cheptou, Adolphe, & Shykoff, 2005; MacDonald & Kotanen, 2010; Schierenbeck, Mack, & Sharitz, 1994; Schutzenhofer, Valone, & Knight, 2009; Williams, Auge, & Maron, 2010), emphasizing the need to further test this hypothesis experimentally—especially for animals in the wild.

Fully understanding the generality of the ERH and how support for it varies by taxa, time since invasion, and other abiotic and biotic factors can inform management decisions to control invasive species and reduce their impacts. For example, if enemy release is demonstrated to be a mechanism of invasiveness, restoring missing enemies to the invader could help control populations and limit their spread, provided that these enemies will not harm native species. This strategy has been suggested to control invasive cane toads *Rhinella marina* in Australia by introducing missing lungworms to toads at the invasion front, which reduce viability of cane toads, their natural hosts, but not native frogs (Pizzatto & Shine, 2012). Alternatively, treating native species could be an effective strategy for improving their ability to compete with the invader. However, if enemy release is ruled out as a cause for invasiveness, then other mechanisms and control options would need to be investigated. Researchers often use antiparasitic drug treatments to examine the consequences of parasitic infections on animal hosts

(Pedersen & Fenton, 2015). This approach can be applied to test the ERH by using antiparasitic drugs to kill parasites in invasive and native individuals, and then comparing the responses (e.g. growth and survival rates) of treated individuals relative to control individuals carrying natural parasite loads. If the ERH is supported, the benefit of parasite removal for native hosts will be greater than for invasive hosts because of native hosts' greater investment in defences against parasitism.

Several studies have observed reduced parasite diversity in introduced amphibians (Marr et al., 2008; Ortega et al., 2015; Schoeman et al., 2019), but none have experimentally tested it as a mechanism of invasiveness. We conducted a 1-year mark–recapture study, in which we used an anthelmintic drug to remove parasitic gut worms from invasive Cuban treefrogs *Osteopilus septentrionalis* and native treefrogs (*Hyla* spp.) in Florida, USA, to investigate whether the loss of parasites in the Cuban treefrog contributes to its invasion success. The Cuban treefrog is native to several Caribbean island groups and was first reported in Florida in 1931 and in our study region (Hillsborough County) in 1996 (Barbour, 1931; Meshaka Jr., 1996). Cuban treefrogs negatively impact native amphibians in Florida through competition and predation (Glorioso, Waddle, Crockett, Rice, & Percival, 2010; Knight, Parris, & Gutzke, 2009; Meshaka Jr., 2001; Rice et al., 2011; Smith, 2005; Tennessen, Parks, Tennessen, & Langkilde, 2016; Wyatt & Forsy, 2004). Cuban treefrogs have a lower helminth species richness in Florida than in their native range, which is consistent with the ERH (Ortega et al., 2015). We predicted that parasite removal would increase growth and survival rates relative to control individuals, and that this response would be stronger in native than invasive species because natives might be investing more in parasite defences. Our findings can be used to guide management decisions and further research into mechanisms underlying the invasion of the Cuban treefrog.

2 | MATERIALS AND METHODS

2.1 | Field methods

Our study took place at 12 wetlands in Flatwoods Wilderness Park, near Tampa, Florida, USA. These wetlands were dominated by bald cypress *Taxodium distichum* and held water continuously during summer months (July–September) and intermittently during other times of the year after heavy rainfall. Wetland size varied from 2,048 to 13,897 m² in area and 172 to 503 m in perimeter at the high-water level. The 12 wetlands were located 129–2,294 m from one another, and an average of 284 m from the nearest wetland (range: 129–901 m). To attract treefrogs, we installed polyvinyl chloride (PVC) pipes (diameter: 3.8 cm, length: 1 m) vertically into the ground at 3-m intervals around each wetland at the high-water mark. We installed a total of 1,170 PVC pipes, with an average of 98 pipes per wetland

(range: 57–168 pipes). We recorded weather data throughout the study using temperature dataloggers and rain gauges.

We sampled all PVC pipes for treefrogs every 2 weeks for 1 year (October 2015–September 2016). Frogs were removed from pipes by gently coaxing them into resealable plastic bags using a ‘plunger’ constructed from a paint roller attached to an aluminium rod. Each frog was marked individually using a visible implant alpha tag (Northwest Marine Technology, Inc.) inserted into the femoral lymph sac in the left hindlimb. We treated all captured frogs at six wetlands for helminth parasites using an oral dose of the anthelmintic drug Ivermectin (Vetrimec, MWI Animal Health) diluted with propylene glycol and administered at a dosage of 0.2 mg/kg (2.5–24 μ l of solution). The other six wetlands served as control sites; frogs at these sites received a sham treatment of propylene glycol in the same amount as frogs that received the drug. Frogs received drug or sham treatments at each capture or at a maximum frequency of once per month. Ivermectin is effective against both arthropod and helminth endoparasites and ectoparasites in amphibians and other taxa (Densmore & Green, 2007; Panayotova-Pencheva, 2016; Walker & Whitaker, 2000). Although our study focused on gastrointestinal (GI) worms, our drug treatment also may have reduced other parasites. At each capture, we recorded each frog's tag identification code, species identity, snout–vent length (SVL), mass and sex when possible. Sex could only be determined in adult frogs during the breeding season (by the presence of nuptial pads or eggs), except for large female Cuban treefrogs that could be distinguished by size throughout the year (≥ 60 mm SVL).

