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FACTORS IMPACTING THE POST RELEASE VIABILITY OF AMERICAN BURYING BEETLE (*NICROPHORUS AMERICANUS* OLIVIER) TO NEW YORK

BY

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THESIS

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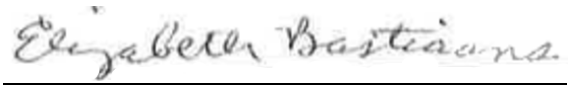

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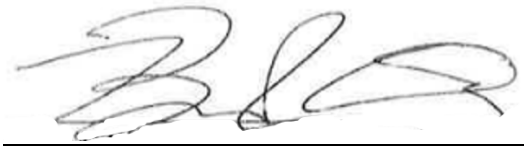

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Preface

Conservation is frequently defined through the human perspective as the care and protection of natural resources for use by our future generations. Conservation based on human necessity has often found sustainable practices to be the key to success and comfort of our species. Sustainable practices attempt to stabilize natural resources. This has been achieved through applied practices. Precision-based agriculture and livestock implementation (Monteiro, 2021), low-impact, selective timber harvesting (Arevalo, 2016), and wild game management all place human well-being at the forefront of conservation. This humanistic approach results in limited efforts to balance and diversify the natural world, placing us at the center of our concerns rather than as a part of the whole.

The science of conservation biology has begun to address anthropocentric takes on conservation. Soulé (1985) defines the field as a mission or crisis-oriented discipline where ethics are a genuine part of the science. His reference to crisis-based disciplines indicates the need to make decisions about design and management based more on our preexisting knowledge, analogous to surgery or war. Conservation biology is a multidisciplinary science which reaches beyond natural resources. It is an expanding field constructed on the foundations of ecology, social sciences, population biology, genetics, and ecological restoration and monitoring. Conservation biology distinguishes between the resources valued for human enhancement and

the continuity of all biotas. This concept is not to exclude resource management. Since conservation biology is an inclusive field of research, the involvement of many disciplines forms a holistic approach to conservation science.

The root of conservation biology is the preservation of biodiversity. More specifically, it is the diversity and abundance of species, their genetics, and the ecosystems and communities in which they occur (Yahner, 2000). Humanity already obtains economic benefits such as food, medicine, and industrial products from biodiversity, for which conservation of such diversity should be well engaged (Ehrlich & Wilson, 1991). More importantly, the conservation of biodiversity nurtures the essential services that ecosystems provide, such as clean air and water, fertile soils, and climate regulation. Still too often we find detriments to ecosystem services through human interactions, such as pollinator species decline (Vanbergen, 2013) and effects to decomposers in microbial communities (Tlili, 2017).

With conservation biology engaging in the complexities of biodiversity, focus is often given to species and ecosystems which require more immediate attention; species with populations facing dramatic decline, or species which are on the brink of extinction. In 1973, the United States Congress passed the Endangered Species Act (ESA), which declared that a variety of fish, wildlife, and plant species in the US have gone extinct due to the consequences of economic growth and development (ESA, 1973). The ESA inducted strong protections for a host of threatened and endangered species to stabilize and recover those species listed (Bean, 2009). Two federal agencies, the United States Fish and Wildlife Service (USFWS) and the National Marine Fisheries Service (NMFS), administer the ESA (ESA, 1973). Successful recovery has been documented under the guidance of both agencies, as in the cases of the bald eagle (*Haliaeetus leucocephalus*) (Winder & Watkins, 2020) and the humpback whale (*Megaptera novaeangliae*) (Bortolotto, 2016). However, the ESA's listing decisions have been viewed as controversial at times. Both habitat ownership, whether federal or non-federal lands, and group-

listing species, as opposed to individual species, have been correlated with ESA listing decisions (Smith-Hicks & Morrison, 2019).

Beginning in the early 1980's Habitat Conservation Plans (HCP) were established to assist with ESA protection on non-federal lands. To fulfill HCPs, the USFWS and private stakeholders worked to set aside large areas of protected habitat for endangered species conservation (Langpap & Kerkvliet, 2012). With conserved habitat as the foundation to species recovery, reintroduction attempts are often the next step in revitalizing populations of endangered species.

Reintroductions are efforts to return species to areas of their historic range where they have since been extirpated (Armstrong & Seddon, 2008). Conservation biology is coupled with the science of reintroduction biology. Since the mid-1990's reintroduction biology has tried to support evidence-based approaches to conservation through reintroduction efforts. As both conservation biology and reintroduction biology are relatively new efforts, the establishment of best practices are still being constructed. Both fields often rely on theoretical deduction rather than strictly observational based evidence when making decisions about reintroduction (Armstrong & Seddon, 2008; Taylor et al., 2017). The effects of rapid decline in species numbers often pressures practitioners to focus primarily on the establishment of populations, arguably foregoing additional key questions about post-release survival, or how the target species will affect the existing ecosystem (Armstrong et al., 2015). It is also understood that the reintroduction of a species cannot be deemed a success simply due to the translocation of a species to its historic home range. Success in reintroduction is often defined as the establishment of a self-sustaining population of locally born individuals. Through persistent monitoring efforts, it may take as long as 20 years or more to determine a self-sustaining population exists (Towns & Ferreira, 2001).

To maintain a population of a reintroduced species the availability of resources within the habitat must be considered. Optimal habitat use by a species balances the maximum energetic uptake while minimizing mortality which benefits the species fitness, the combination of its reproduction and survival (Ofstad et al., 2018). Hutchinson's (1957) niche theory claims a fitness gradient runs across environmental conditions. In niche theory, an individual's fitness is a multidimensional function of all biotic and abiotic resources in which they encounter (DeCesare et al., 2014). The partitioning of habitat and resources can lead to spatial niche segregation which may allow for the coexistence of species within a shared habitat. The dynamics of partitioning can be difficult as fluctuations in species richness and abundance can provide substantial overlap, increasing the pressure of competition for optimal habitat (Wereszcuk & Zalewski, 2015). In ecological systems, habitat may not always be optimal. Multiple factors such as predation risk, seasonal effects on survival, and the availability of food and reproductive resources result in trade-offs between fitness traits, which can drive decisions that either grow populations or result in serious decline (DeCesare et al., 2014; Ofstad et al., 2018). One group in serious decline in North America are burying beetles.

Burying beetles (Silphidae: *Nicrophorus*) are a genus of roughly 75 species in the northern hemisphere which rely on vertebrate carrion, an unpredictable resource in both space and time, as a brood chamber for their larvae (Lomolino & Creighton, 1996; Scott, 1998). Although no preference between small mammals or bird carcasses has been observed, preferred carcass size is known to be partitioned between species of *Nicrophorus* beetles which decreases interspecific competition during times of reproduction (Scott, 1998). Intraspecific conflicts over carrion resources are in most cases settled by the size of the beetles in competition, where the larger secures the resource (Otronen, 1988). Burying beetle reproduction exhibits unique biparental strategies from preparing a carcass to provisioning larvae (Smith et al., 2017). Biparental care in

Nicrophorus species results in significantly more offspring than in uniparental care by either the female or the male (Benowitz & Moore, 2016). Upon locating an appropriately sized carcass, a breeding pair will remove the feathers or hair, preserve it with anal and oral secretions, and bury it in soil as food for their future offspring (Trumbo & Robinson, 2004). In addition to carrion size provisioning, burying beetle communities will create temporal patterns when seeking carrion to limit competition among species. In North America, burying beetle species will alternate reproductive periods from late April through September with minimal overlap (Scott, 1998). During the remaining months, burying beetles overwinter either as larvae or adults depending on the species, with adults having greater control over the habitat choice due to their mobility (Schnell, 2008). Since burying beetles are often deemed habitat generalists (Scott, 1998), little is known of their overwintering site selection preferences.

In July of 1989, the American burying beetle (*Nicrophorus americanus* Oliver; ABB) was listed as Endangered in accordance with the ESA by the Department of the Interior (USFWS, 1991). Once found in three Canadian provinces and over 30 states in the eastern United States, ABB are thought to be present in seven states with Oklahoma and Nebraska supporting the largest populations (Leasure & Hoback, 2017*).* The Easternmost populations are found along the Atlantic Seaboard on Block Island, RI and Nantucket Island, MA (McKenna-Foster et al., 2016). American burying beetle are the largest member of the *Nicrophorus* genus with body lengths between 27 – 35 mm and require carrion for reproduction in the range of 50 – 300 g (Lomolino, 1995). The American burying beetle is considered an univoltine species. Each cohort must survive over winter as adults to reproduce upon reemergence in Spring (Amaral et al., 1997). Abrupt disruption to forested habitats such as tree removal and soil disturbance can kill off both pre-emergent adult beetles and pre-reproductive individuals (Creighton, 2009). Such habitat loss will result in a

decreased carrion prey base and increased competition from vertebrate scavengers (Sikes & Raithel, 2002).

The 1991 American burying beetle recovery plan drafted by the Rhode Island Division of Fish and Wildlife for the USFWS aims to restore and protect ABB populations. The interim objective of this plan is to reduce the threat of extinction to the species. The long-term goal is to improve ABB's status to a degree that allows the reclassification from Endangered to Threatened (USFWS, 1991). With support from a recovery challenge grant provided by the USFWS to reintroduce ABB to New York, the research conducted as part of this thesis will address overwinter survival and site selection of *Nicrophorus orbicollis*, the congener phylogenetically closest to ABB (Szalanski, 2000). In addition to overwintering studies, research of carrion competition among *Nicrophorus* beetles, vertebrate scavengers, and fly colonization will be discussed.

Chapter 1. Fate of Carrion: Competition for reproductive resources of *Nicrophorus* beetles in New York forests.

Due to their abundance, small vertebrate carcasses make up a sizable portion of carrion biomass. In northern latitudes, competition for carrion is highest among carrion flies, vertebrate scavengers, and *Nicrophorus* beetles (Trumbo, 2016). Beetles that breed on carrion provide an important ecosystem service through increased nutrient cycling in woodland soils (Ilardi et al., 2021). By out-competing fly colonization for carrion, burying beetles can also decrease fly populations (Trumbo, 2016). Adult burying beetles directly destroy both fly eggs and larvae found on carrion and carry phoretic mites that will pierce fly eggs found on vertebrate carcasses (Scott, 1998). As *Nicrophorus* beetles rely exclusively on vertebrate carrion for reproduction, this chapter will assess the competition for such carrion in forested habitat at a future ABB release site,

Greenwoods Conservancy in Hartwick, NY. The results of this study show *Nicrophorus* beetles buried 74% of the 180 total carcasses available during the trials, indicating they are the dominant competitor for small vertebrate carrion. Air temperature above 22 °C had a significant effect on the increased probability of fly colonization. These results may influence management strategies for the reintroduction of the endangered American burying beetle to NY.

