



Long-term changes in mole cricket body size associated with enemy-free space and a novel range

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Abstract Exotic species can cause ecosystem and landscape-level changes in their novel ranges, but factors associated with novel ranges can also change the invaders. By tracking trait changes over space and time, we can learn about the future ecological and economic implications of invasive species' dispersal. Here, we investigated body size changes of two invasive mole cricket species, *Neoscapteriscus borellii* and *N. vicinus*, introduced to the U.S. from South America (≈ 1904) without natural enemies, and later exposed to them (≈ 1980) through classical biological control. We compared body sizes of *N. vicinus* and *N. borellii* in the novel range from before biological control and 30 years after, as well as *N. borellii* in its native range at the same time period. Contrary to expectations, our data suggest that *N. borellii* and *N. vicinus* body sizes have increased since re-establishment of interactions with their natural enemies. Our results also suggest that *N. borellii* body size decreased in enemy-free space after U.S. invasion and prior to

biological control. Selection or reduced intraspecific competition, both likely associated with biological control, may explain the changes in body size over time. Although these results warrant further research, they provide valuable insights into the long-term effects of invasion and classical biological control.

Keywords Enemy release hypothesis · Density-dependence · Entomopathogenic nematodes · Invasive species · Parasitism

Introduction

Exotic organisms may colonize novel ranges free of their endemic natural enemies ('Enemy Release Hypothesis', Dunn et al. 2012), which can result in exponential population growth (Scott 1987) and have a wide range of ecological and economic consequences (Didham et al. 2005). Additionally, abiotic and biotic selective pressures associated with novel habitats may cause exotic species to diverge genetically and/or phenotypically from their native populations (Huey et al. 2000; Schäfer et al. 2018), generating fitness advantages that increase the invasive potential and impact of the introduced organism (Phillips et al. 2006; Masson et al. 2018). Thus, following introduced species and their traits through time and space may elucidate how biological

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invasions behave across broad ecological landscapes (Masson et al. 2018).

From 1899 to 1925 three mole cricket species in the genus, *Neoscapteriscus* (Orthoptera: Gryllotalpidae), invaded ports of entry in the southeastern United States (Walker and Nickle 1981). Within less than three decades, two of them, *N. borellii* Giglio-Tos and *N. vicinus* Scudder, became economic pests of turfgrasses and pastures through much of the southeastern U.S. (Parkman et al. 1996; Mhina et al. 2016). Both species disperse by flight and damage plants by tunneling through soils and uprooting or consuming plant material. To reduce economic and agricultural losses, researchers identified natural enemies in each species' native range (Bolivia, Uruguay, and Brazil) and introduced them to Florida. Biological control agents included a parasitic wasp, *Larra bicolor* Fabricius (Hymenoptera: Crabronidae), a parasitic fly, *Ormia depleta* Wiedemann (Diptera: Tachinidae), and an entomopathogenic nematode, *Steinernema scapterisci* Nguyen and Smart 1990 (Rhabditida: Steinernematidae) (Parkman et al. 1996).

Although never attributed to a single natural enemy, 25 years of mole cricket survey data from several locations in central Florida (Frank and Walker 2006) illustrate a significant decline in *N. borellii* and *N. vicinus* abundance following the establishment of biological control after 1987 (Fig. 1) (Parkman et al. 1996). Thus, classical biological control efforts are

considered a success and have been attributed with saving Florida's cattle industry over \$13 million annually since their establishment (Mhina et al. 2016). Despite this history, both invasive *Neoscapteriscus* species have continued to cause economic damage in the southeastern U.S. (Mhina et al. 2016) and evidence suggests they are expanding their ranges into the western U.S. and to higher latitudes (Dillman et al. 2014; iNaturalist.org 2018). To date, there are limited data on the current distribution and rate of spread of the introduced natural enemies and both *Neoscapteriscus* species. Although mole cricket dispersal is dependent upon local weather conditions (Hayslip 1943; Beugnon 1981; De Graaf et al. 2004), we have a poor understanding of how mole cricket morphology affects flight and what biotic or abiotic factors may affect their continued invasion (Dong and Beck 1982).