2.2 | Parasites observed and effectiveness of the anthelmintic drug

To identify parasite species and assess the effectiveness of the anthelmintic drug in reducing parasite loads, we quantified helminths present in the GI tracts and faecal samples of invasive and native frogs. See Appendix S1 for details on these methods.

2.3 | Survival and recapture probabilities

We used Cormack–Jolly–Seber (CJS) models to estimate survival and recapture probabilities. CJS models cannot distinguish between mortality and dispersal, and therefore estimate ‘apparent survival’, which is the product of the probabilities of true survival and study site fidelity. Each CJS model separately estimates the probabilities of survival and recapture. We fitted CJS models in which survival and recapture probabilities were held constant, varied over time, or varied by treatment (anthelmintic drug or sham), species, SVL, the interaction of time and species, or the interaction of treatment and species. We included models with all possible combinations of these variables. We assessed the fit of CJS models by comparing their AICc values. Analyses were performed in MARK (White & Burnham, 1999) and executed using the R_{MARK} package (Laake, 2013) in R software. After we obtained survival and recapture probabilities from the top

model, we used linear models (*lm* function) in R software to examine how these probabilities were affected by temperature (average temperature during the 2-week period prior to each sample), precipitation (total amount during the 2-week period prior to each sample), species and interactions among these variables.

2.4 | Growth rates

We used a linear mixed-effects model (*lme* function in package NLME, R software) to examine the main and interactive effects of the anthelmintic drug, species, starting season and starting SVL on monthly growth rates. For frogs that were recaptured more than once during our study, we included each growth interval between recaptures, rather than using one growth interval between initial capture and final recapture for each frog. We included frog and field site identity as random effects in the model to account for possible differences in growth rates among frogs or sites. Probability values were calculated using the *Anova* function in the CAR package in R software. We constructed partial residual plots to examine the relationships between variables using the *visreg* function in the VISREG package in R software.

To generate age–size relationships to display growth curves and estimate time to sexual maturity, we fitted mark–recapture data to von Bertalanffy growth models (Fabens, 1965). We used the non-linear, least-squares regression procedure (Nonlinear fit, JMP software) to fit von Bertalanffy growth models, where the parameters for intrinsic growth rate and asymptotic body size were first seeded with initial best guesses (Webb, Pike, & Shine, 2008). These models are unable to incorporate or test the significance of covariates, such as the effects of treatment, species, season, individuals and sites that we included in our linear mixed-effects model. Therefore, we used separate von Bertalanffy growth models for different treatments and species, and we included one growth interval between initial capture and final recapture for each frog, rather than including each growth interval between recaptures. We used the results from these models to generate age–size relationships (Frazer, Gibbons, & Greene, 1990; Webb et al., 2008). The mean SVL for newly metamorphosed frogs of each species (18 mm), and the mean SVL at sexual maturity for male Cuban treefrogs (40 mm), female Cuban treefrogs (60 mm) and both sexes of native treefrogs (30 mm) were determined for our populations by our mark–recapture dataset.

3 | RESULTS

3.1 | Frog captures

We captured four species during our study: Cuban treefrogs *O. septentrionalis*, green treefrogs *Hyla cinerea*, pinewoods treefrogs *Hyla femoralis* and squirrel treefrogs *Hyla squirella*. We marked a total of 4,191 individual frogs, and recaptured 2,216 (53%) of these frogs at least once (range: 1–21 recaptures), for a total of 11,004 captures during the study. We recaptured 1,732 of 3,258 (53%)

Cuban treefrogs, 12 of 19 (63%) green treefrogs, 173 of 361 (48%) pinewoods treefrogs and 299 of 553 (54%) squirrel treefrogs. The Cuban treefrog was the dominant species and accounted for 78% of all individual frogs marked and 79% of total captures. Because green treefrogs were rarely encountered and not captured at all sites, this species was excluded from further analyses. We did not detect any dispersal between wetlands (mean nearest neighbour distance: 284 m; range: 129–901 m); all recaptured frogs were found at the wetlands at which they were first captured and marked.

3.2 | Parasites observed and effectiveness of the anthelmintic drug

We observed fewer species of parasites in Cuban treefrogs than has been reported in their native range (Appendices S1 and S2). The nematode *Aplectana hamatospicula* was the dominant parasite, accounting for 97% of all parasites recorded. The anthelmintic drug successfully reduced worm loads in invasive and native species (Appendix S1; Tables S1 and S2; Figures S1 and S2).