Chapter 2. Overwintering site selection of *Nicrophorus orbicollis* Say in New York

The teneral adults of *Nicrophorus* beetles which emerge in late July and August will enter a reproductive diapause over winter, reproducing the following late Spring and Summer (USFWS, 1991). Burying beetles, named for the reproductive behavior in which they bury vertebrate carrion in soil, may only be assumed to bury themselves in soil over winter. Like many *Nicrophorus* species, ABB seek overwinter locations as adults, which allows for some control over what site they chose. With research demonstrating a greater overwinter survival of ABB when provisioned with carrion than without (Schnell, 2008), it is possible that ABB seeks an overwinter food source when confronted with seasonal changes approaching winter months. This olfactory laboratory study researched the site selection of two populations of *N. orbicollis,* the sister taxon of ABB, when acclimated to near-winter photoperiods and air temperature. One population came from Hartwick, NY and the other from Block Island, RI. A four-chamber olfactometer provided the same four choices to all beetles within this study: forest soil, *Peromyscus* spp nest material, leaf litter from a forested site, and a blank control. This study aimed to determine if *N. orbicollis* preferred a particular choice more than the other provided choices and whether there was a difference in site selection between the two populations. Results from this study found no significant difference among the choices made by all *N. orbicollis*. Leaf litter was chosen most often by both populations. Population was found to have no effect on the choices made. Similarity among the choices made

by both populations may indicate that alterations to habitat for translocated ABB from Block Island, RI is not necessary when reintroducing ABB to NY.

Chapter 3. Overwinter survival of two populations of *Nicrophorus orbicollis* Say in New York forests

American burying beetle (ABB) for the NY reintroduction will be provided from the current Northeastern population found on Block Island, RI. Similarities among the RI site and the reintroduction site in NY may indicate that overwinter survival rates of the two populations will be comparable. Two populations of a surrogate species, *Nicrophorus orbicollis*, one from Block Island, RI, and one indigenous to Hartwick, NY, will be placed out over winter at Greenwoods Conservancy, in Hartwick, NY to determine survival success rates. As *N. orbicollis* is phylogenetically the closest congener to ABB, results of this study may help determine the number of ABB that should be released annually to maintain a wild population in NY based on the number of Block Island beetles that survive. Additionally, this study will provide survival results for the local *N. orbicollis* population, as well as the soil depth at which surviving beetles buried themselves over winter. This study may also determine if there is significance to sex, weight, and size of *N. orbicollis* when surviving over winter at a reintroduction site in NY. A total of 39 of 60 beetles survived overwinter. Population had a significant effect on the rate of overwinter survival in *N. orbicollis* with more beetles from the local population surviving through the winter months. Most of the beetles which survived were found between 6 and 10 cm below the soil surface. Additional variables had no significant effect on the survival of all beetles.

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Chapter 1
Fate of Carrion: Competition for reproductive resources of Nicrophorus beetles in New York forests

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Abstract

Small vertebrate carrion is a nutrient resource for a variety of organisms. Although small vertebrate carrion can be abundant, it is spatially and temporally unpredictable, which leads to competition among species that rely on it. Carrion competition in the northeastern United States is greatest among vertebrate scavengers, carrion flies, and *Nicrophorus* beetles. The purpose of this study was to determine the fate of small vertebrate carrion among mixed deciduous forest located in central New York between May and July 2022. *Nicrophorus* beetles buried 74% of carcasses (n=180) available during the trials, indicating they are the dominant competitor for small vertebrate carrion. A logistic regression model based on this study predicts 75% - 80% of carrion would be buried by *Nicrophorus* beetles when average daily air temperatures are in a range of 15 °C to 22 °C. Average daily air temperature above 22 °C was associated with an increased probability of fly colonization from 8% at 22 °C to 90% at 28 °C. These results may influence management strategies for the reintroduction of the endangered American burying beetle (*Nicrophorus americanus* Olivier: ABB) to NY.

1 | INTRODUCTION

Once deceased, a vertebrate carcass becomes an ephemeral nutrient resource for a wide array of organisms (Benbow et al., 2015; Owings & Picard, 2016). The decomposition process of carrion is critical to nutrient cycling (Benbow et al., 2013). Carrion has a low carbon-to-nitrogen ratio, which increases the rate of decomposition and provides a higher-quality source of nutrients to soils than plant detritus (Farwig et al., 2014; Ilardi, 2021). Carrion also contributes to ecosystem conditions by facilitating trophic interactions (Sawyer et al., 2022). For a limited period of time, an individual carrion can function as a decomposing resource patch which accelerates the biological activity of specialized necrophagous invertebrate species (DeVault et al., 2011; Farwig et al., 2014; Stiegler et al., 2020). Although necrophagous invertebrates are responsible for most carrion decomposition (Payne, 1965), the resource is sought by vertebrate scavengers, arthropods, and microbes alike (DeVault et al., 2004). The community composition within a necrobiome can vary based on several factors, such as the time of day, habitat, carrion size, or season (DeVault et al., 2004; Benbow et al., 2013). Due to the abundance of small vertebrate species in terrestrial ecosystems, a substantial portion of carrion biomass is made up of small vertebrate carcasses (Trumbo, 2016). As the presence of carrion is short-lived and unpredictable, competition for the resource can be intense among species (Wettlaufer et al., 2021).

Competition for small vertebrate carrion in temperate regions of North America includes vertebrate scavengers (DeVault et al., 2011; Olson et al., 2016), carrion flies (Putnam, 1978), and burying beetles (*Nicrophorus* spp.) (DeVault et al., 2004; Trumbo, 2016). Vertebrate scavengers can be dominant competitors for carrion as scavenging is a behavior in which vertebrate species can obtain nutritional benefits without active predation efforts (DeVault et al., 2003; Wilson &

Wilkovich, 2011; Allen et al., 2015). Scavenging plays an important role in ecosystem function and energy transfer between trophic levels (Moreno-Opo & Margalida, 2013; Allen et al., 2015). In some cases, more energy transfer has been defined through the scavenging of carrion than through predation by vertebrates (Wilson & Wilkovich, 2011). Vertebrate meso-scavengers can move small carrion from the carrion's point of origin, resulting in a loss of resources for necrophagous invertebrate competitors. The relocation of carrion by meso-scavengers allows for greater diffusion of nutrients throughout a terrestrial ecosystem (Olson et al., 2016). DeVault et al. (2011) determined that 88% of mouse carcasses were removed from farmland in Indiana by meso-scavengers, primarily raccoons (*Procyon lotor*) and Virginia opossums (*Didelphis virginiana*). Although meso-scavengers can locate carrion throughout the year, increased air temperature (over ~22 ˚C) is inversely related to their carrion acquisition (DeVault et al., 2011).

Additionally, similar increases in air temperature can accelerate carrion fly colonization and the development of fly larvae on small vertebrate carrion (Joy et al., 2006, Beasley et al., 2012). Sarcophagid flies may begin to feed on vertebrate carrion within minutes after death and can lay eggs within the first six hours postmortem (Payne, 1965). These colonizing carrion flies rely on fresh carrion as a high-quality nutrient source for larval development (Dawson et al., 2022). Female carrion flies will often deposit their young in the initial stages of carrion decay (Archer & Elgar, 2003). During summer months, the colonization of a small vertebrate carrion by either calliphorid or sarcophagid larvae can take place in as early as 48 - 60 hours (Payne, 1965; Putnam, 1978). Scott (1998) determined competition between carrion flies and burying beetles increases over the summer in New Hampshire as air temperatures continue to rise. Scott's The study identified two species of burying beetle (*N. orbicollis* and *N. defodiens*) which abandoned more carrion to fly colonization in August than in either June or July. A result which indicates fly

colonization through rapid larval development can out compete burying beetles for reproductive resources as summer air temperatures increase.

Burying beetles, like carrion flies, rely on carrion as a source of nutrition for their developing larvae (Scott, 1998). Burying beetles depend on sensitive chemical receptors in their antennae to quickly locate small vertebrate carrion (Scott, 1996). Upon locating an appropriately sized carcass, a breeding pair will remove the feathers or hair, shape the carrion into a ball, preserve it with anal and oral secretions, and bury it in soil before the female will lay eggs (Trumbo & Robinson, 2004). Upon hatching, the larvae will be fed carrion by either one or both parents (Scott, 1998). This unique biparental behavior in burying beetles allows for both the extended care and protection of the larvae and the regulation of brood size through filial cannibalism (Benowitz & Moore, 2016; Smith et al., 2017). The protection of the larval brood and carrion by the male burying beetle limits predation by other invertebrate species and carrion takeover by congeneric and conspecific competitors (Scott, 1998). Male defense against other burying beetles is not always successful. Aggressive conflicts between burying beetles over a carrion resource will often result in the larger beetle warding off the smaller beetles (Otronen, 1988). Competition among burying beetles is reduced by temporal resource partitioning. The emergence of *Nicrophorus* species is staggered throughout the warmer months from May through August resulting in only a few species seeking carrion for reproduction at any given time (Wettlaufer et al., 2021). Additional ecological characteristics such as carrion size and preferred habitat also separate species of *Nicrophorus* beetles when searching for reproductive resources (Scott, 1998).

Evaluating carrion competition between burying beetles, vertebrate scavengers, and carrion flies provides a better understanding of species interaction within a particular habitat. The results of a carrion competition study in New York forests may reflect similar studies (Scott 1996; Trumbo, 2016) throughout the northeastern US which have defined burying beetles as the most successful competitors of carrion acquisition. Results of burying beetle success over flies and vertebrate

scavengers in allocating carrion resources may indicate an appropriate habitat in which burying beetles have access to vital reproductive resources. Research in carrion competition is recommended by the US Fish and Wildlife Service (USFWS) in their recovery plan for the endangered American burying beetle (*Nicrophorus americanus* Oliver: ABB) as a way of determining habitat suitability among a potential reintroduction site (U.S. Fish and Wildlife Service, 1991). The primary objectives of this study are to determine suitability of forested sites in New York for ABB reintroduction and to understand which competitors, congeneric or otherwise, ABB would interact with during their breeding season through the evaluation of a carrion competition study. Additionally, assessing the impact of variables (air temperature, carrion size, trial month) on carrion fate for significant influence throughout this competition study would better inform species management and reintroduction efforts of ABB.

2 | METHODS

We conducted research at Greenwoods Conservancy, a 4.86 km^2 conservation refuge located in Otsego County, NY, USA (42.720933, -75.088947). Forested habitat within the conservancy is defined as mixed hardwood with red oak (*Quercus rubra*), sugar maple (*Acer saccharum*), and red maple (*Acer rubrum*) being the dominant species. We ran three trials in forested habitat at Greenwoods Conservancy in 2022 (May 22 – 27, June 19 – 24, and July 17 – 22) during the time in which ABB are reproductively active (Scott, 1998; McKenna Foster et al., 2019). For each trial, we used a total of sixty mice (*Mus musculus*) and rat (*Rattus norvegicus*) carcasses (Rodent Pro®, Inglefield, Indiana, U.S.A.). We evenly divided the carcasses into three vertebrate carrion size classes: small (18.00 g – 29.99 g), medium (85.00 g – 174.99 g), and large (175.00 g – 274.99 g) (DeVault et al., 2004; Trumbo, 2016). We chose the carcass size classes which represented the host vertebrate species available at Greenwoods Conservancy which would be

sought by *Nicrophorus* beetles during the trials. We tied a 1 m long piece of unscented dental floss to the hind leg of each carrion (Trumbo & Bloch, 2002). On the opposing end of the floss, we tied a 5 cm piece of flagging tape marked with the carrion's size class and identification number. We thawed all carrion at room temperature (21 °C ± 2 °C) 24 hours prior to deployment in a trial (DeVault et al., 2004).