The long-term consequences of novel habitats or the absence and reintroduction of parasites on important life history traits like body size are poorly understood. Both *Neoscapteriscus* species proliferated in the southeastern U.S. in enemy-free space for approximately 80 years until being re-established with parasites. Empirical evidence is mixed regarding the effect of enemy free space on a newcomer's body size (Campbell and Echternacht 2003; Dlugosch and Parker 2008). Furthermore, parasitic infections can reduce host body size in a wide range of taxa, although

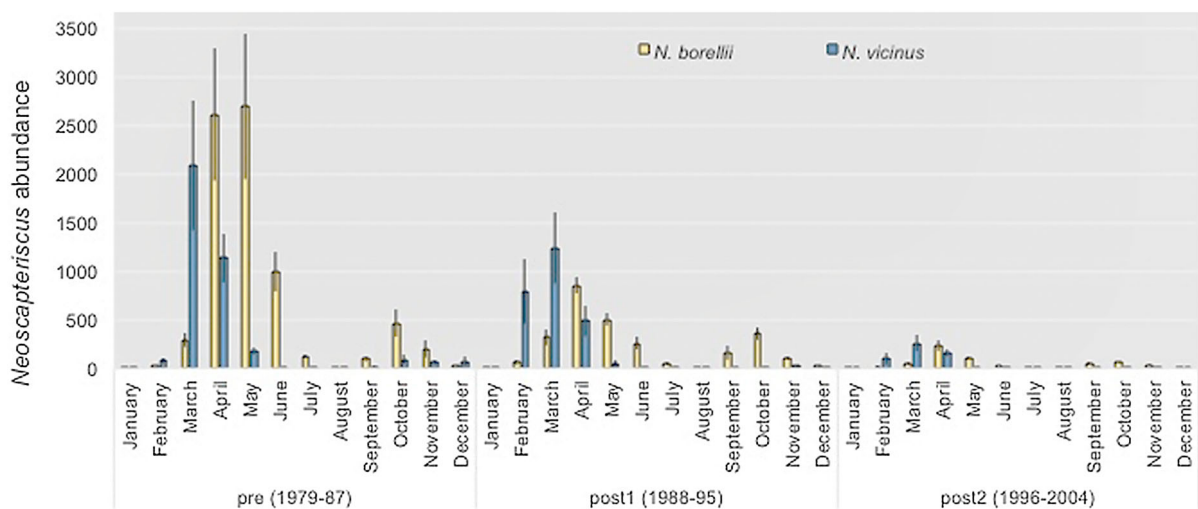


Fig. 1 Monthly (mean \pm SE) mole cricket abundance from 1979 to 2004 in north-central Florida, pre- and post-establishment of biological control agents (1988). The post-biological

control period was divided into 7 and 8-year periods for better resolution. Data are from the University of Florida Institutional Repository (<http://ufdc.ufl.edu/UF00089433/00001>)

primarily among marine arthropods and mollusks (Torchin et al. 2001). In contrast, evidence among terrestrial and marine invertebrates suggests an increase in body size due to parasite infection, typically associated with reduced fitness (Baudoin 1975; Poulin and Thomas 1999; Sorensen and Minchella 2001). Hence, the release and re-establishment of host-parasite interactions over extended periods may unpredictably affect the exotic host and may be partially due to novel biotic conditions of the new range in which the interactions are taking place. For both invasive *Neoscapteriscus* species, body size affects fitness, which has implications for invasive potential. For example, larger females are more fecund (Forrest 1986) and larger males produce louder mating calls (higher intensity), which attracts more female mates (Forrest 1980).