3.3 | Survival and recapture probabilities

Survival and recapture probabilities for the two native species commonly captured in our study (pinewoods treefrogs and squirrel treefrogs) were similar (Figure S3); therefore, we combined these two species into one group and compared them to the invasive

species. Of the 161 CJS models that we fitted to examine factors affecting probabilities of survival and recapture in native and invasive frogs, we obtained one model with $\Delta AICc < 2$ that accounted for 96% of model weight and suggests that frog survival was affected by time, the anthelmintic drug, species, and SVL (Figure 1; Table S3), and recapture rates were affected by SVL and the interaction between time and species (Figure 2; Table S3). None of the other models we tested were strongly supported by our data (Table S3); the $\Delta AICc$ for the second-ranked model was 7.045, which is well above the recommended cut-off of 2 $\Delta AICc$ (Burnham & Anderson, 2002).

Two-week apparent survival probabilities varied over time (range: 21%–98%, Figure 1a), were higher for the invasive than native species by an average of 8% (Figure 1b) and were negatively related to SVL (Figure 1c). Survival probabilities were also higher in frogs that were treated with the anthelmintic drug than the sham treatment, by an average of 1.4% (Figure 1d); the drug had similar effects on native and invasive frogs (no support for an interaction between species and treatment; Table S3). Survival probabilities for native and invasive species were similarly affected by weather (Figure 1a; Table S4); survival probabilities were negatively related to both temperature and precipitation, indicating that survival was highest during winter (cool, dry conditions) and lowest during summer (warm, wet conditions). Direct observations of mortality were rare; we found 10 dead Cuban treefrogs inside PVC pipes, and three of these were found during the coldest sampling period of the study.

Recapture probabilities were affected by the interaction between time and species (Figure 2a; Table S3) and were positively related to SVL (Figure 2b; Table S3). Recapture probabilities were

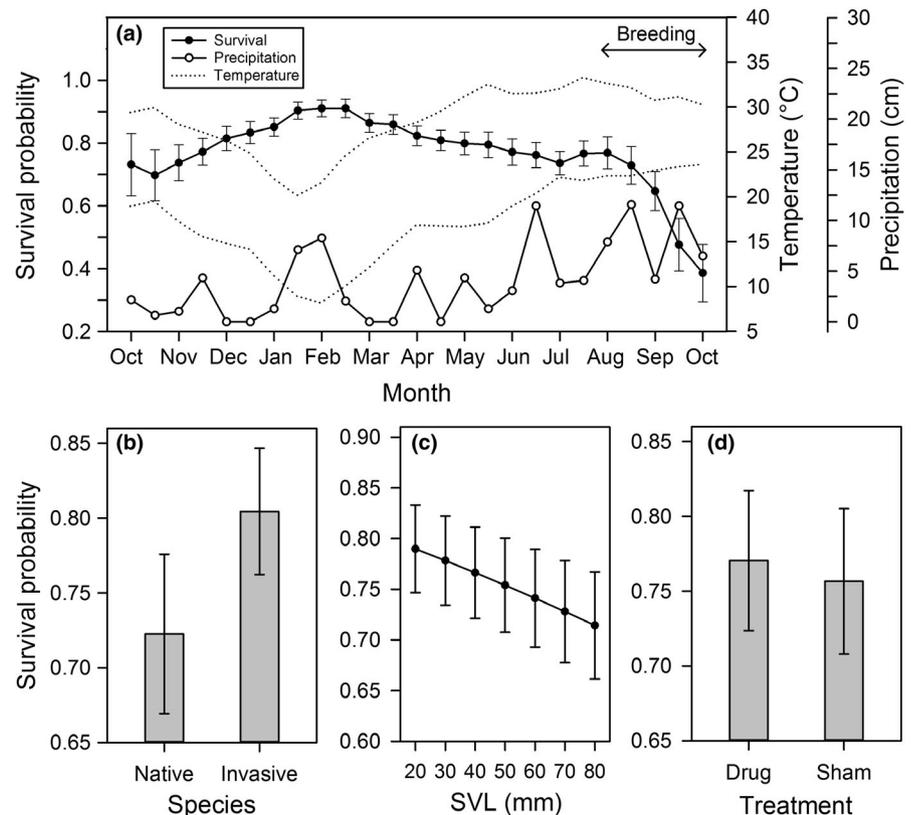


FIGURE 1 Two-week survival probabilities (\pm SE) from the top Cormack–Jolly–Seber model (a) over a 1-year period, averaged across species and treatments and controlling for snout–vent length (SVL; each survival probability is shown as a moving window by averaging the previous, current and subsequent probabilities; also shown are the average daily minimum and maximum temperatures and the total amount of precipitation received during the 2-week period prior to each sample), (b) for invasive and native treefrogs, averaged across time and treatments and controlling for SVL, (c) for frogs of different body sizes (SVL), averaged across time, species, and treatments and (d) for frogs treated with an anthelmintic drug or sham, averaged across time and species and controlling for SVL