For the placement of carrion in each trial, we randomized sixty locations within forested habitat at Greenwoods Conservancy using Geographic Information System (GIS) software (ersi ™, ArcMAP 10.8, 2020). We deployed carrion a minimum of 100 m apart and 50 m from road access (DeVault et al., 2004). We then randomized which carrion would be placed at which location based on the carrion's identification number and size classification, using Microsoft Excel. We began placing carrion in the morning of Day 0 during each of the five-day trials. We located carrion placement sites using Google Maps with the coordinates determined above. We assured the dental floss and identification labels were tucked neatly under the carrion as to not interfere with potential competitor interactions with the carrion. We also placed a 12 cm long metal pin 8 cm into the ground at the base of the tail of each carrion as a placement marker. We were able to measure from the marker to determine any distance a carrion was moved during the trials.

Through Microsoft Excel, we randomized the placement of 12 Browning Strike Force Extreme model # BTC-5HDX trail cameras (Browning ® Trail Cameras, Birmingham, AL) within each trial. We assigned four cameras to each of the three carrion size classifications. We placed the cameras during Day 0 of each five-day trial. We suspended the cameras from trees between 0.5 m – 1 m off the ground. We positioned the cameras at a downward angle to face the carrion at 1 m – 2 m away and programmed each camera to capture three images per activation (DeVault et al., 2011).

We made observations of all carrion in the morning and evening of each day beginning at the time of placement. In addition to recording all observations on a field datasheet, we captured photos from 30 cm directly above each carrion using a cellphone camera (LG model V-20). We

included in each photo an identification card which denoted the time and date, the carrion identification, and the observer's initials.

We categorized the fate of each carrion as either buried by a *Nicrophorus* beetle, taken by a vertebrate scavenger, buried by a *Nicrophorus* beetle then taken by a vertebrate scavenger, colonized by flies, or decomposed. If we observed that carrion was buried by *Nicrophorus* beetles we would record the distance the carrion was moved (cm), the depth at which it was buried (cm), and the number and species of *Nicrophorus* beetles present. We would define a carcass as scavenged if the carrion were absent from its point of placement or if photographic evidence were captured on a designated trail camera. With fly colonization, we monitored and quantified both eggs and larvae on a carcass. We defined the fate of carrion to be fly colonization when more than 100 fly larvae were present on a carcass. At the end of the five-day trials, if a carrion was decayed to a degree in which it was no longer viable to any competitor, we categorized it as decomposed.

2.1 | Data analysis

We used multinomial logistic regression models to determine which factors contributed most to the fate of carrion using the XYZ package (Venables & Ripley, 2002) in R Statistical Software (*v4.2.2*; R Core Team 2022). Carcass fate was our dependent variable with trial (May, June, or July), carcass size (small, medium, or large), and average daytime air temperature the independent variables. We conducted a Tukey pairwise comparison on all models using the emmeans package (Lenth, 2023). The model selection we determined was based on Akaike information criterion (AIC) with the AICmodavg package (Mazerolle, 2023). We made predictions for the model of best fit and plotted them using ggplot2 (Wickham, et al., 2019). All analyses we performed used R Statistical Software (*v4.2.2* R Core Team 2022).

3 | RESULTS

In total, 133 of 180 carrion were buried by *Nicrophorus* beetles (74%). Vertebrate scavengers removed 23 (13%) carrion over the three trials. Fifteen (8%) of the total carrion were colonized by flies, five (3%) were first buried by *Nicrophorus* beetles and then scavenged by vertebrates, and the remaining four (2%) carrion had decomposed by the end of the trial. *Nicrophorus* beetles were the dominant competitors for all carrion size classes (small = 80%, medium = 73%, large = 68%). The average distance *Nicrophorus* beetles dragged a carcass was 17 cm ± 1.1 (SE) in a range of distance from 1 cm to 102 cm. The average depth at which a carcass was buried by *Nicrophorus* beetles was 3 cm ± 0.2 (SE) in a range of 1 cm to 10 cm. Trail camera photographs indicate vertebrate scavengers to include racoons (*Procyon lotor*), fishers (*Pekania pennanti*), long-tailed weasels (*Mustela frenata*), and red-tailed hawks (*Buteo jamaicensis*).

The logistic regression analysis found the model of best fit to include the effects of average daily air temperature on the fate of carrion (Table 1). Model fit declined for the remaining models of predictors of carrion fate (ΔAIC > 32.3) (Mazerolle, 2023). The average daily air temperature model showed a significant effect on the fate of carrion ($\chi^2 = 52.889$, df = 4, $p < .01$). Average daily air temperatures between 15 °C and 22 °C indicate the probability of carrion buried by *Nicrophorus* beetles to range between 75% and 80%. The probability of fly colonization increased from 8% when average daily air temperatures were 22 °C up to 90% probability at 28 °C (Table 2) (Figure 1).

4 | DISCUSSION

Burying beetles were the dominant competitor during all trials and across all carrion size classes within this study, outcompeting both vertebrate scavengers and fly colonization in forested sites throughout Greenwoods Conservancy. *Nicrophorus sayi* was the predominant species of burying beetle during the May trial, with *N. orbicollis* being the primary species in the June and July trials. The burying beetle, *N. sayi*, is an early-emerging species in North America (Scott, 1998; Wettlaufer et al., 2021) which breeds in cooler temperatures (Benowitz et al., 2019) and seeks reproductive resources from April until June (Scott, 1998). In contrast, *N. orbicollis* begins searching for a reproductive host in mid-June through early August, which overlaps with ABB reproduction (Trumbo & Bloch, 2000). Although burying beetle reproduction is divided among congeners throughout the spring and summer, there is some overlap among species (Scott, 1998). Reproductive activity of *N. orbicollis* and ABB occur simultaneously during the months of June and July. However, reproductive host size is also partitioned, with *N. orbicollis* utilizing vertebrate carcasses ranging from 7 g to 150 g, while ABB seeks slightly larger carrion from 30 g up to 500 g (Trumbo & Bloch, 2000). This partitioning of carrion by size is thought to decrease competition among congeners which seek reproductive hosts at the same time.

The results of this competition study, in which *Nicrophorus* beetles are the dominant competitor, align with similar studies in northern latitudes of North America. Trumbo (2016) determined that 77.5% of mouse carcasses were buried by *Nicrophorus* beetles in Connecticut forests during the reproductive season. Scott (1998) found that the greatest competition *N. orbicollis* faces during its reproductive period in New Hampshire, Northern Michigan, and Ontario Canada is from conspecifics. Alternatively, southern regions of North America find either fly colonization, ants, or vertebrate scavengers to be the superior competitor for carrion (DeVault, et al., 2004, Sawyer, et

al., 2022). In addition to greater success in northern habitats, burying beetle species diversity is greater, with northern locations supporting both habitat specialist and generalist species (Trumbo, 1990). Temperature may play a role in decreased success among burying beetles in the southern portion of North America, as habitat specialists may be outcompeted by carrion flies and ants making it difficult for them to maintain a viable population (Trumbo, 1990).

Temperature can be a factor which affects competition for carrion across a variety of ecosystems. DeVault et al. (2004) discovered that vertebrate scavenging activity declined greatly when temperatures exceeded 17 °C among forested sites in South Carolina. In Indiana agricultural land, scavenging activity declined when ambient air temperature increased above ~ 22 °C (DeVault et al., 2011). Similar air temperatures have an opposing effect on fly colonization, where temperatures above 22 °C show an increase in fly activity and development (Archer & Elgar, 2003) and temperatures below 17 °C slow third instar development in carrion fly larva (Diptera: Calliphoridae) (Joy et al., 2006). The results of this study align with temperature effects on fly development, where the probability of fly colonization increased substantially when average day-time air temperatures exceeded 22 °C. The resulting increase of fly colonization at higher temperatures may influence reintroduction timing of ABB. Release of ABB may be more appropriate during the earlier portion of their reproduction period in mid-June when air temperatures are cooler to decrease the potential of fly competition.

If release of ABB is timed based on temperature to decrease competition from both vertebrate scavengers and carrion fly colonization, they will still face abundant competition from the congener, *N. orbicollis*. The results of this study determine that *N. orbicollis* can use carrion up to 274.99 g, although they are more proficient in burying carrion of smaller sizes (18.00 g – 174.99 g). This may indicate that the niche for larger carcasses (> 175 g) is still available for ABB among forested habitats such as those available at Greenwoods Conservancy during June and July. Congeneric *Nicrophorus* beetles often dispute carcasses through aggressive behavior (Scott,

1998) where larger body size is the best predictor of dominance and success in competition for carrion (Otronen, 1988; Schrempf et al., 2021). As ABB is the largest species of its genus (Lomolino et al., 1995), they should outcompete congeners for carrion resources. Interspecific competition for reproductive resources may not be the greatest challenge for ABB recovery in NY; however, an abundance of appropriate carrion could be the foundation to success. The continued monitoring of small vertebrate populations and their habitat, along with *Nicrophorus* beetle community composition research is essential to this conservation effort. Management practices which could facilitate an abundant and diverse small mammal and bird population at a reintroduction site where competition from meso-scavengers and carrion flies is low, may lead to the development of a self-sustaining ABB population once reintroduced.

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TABLES

Table 1. Akaike information criterion corrected for sample size (AICc), number of parameters (K), the difference between each model and the best (ΔAICc), model likelihood (L), and AICc weight (Wt) for values for the logistic regression models on the fate of small vertebrate carrion in forested sites at Greenwoods Conservancy, Hartwick, NY from May to July 2022. The best-supported model included the effect of average daily air temperature on carrion fate.

Model	K	AICc	ΔAICc	L	Wt
average air temp	8	279.93	0.00	1	0.99999991
trial	12	312.39	32.46	8.93E-08	8.93E-08
carrion size + trial	20	319.57	39.65	2.46E-09	2.46E-09
null model	4	324.20	44.28	2.43E-10	2.43E-10
carrion size	12	330.27	50.34	1.17E-11	1.17E-11

Table 2. The probability of small vertebrate carrion fates within forested sites at Greenwoods Conservancy, Hartwick, NY, across a range of air temperatures spanning from 15 °C to 28 °C during the months of May, June, and July 2022. Temperatures at 22 °C or below saw the highest probability of carcasses being buried by *Nicrophorus* beetles. Above 22 °C the probability of fly colonization becomes the highest.