In this study, we surveyed *N. borellii*, *N. vicinus*, and their introduced parasitic nematode, *S. scapterisci*, for 2 years. We compared body sizes of present-day field-collected mole crickets with those collected from the same geographic area in 1981–1982, prior to the introduction of natural enemies. Additionally, we compared body sizes between a native (Brazil) and novel (Florida, USA) population of *N. borellii* to determine if there were changes following introduction to Florida in enemy-free space. *This unique ecological scenario allows us to determine if the release and re-establishment of host-parasite interactions can affect body size trends in a novel range.* We also investigated if parasitism was associated with body size patterns. We predicted that *Neoscapteriscus* spp. body size had decreased since parasite introduction in Florida, as the drastic decline in mole cricket abundance (Fig. 1) suggests reduced fitness.

Methods

Study species: distribution

Neoscapteriscus borellii (see Appendix S1: Fig. S1) is broadly distributed throughout the southern U.S. from Florida to North Carolina and Texas (Walker and Nickle 1981), as well as southern Arizona and California (Dillman et al. 2014). *Neoscapteriscus vicinus* has a similar but more constricted distribution, ranging from Florida to North Carolina to eastern

Texas (Nickle 2003). Both species are endemic to Brazil, Uruguay, and Bolivia.

Mating behavior and acoustic trap

Male *N. borellii* and *N. vicinus* produce acoustic mating calls at night from the entrance of their subterranean tunnels by stridulating their hind wings to attract female mates (Ulagaraj and Walker 1973). In the 1970s, it was discovered that playing recorded or synthetic mating calls of both species attracts large numbers of mole crickets, especially females (Ulagaraj and Walker 1973; Walker 1982). In 2017 and 2018, we deployed acoustic traps described in Rohde et al. (2019), using recorded mating calls to capture *N. borellii* and *N. vicinus* in north-central Florida. The traps broadcasted a single prerecorded audio file composed of 4-s recordings of a *N. borellii* call (2.7 kHz, 50 pulses/s at 106 dB measured at 15 cm from the audio source) and a *N. vicinus* call (3.3 kHz, 130 pulses/s) (Walker 1982; Rohde et al. 2019), which played on loop every night at dusk for 2 h, during peak female flight (Forrest 1980).

Impact of biological control agents

By the late 1980s, *S. scapterisci* was considered established in north-central Florida and frequently field-collected from *N. borellii* and *N. vicinus* (Parkman et al. 1993). This parasitic nematode attacks and kills adult *N. borellii* and *N. vicinus* by infiltrating the insect's hemocoel and vectoring a pathogenic bacterium (*Xenorhabdus* spp.) harbored in the nematode gut (Dillman and Sternberg 2012), and has been associated with reduced mole cricket abundance (Parkman et al. 1996). The other two introduced biological control agents, *L. bicolor* and *O. depleta*, are established in Florida and beyond. However, there is limited evidence that either have reduced mole cricket abundance (Frank et al. 1995, 1996); although it cannot be ruled out.

Data sets

To compare *N. borellii* and *N. vicinus* body size before and after biological control agent introduction, we obtained mole cricket pronotum lengths (PL) as a proxy for body size (Appendix S1: Fig. S1, Table S1; Forrest 1987) at two time points. We collected adults

of both species in 2017 and 2018 using acoustic traps (Rohde et al. 2019). In 2017, we collected mole crickets weekly from April 23rd to July 6th (late spring) at nine sites in north-central Florida. In 2018, mole crickets were collected from February 7th to April 5th (early spring) at six sites in north-central Florida. These collections represent invasive mole crickets about 110 years after their introduction and establishment in north-central Florida (Walker and Nickle 1981).

Secondly, we obtained *N. vicinus* and *N. borellii* PLs collected in 1981–1982 from north-central Florida (Alachua county, Gainesville, 29°38'N 82°16'W) also using acoustic traps playing recorded mating calls (Walker 1982), from previously published research (Forrest 1987).