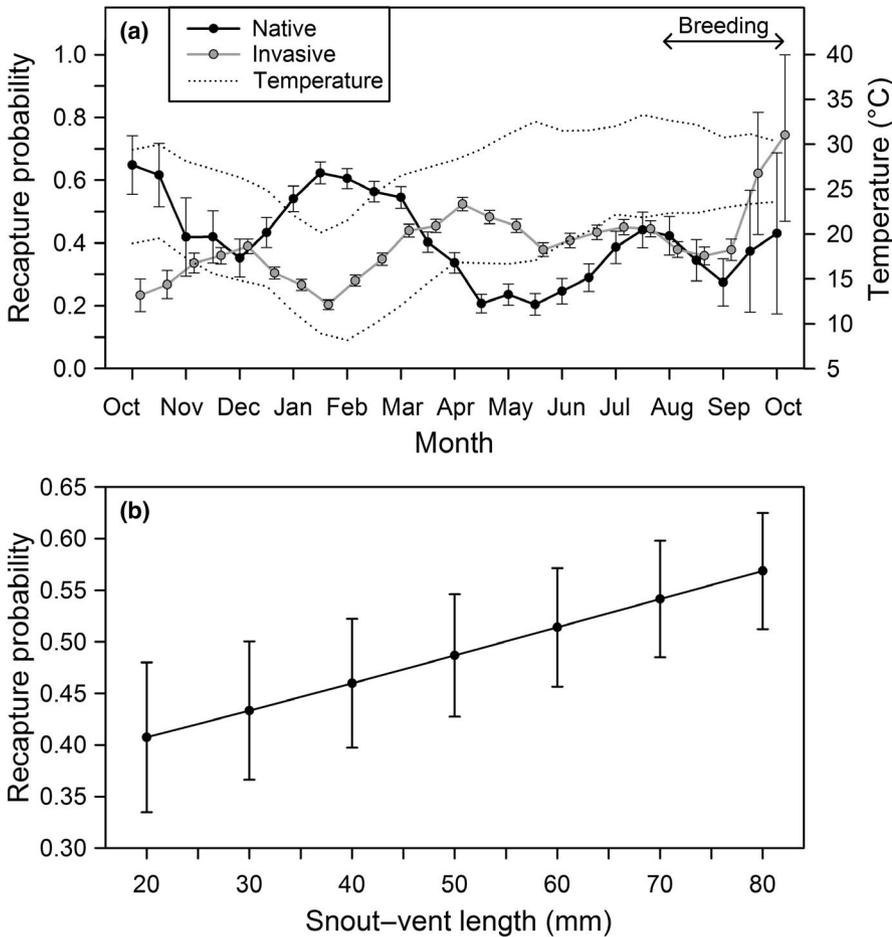


FIGURE 2 Two-week recapture probabilities (\pm SE) from the top Cormack-Jolly-Seber model (a) over a 1-year period for invasive and native treefrogs showing the interaction between time and species and controlling for snout-vent length (SVL; each recapture probability is shown as a moving window by averaging the previous, current and subsequent probabilities. Dotted lines show the average daily minimum and maximum temperatures for the 2-week period prior to each sample) and (b) the positive relationship between recapture probability and SVL

largely driven by seasonal changes in temperature; they were affected by the interaction between temperature and species, but were not affected by precipitation (Table S5; Figure 2a). Temperature was positively related to recapture rates in the invasive species and negatively related to recapture rates in the native species (Figure 2a). This indicates that recapture rates were lowest for invasive frogs and highest for native frogs in winter, and highest for invasive frogs and lowest for native frogs in summer.

3.4 | Growth rates

We examined 2,351 growth intervals from 674 female Cuban treefrogs, 1,890 growth intervals from 488 male Cuban treefrogs, 454 growth intervals from 175 pinewoods treefrogs and 915 growth intervals from 303 squirrel treefrogs. Growth rates for the two native species were similar (Table S6); therefore, we combined these species into one group and compared them to the invasive species. Growth rates were analysed separately for each sex of the invasive species because of the strong sexual size dimorphism present in this species (McGarrity & Johnson, 2009; Meshaka Jr., 2001; Vargas-Salinas, 2006). Our linear mixed-effects model indicated that monthly growth rates were influenced by the three-way interaction among species (and sex in Cuban treefrogs), season and starting SVL (Table 1; Figure 3). Overall, the invasive species grew faster than the native

TABLE 1 Statistical results from a linear mixed-effects model that tested for the main and interactive effects of treatment (anthelmintic drug or sham), species (invasive female, invasive male, native), starting season (spring, summer, autumn, winter) and starting snout-vent length (SVL) on monthly growth rate. Individual and field site identity were used as random effects. Significant probability values are shown in bold typeface

Effects	χ^2	df	p
Treatment	0.0455	1	0.8310
Species	633.7580	2	<0.0001
Season	997.5239	3	<0.0001
SVL	236.5778	1	<0.0001
Treatment \times Species	2.2398	2	0.3263
Treatment \times Season	0.0119	3	0.9997
Species \times Season	210.9858	6	<0.0001
Treatment \times SVL	0.1691	1	0.6809
Species \times SVL	55.7681	2	<0.0001
Season \times SVL	162.8786	3	<0.0001
Treatment \times Species \times Season	1.6849	6	0.9463
Treatment \times Species \times SVL	0.6505	2	0.7223
Treatment \times Season \times SVL	6.3349	3	0.0964
Species \times Season \times SVL	24.6782	6	0.0004
Treatment \times Species \times Season \times SVL	1.8977	6	0.9289