Avg Daily Air Temp °C	Buried then Scavenged	Buried	Decomposed	Fly Colonization	Scavenged
15	0.016	**0.795**	0.027	0.000	0.161
16	0.019	**0.799**	0.027	0.001	0.155
17	0.021	**0.801**	0.026	0.002	0.150
18	0.024	**0.802**	0.025	0.004	0.145
19	0.028	**0.801**	0.024	0.008	0.139
21	0.035	**0.780**	0.022	0.038	0.125
22	0.039	**0.746**	0.020	0.079	0.115
26	0.024	0.269	0.006	**0.665**	0.036
27	0.015	0.150	0.003	**0.812**	0.019
28	0.009	0.076	0.002	**0.904**	0.009

FIGURES

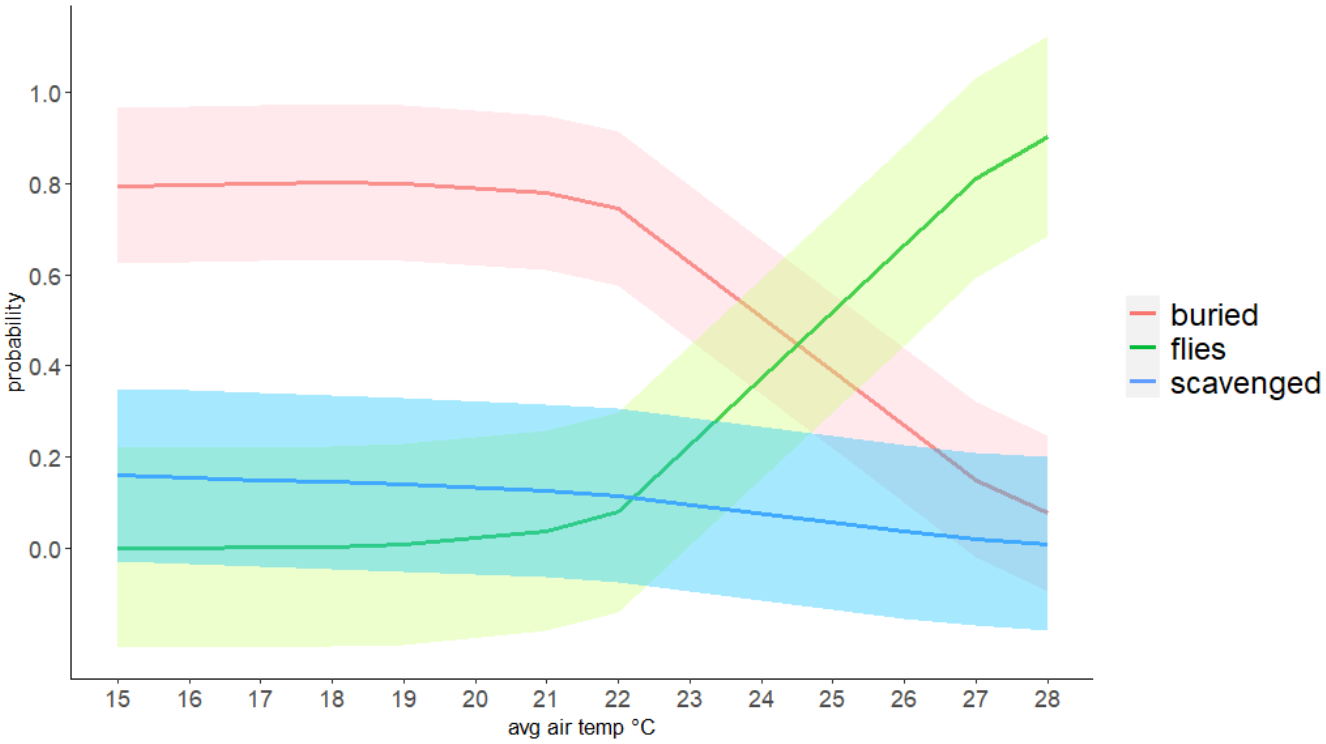

Figure 1. The probability of small vertebrate carrion fates including ± std. err. of carrion either buried by *Nicrophorus* beetles, colonized by carrion flies, or taken by vertebrate scavengers across a gradient of average air temperature ranging from 15 °C to 28 °C within forest habitats at Greenwoods Conservancy, Hartwick, NY, from May through July 2022.

Chapter 2
Overwinter site selection of *Nicrophorus orbicollis* Say (Coleoptera: Silphidae)

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Abstract

Adult insects which overwinter in temperate regions are faced with many challenges including low temperatures, energy loss, and desiccation. Their ability to select an over winter location may mitigate some of the challenges they face throughout the cold season. Overwintering site selection of burying beetle (*Nicrophorus* spp.) populations throughout the northeastern United States is seldomly studied. The long and erratic flight patterns coupled with the highly sensitive chemoreceptors of adult burying beetles may direct the choices they make in securing an overwintering habitat. As environments vary throughout the northeast, local adaptation among some populations of burying beetles may have evolved. Efforts in reintroducing the endangered American burying beetle (*Nicrophorus americanus* Olivier; ABB) from the extant population on Block Island, Rhode Island back to the state of New York may be faced with difficulties based on such local adaptations. Through a laboratory olfactometer study, we compared the choices (forest soil, forest leaf litter, *Peromyscus* spp. nesting material, and a control) made by two populations of *Nicrophorus orbicollis* Say, one indigenous to central NY and one from Block Island, RI, when acclimated to near-winter conditions in NY. Results indicate similarity among choices made by the two populations, with leaf litter from hardwood forests in NY being the most preferred. From these results, we have determined that population had no discernable effect on the choices made by the burying beetles. However, the volatile organic compounds from leaf litter may have some influence on the overwinter site selection of *N. orbicollis* found in NY.

1 | INTRODUCTION

Winter in the northeastern United States is often considered a season of dormancy in which many ecological processes have historically been thought to slow as air temperatures fall below freezing (Cambell et al., 2005). However, recent research suggests the seasonal change into winter is a key driver of many ecological processes among different ecosystems (Dinh et al., 2023). As this seasonal change commences, so begins a period of transition and preparation for many species (Lehmann et al., 2012). Trees in temperate forests drastically reduce water and nutrient uptake upon entering dormancy to conserve energy (Nilsson, 2022). Half of the world's bird species engage in migratory flights, with even residential species of northern latitudes making short migrations to more suitable winter habitat (Marchand, 2013). The scatter-hoarding behaviors of rodent species to cache food in the process of preparing for the long, harsh winter months begins as air temperatures decrease and the photoperiod changes (Bartlow et al., 2018). These seasonal developments also institute the seeking and engineering of shelter by many species to avoid exposure to winter conditions (Swihart, 1995; Caceres-Charneco & Ransom, 2009; Bearman-Brown et al., 2020; Pustilnik et al., 2020).

For ectotherms such as amphibians and invertebrates, the fluctuation in air temperature within seasonal environments can have a dramatic effect on their survival, due to the limitations of their own body temperature regulation (Alford et al., 2014; Urbanski, et al., 2017). Provisioning habitat for these species can be a crucial component of their overwinter survival (Miyashita & Takada, 2007; Machăc & Tuf, 2021). Several cold-blooded species overwinter in the subnivium, the thermally stable microhabitat between the ground surface and snowpack (Pauli et al., 2013;

Fitzpatrick et al., 2019). However, the existence of the subnivium is contingent on the duration and depth of the snow. Other ectotherms seek shelter in pre-existing burrows or nests constructed by other wildlife and at times even share a hibernaculum with other ectothermic species (Greene et al., 2016; Hartzell, 2019). Still others burrow into the soil, leaf litter, or the bark of trees to diapause through the cold season (Rooney & Lewis, 2000; Boychuk et al., 2015; Javahery, 2019).

The strategies of insects for acquisition of an overwinter microhabitat vary. While numerous insects overwinter in an immature development stage (Turnock et al., 1983; Block et al., 1987; Smith, 2002), many insects in temperate regions enter overwinter diapause as adults (Rusch et al., 2012; Boychuk et al., 2015; Mikat & Straka, 2021). These actions are not only entrained by temperature and photoperiod (Tougeron, 2019; Obrycki, 2022), but also olfactory and chemical cues. Species such as the brown marmorated stink bug (*Halyomorpha halys),* boxelder bug (*Leptocoris trivittatus)*, and many cluster flies of the genus *Pollenia* seek shelter in artificial structures in considerable numbers signaled by others of the same species (Tinker, 1952; Nielsen & Hamilton, 2009; Vezsenyi et al., 2022). The convergent lady beetle (*Hippodamia convergens*) leaves a cuticular hydrocarbon, which acts as a pheromone at hibernacula sites to congregate conspecifics to the overwinter location (Wheeler & Cardé, 2014). Chemical cues are also used by certain species of carpenter bees of the genus *Ceratina*, to rediscover old nests or locate the burrows of other hymenopteran insects to avoid winter conditions (Mikát & Straka, 2021).

Olfactory senses are critical to the existence of burying beetles (*Nicrophorus* spp.). This genus relies on sensitive chemosensory receptors to locate small vertebrate carrion for preparation as a food source for their young (Scott, 1998). The teneral adults overwinter in a state of reproductive diapause, to emerge during the following spring and summer (USFWS, 1991; Amaral et al., 1997). As most burying beetles overwinter as highly mobile adults, they possess some control over the selection of their overwintering site. This may indicate that habitat selection plays a role in the persistence of *Nicrophorus* spp. (Schnell et al., 2008). Burying beetles, named for the

reproductive behavior whereby they bury vertebrate carrion in soil, may bury themselves in soil over winter (Scott 1998; Schnell et al., 2008; Hoback & Conley, 2014), though this assumption has not been explicitly tested. Burying beetles may participate in alternative strategies, such as habitat provisioning. Research demonstrates higher overwinter survival of the endangered American burying beetle (*Nicrophorus americanus* Oliver; ABB) when provisioned with carrion than without (Schnell et al., 2008). Therefore, it is possible that burying beetles also seek an overwinter food source when confronted with seasonal cues suggesting the approach of winter.

Understanding more about the overwintering behaviors of *Nicrophorus* beetles can assist in directing the conservation goals of ABB reintroduction efforts in the northeastern United States, which are currently underway in inland forest sites in New York. The source population for this reintroduction is an ABB population from Block Island, Rhode Island. Although ABB from Block Island experience more similar winters to New York than ABB from other extant populations (Schnell et al., 2008), habitat conditions on Block Island are not identical to those in New York. As a coastal island, Block Island's vegetation is composed of maritime shrubs and grasslands (McKenna-Foster et al., 2016; Leasure & Hoback, 2017). To determine if source population influences overwintering site choice, two populations of the congener most closely related to ABB phylogenetically (Szalanski et al., 2000) *Nicrophorus orbicollis* were used in a laboratory olfactometry study. One population was sourced from Block Island, RI and the other from central NY. In this study the two populations were presented with the same substrate choices from NY forests, after acclimation to near-winter air temperature and photoperiod. Similarities between the two populations may provide evidence for how ABB will be suited for over winter habitat within NY, regardless of localized adaptation to Block Island. Additionally, the inclusion of *Peromyscus* spp. nesting material in this study seeks to test the beetle's preference for potential habitat provisioning or food source allocation over forest soil and leaf litter under simulated near-winter conditions.

