Biol Invasions (2025) 27:47
https://doi.org/10.1007/s10530-024-03511-2

ORIGINAL PAPER

Higher heat acclimation ability in a non-native versus a native dung beetle (*Onthophagus* spp.)

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Received: 9 April 2024 / Accepted: 8 December 2024 / Published online: 21 December 2024

Abstract Invasive species may be more capable of adjusting to climate warming via phenotypic plasticity than native species since plasticity is thought to increase invasion success. Physiological plasticity via acclimation is one way in which organisms can adjust their thermal tolerance in response to temperature change, but few studies have addressed whether invasive species have greater thermal plasticity compared to native congeners. Here we investigated whether thermal plasticity via temperature acclimation varies between two *Onthophagus* dung beetle species, the non-native *Onthophagus taurus* and the native *Onthophagus hecate*, collected from both Florida and Tennessee, USA. We expected the non-native *O. taurus* to demonstrate greater plasticity than the native *O. hecate*; we also predicted that beetles from Florida would have reduced plasticity since their environment is less thermally variable. To examine thermal plasticity, we measured shifts in time until loss of function (i.e., leg mobility) following acclimation to hot or cold temperature treatments. We found that non-native *O. taurus* from Florida acclimated to warm temperatures, increasing time to loss of function following warm treatments; unexpectedly, *O. taurus* from Tennessee showed no warm acclimation ability. *Onthophagus hecate* did not acclimate to warm temperatures in either location. In contrast, both species showed similar levels of cold acclimation. Taken together, our results suggest that the non-native species, *O. taurus*, will be more capable of using physiological adjustments to respond to climate warming than the native species, *O. hecate.*

Keywords Climate change · Heat knockdown · Introduced species · Invasive species · Scarabaeinae · Thermal physiology

Introduction

Theory and empirical work suggest that invasive species have greater phenotypic plasticity than native species (Baldwin 1896; Agrawal 2001; Sol et al. 2002; Nicolakakis et al. 2003; Gross et al. 2010; Wright 2010; Davidson et al. 2011; Engel et al. 2011; Tepolt and Somero 2014; Amiel et al. 2011), which not only allows invasive species to establish in new environments but may also buffer them against environmental change. In contrast, native species have a longer history of evolution in their environments and may demonstrate local adaptation rather than phenotypic plasticity since plasticity is costly to maintain (Dewitt et al. 1998; Gotthard and Nylin 1995). The greater capacity for phenotypic plasticity of invasive species compared to native species may become especially concerning due to climate change; biological invasions could act synergistically with increases in

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temperature and the frequency of extreme thermal events to drive the decline of native species (Chown et al. 2007; Penk et al. 2016; Allen et al. 2018).

Plasticity of thermal physiology could increase survival during extreme events (Stillman 2003; Seebacher et al. 2014), but it's not clear whether invasive species have greater thermal plasticity to respond to climate change. Empirical tests of plasticity generally conclude that invasive species have greater behavioral and morphological plasticity than native species (Davidson et al. 2011; Engel et al. 2011; Penk et al. 2016; Hiatt and Flory 2020). The limited evidence available on thermal plasticity of invasive species suggests that thermal plasticity may drive invasion success of some plant (Richards et al. 2006) and animal (Nyamukondiwa et al. 2010; McCann et al. 2018; Claunch et al. 2021) species, but few studies have quantified whether thermal plasticity is greater in invasive compared to native species (but see Coccia et al. 2013; Penk et al. 2016; Barker et al. 2018). Yet, such physiological knowledge is critical for informing invasion science (Lennox et al. 2015; Kelley 2014); physiological processes impact all stages of biological invasions, and thus, physiological knowledge can provide insight on species' ability to establish and spread outside their native range (Pertierra et al. 2012; Boardman et al. 2022).

Thermal physiology varies with climate regimes. Organisms experiencing more seasonal and diurnal temperature variation have broader thermal tolerance and increased physiological plasticity (Janzen 1967; Chown et al. 2004; Sheldon et al. 2018; Chown and McGeoch 2023). Depending on environmental conditions, thermal tolerance and plasticity may vary among populations of the same species (Lenz et al. 2011; Narum and Campbell 2015; Cvetanovska et al. 2021). This suggests that any differences in thermal physiology between a native and an invasive species may vary among populations where they co-occur, altering the combined impacts of the biological invasion and climate change across the range of the native species.