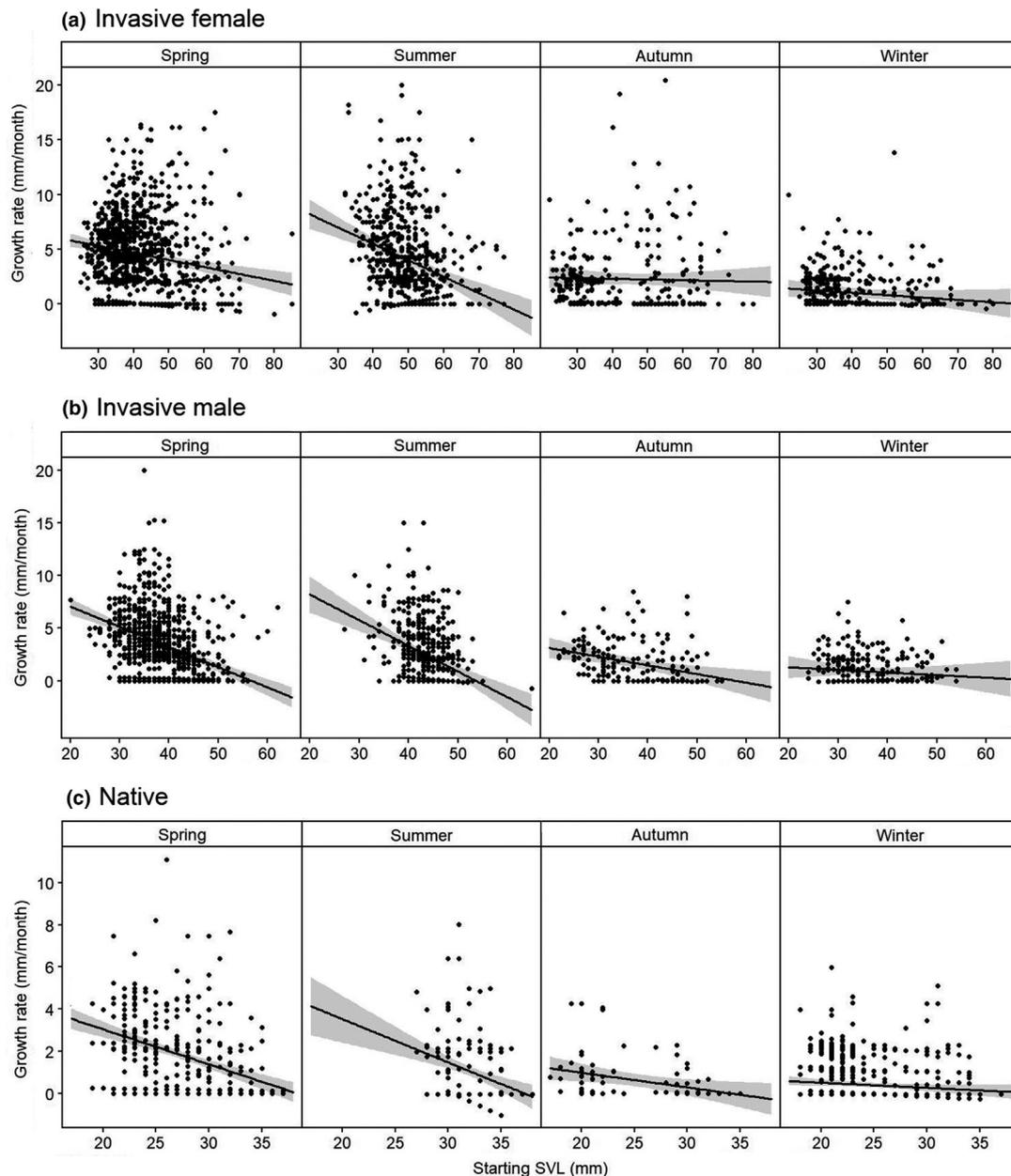


FIGURE 3 Partial residual plots with 95% confidence bands (shaded) showing the interactive effects of species, starting season, and starting snout-vent length (SVL) on monthly growth rates. Species groups are (a) invasive female treefrogs, (b) invasive male treefrogs, and (c) native treefrogs

species, and all species grew faster in summer and spring than in winter and autumn. Growth rates were negatively related to starting body size, but the strength of this relationship differed among species and seasons. This relationship was stronger during seasons with higher growth rates (summer and spring) than in seasons with lower growth rates (winter and autumn). Growth rates were not affected by the anthelmintic drug or any interactions involving the drug (Table 1).