2 | METHODS

2.1 | Study specimen rearing

For this study, we chose *N. orbicollis*, the congener most closely related to *N. americanus* phylogenetically (Szalanski et al., 2000) as a surrogate species for research. On June 23, 2022, 28 (11 males, 17 females) wildtype specimens of *N. orbicollis* were collected from Block Island, RI with assistance from the Nature Conservancy on Block Island using baited pitfall traps (RIDEM Division of Fish and Wildlife Scientific Collector Permit # 2022-44-W) (McKenna-Foster et al., 2016). We collected a second population of wildtype *N. orbicollis* from Greenwoods Conservancy in Hartwick, NY using baited, above-ground pitfall traps throughout the month of June 2022. We housed the beetles individually in 1.37 l transparent plastic containers (9 x 19 x 8 cm) (Pioneer Plastics Inc #149c). We loosely placed damp paper towels (Georgia-Pacific, Pacific Blue basics #23304) into each container to prevent desiccation of the beetles and changed the towels weekly. We fed a 1 cm^3 piece of cow liver to each beetle twice a week (Delclos et al., 2020). We organized housing containers by population and stored them on shelving in the laboratory space at the State University of New York (SUNY) Cobleskill. The laboratory air temperature was programmed by building facilities to maintain at 21 °C ± 2 °C. We programmed overhead LED lighting to provide a photoperiod cycle of 12:12 (L:D) hours a day (Akotsen-Mensah & Fadamiro, 2015; DeVries et al., 2019; Karmakar et al., 2020). After an initial 5 day waiting period, we placed breeding pairs of *N. orbicollis* into individual 7.8 l clear plastic terrariums (17 x 27 x 17 cm) which we filled halfway with a blend of equal parts topsoil, sand, and peatmoss. We provided each breeding pair with a large white previously frozen mouse carcass (*Mus musculus*) weighing between 18.00 g and

29.99 g (RodentPro.com). We then placed a damp layer of paper towel over the soil mixture and carcass which we sprayed with water daily to prevent desiccation of the beetles during reproduction. Newly eclosed *N. orbicollis* emerged 38 days from the placement of the mouse carcass at which time we placed them into individual 1.37 l containers. We recorded the date of eclosion, sex, population, and the lineage for each specimen. We disposed of all soil once reproduction was completed. We continued rearing *N. orbicollis* until more than one hundred, second filial generation (F2) individuals of each population had been reached. All beetles used in this study were F2 *N. orbicollis*.

2.2 | Olfactometer

We constructed a modified four chamber olfactometer for use in this experiment (Petersson, 1970; Vet et al., 1983; Said et al., 2006) (Figure 1). We designed identical, independent air systems for each of the four substrates included in the study. The air was supplied by four electric aquarium air pumps (Tetra Whisper model 10). Air was passed through 4.0 g of activated charcoal (AquaClear # A-1384) for air purification (Vinauger et al., 2011). It was then pumped through 15 mL of deionized water for humidification (Said et al., 2006), before passing over 20 mg of a substrate. Air flow was independently dictated by acrylic air flow meters (BQLZR model M4170509042) at 500 mL/min (Said et al., 2006). The essence of each substrate entered the arena from one of four corners. Air was then vacuumed from the center of the olfactometer arena using a modified air pump (Tetra Whisper model 100) at a rate of 600 mL/min. All air was distributed through a standard aquarium 1.4 cm air hose. We constructed the arena using clear epoxy resin with an 8 mm thick black plastic base and a 1 mm thick clear plexiglass removable lid. We affixed a 9 cm plastic screw cap in the center of the plexiglass lid for ease of beetle deployment (Said et al., 2006). We included threshold lines 11 cm from the center of the arena to

determine the choice made by individual beetles within the study (Marler & Marler, 2018). We placed a removable 7 cm diameter acclimation cage under the screw cap at the center of the arena which allowed beetles to settle for 30 seconds before each trial. This was derived from our preliminary test trials to allow for a standard amount of time for each beetle to acclimate to the arena after being removed from their individual housing container and placed into the olfactometer.

2.3 | Study design

We fed a total of 216 F2 *N. orbicollis* (n=108 NY, n=108 RI) a 1 cm^3 piece of cow liver 18 hours before acclimation. We recorded the sex, weight (g), age (days since eclosion), and pronotum width (mm) of each beetle before moving them to an environmental control room located at SUNY Cobleskill for a pre-trial, 24-hour acclimation period. We set the control room air temperature to 5 °C (Lehmann et al., 2012) and timed overhead LED lighting to operate for 11:13 (L:D) a day. After the 24-hour acclimation, we ran the olfactometer trials in the control room under red light (Kulkarni et al., 2017). We ran the olfactometer for 10 minutes before use (DeVries et al., 2018). We haphazardly selected beetles one at a time and placed them into the arena's acclimation cage for 30 seconds. We then removed the cage without disturbing the beetle and reinstalled the screw cap. We provided each beetle five minutes to make a choice (Said et al., 2006; Chen et al., 2016; Vera, et al., 2016; DeVries et al., 2019). We determined that a beetle made a choice once its entire body crossed a threshold line in the arena. After each beetle trial we removed the entire plexiglass lid and wiped the interior of the arena with 70% ethanol and left it to dry before reinstalling the lid and running another trial (Vera et al., 2016; Kulkarni et al., 2017; DeVries et al., 2019). After 10 consecutive trials, we removed the air supply lines from the arena, turned the arena one quarter rotation, and reinstalled the air supply lines. We ran each beetle once through

the olfactory trial (Vera et al., 2016; Camara Siqueira da Cunha et al., 2022). We used a total of 200 *N. orbicollis* (NY; n = 100, RI; n = 100) in this study.

2.4 | Data analysis

All analyses we performed were in R Statistical Software (*v4.2.2*; R Core Team 2022).We compared observed choice outcomes made by all *N. orbicollis* in this study to expected outcomes in a Chi-square test for probability with a p-value of less than .05 used to indicate statistical significance (*v1.3.2*; Wickham et al., 2019). We then used the same Chi-square test to compare observed outcomes of individual choices (forest leaf litter, forest soil, and *Peromyscus* spp. nest material) against the control to the expected outcome in each test. We corrected the probability (p = .05) for the multiple comparisons using the Bonferroni procedure due to the increased risk of a type I error. With the correction we made to type-I error rate, we used an adjusted p-value of less than .02 to indicate statistical significance.We prepared multinomial logistic regression models using the *nnet* package (Venables & Ripley, 2002) to determine which factors contributed most to the choices made by all *N. orbicollis* across populations. We used the *emmeans* package (*v1.8.5*; Lenth, 2023) to conduct a Tukey pairwise comparison on all models. Our model selection was determined based on Akaike information criterion corrected for sample size (AICc) with the *AICcmodavg* package (*v2.3.2*; Mazerolle, 2023). We made predictions from models and plotted them using the *tidyverse* package (Wickham et al., 2019).

3 | RESULTS

Choices were made by all 200 *N. orbicollis* (NY; n = 100, RI; n = 100) within this study. Forest leaf litter was chosen most by both populations (NY; n = 34, RI; n = 35) followed by the control (NY; n = 27, RI; n = 30), forest soil (NY; n = 21, RI; n = 21) and then *Peromyscus* spp. nesting material

(NY; n = 18, RI; n = 14) (Figure 2). When the observed choices made by all *N. orbicollis* were compared to the equally distributed expected outcomes in a Chi-square test of probability, results concluded that the choices made by *N. orbicollis* were significantly different from the null expectation of 25% of beetles choosing each substrate type (X^2 = 15.96, df = 3, p = .001). A significant difference was determined between the observed outcomes of *Peromyscus* spp. nesting material (n = 32) and the control (n = 57) (X^2 = 7.02, df = 1, p = .01). No discernable difference between the observed outcomes of forest leaf litter (n = 69) and the control (n = 57) (X^2 = 1.14, df = 1, p = .29) nor forest soil (n = 42) and the control (n = 57) (X^2 = 2.27, df = 1, p = .13) were determined.

The results of the multinomial logistic regression analysis for all *N. orbicollis* found the null model to be the best supported model of choice, suggesting that while probability of choosing a given substrate varied, it was not affected by explanatory variables (population, beetle sex, beetle size, beetle weight) of interest. Competing models included the effects of the beetle's sex on choice (∆AIC = 3.59), the beetle's body size on choice (∆AIC = 5.58), and the effects of population on choice (∆AIC = 5.64) (Table 1). However, no significant association was found between the sex of all beetles and the observed choices (X^2 = 2.72, df = 3, p = .44), the size of all beetles and the observed choices (X^2 = 0.73, df = 3, p = .87), nor the population of beetles and the observed choices (X^2 = 0.67, df = 3, p = .88).

A significant association was determined among the interaction of population and body size (X^2 = 9.37, df = 3, p = .02) when making a choice (Figure 3a, 3b, 3c). The model indicated that the probability of *N. orbicollis* from the NY population choosing forest leaf litter increased from 7.0% to 60.1% as body size increased from a pronotum width of 4.3 mm to 7.3 mm (Figure 3a). Alternatively, the probability of NY beetles choosing *Peromyscus* spp. nesting material declined from 45.1% to 6.2% as the body size increased from a pronotum width of 4.3 mm to 7.3 mm (Figure 3b).

4 | DISCUSSION

Although burying beetles are highly mobile (Schnell et al., 2008) and often thought to be habitat generalists (Scott, 1998), their affinity towards mature oak dominated forests for reproduction (Anderson, 1982(a), 1982(b); Lomolino & Creighton, 1996) may also be associated with overwintering habitat due in part to forest leaf litter. Even though burying beetles are often affiliated with burying carrion in soil (Milne & Milne, 1976), it may be the volatile organic compounds (VOCs) from leaf litter that signify the importance of a habitat, whether that pertains to carrion resource allocation or overwinter site selection. While most species of burying beetle are highly adept at locating small vertebrate carrion through the VOCs the carrion emits (Trumbo, 2016; Delcos et al., 2021), they are less likely to discover the carrion when it is covered by leaf litter or soil (Trumbo & Bloch, 2002). It is possible that burying beetles associate leaf litter VOCs with carrion resources, as many small mammals and birds rely on hardwood forest habitats for food and shelter (Chace et al., 2009; Hsia & Franci, 2009; Kellner et al., 2013; Dorigo et al., 2021). Locating such habitat may be an effective approach to discovering an otherwise ephemeral resource whose abundance and location can be difficult to predict (DeVault et al., 2003; Creighton et al., 2009; Wettlaufer et al., 2021). As burying beetles are more likely to survive overwinter with a food source (Schnell et al., 2008), these forested habitats may provide adequate resources for burying beetles year-round. The leaf litter samples for this study were collected from hardwood forest sites in NY and consisted primarily of oak (*Quercus* spp) and maple (*Acer* spp). Further olfactometry studies comparing multiple leaf litter types may reveal preference for a particular tree species or forest type among *Nicrophorus* species. Modeling of the interaction between population and body size indicates that larger bodied *N. orbicollis* of the NY population are more likely to choose leaf litter

than smaller bodied individuals of the same population (Figure 3a). This can be biologically significant as it may suggest that these forests are a favored habitat for adult burying beetles. In the presence of many conspecifics, adult burying beetles decrease their brood size through infanticide (Trumbo, 1990(a), 1990(b)) resulting in larger bodied offspring (Woelber et al., 2018). It is also possible that larger carrion are found among these forest sites as greater resource availability produces larger burying beetles (Smiseth et al., 2013). An abundance of larger bodied burying beetles at a specific site would indicate high densities of such species among that habitat, potentially larger carrion resources, or both. Whether competition over habitat takes place among burying beetles is unknown, however competition for carrion often finds the larger bodied beetle the victor (Otronen, 1988; Schrempf et al., 2021).