Here we investigated whether thermal plasticity via temperature acclimation varies between a native and a non-native *Onthophagus* dung beetle species from two populations separated by latitude. The non-native species, *Onthophagus taurus*, is native to Europe and was first recorded in the USA in 1974 on cattle pastures in northwestern Florida (Fincher and Woodruff 1975; Hoebeke and Beuchke 1997). The species established and began to expand northwards into much of the southeastern USA, helped by intentional introductions in the 1980s in California, Texas, New Jersey, and Georgia to decrease dung build-up. Currently, *O. taurus* occurs throughout much of the eastern USA and southward into the Caribbean (Floate et al. 2017; Pokhrel et al. 2021). Environmental niche models indicate that *O. taurus* may continue to expand into most of the USA, Mexico, and the Caribbean (Floate et al. 2017). *Onthophagus taurus* overlaps in range with the native beetle *Onthophagus hecate*, which occurs from Florida to southern Canada. *Onthophagus taurus* and *O. hecate* have similar seasonal and diel activity patterns, dung use, and breeding behaviors and are often collected within the same dung pats. The two species are small-bodied dung beetles relative to the community as a whole, though the non-native *O. taurus* are larger than the native *O. hecate* (e.g., mean mass of 77 female *O. taurus* is 0.07 g; mean mass of 79 female *O. hecate* is 0.05 g). Both species show sexual and male dimorphism; in populations of both species, there are major males with large, prominent horns, minor males with small horns, and females. In this study, we only included major males and females.

We measured thermal plasticity in these species by acclimating them to either a warm or cold temperature treatment and then quantifying shifts in their ability to withstand extreme temperatures. Different techniques are used to quantify insect thermal tolerance, including various static assays (Hoffmann et al. 2003; Ørsted et al. 2022). In static assays, insects are exposed to a constant, stressful warm or cold temperature, and the time it takes to reach a predetermined endpoint, such as onset of muscle spasms, recovery from coma, loss of coordinated leg movements, knockdown, or death, is recorded (Hoffmann et al. 2003). Following Sheldon and Tewksbury (2014), we defined the "failure" endpoint as loss of coordinated leg movements, a critical ability for organisms escaping stressful temperatures. We collected beetles of both species from two areas, northern Florida and eastern Tennessee, USA. Based on standard deviation of mean monthly air temperatures, Florida (8.5 °C) is less seasonal than East Tennessee (14.9 °C) (data from the years 2011–2021; NOAA 2024). We examined variation in thermal plasticity both within and between species. Specifically, we investigated the following questions: (1) Does thermal plasticity vary between the non-native beetle, *O. taurus*, and the native beetle, *O. hecate*?, and (2) Does thermal plasticity vary between populations of a species? We predicted that the non-native *O. taurus*, regardless of source population, would demonstrate greater thermal plasticity than the native *O. hecate*. We also expected that beetles from Tennessee, where temperatures are more seasonally variable, would show greater thermal plasticity than beetles from Florida, where temperatures are more stable. Finally, we predicted that both species would show greater thermal plasticity to cold versus warm temperatures since previous research on dung beetles has shown limited plasticity of upper thermal limits (Machekano et al. 2021) and cold tolerance of ectotherms is more responsive to acclimatization than warm tolerance (Gunderson and Stillman 2015).

Methods

Study sites

We collected adult dung beetles from two areas, northern Florida and eastern Tennessee. In Florida, we collected adults of both species from the University of Florida Sante Fe River Ranch Beef Unit in Alachua, FL (29° 55′ 308″ N, − 82° 29′ 269″ W), which contains approximately 1600 acres of pasture and supports 300 beef cattle. The pastures are primarily open with cultivated Bermuda grass and a few forested areas. During the dung beetle breeding season (May–August), average maximum and minimum air temperatures in Florida are 32.4 °C and 21.7 °C, respectively (data from the years 2011–2021; NOAA 2024).

In eastern Tennessee, we collected *O. hecate* from Seven Islands State Birding Park (35° 57′ 143″ N, − 83° 41′ 221″ W), a 416-acre protected area with a combination of managed grassland and wooded areas. We collected *O. taurus* from a small, 15-acre private beef farm with 40 grazing cattle in Powell, TN (36° 03′ 258′ N, 84° 04′ 198″ W). Both sites are in rural areas outside of Knoxville, Tennessee and are approximately 40 km apart. The average maximum and minimum air temperatures during the breeding season (May–August) are 29.3 °C and 17.4 °C, respectively (data from the years 2011–2021; NOAA 2024).