Finally, we obtained PL measurements of *N. borellii* from its native range in Brazil. *Neoscapteriscus borellii* were collected in Rio Claro, São Paulo, Brazil (22°24'S 47°36'W) from 1983 to 1985 and their pronotum lengths were recorded. These data were extracted from Saes and Fowler (1985), which is part of the Mole Cricket Research 1984–1985 Annual Report produced by the University of Florida. These data represent *N. borellii* body size in their native range in enemy-free space during the same period as our north-central Florida enemy-free data.

To compare *Neoscapteriscus* body size over time (and provenance for *N. borellii*), we used comparable data sets. For Florida data (1981–1982, 2017–2018), spring (February–July) data were used, as this is when both species are most active (Fig. 1). For Brazilian *N. borellii* data (1983–1985) we used PL measurements collected during the Southern Hemisphere spring (August–November), which is also peak mole cricket abundance in their native range (Fowler 1987).

Parasite surveys

We used the White trap method (White 1927) to determine if collected *N. borellii* and *N. vicinus* were parasitized by *S. scapterisci*. Using this method, juvenile nematodes are detected and collected as they leave the cadaver of a parasitized host (Nguyen and Smart 1991). We quantified infection rates (Parkman et al. 1994, 1996) and investigated the relationship between *S. scapterisci* infection, host species, and body size.

Morphometrics

To quantify mole cricket body size, we obtained dorsal photographs of each individual after White trapping using a Cannon 7D DLSR camera (lens: EFS 60 mm f/2.8 Macro USM) mounted to a focus rail. Mole cricket PL has been used to quantify mole cricket body size for several decades (Forrest 1987; Xu et al. 2013). However, we also measured the shortest pronotum width and longest pronotum width for each individual, to better describe the overall size and shape of these organisms (Appendix S1: Fig. S1). We used ImageJ software (Schneider et al. 2012) to measure all traits. Each mole cricket was measured with high precision by three or four trained researchers. For example, measurement error for PL was 1.3% for a sample of 290 individuals based on 934 images.

Data analysis

All analyses were conducted using IBM® SPSS® ver. 24. To examine sexual dimorphism in 2017 and 2018 for both species, we used multivariate analysis of variance (MANOVA) including the three pronotal traits in our analyses. We used Chi-square tests to compare nematode infection rates for each species between sexes, and across years only for *N. borellii*.

To investigate if *S. scapterisci* has exerted selective pressures on mole cricket body size, we compared PL between infected and uninfected individuals for both *Neoscapteriscus* species.

We separated the *N. borellii* analyses by year due to a large difference in infection rates across years (see “Results”). Thus, to compare body size between infected and uninfected individuals, we used two-sample *t* tests for each species, separated by year and sex for a total of six comparisons.

To determine if *N. borellii* or *N. vicinus* body size differs between pre-biological control (1981–1982) and post-biological control (2017–2018) time periods, we compared mean PL between individuals collected during both time periods (for *N. borellii* and *N. vicinus*) and geographic locations (for *N. borellii*). For *N. borellii*, we also compared body sizes in both Florida time periods to the Brazilian body sizes (1983–1985). We used simple Analysis of Variance (ANOVA) to compare across groups (period/site) and sexes, both fixed factors.

Results

In 2017 (late spring), we collected 639 *N. borellii* adults in north-central Florida, composed of 563 females and 76 males. We collected less than 15 *N. vicinus* in 2017 since they primarily fly in early spring (Fig. 1). Therefore, we excluded them from all 2017 analyses. In 2018 (early spring), we collected 73 *N. borellii* adults (38 females and 35 males), and 433 *N. vicinus* adults (417 females and 16 males). Both species were included in 2018 analyses.

Neoscapteriscus borellii exhibit sexual dimorphism where males are larger than females (Fig. 2, Appendix S1: Fig. S2). In 2017, all male body size metrics were significantly larger than female traits (MANOVA: Wilks’s lambda $F_{3,635} = 28.77, p < 0.0001$; Appendix S1: Fig. S2). In 2018, we found the same pattern (MANOVA: Wilks’s lambda $F_{3,69} = 14.58, p < 0.0001$; Fig. 2). *Neoscapteriscus vicinus* males are also larger than females (MANOVA: Wilks’s lambda $F_{3,429} = 5.39, p = 0.001$), but not as drastically (Fig. 2).