The nesting material of *Peromyscus* spp. was chosen significantly less than the expected outcome and was the choice made least often by both populations. This may suggest that *N. orbicollis* does not seek to provision habitat created by other species when confronted with decreased air temperature and photoperiod. Although burying beetles rely upon chemoreception to locate carrion (Delclos et al., 2021), the pungent volatiles given off by the nesting material may deter *N. orbicollis* from seeking mouse nesting sites for their overwinter habitat. Further research into which volatiles were given off by the mouse nest may indicate odors least favored by burying beetles.

The second most common choice made by both populations of *N. orbicollis* was the control. The components used in the olfactometer to hold the substrate choices were constructed of similar plastic material to that of the containers used to house the individual F2 beetles before the choice trials. The control was left without a substrate in the olfactometer, which potentially resulted in the odor not being of just purified air, but of the plastic used to house the substrates within the olfactometer. This odor may have created bias toward the control as the beetles were familiar with

a similar odor through prior exposure. Corrections to avoid such bias could be made using wild-caught beetles, alternative olfactometer or housing materials, or the elimination of a blank control.

Many abiotic factors including photoperiod and temperature initiate dormancy in insects (Hwang & Shiao, 2011). Preparing for a state of dormancy may require the security of food or shelter within a preferred habitat. Understanding how a species interacts with a habitat can inform conservation efforts involving the translocation or reintroduction of a species (Kappeler et al., 2013; Hawkes & Gerwing, 2019; Bastille-Rousseau & Wittemyer, 2020; Jones et al., 2021), as adaptation to a new habitat can be disruptive and stressful to introduced wildlife (Teixeira et al., 2007; Jenni et al., 2015; Hilbers et al., 2019). In the case of this study, a population of *N. orbicollis* from Block Island, RI was presented with substrate choices found among forested sites in NY and compared to the choices made by an indigenous population of *N. orbicollis*. The composition of Block Island, RI is quite different than that of central NY. Block Island consists of coastal shrub, grassland communities and pastureland (Sikes & Raithel, 2002; Leasure & Hoback, 2017). Similarities between the choices made by the two populations may indicate that adaptation to a change in habitat composition may result in the successful translocation of a burying beetle species, such as ABB, from Block Island to NY. Although *N. orbicollis* is the species best suited as a surrogate for this study (Szalanski et al., 2000), a study conducted in Arkansas by Lomolino, et al. (1995), found that *N. orbicollis* preferred forested sites, whereas ABB, a species believed to be more capable of tolerating varied habitat, preferred soil types with higher percentages of sand over silt and clay. Replication of this study using ABB from Block Island could provide more informative results.

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TABLES

Table 1. Akaike information criterion corrected for sample size (AICc), number of parameters (K), the difference between each model and the best (ΔAICc), model likelihood (L), and AICc weight (Wt) for the logistic regression models on the variables which may affect the choices made by *Nicrophorus orbicollis* in the overwintering site selection trials. The best-supported model was the null model.

Model	K	AICc	ΔAICc	L	Wt
null	3	544.46	0.00	1.00	0.72
beetle sex	6	548.05	3.59	0.17	0.12
beetle size	6	550.04	5.58	0.06	0.04
population	6	550.10	5.64	0.06	0.04
beetle weight	6	550.60	6.13	0.05	0.03
population * beetle size	12	553.43	8.97	0.01	0.01
population + beetle sex	9	553.74	9.27	0.01	0.01
beetle size + beetle sex	9	553.84	9.38	0.01	0.01
population * beetle weight	12	554.24	9.77	0.01	0.01
beetle sex + beetle weight	9	554.39	9.92	0.01	0.01
beetle size + beetle weight	9	555.63	11.16	0.00	0.00
population * beetle sex	12	555.71	11.24	0.00	0.00
population + beetle size	9	556.08	11.62	0.00	0.00
beetle size * beetle sex	12	556.43	11.96	0.00	0.00
population + beetle weight	9	556.49	12.02	0.00	0.00
beetle sex * beetle weight	12	557.14	12.67	0.00	0.00
beetle sex + beetle weight + beetle size	12	559.65	15.19	0.00	0.00
population + beetle sex + beetle size	12	559.95	15.48	0.00	0.00
population + beetle sex + beetle weight	12	560.33	15.87	0.00	0.00
beetle size * beetle weight	12	562.20	17.74	0.00	0.00
population * beetle sex * beetle size	24	565.28	20.81	3.02E-05	2.16E-05
population + beetle sex + beetle weight + beetle size	15	566.18	21.72	1.92E-05	1.38E-05
population * beetle sex * beetle weight	24	568.55	24.08	5.89E-06	4.22E-06
beetle sex * beetle weight * beetle size	24	578.10	33.64	4.96E-08	3.55E-08
population * beetle sex * beetle weight * beetle size	48	617.78	73.31	1.20E-16	8.62E-17

FIGURES

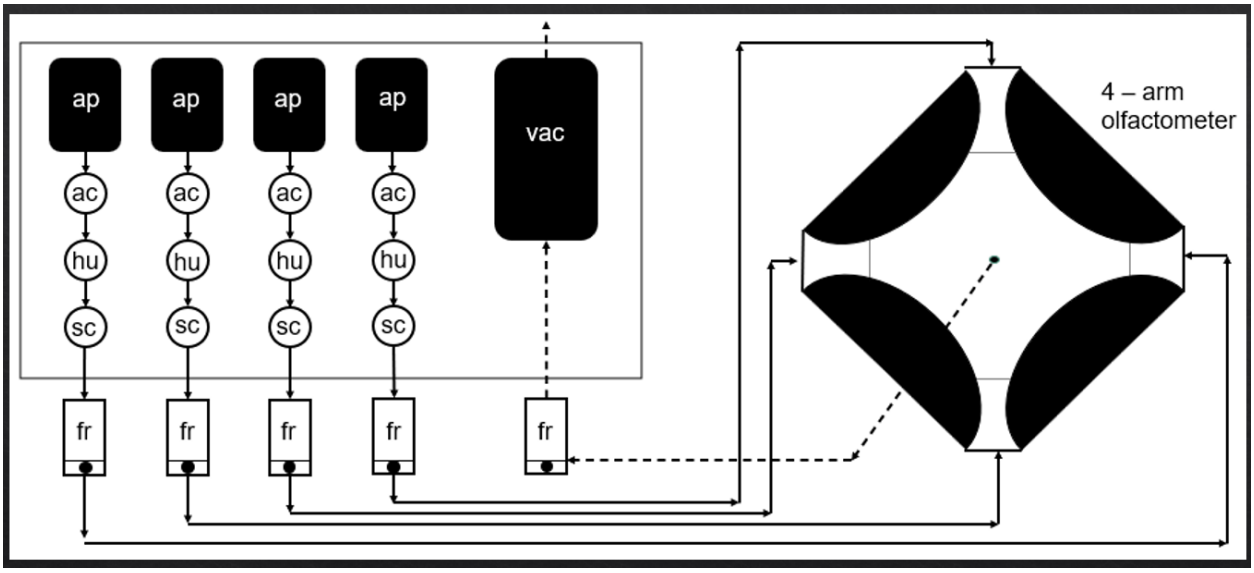

Figure 1. Diagram of the four-arm olfactometer attached to the volatile delivery system. ap: air pump, ac: activated charcoal, hu: humidifier, sc: substrate container, fr: flow regulator, vac: vacuum pump.

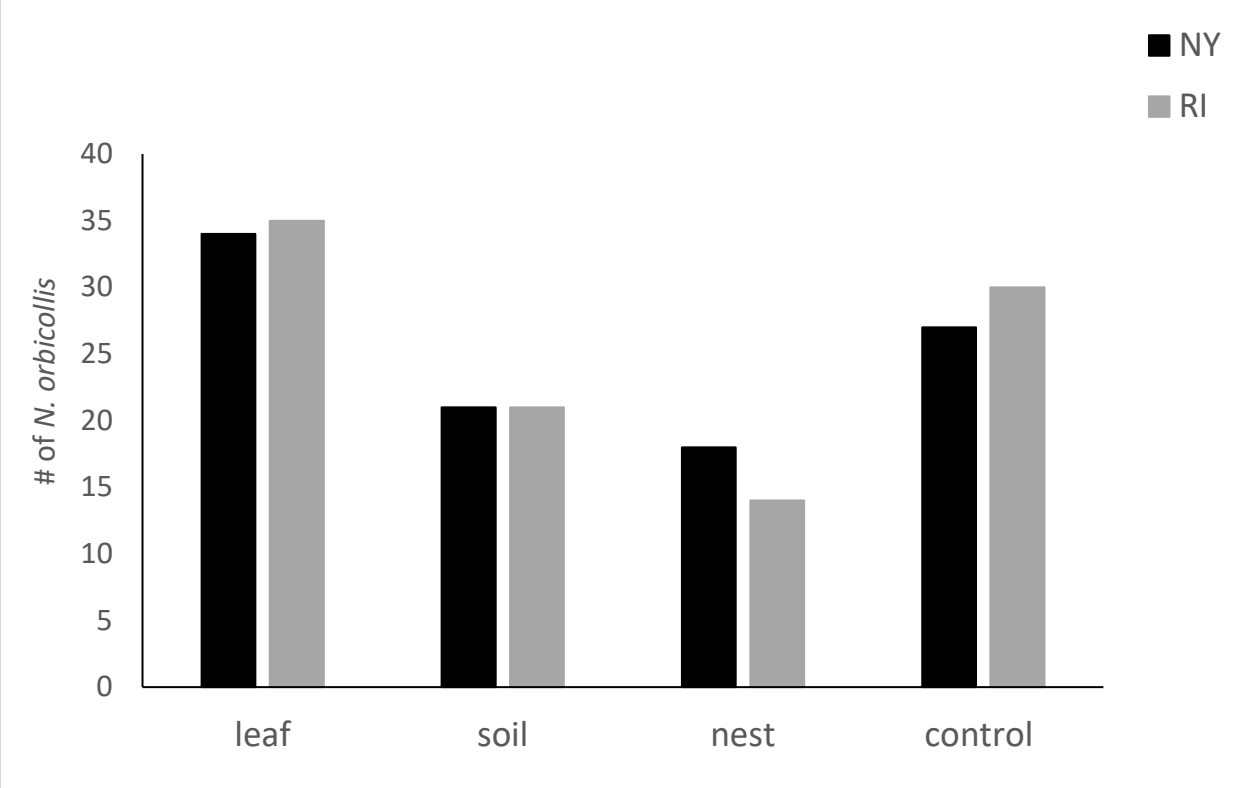

Figure 2. Observed choices made by the two populations (NY; RI) of *Nicrophorus orbicollis* of four options (leaf litter, forest soil, control, and *Peromyscus* spp. nesting material) provided in an olfactometry study when acclimated to overwinter conditions (air temperature 5 °C; photoperiod 11:13 hours (L:D)).