Field collection

We collected adult *O. taurus* and *O. hecate* beetles in Florida (May 2019) and Tennessee (May and June 2021) using baited pit-fall traps and manually searching through cow dung. In Florida, we held beetles in conspecific groups of ~ 50 individuals in 2 L rectangular containers (135 × 102 × 282 cm) filled with a 4:1 mixture of topsoil:sand at constant room temperature (25 °C). We fed colonies ad libitum with field collected cow dung. After 3 days of collection, we transported all beetles to the laboratory at the University of Tennessee in a temperature-controlled vehicle (24.2–25.3 °C). In Tennessee, we collected and transported all field-caught beetles to the lab on the same day. We transported Tennessee beetles in plastic containers with damp paper towels in a temperature-controlled vehicle (24.2–25.3 °C).

Once in the laboratory, we held beetles in conspecific groups of 40–50 individuals in the 2 L rectangular containers and 4:1 mixture of topsoil:sand for 7 days at room temperature (24.5–25.0 °C) and fed them ad libitum with autoclaved cow dung, which provided nutrition and moisture.

Acclimation treatments

To measure thermal plasticity, we quantified shifts in thermal tolerance, which we defined as the amount of time beetles could function in hot and cold extremes following acclimation to either warm or cool temperature treatments, respectively. To do this, we randomly assigned dung beetles to either the cold or warm acclimation treatment. For both acclimation treatments, we housed beetles in groups of 6–10 individuals in 1 L plastic containers filled with soil. We provided the group with 77.5 ± 2.5 g of autoclaved cow dung, and we acclimated beetles in Panasonic (MIR-554) or Percival (PGC-10) incubators at 50% relative humidity. For Tennessee beetles, we used female beetles of both species because we were able to collect larger sample sizes. For Florida beetles, we did not collect enough females and used both males and females to increase sample size, with each treatment having roughly the same number of male to female beetles. Based on our analyses (see below), the inclusion of males did not qualitatively impact our results and conclusions, and thus, we used both males and females for analyses.

To measure shifts in cold tolerance (i.e., shifts in the amount of time beetles could function in cold extremes), we used one set of beetles and placed half the individuals in a cold acclimation treatment of 15 °C and the other half in a control temperature of 22.5 °C for 4 days (Table 1). To measure shifts in heat tolerance (i.e., shifts in the amount of time beetles could function in hot extremes), we used a second set of beetles and placed half the individuals in a warm treatment of 29.5 °C and the other half in a control temperature of 22.5 °C for 4 days (Table 1).

The cold (15 °C) and warm (29.5 °C) acclimation temperatures reflect conditions that the beetles would experience in the field that are still well above and below, respectively, the critical thermal limits measured for other temperate dung beetle species (Sheldon and Tewksbury 2014). We used 22.5 °C as our control temperature because beetles reproduce readily at this temperature throughout the breeding season (Mamantov and Sheldon 2021), suggesting this temperature does not induce thermal stress.

Time to loss of function trials

After acclimation periods, we quantified the degree of thermal plasticity by comparing time until loss of function between beetles acclimated in control versus warm or cold acclimation treatments. To measure time until loss of function, we removed beetles from the incubator, gently brushed off any sand and soil with a paintbrush, and recorded mass (Mettler Toledo analytical balance model ML54T). We then placed beetles individually into separate clear plastic containers with lids that had been submerged into a water bath up to the container lip (see Sheldon and Tewksbury 2014). We placed a layer of white sand on the bottom of the containers to increase traction for the beetles. We held the water bath at 6 °C or 48 °C for cold or warm trials, respectively. We chose water bath temperatures based on previous thermal tolerance research with dung beetles (Sheldon and Tewksbury 2014) and to allow for variation in time until loss of function while also ensuring trials were not long enough to cause desiccation in beetles. To ensure that air temperature within the containers matched the water bath temperature, we kept an empty plastic container submerged in the water bath during all trials and monitored the air temperature inside it (Sheldon and Tewksbury 2014).

Table 1 Sample sizes of *O. taurus* and *O. hecate* beetles from Tennessee and Florida study sites used in cold and warm tolerance experiments

	Cold tolerance		Warm tolerance	
	Control 22.5 °C	Cold acclimation 15 °C	Control 22.5 °C	Warm acclimation 29.5 °C
Onthophagus taurus				
Florida	20	17	18	18
Tennessee	20	20	19	18
Onthophagus hecate				
Florida	5	6	7	6
Tennessee	20	19	20	20