We collected *S. scapterisci*-infected individuals of both *Neoscapteriscus* species from all study sites in

both years. In 2017, 33% of *N. borellii* were infected and there was no difference in infection rate between sexes ($X^2 = 1.262, df = 1, p = 0.74$; Appendix S1: Fig. S3). In 2018, infection rates were around 54% for both species and we, again, did not detect differences between sexes for either *N. borellii* ($X^2 = 0.41, df = 1, p = 0.52$; Appendix S1: Fig. S3) or *N. vicinus* ($X^2 = 1.03, df = 1, p = 0.31$; Appendix S1: Fig. S3). Thus, infection rates were much higher in the early spring (2018) than late spring (2017) ($X^2 = 44.3, df = 2, p < 0.0001$; Appendix S1: Fig. S3).

Interestingly, in 2017, infected female *N. borellii* were larger than uninfected females ($t = 3.43, df = 404.4, p = 0.0007$; 95% confidence interval: [0.068, 0.250]; Appendix S1: Fig. S4a), but we found no differences in males ($t = -0.336, df = 30.0, p = 0.74$; 95% CI [-0.50, 0.36]; Appendix S1: Fig. S4a). Again in 2018, infected *N. borellii* females were larger than uninfected females ($t = 3.35, df = 28.7, p = 0.0023$; 95% CI [0.25, 1.03]), and we also found the same trend for males ($t = 2.11, df = 29.3, p = 0.043$; 95% CI [0.020, 1.20]) (Appendix S1: Fig. S4b). We found no difference in body size between infected and uninfected *N. vicinus* females