We fitted von Bertalanffy growth models to our data to generate age-size relationships to display growth curves and to estimate time to sexual maturity. These models indicated that Cuban treefrogs reached a larger average maximum size than native frogs during our study, and Cuban treefrogs also showed a large degree of sexual size dimorphism, with females reaching larger body sizes

than males (Table 2; Figure 4). Although our von Bertalanffy growth models cannot be compared quantitatively, they agreed with our linear mixed-effects model that the invasive species grew faster than the native species. However, they also suggested that invasive males grew slightly faster than invasive females when not controlling for seasonality (Table 2). The von Bertalanffy growth models also support the results of our linear mixed-effects model that growth rates were not affected by the anthelmintic drug (Figure 4). The models predicted that invasive females that received the drug reached a slightly larger body size than invasive females that received the sham treatment (Table 2; Figure 4); however, this result was likely caused by a larger maximum body size of females present at drug sites than sham sites (90 and 80 mm, respectively) at first capture, before

TABLE 2 Results from von Bertalanffy growth models fitted to snout-vent length (SVL) growth data from invasive (separate for each sex) and native species. Shown are the intrinsic growth rate and asymptotic SVL (mm), and associated standard errors

Species	Sex	Treatment	Growth rate (SE)	Asymptotic SVL (SE)
Invasive	Female	Drug	0.099 (0.011)	76.4 (3.1)
Invasive	Female	Sham	0.129 (0.016)	68.2 (2.7)
Invasive	Male	Drug	0.234 (0.018)	51.3 (0.7)
Invasive	Male	Sham	0.257 (0.022)	51.1 (0.7)
Native	Both	Drug	0.071 (0.010)	40.9 (1.9)
Native	Both	Sham	0.065 (0.013)	41.0 (2.9)

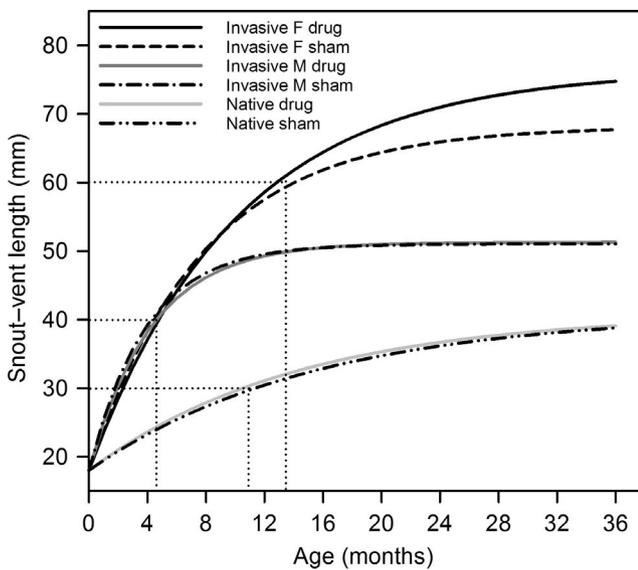


FIGURE 4 Relationship between age and snout-vent length for invasive male and female Cuban treefrogs and native treefrogs that were treated with an anthelmintic drug or sham. The von Bertalanffy growth model was used to fit mark-recapture data for all groups. Dotted lines indicate age and body size at sexual maturity

treatments were administered. The length of time required from metamorphosis to sexual maturity (Figure 4), averaged across treatments, was shortest for invasive males (4.5 months to reach 40 mm), longest for invasive females (13.4 months to reach 60 mm) and intermediate for the native species (10.9 months to reach 30 mm).

4 | DISCUSSION

After observing that Cuban treefrogs have fewer helminth species in their introduced than native range (Appendix S2; Ortega et al., 2015),

we experimentally tested whether this enemy release contributes to their invasiveness. We hypothesized that reducing worm loads would increase growth and survival rates in all species relative to controls, and that this response would be stronger in native than invasive species because native species might be investing more in parasite defences. Although our drug treatment successfully reduced parasite loads (Appendix S1; Tables S1 and S2; Figures S1 and S2), invasive and native species responded similarly to the anthelmintic drug; these patterns are not consistent with enemy release facilitating the invasion. Other experimental tests of the ERH have been largely restricted to terrestrial plants and have yielded mixed results. Field experiments have shown that although invasive plants often experience less damage from herbivores and pathogens than native plants, and less damage in their introduced than native range, their enemy release is not consistently associated with improved individual fitness or population growth rates (DeWalt et al., 2004; Genton et al., 2005; MacDonald & Kotanen, 2010; Schierenbeck et al., 1994; Schutzenhofer et al., 2009; Williams et al., 2010).

Native and invasive frogs could have had similar responses to the anthelmintic treatment if they carried similar parasite loads. Although we observed lower species richness in Cuban treefrogs post-invasion, there appear to be similar worm abundances in their introduced (12.1 in our study, 14.7 in Ortega et al., 2015) and native (4.6 in Coy Otero & Ventosa, 1984, 12.7 in Goldberg, Bursley, & Tawil, 1994) ranges. In addition, seven helminth species have been reported from squirrel treefrogs in the wild, although some may not have occurred in the GI tract (Connier, Fulmer, McAllister, Trauth, & Bursley, 2014), which is similar to the eight helminths found in introduced Cuban treefrogs in our study area (Appendix S2). We found similar numbers of juvenile worms shed in faecal samples of native and invasive frogs (Table S2; Figure S2), suggesting that the abundance of adult worms parasitizing the frogs may also be similar. Another potential explanation for our results is differences in parasite virulence between frog species; however, native and invasive frogs experimentally infected by *A. hamatospicula*, the dominant parasite in our study, both lost weight relative to controls, suggesting that virulence might be similar (Knutie, Wilkinson, Wu, Ortega, & Rohr, 2017; Ortega, 2018). Overall, based on data from our study and the literature, it appears possible that the response of native frogs to the anthelmintic drug was similar to that of invasive frogs because they were just as heavily parasitized.