We monitored individuals in the trials for loss of function, which we defined as the ability to move legs in coordinated movements. Coordinated leg movements are important for allowing an organism to seek refuge and escape stressful temperatures. During trials, beetles usually attempted to walk or fly around the container; we monitored this movement and recorded the time when the beetles were no longer able to move limbs, which was shortly after forward motion and flight were impeded. If an individual did not attempt movement but instead tucked legs under its body, we removed the lid, used a paintbrush to disturb the beetle and encourage movement, and quickly replaced the lid. If the beetle did not respond to this, we removed the individual from the water bath container and the trial ended (occurred in less than 2% of beetles). If an individual flipped upside down and was unable to right itself, we also used a paintbrush to flip the individual upright. To confirm that this procedure did not change the temperatures inside the submerged container, we did mock flips in the empty container housing the thermocouple and found that this did not alter air temperature. After trials, we again recorded the mass of every individual to monitor water loss over the course of the trial. Data we collected during trials is available in Dryad.

Statistical analyses

To examine differences in thermal plasticity between the two species and two populations, we used separate linear models for cold and warm tolerance trials in R Version 3.6.3 (R Core Team 2020). For both models, we used the response variable of time until loss of function and the predictors of acclimation treatment (warm or cold versus control), species (*O. hecate* or *O. taurus*), population site (FL or TN), and beetle mass at the start of the trial (hereafter "starting mass"), and the interactions among species, treatment, and population site. We included treatment in our model to test whether time until loss of function varied in response to either warm or cold acclimation relative to the control. We included species to test whether time until loss of function varied between *O. taurus* and *O. hecate*, and we included population site in our model to test whether time until loss of function varied between Florida and Tennessee beetles. To test for differences in acclimation ability between the two species living in the two population sites, we included the interactions between species, site, and treatment. We included starting mass as a predictor due to allometric relationships between thermal physiology and body size; larger organisms have a reduced surface area to volume ratio, increasing heat and moisture retention. To meet assumptions of normality, we log transformed time to loss of function for the cold acclimated beetles. To determine best-fit models, we performed model selection using Akaike Information Criterion (AIC) values and the normality of residuals (Burnham and Anderson 2002; Zurr et al. 2009; Symonds and Mousalli 2011).

Because time until loss of function at high temperature could be influenced by acclimation ability and the ability to shed heat via evaporative cooling, we also examined if water loss varied between *O. taurus* and *O. hecate* during the warm trials (48 °C). To approximate water loss, we calculated the percent of body mass lost during the trial. To do this, we subtracted the mass at the end of the trial from the mass at the start of the trial, divided this value by the mass at the start of the trial, and then multiplied by 100. We then examined whether the percent of body mass lost varied using the same predictors and model selection as above.

Because we used females from Tennessee and females and males from Florida in our experiments, we ran the same analyses (above) with males from Florida removed. Our qualitative results were the same; excluding males did not impact the AIC comparisons or whether a result was significant. Thus, we kept all individuals in our models, and we present results based on female and male beetles.

Results

Our goals were to test whether thermal plasticity in response to warm and cold acclimation temperatures varies between the non-native beetle, *O. taurus*, and the native beetle, *O. hecate*, and whether degree of thermal plasticity varies between beetles from Florida and Tennessee populations.

The non-native *O. taurus* from both populations had greater heat tolerance, measured as time until loss of function while held at 48 °C, compared to the native *O. hecate*. Following warm acclimation treatments, neither species in Tennessee nor the native *O. hecate* in Florida demonstrated shifts in time to loss of function. However, the non-native *O. taurus* collected in Florida showed a significant increase in time until loss of function after the warm acclimation (Fig. 1). The best model for time until loss of function following warm acclimation treatments included the three-way interaction between treatment, species, and site ($p < 0.01$), indicating that *O. taurus* and *O. hecate* collected in different sites varied in their response to warm acclimation. To better understand this significant interaction among the predictors, we performed separate analyses on beetles from Florida and Tennessee with treatment and starting mass as predictors. For beetles collected in Florida, *O. taurus* significantly increased time until loss of function after warm acclimation ($p < 0.001$), but *O. hecate* did not show significant adjustment ($p = 0.96$). For beetles collected in Tennessee, *O. hecate* showed a marginally significant increase in time until loss of function ($p = 0.06$), but *O. taurus* did not show significant adjustment in time until loss of function after warm acclimation ($p = 0.21$). The best model for *O. hecate* from Tennessee included beetle starting mass ($p < 0.001$) such that in response to warming, larger *O. hecate* beetles had significantly longer time to loss of function in warm temperatures. In contrast, body size did not influence time until loss of function in *O. hecate* from Florida ($p = 0.94$) or in *O. taurus* from Tennessee ($p = 0.08$) or Florida ($p = 0.41$) (Fig. 2).