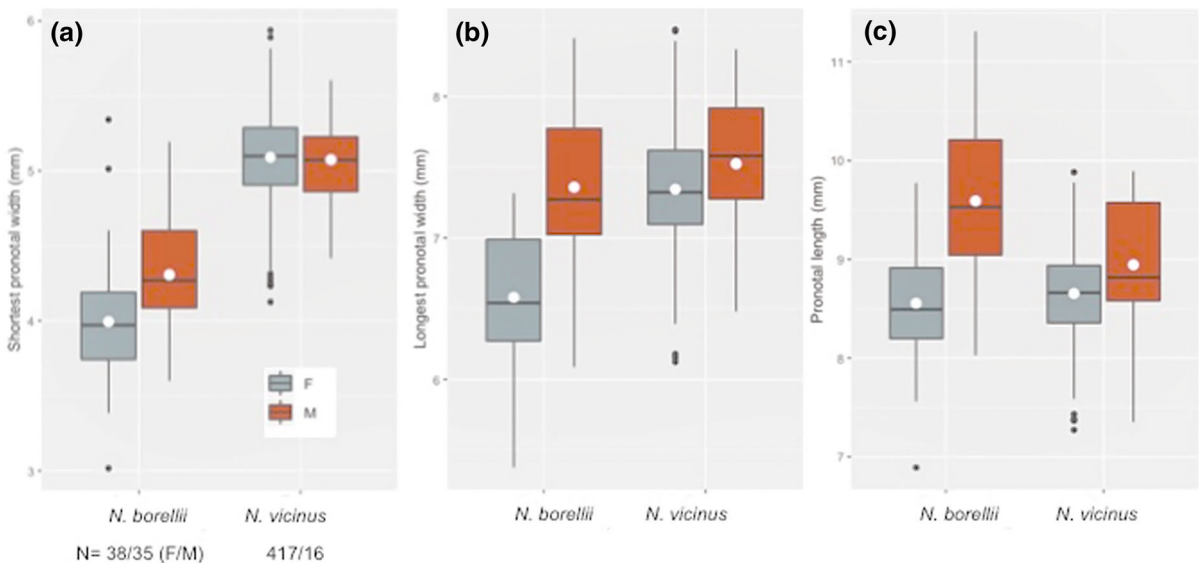


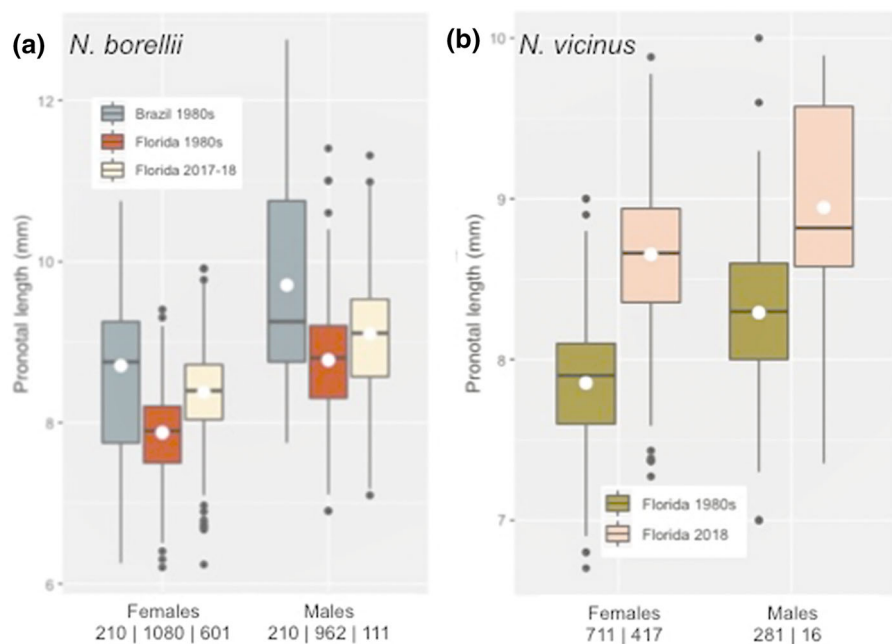
Fig. 2 Sexual size dimorphism in *N. borellii* and *N. vicinus* collected in 2018 (early spring). Boxplots and means (white dots) of the three pronotum measurements for each species, separated by sex (grey = females, red = males). For *N. borellii*, all traits were significantly larger in males; MANOVA between-subject effects: **a** SPW – $F_{1,71} = 10.59, p = 0.002$; **b** LPW – $F_{1,71} = 41.2, p < 0.0001$; **c** PL – $F_{1,71} = 33.7,$

$p < 0.0001$. For *N. vicinus* only PL was longer in males, while LPW was marginally longer in males; MANOVA between-subject effects: **a** SPW – $F_{1,431} = 0.048, p = 0.83$; **b** LPW – $F_{1,431} = 3.22, p = 0.073$; **c** PL – $F_{1,431} = 5.9, p = 0.015$. Sample sizes: *N. borellii* 38/35 [F/M], *N. vicinus* 417/16

($t = -0.370$, $df = 333.3$, $p = 0.71$; 95% CI [-0.11, 0.08]) or males ($t = 0.71$, $df = 5.22$, $p = 0.51$; 95% CI [-0.87, 1.54]) (Appendix S1: Fig. S4c).

Female and male *N. borellii* inhabiting north-central Florida are larger now (2017–2018) than they were 30 years ago in the same geographic region, but smaller than in their native range [Brazil] (Group: $F_{2,3168} = 318.89$, $p < 0.0001$; Fig. 3a). Sexual size dimorphism (SSD) is conserved across time periods and locations (Sex: $F_{1,3168} = 677.82$, $p < 0.0001$), with a slight reduction of SSD in 2017–2018 (Group \times sex interaction: $F_{2,3168} = 4.29$, $p = 0.014$). Due to the significant interaction we conducted separate ANOVAs by sex; in both cases we obtained similar results (females $F_{2,1888} = 259.3$, $p < 0.0001$; males $F_{2,1280} = 119.7$, $p < 0.0001$). Male and female *N. borellii* are on average 3.7% and 6.3% larger now (2017–2018), respectively, than in the 1980s. Additionally, male and female *N. vicinus* are 8% and 10%, respectively, larger now (2018) than they were in the 1980s (Group: $F_{1,1421} = 159.75$, $p < 0.0001$; Fig. 3b), with no change in sexual size dimorphism ((Sex: $F_{1,1421} = 40.66$, $p < 0.0001$; period \times sex interaction: $F_{1,1421} = 1.81$, $p = 0.18$).