Anthelmintic treatments increased 2-week survival rates by 1.4% (Figure 1d; Table S3), which compounds to a maximum of 2.4% after 2 months, and did not affect growth rates (Tables 1 and 2; Figures 3 and 4). These small effects of parasitic worms on hosts were unexpected, given the potential costs of parasitic infections on hosts as host resources are consumed directly by parasites and additional energy is lost to immune defences and repair of tissues damaged by feeding, attachment and migration (Bonneaud et al., 2003; Civitello, Allman, Morozumi, & Rohr, 2018; Civitello, Fatima, Johnson, Nisbet, & Rohr, 2018; Cressler, Nelson, Day, & McCauley, 2014; Medzhitov, Schneider, & Soares, 2012). Frogs may have been able to compensate for energy lost to worms by increasing their food intake, as has

been shown experimentally in captive Cuban treefrogs that were parasitized by *A. hamatospicula* (Knutie et al., 2017). Although our study species appear to tolerate their gut parasites, our findings may underestimate the costs of parasitic worms on frog growth and survival rates because our drug treatment did not completely eliminate parasites in all frogs, partly due to high reinfection rates. The life cycle of *A. hamatospicula* facilitates high infection rates because juvenile worms are shed through faeces and infect the same or new hosts by penetrating the skin and migrating to the large intestine (Knutie et al., 2017).

Two-week survival probabilities varied over time (21%–98%) and were highest during winter (cool, dry) months and lowest during summer (warm, wet) months (Figure 1a; Tables S3 and S4). These are 'apparent' survival probabilities, which are the product of the probabilities of true survival and study site fidelity. During warmer and more humid weather, frogs are more active (McGarrity & Johnson, 2010; Meshaka Jr., 2001), which could increase both dispersal rates and predator exposure at breeding ponds and in surrounding terrestrial habitat. Conversely, frogs are less active and should have higher site fidelity and lower predation rates during cooler and drier weather, when survival rates were estimated to be higher. Although low temperatures can cause mortality of invasive Cuban treefrogs that are adapted to a warmer climate (Haggerty & Crisman, 2015), freezing temperatures were rare during our study, and consequently, winter mortality rates were estimated to be low.

Survival probabilities were higher overall for invasive than native species, by an average of 8% (Figure 1b). This could be caused by lower predatory or competitive pressure on Cuban treefrogs than native treefrogs. Because Cuban treefrogs compete with native treefrogs and prey on them, lower survival rates in the native species could be caused by a combination of competition and predation by this much larger competitor (Glorioso et al., 2010; Meshaka Jr., 2001; Rice et al., 2011; Wyatt & Forsy, 2004). Alternatively, because our model cannot distinguish between mortality and dispersal, it is possible that invasive frogs have higher fidelity to the PVC pipes that we used to sample them. Although we did not document any individuals moving between our study wetlands, they could have moved elsewhere. Two-week survival probabilities were fairly low overall, averaging 80% for invasive frogs and 72% for native frogs. When compounded over time, annual survival probabilities were less than 1% for all species, suggesting that they have high dispersal rates or short life spans.

Although the survival probabilities of native and invasive species varied similarly throughout the year, their recapture probabilities varied strikingly (Figure 2a; Table S3). Recapture rates were largely driven by seasonal changes in temperature but were not affected by precipitation (Table S5; Figure 2a). Temperature was positively related to recapture rates in the invasive species and negatively related to recapture rates in the native species (Figure 2a). Overall, recapture rates were lowest for invasive frogs and highest for native frogs in winter, and highest for invasive frogs and lowest for native frogs in summer. These patterns could be caused by shifts in habitat use and/or competition between native and invasive frogs for shelter sites.

Invasive Cuban treefrogs are adapted to a tropical climate and are more vulnerable to low temperatures and dry conditions than native treefrogs (Haggerty & Crisman, 2015; Roznik, Rodriguez-Barbosa, & Johnson, 2018), so their low recapture rates during winter could be caused by a shift in habitat use from PVC pipe refugia to warmer, moister shelters, such as burrows or crevices in vegetation. The corresponding high recapture rates of native frogs during winter could also reflect a habitat shift, potentially caused by decreased competitive pressure from invasive frogs for PVC pipes. Removing Cuban treefrogs from an area increased the estimated abundance of native treefrogs (Rice et al., 2011), supporting this hypothesis. Recapture probabilities were positively related to body size (Figure 2a), suggesting that larger frogs have higher site fidelity or exclude smaller frogs from pipes. Further research on movements, habitat selection and competitive interactions between these species would help elucidate these patterns.