Because heat tolerance could be impacted by the ability to shed heat via evaporative cooling, we also examined water loss (i.e., percent change in body

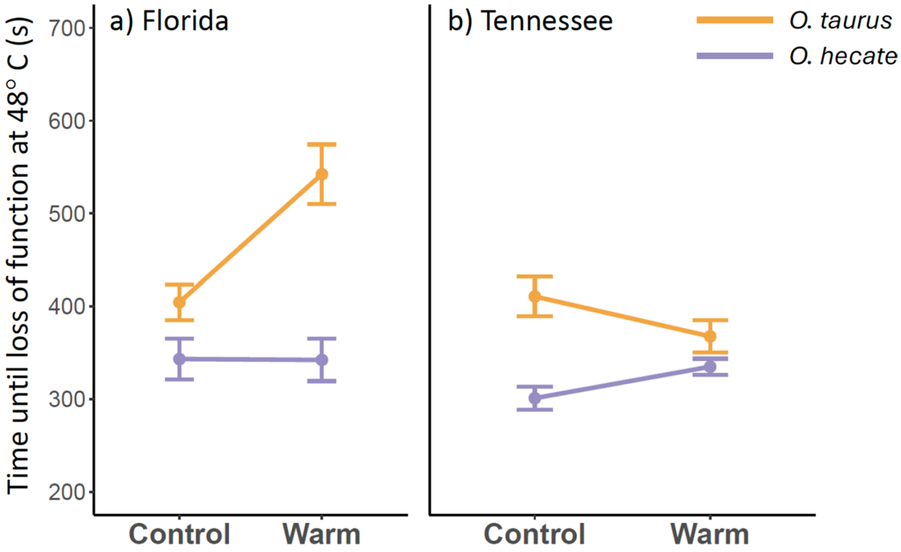

Fig. 1 Time until loss of function for native and non-native *Onthophagus* dung beetles from Florida and Tennessee following warm acclimation treatments. Plots show results for beetles collected in Florida (**a**) and Tennessee (**b**). Orange and purple lines represent non-native *O. taurus* and native *O. hecate* beetles, respectively. The mean and standard error of treatment group are represented by the point and bars, respectively

mass) during loss of function trials. In warm acclimated beetles, we found that shifts in time until loss of function were not caused by increased water loss (Fig. 3). The best model of percent change in body mass following warm temperature treatments included site ($p < 0.0001$), but not species ($p = 0.39$) or treatment ($p = 0.21$). Beetles from Florida, regardless of species or treatment, lost more mass during warm trials than Tennessee beetles, suggesting higher rates of evaporative cooling in Florida populations (Fig. 3).

In response to cold acclimation treatments, both species from both populations demonstrated shifts in time to loss of function (Fig. 4). The best model for time to loss of function following cold acclimation treatments included the interaction between site and

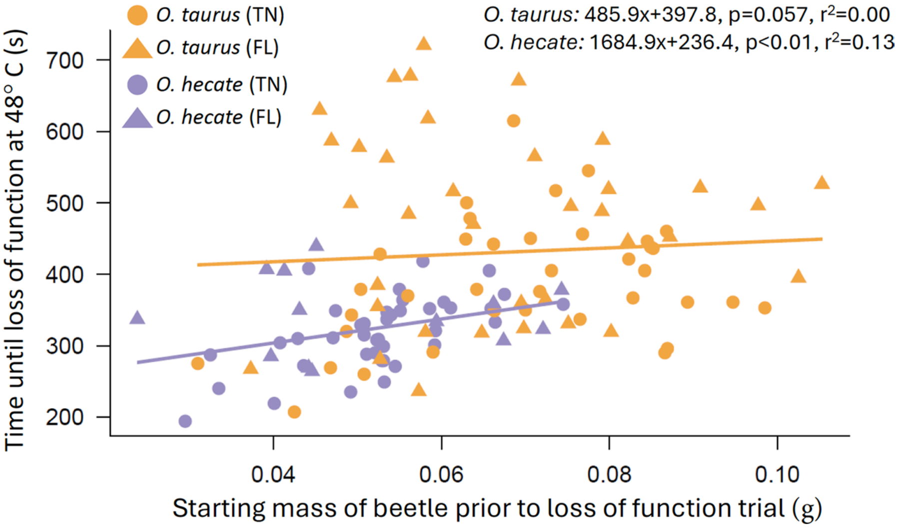

Fig. 2 Time until loss of function in native and non-native *Onthophagus* dung beetles in relation to body mass following warm acclimation. Orange and purple colors represent individuals of the non-native *O. taurus* and native *O. hecate* beetles, respectively, following either control or warm acclimation incubation but prior to warm tolerance tests. Circles and triangles represent beetles from Tennessee and Florida, respectively. The best fit lines and r^2 values were calculated via regression of time until loss of function and beetle mass