Fig. 3 Boxplots and means (white dots) of body size (pronotal length) for **a** *N. borellii* and **b** *N. vicinus* males and females in Florida in the 1980s and 2017–2018, and of *N. borellii* males and females in Rio Claro, São Paulo, Brazil in 1983–1985. Both invasive *Neoscapteriscus* species in north-central Florida are larger in 2017–2018 than 30 years ago, and 2017–2018 Florida *N. borellii* are smaller than in their native range. Sample sizes are on the X-axis



Discussion

Invasive organisms and classical biological control programs present unique opportunities to investigate the regulatory pressures that can act in concert, or synergistically, to govern their abundance and distribution (Hawkins et al. 1997). Our results indicate a 4–10% increase in the body size of two invasive *Neoscapteriscus* mole cricket species over a 30-year period, during which they were re-introduced to top-down biotic regulation from parasitic invertebrates. Florida *N. borellii*, but not *N. vicinus*, showed seasonal differences in body size in the early 1980s (Forrest 1987), and we found the same seasonal body size patterns in 2017–2018 (Appendix S1: Fig. S5), suggesting that the increase in body size over 30 years is associated with more than nutritional or seasonal changes. Since 1900, Florida has experienced significant land use change through deforestation, agricultural development, and urbanization (Volk et al. 2017). Land use change and the influx of people introduce substantial unexplained variability that may have affected mole cricket morphology and distribution. However, pasturelands, primary mole cricket habitat, continue to occupy the fifth largest land area in the state (Volk et al. 2017) and our study sites have not changed land use type since 1980. Although we cannot isolate the mechanism behind the morphological

change in mole crickets, we argue that it is a direct or indirect effect of the re-establishment of biological control in a novel habitat.

Interestingly, *N. borellii* from Brazil in 1983–1985 are drastically larger than those from Florida during the same time period, which are smaller than *N. borellii* from the same region of Florida in 2017–2018 (Fig. 3). Unfortunately, we do not know the size of *N. borellii* at the time of North American invasion. If invading *N. borellii* were smaller than 1980 Florida *N. borellii*, it would suggest that body size in Brazil and Florida has similarly increased over the past century. Due to drastically different evolutionary histories between these geographies, we argue that this scenario is unlikely. If invading *N. borellii* were the same size as 1980 Florida *N. borellii*, it would suggest that body size did not change during the 80 years post-invasion but that *N. borellii* in Brazil became significantly larger from 1900 to 1980. Since selection pressures on morphology often follow biological invasions (Huey et al. 2000; Schäfer et al. 2018) and there is no evidence supporting a 10.5% increase in *N. borellii* body size in their native range between 1900 and 1980, this scenario also seems unlikely. Based on our 1980 Brazilian data, we hypothesize that South American *N. borellii* invading Florida were larger than those collected in Florida in 1980. Therefore, we argue our results suggest that *N. borellii* body size likely decreased after colonizing Florida approximately 80 years earlier, and then increased (Fig. 3) after the establishment of their endemic parasites and subsequent decline in abundance (Fig. 1). Though we do not have *N. vicinus* body size data from their native range, it is plausible that the same process occurred for both species given that each has significantly increased in body size in Florida since 1980.