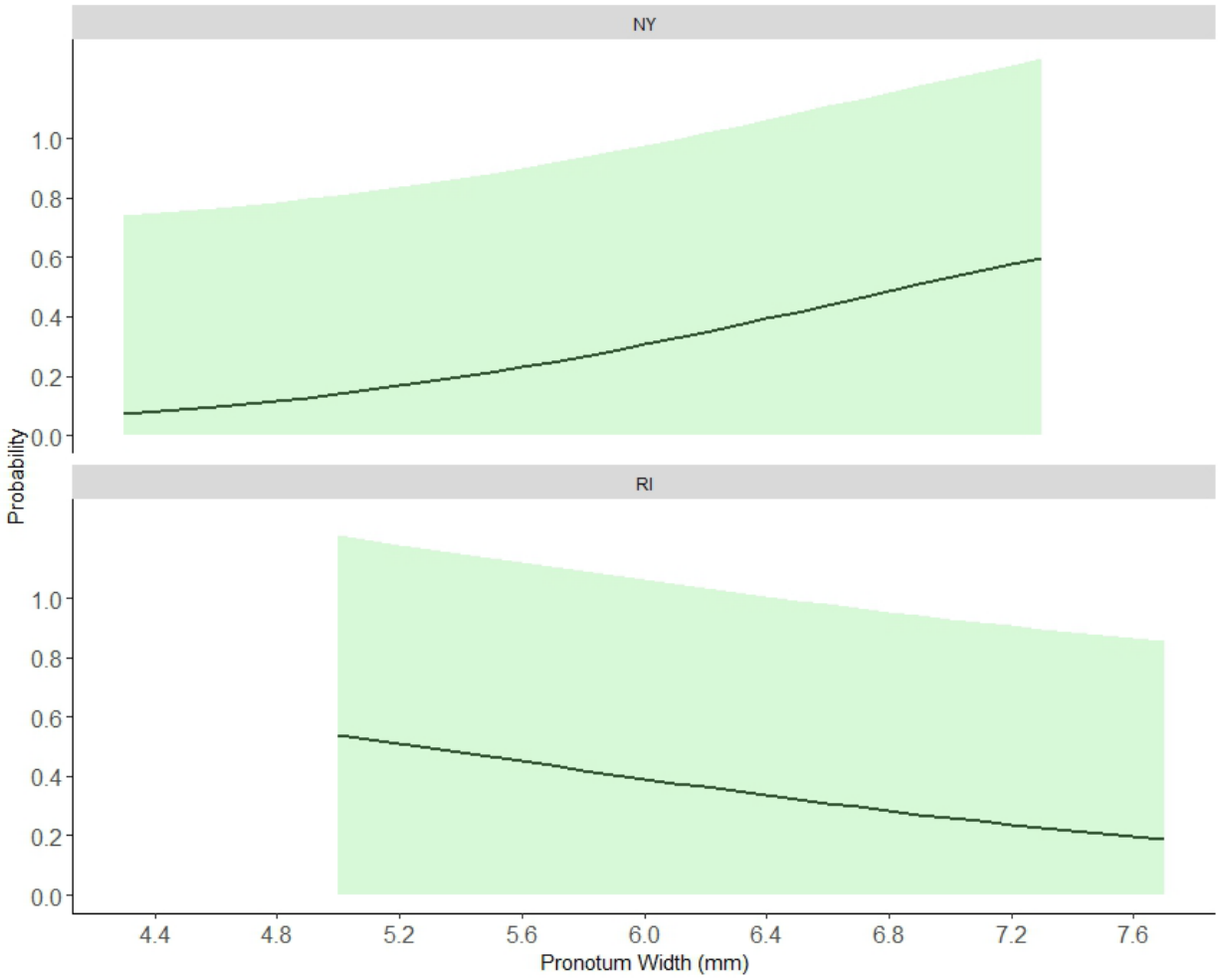

Figure 3a. Probability of *N. orbicollis* from two populations (NY, RI) choosing forest leaf litter as an overwintering site in NY forests based on the beetle's body size, represented as the measured width of their pronotum (mm).

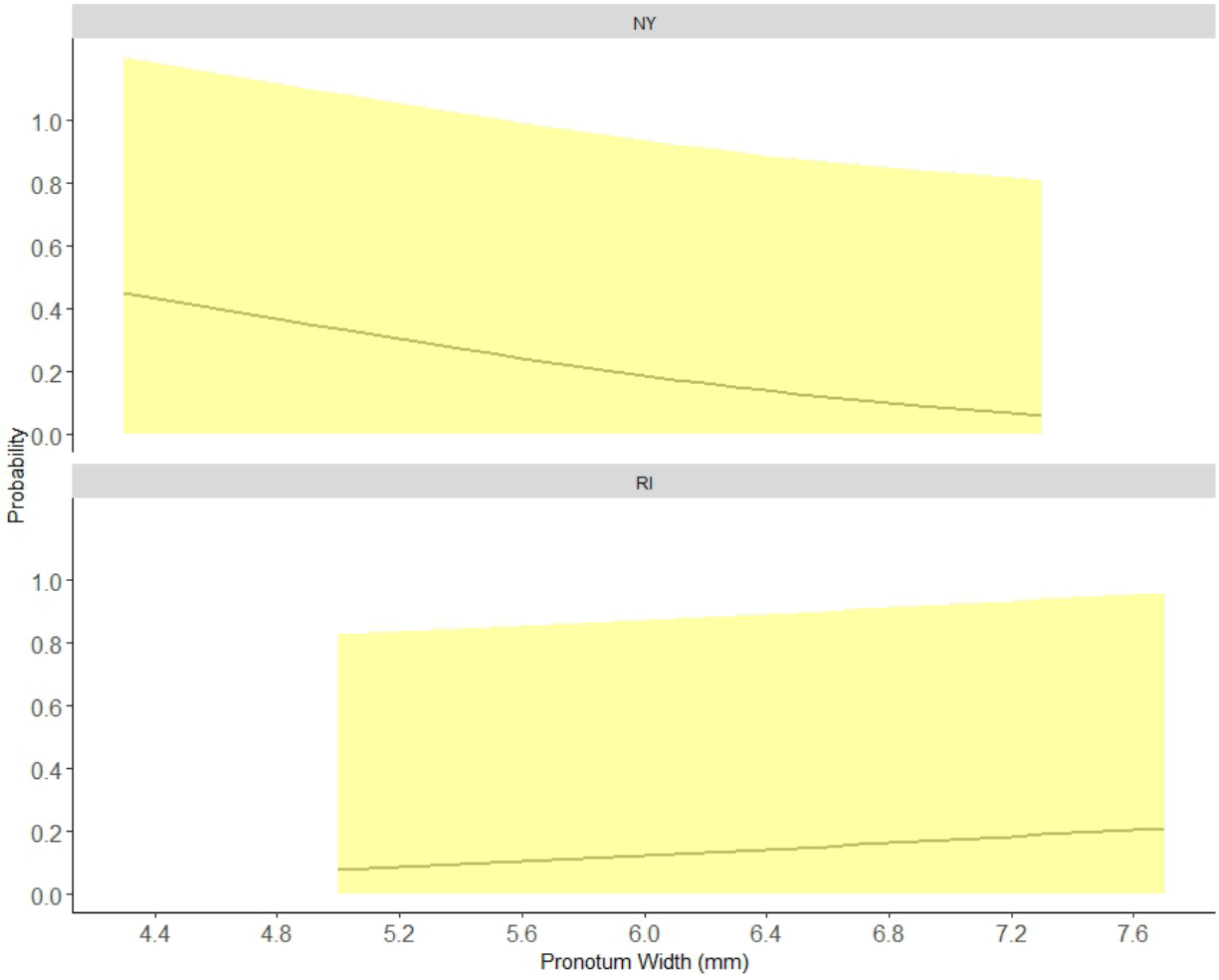

Figure 3b. Probability of *N. orbicollis* from two populations (NY, RI) choosing *Peromyscus* spp. nesting material as an overwintering site in NY based on the beetle's body size, represented as the measured width of their pronotum (mm).

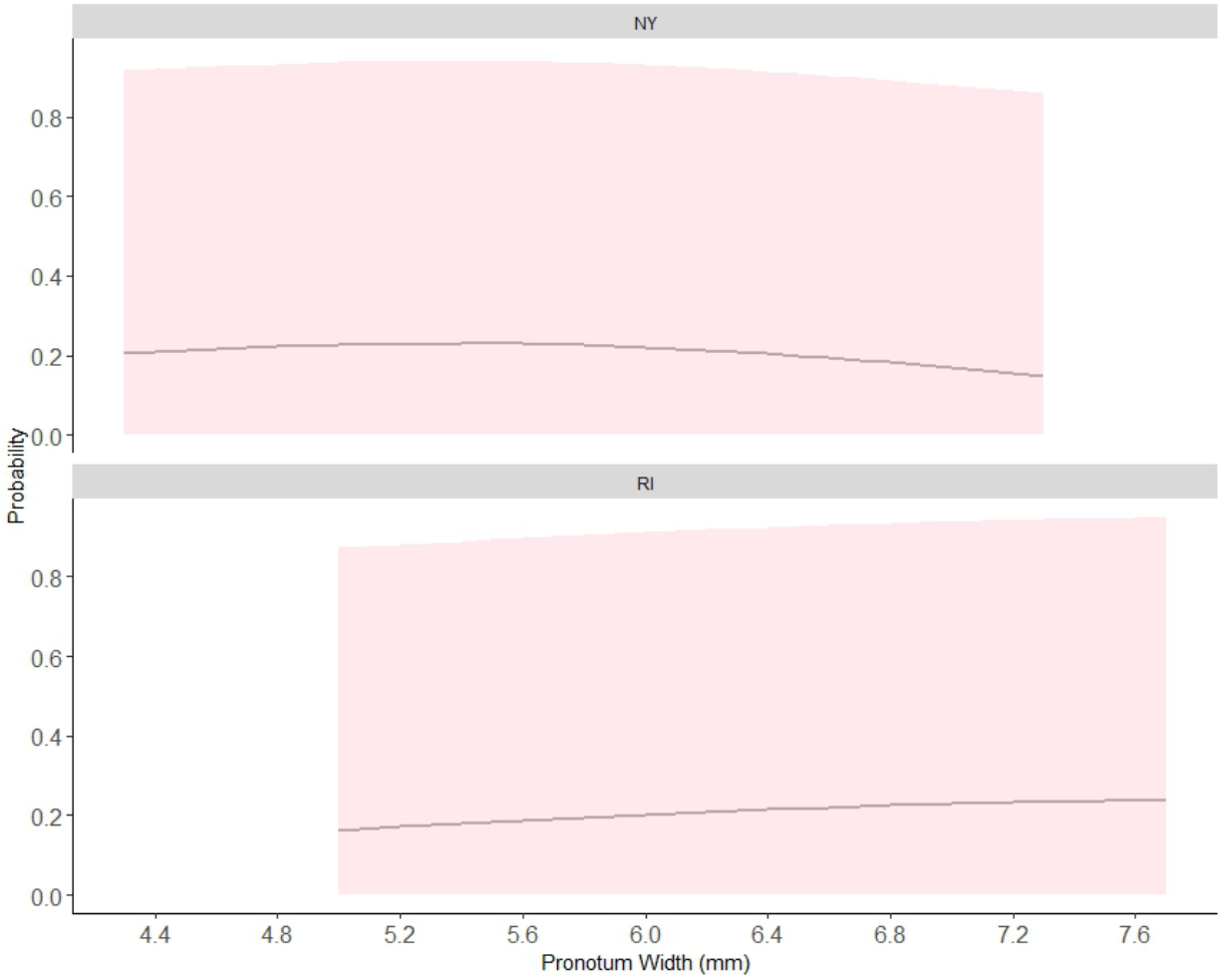

Figure 3c. Probability of *N. orbicollis* from two populations (NY, RI) choosing soil as an overwintering site in NY forests based on the beetle's body size, represented as the measured width of their pronotum (mm).