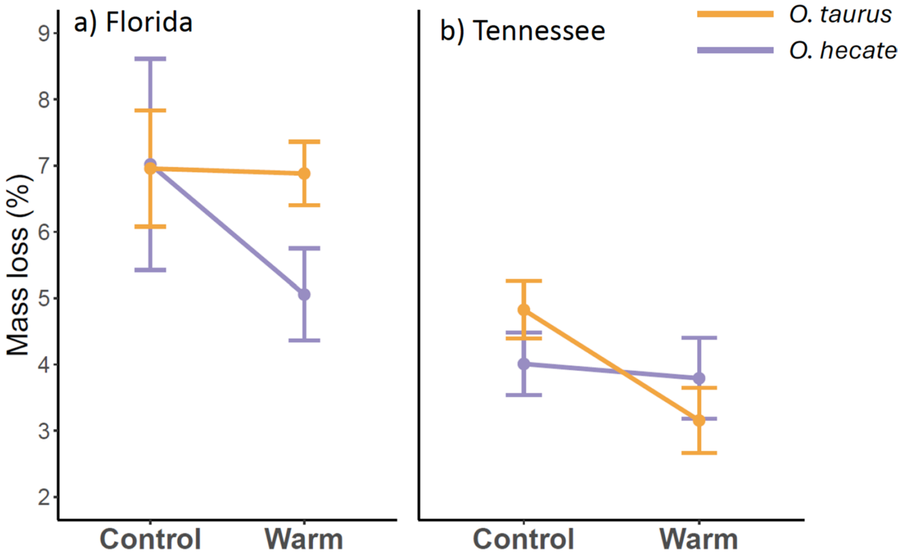

Fig. 3 Percent mass loss of control and warm-acclimated beetles during warm tolerance trials. Plots show results for beetles collected in Florida (**a**) and Tennessee (**b**). Orange and purple lines represent non-native *O. taurus* and native *O. hecate* beetles, respectively. The mean and standard error of treatment group are represented by the point and bars, respectively

treatment ($p < 0.05$) and site and species ($p < 0.001$), as well as the predictors of site, treatment, starting mass, and species. This suggests that both species acclimate to cold temperatures, but the response varies by population. Thus, while acclimation increases the time that beetles can tolerate cold temperatures, this plasticity does not vary by species (Fig. 4). The inclusion of starting mass significantly improved the statistical model ($p < 0.05$; Fig. 5). To better understand the interactions between site and treatment and site and species in cold-acclimated beetles, we examined time until loss of function separately for beetles collected in Florida and Tennessee. For Tennessee beetles, both species showed significant acclimation to cold temperatures ($p < 0.0001$). For Florida beetles, *O. taurus* significantly increased time until loss of function after cold acclimation treatments ($p < 0.001$), but *O. hecate* demonstrated only a marginally significant increase in time until loss of function ($p = 0.07$). Thus, in Florida, *O. taurus* appears to have greater cold acclimation ability than *O. hecate*.