Another important difference between native and invasive species that our study revealed is variation in growth rates. Overall, the invasive species grew much faster than the native species, and both sexes also reached larger body sizes (Tables 1 and 2; Figures 3 and 4). The invasive species showed a large degree of sexual size dimorphism, with females reaching much larger body sizes than males (Table 2; Figure 4), as previously reported (McGarrity & Johnson, 2009; Meshaka Jr., 2001; Vargas-Salinas, 2006). Invasive males reached sexual maturity in less than half the time (4.5 months) required for native males to mature (10.9 months). Female Cuban treefrogs reached maturity after 1 year (13.4 months) at a body size that is at least twice that of mature native females, which facilitates large clutch sizes averaging 4,000 eggs (Meshaka Jr., 2001; Vargas-Salinas, 2006). The rapid growth and maturation and high fecundity of Cuban treefrogs contribute to their invasion success by allowing them to rapidly colonize new areas and reach high densities.

At least 174 amphibian species have been introduced at least once outside of their native ranges, with over 50% of these species establishing populations (Kraus, 2009). These introductions have resulted in a broad diversity of ecological and evolutionary impacts (Kraus, 2015). Because introduced individuals can carry parasites and pathogens, one significant impact of amphibian introductions is disease transmission to native species (Fisher & Garner, 2007). For example, current evidence suggests that the world trade in amphibians has caused the emergence of the fungal disease chytridiomycosis, which has caused declines in over 500 amphibian species world-wide (Scheele et al., 2019). Amphibians have been transported to new locations unintentionally (e.g. as stowaways on vehicles, boats and transported plants) and intentionally for pets, food, research and biocontrol (Kraus, 2009). Once amphibians and any co-introduced parasites have been introduced to an area, control options are often limited and unsuccessful. Therefore, actions to prevent the introduction and establishment of amphibians and biosecurity measures to prevent disease spread are keys to preserving biodiversity (Fisher & Garner, 2007). As an example, the US Fish and Wildlife Service banned the importation and interstate transport of salamanders in 2016 to prevent introduction of the

deadly fungus *Batrachochytrium salamandrivorans* into the United States.

We did not find strong support for the ERH as a mechanism for the invasion of the Cuban treefrog in an area where they have been established for 20 years. However, we cannot rule out an advantage of enemy release at the invasion front, where this species has a reduced investment in immune defences (Goetz, Romagosa, Appel, Guyer, & Mendonça, 2018). Parasite diversity often increases over time in introduced species because known parasites lag behind their hosts and new parasites have not been acquired yet (Gendron, Marcogliese, & Thomas, 2012; Kołodziej-Sobocińska, Brzeziński, Niemczynowicz, & Zalewski, 2018; Phillips et al., 2010; Schultheis, Berardi, & Lau, 2015). Our findings suggest that any manipulation of parasites in invasive or native hosts in established populations would not be an effective method of controlling Cuban treefrogs. Instead, other mechanisms may facilitate the invasion success of Cuban treefrogs, such as predation of Cuban treefrogs on native treefrogs (Glorioso et al., 2010; Meshaka Jr., 2001; Wyatt & Forsy, 2004), or the life-history traits of Cuban treefrogs that we observed, including faster rates of growth and maturation, higher survival rates and larger body sizes than native treefrogs. Further research into these and other alternative hypotheses is needed to explain the Cuban treefrog's success and help guide management actions to reduce their spread and negative impacts. Our study demonstrates that enemy release may not be a primary driver of invasiveness, highlighting the need for more experimental tests of the ERH to examine its generality.

ACKNOWLEDGEMENTS

We thank Nicole Ortega for assistance with setting up this project, and we thank Keith Ballou, Jessica Cintron-Frett, Megan Handfield, May Ibrahim, Andres Manrique, Nicole Ortega, David Pike, Jenna Pochy, Jake Pristupa, Chloe Ramsay and Talya Rejtman for help with fieldwork. We also thank Jeremy Cohen for help with one of the figures. We are grateful to the Southwest Florida Water Management District for access to Flatwoods Wilderness Park. This research was supported by grants to J.R.R. from the National Science Foundation (EF-1241889), National Institutes of Health (R01GM109499, R01TW010286), US Department of Agriculture (NRI 2006-01370, 2009-35102-0543) and US Environmental Protection Agency (CAREER 83518801). This project was conducted under permit LSSC-15-00014 issued by the Florida Fish and Wildlife Conservation Commission, and protocol WIS00000587 approved by the Institutional Animal Care and Use Committee at the University of South Florida.

AUTHORS' CONTRIBUTIONS

E.A.R. and J.R.R. designed the study; E.A.R., K.L.S. and N.C. collected the data; E.A.R. analysed the data with support from J.R.R.; E.A.R. wrote the first draft of the manuscript. All authors contributed to the final manuscript and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.nvx0k6dp0> (Roznik, Surbaugh, Cano, & Rohr, 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Roznik EA, Surbaugh KL, Cano N, Rohr JR. Elucidating mechanisms of invasion success: Effects of parasite removal on growth and survival rates of invasive and native frogs. *J Appl Ecol*. 2020;57:1078–1088. <https://doi.org/10.1111/1365-2664.13634>