One possible explanation for changes in body size after *N. borellii* and *N. vicinus* invaded Florida is the climate. Rio Claro (São Paulo, Brazil) and the remaining native range of *Neoscapteriscus* spp. (Uruguay to Bolivia) is cooler than north-central Florida, which based on Bergmann's rule, suggests that individuals could be larger in their native range because it is colder (Riemer et al. 2018). However, since mean annual temperatures have increased since 1980 in the southeastern U.S. (PRISM Climate group 2018), Bergmann's rule does not support our observation that both species have grown larger since the 1980s. In contrast, converse Bergmann's rule

(Mousseau 1997), which has been supported in multiple other Orthopteran species (Lutz 1908; Blankenhorn and Demont 2004), supports an increase in body size with warmer climates. Therefore, Florida's warmer climate and rising regional and global temperatures over time may be associated with our observed increase in *Neoscapteriscus* body size from 1980 to 2018. Similarly, warming and Converse Bergmann's rule could support that invading mole crickets grew larger in Florida from 1900 to 1980, nonetheless, it does not explain why Brazilian mole crickets are larger than those in Florida.

The observed body size changes since the 1980s may also be due to direct and/or indirect effects of *S. scapterisci* parasitism. Host-parasite interactions can alter a host's phenotype, creating population-level differences in infected and uninfected individuals, which may affect host abundance and/or host trait functionality (Wood et al. 2007; Lefèvre et al. 2009; Johnson et al. 2015). Therefore, parasitism can act as a selection agent, shifting host phenotype distributions (reviewed in Poulin and Thomas 1999). Since both species are larger now and remain highly infected at the population level (30–50%), it suggests an advantage to larger body size. *Steinernema scapterisci* juveniles infect adult mole crickets, but do not inhibit flight (Parkman et al. 1993), which means the selection pressure is on adults and their ability to mate and reproduce before succumbing to infection. Increased body size may increase host survival (Baudoin 1975). For example, larger, more resilient mole crickets may also take longer to succumb to nematode infection and therefore survive longer post-infection allowing for more breeding opportunities (Boff et al. 2000). Although highly variable, nematode-infected *N. borellii* were generally larger than those not infected (Appendix S1: Fig. S4), supporting the notion that larger individuals can sustain infection long enough to fly to a mate and potentially reproduce. Body size may also affect mole cricket dispersal ability and thus the movement of *S. scapterisci* and the selection for larger body size, although there is currently no evidence for this. This increase in body size may also result from reduced energy allocation to reproduction (Sousa 1983), or increased feeding rate to offset energy lost to parasites (Sorensen and Minchella 2001). No such pattern was found for *N. vicinus*. Although further investigation is required, these may be potential mechanisms by which at least one invasive

Neoscapteriscus species has become larger since re-establishment with *S. scapterisci*.

Density-dependent selection over extended time periods can also alter life history traits (Fowler 1981; Calsbeek and Smith 2007). Thus, the *S. scapterisci*-induced reduction in mole cricket densities after 1988 (Fig. 1) may have indirectly affected *Neoscapteriscus* body size. *Neoscapteriscus* population densities increased dramatically over 80 years after the U.S. invasion, which may have imposed strong density-dependent selection (e.g. competition), leading to a smaller body size (Wilbur 1977). Those same density-dependent factors may have facilitated the observed increase in *Neoscapteriscus* body size after the establishment of biological control (Dunn et al. 2012). However, higher densities can also increase population-level body size when larger individuals have a competitive advantage (Calsbeek and Smith 2007). Therefore, it is unclear why *N. borellii* body size would have decreased after invasion, but it is clear that both *Neoscapteriscus* species' body size increased after re-establishment with their parasite.

This unique ecological history and study system allows us to explore the consequences of enemy-free space and its re-establishment in a novel range on host body size. Our results indicate that a novel range and enemy-free space led to a demographic explosion, accompanied by reduced host body size. The re-establishment of parasitism and subsequent reduction in host abundance coincides with an increase in host body size. Although we cannot untangle the direct and indirect effects of the parasite and novel habitat on host body size, it is clear that these interactions have important consequences on the fitness, abundance, and distribution of two invasive insect pests. Evidently, untangling the mechanism(s) responsible for this pattern is the next logical step.

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