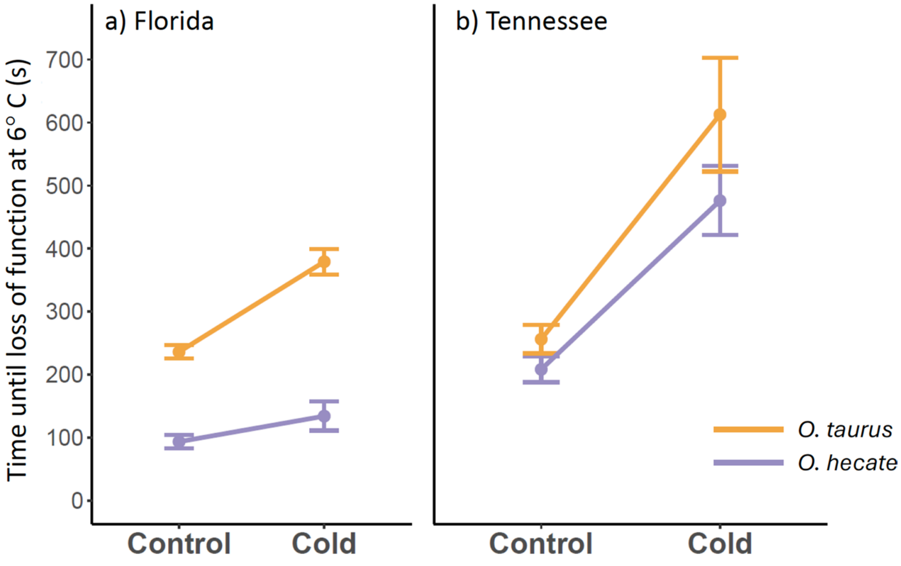

Fig. 4 Time until loss of function for native and non-native *Onthophagus* dung beetles from Florida and Tennessee following cold acclimation treatments. Plots show results for beetles collected in Florida (**a**) and Tennessee (**b**). Orange and purple lines represent non-native *O. taurus* and native *O. hecate* beetles, respectively. The mean and standard error of treatment group are represented by the point and bars, respectively

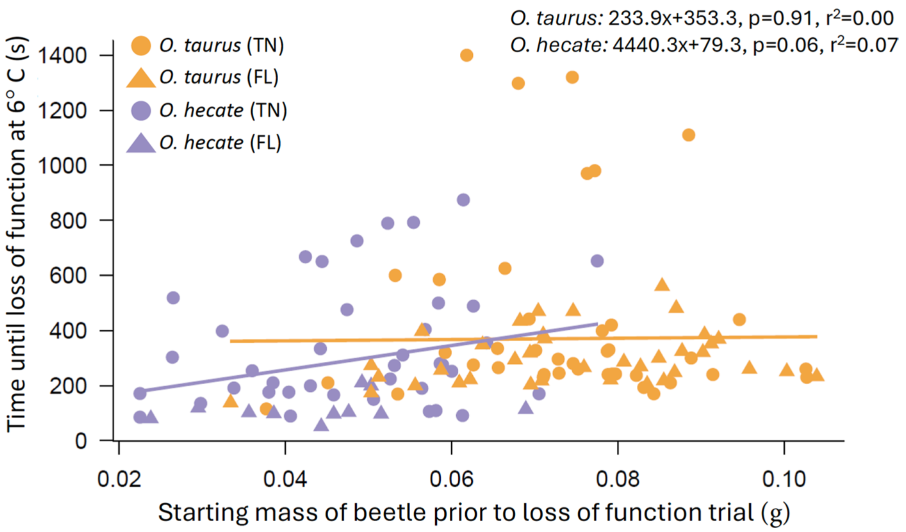

Fig. 5 Time until loss of function in native and non-native *Onthophagus* dung beetles in relation to body mass following cold acclimation. Orange and purple colors represent individuals of the non-native *O. taurus* and native *O. hecate* beetles, respectively, following either control or warm acclimation incubation but prior to warm tolerance tests. Circles and triangles represent beetles from Tennessee and Florida, respectively. The best fit lines and r^2 values were calculated via regression of time until loss of function and beetle mass

Discussion

To investigate whether increased thermal plasticity may favor invasive species over native species under climate warming, we measured shifts in thermal tolerance of a non-native dung beetle, *O. taurus*, compared to a native congener, *O. hecate* from two different sites with varying climates. We expected that the non-native *O. taurus* would demonstrate thermal plasticity in response to warm temperatures regardless of location, but unexpectedly, we only observed this plasticity in the non-native *O. taurus* from Florida but not from Tennessee where temperatures are more variable (Fig. 1). The native *O. hecate* beetles did not demonstrate significant adjustments in warm tolerance at either geographic location. As predicted, plasticity in response to cold temperatures was greater than in response to warm temperatures, and all populations demonstrated the ability to acclimate to colder temperatures except for *O. hecate* beetles from Florida. Beetles of both species collected from Tennessee had greater acclimation to cold temperatures relative to beetles collected from Florida.

Acclimation to warm temperatures was only seen in the non-native *O. taurus*, suggesting that thermal plasticity may contribute to the spread of invasive species under climate warming. Previous research has indicated that invasive species have greater physiological tolerance (Zerebecki and Sorte 2011; Cortes et al. 2016; Pertierra et al. 2012) and can benefit from warming temperatures, allowing them to exploit new areas or become more competitive (Dukes and Mooney 1999; Morrison et al. 2005; Hellman et al. 2008; Walther et al. 2009; Bradley et al. 2010; Mainka and Howard 2010; Huang et al. 2011; Pertierra et al. 2012). In a previous study on dung beetles, Machekano et al. (2021) showed that adult beetles acclimated to high temperatures made significantly bigger brood balls and removed significantly more dung compared to beetles from control and low temperature acclimation. Thus, in the case of *Onthophagus* dung beetles, increased ability to acclimate to warmer temperatures may provide a competitive advantage and favor the non-native *O. taurus* over its native congener, *O. hecate*, which showed no acclimation to warmer temperatures. Interestingly, we only observed this acclimation ability in *O. taurus* from Florida, not from Tennessee, indicating that exposure to higher average temperatures may select for maintenance of warm acclimation ability (Carbonell and Stoks 2020). Furthermore, this result indicates that thermal plasticity may vary across the range of an invasive species.

We expected that beetles from Tennessee, where temperatures are more seasonally variable, would show greater acclimation ability than beetles from Florida, where temperatures are warmer but less seasonally variable (Janzen 1967; Chown et al. 2004; Sheldon et al. 2018). However, exposure to greater seasonal variation only seems to have increased the beetles' ability to acclimate to cold temperatures. Previous research indicates that cold but not warm tolerance often shifts after acclimatization (Diffenbaugh and Field 2013; Seebacher et al. 2014; Gunderson and Stillman 2015), and this pattern has been observed in both native and invasive invertebrates (Janion-Scheepers et al. 2018). Our results support this conclusion, indicating that cold tolerance is generally more plastic than warm tolerance in these beetle species. *Onthophagus hecate* from Florida had reduced acclimation ability to cold temperatures compared to the other populations (Fig. 4), which is expected; rather than maintaining physiological plasticity, these populations may be locally adapted to the warm and stable environment of their breeding season (Gotthard and Nylin 1995; Agarwal 2001).

Our results indicate that the spread of the non-native *O. taurus* into warmer regions may be facilitated by its ability to adjust to warmer temperatures through acclimation. Currently, *O. taurus* is spreading across Central America and has been collected in parts of northern South America (Floate et al. 2017; Pokhrel et al. 2021). In our study, *O. taurus* in Florida showed thermal plasticity in response to warmer temperatures and the greatest ability to withstand elevated temperatures, indicating that some populations of *O. taurus* can adjust to warming through acclimation. In previous work, we also found that, in response to temperature increases, *O. taurus* beetles alter their reproductive behaviors, buffering developing larvae from warmer temperatures and leading to greater offspring survival compared to *O. hecate* beetles (Mamantov and Sheldon 2021). Taken together, *O. taurus* adults and offspring are less likely to be negatively impacted by climate change due to both physiological and behavioral adjustments, respectively, which may allow this non-native species to expand its range under warming conditions. In contrast, the native beetle *O. hecate* will need to utilize other strategies to adjust to climate change or may experience population declines. For example, when air temperatures get too hot or cold, adult dung beetles can move to more favorable microclimates (Caveney et al. 1995; Menéndez and Gutiérrez 2004), dig deeper in the soil (Macagno et al. 2016; Kirkpatrick and Sheldon 2022), or shift activity times (Gotcha et al. 2021). Such strategies could provide refuge and protect native *O. hecate* from temperature fluctuations.

Variation in thermal plasticity may be a mechanism through which climate change will exacerbate the spread and impact of invasive species. The greater potential to acclimate to warmer temperatures found in some invasive species combined with broader physiological tolerance (Zerebecki and Sorte 2011) and greater heat tolerance (Kelly 2014) suggests invasive species will have greater capacity to handle or even take advantage of climate warming compared to native species (Pertierra et al. 2012). However, the potential for biological invasions to act synergistically with increases in temperature may vary across the invaded range; thermal physiology changes across invasive populations (Lenz et al. 2011; Cvetanovska et al. 2021), highlighting the importance of considering physiological variation when predicting the combined impacts of biological invasions and climate change.

Acknowledgements We thank Kevin Null, Susan Riechert and Mac Post, The University of Florida Santa Fe River Ranch, and Seven Islands State Birding Park for allowing us to collect beetles on their properties. This research was funded by the US National Science Foundation (grant nos. 1930829 and 2046368 to KSS) and funds from the University of Tennessee.

Author contributions MAM and KSS contributed to the study conception and design, MAM performed data collection and analysis, MAM drafted the manuscript and KSS contributed substantially to drafts. Both authors read and approved the final manuscript.

Funding This research was funded by the US National Science Foundation (grant nos. 1930829 and 2046368 to KSS) and funds from the University of Tennessee.

Data availability Data are available from the Dryad Digital Repository under https://doi.org/105061/dryadsn02v6xc2.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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