Chapter 3
Overwinter survival of two populations of *Nicrophorus orbicollis* Say (Coleoptera: Silphidae) in a northeastern forest.

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Abstract

In the northeast United States, the only extant population of the endangered American burying beetle (*Nicrophorus americanus* Olivier; ABB) exists on Block Island, Rhode Island (RI). Now missing from 90% of its native range, efforts to reintroduce ABB sourced from Block Island back to the continental US would aid in the recovery of the species. One factor relevant to the persistence of ABB is its ability to survive over winter. A better understanding of overwinter survival rates in burying beetles (*Nicrophorus* spp.) prior to the translocation of ABB may enhance the chance of successful reintroductions. Using a sister species of ABB as a surrogate, this study compares the overwinter survival rate of two populations of *Nicrophorus orbicollis* Say in central New York (NY); one indigenous to the study site and one introduced from Block Island, RI. We determined that 65% of all *N. orbicollis* survived over winter, but burying beetles from NY had a significantly higher survival rate than beetles from RI. Of the NY population, 83% survived over winter, whereas 47% *N. orbicollis* survived over winter from the RI population. Although their survival was lower than that of local beetles, the finding that nearly half of the translocated population of burying beetles from Block Island, RI survived through the winter in NY supports the choice of central NY as an initial reintroduction site for Block Island ABB.

1 | INTRODUCTION

The American burying beetle (*Nicrophorus americanus* Oliver; ABB) was once widespread across the eastern United States and portions of Canada (Creighton et al., 1993; Lomolino & Creighton, 1996; Butler et al., 2013). In the northeastern US specifically, there are historic records of ABB once existing from Maine through New Hampshire, into Massachusetts, Connecticut, and New York. However, they are now missing from 90% of their contemporary range (USFWS, 1991; Lomolino et al., 1995; Amaral et al., 1997; Sikes & Raithel, 2002). The only extant population of ABB known in the northeast currently resides on Block Island, a small island of maritime shrub and grasslands, 26 km off the coast of Rhode Island along the Atlantic Seaboard (Kozol et al., 1988; Raithel et al., 2006; McKenna-Foster et al., 2016; Leasure & Hoback, 2017). Multiple hypotheses have attempted to explain the dramatic decline of the species in the early to mid-20th century (Sikes & Raithel, 2002). Most notable are the loss and alteration of habitat (Anderson, 1982a; Lomolino & Creighton, 1996) and the loss of ideal carrion resources (Pollock, 2003; Silvy et al., 2004; Williams et al., 2004; Leasure & Hoback, 2017; Gutowsky et al., 2020). The persistence of ABB on Block Island has been associated with both the lack of competition by vertebrate scavengers and the presence of large nesting birds used as carrion resources for reproduction (Amaral et al., 1997; Raithel, 2002; Schnell et al., 2014). The provisioning of carrion on Block Island since 1994 has also resulted in an increased abundance of ABB during years of provisioning (Raithel et al., 2006). In 1989, the US Fish & Wildlife Service (USFWS) designated ABB an endangered species and drafted a recovery plan to protect existing populations and restore the species throughout its historic range (USFWS, 1991). One recovery objective includes the reintroduction of the Block Island population back to the US mainland (USFWS, 1991). The loss of genetic variation as well as the adaptation to island environments can contribute to higher extinction rates on islands (Frankham, 1997). Island populations are also susceptible to climate change through sea level rise, temperature shifts, and intense storms (Connell, 2015; Petzold &

Magnan, 2019; Veron et al., 2019) increasing the urgency for the translocation of this population of ABB to the continental US.

The transfer of wildlife in the reintroduction of a species to an area within its historical range has been a successful means of conservation (Osterberg et al., 2015; Bouley et al., 2021) and is a common strategy when either supplementing a declining population or restoring a population that has been extirpated (Gross et al., 2023). A successful reintroduction is most often defined by establishment of a free-living, self-sustaining population post-release (Griffith et al., 1989; Ashbrook et al., 2015). Prior to the translocation of a species, critical life history traits should be assessed to enhance the chances of a successful reintroduction (Griffith et al., 1989). In the case of ABB, suitable habitat should be determined, as well as reproductive resource availability and overwinter survival rates (USFWS, 1991; Lomolino & Creighton, 1996; Schnell et al., 2008; Jurzenski et al., 2014). As ABB has been extirpated from the northeastern continental US, it is not possible to determine survival rates within the region prior to reintroduction. However, in this study the use of a surrogate species, *Nicrophorus orbicollis* Say, one most closely related to ABB phylogenetically (Szalanski et al., 2000), aims to provide an overwinter survival rate of both a translocated population from Block Island and an indigenous population at forested sites in NY. Similarities in survival rates between the two populations may indicate an improved chance for success in the relocation of ABB from Block Island back to the northeastern contiguous states. Differences between the populations may influence management strategies related to ABB reintroduction efforts through the number of ABB released, the necessity of carrion provisioning, and the reevaluation of habitat. Additionally, this study aims to provide insight into the overwintering biology among burying beetle populations of the northeastern US.

2 | METHODS

2.1 | Study specimen rearing

We acquired specimens from two populations of wildtype *N. orbicollis* for laboratory rearing of beetles for use in this study. Eleven males and 17 females were collected from Block Island, RI in June 2022, with assistance from The Nature Conservancy on Block Island using baited pitfall traps (RIDEM Division of Fish and Wildlife Scientific Collector Permit # 2022-44-W) (McKenna-Foster et al., 2016). During the same time, we collected wildtype *N. orbicollis* from Greenwoods Conservancy, a 4.86 km^2 conservation refuge located in Otsego County, NY, USA (42.720933, -75.088947) using baited, above-ground pitfall traps (Leasure et al., 2012). We housed individual beetles in 1.37 l transparent plastic containers (9 x 19 x 8 cm) (Pioneer Plastics Inc #149c) with damp paper towels (Georgia-Pacific, Pacific Blue basics #23304) to prevent desiccation. We fed a 1 cm^3 piece of cow liver to each beetle twice a week (Delclos et al., 2020) and replaced the paper towels weekly. We housed and reared all beetles in a laboratory provided by the State University of New York (SUNY) at Cobleskill. We programmed overhead LED lighting to provide a 12:12 (L:D) hours a day cycle (Akotsen-Mensah & Fadamiro, 2015; DeVries et al., 2019; Karmakar et al., 2020). The air temperature in the laboratory was programmed by facilities management to maintain 21 °C ± 2 °C.

We bred all *N. orbicollis* on mouse carcasses (*Mus musculus*) weighing between 18.00 g and 29.99 g (RodentPro.com) in individual 7.8 l transparent plastic terrariums (17 x 27 x 17 cm) which we filled halfway with a blend of topsoil, peatmoss, and sand. Newly eclosed beetles emerged around 38 days from the day we initiated breeding. We used laboratory reared, second filial generation (F2) *N. orbicollis* from both populations in this study.

2.2 | Study site

We conducted this study among three forested sites within Greenwoods Conservancy: Site 1 (42.722799, -75.086460), Site 2 (42.719719, -75.095332), Site 3 (42.715309, - 75.086173). All our study sites were within 1 km of each other and no more than 0.5 km from road access. The forested sites were a mix of tree species: maple (*Acer* spp.), oak (*Quercus* spp.), eastern white pine (*Pinus strobus*), and eastern hemlock (*Tsuga canadensis*).

2.3 | Field study design

We modified methods from Schnell et al. (2008) to conduct field studies. On August 18, 2022, we established a 4 x 5 grid of 20 18.9 l buckets (30.2 cm top diameter, 26.2 cm bottom diameter, 36.8 cm height) at each site. We measured 5 m between buckets within each of the grids. We drilled holes into the bottom and side of each bucket for sufficient drainage. We buried each bucket by carefully removing a soil plug 28 cm deep and the approximate width of each bucket, placing a bucket into each hole, and reinserting the soil plug into the bucket. We assured that each soil plug was compressed gently into each bucket with no air gaps on either the inside or outside of the bucket, to which the bucket became a barrier in the soil. In total we buried 60 buckets among the three sites. We left the buckets undisturbed without lids for two months to acclimatize the conditions inside of the buckets to that of the soil outside of the buckets. One day prior to the start of the experiment, we documented the weight (g), age (number of days from eclosion), sex, and source population of all 60 beetles. The field experiment began on October 26, 2022, when we placed individual *N. orbicollis* into each bucket. Ten beetles from each population were used at each of the three sites for a total of 30 beetles from each population. We used Microsoft Excel to randomize which beetle was placed into which bucket. We provisioned each beetle with a small mouse carcass (18.00 g – 29.99 g) (Rodent Pro®, Inglefield, Indiana, U.S.A.) before sealing the

buckets securely with lids. We replaced the material from the lid centers with a heavy-duty metal wire mesh (0.64 cm x 0.64 cm) to allow for exposure to natural elements (air, light, precipitation) while still allowing the lids to seal tightly to the buckets. We used buckets with secure lids to ensure beetles could not escape during the study by either flying away or digging through the soil. If we could not locate a beetle, we assumed that the beetle died and decomposed rather than escaped so long as the bucket and lid remained sealed and intact throughout the study. We left the beetles to overwinter in the buckets for six months.

On April 13, 2023, overnight low air temperatures reached 16 °C for a third consecutive evening (Schnell et al., 2008), which determined the end of my study prior to the beetle's natural emergence. We carefully pulled buckets one at a time, removed the lids, and placed the soil plugs on to a plastic sheet. Starting at the soil surface end, we dissected each plug carefully to locate the beetle. Once we located a beetle, we recorded whether it was alive or dead and the depth (cm) at which we located it in the soil plug. We then placed the individual beetle into a container with a damp paper towel. We brought all beetles back to the laboratory at SUNY Cobleskill where we reweighted (g) and confirmed the sex of each living beetle.

2.3 | Temperature data

We recorded both air and soil temperature hourly from October 4, 2022, through April 13, 2023, at each of the three sites using Thermochron iButton model # DS1921G temperature loggers (Thermochron® Temperature Loggers, Castle Hill, Australia). We recorded soil temperature by placing two loggers inside of a sealed PVC pipe (1.9 cm diameter, 91.5 cm height). We positioned one logger 5 cm from the base of the pipe and the other logger 23 cm from the base of the pipe. We filled the gaps inside of the pipe between the loggers with foam insulation. We then inserted the PVC pipe into the ground vertically so that 33 cm of the pipe was below the soil surface leaving

58.5 cm exposed above the soil surface. This allowed us to record soil temperature at a depth of 28 cm (equivalent to the bottom of the buckets) as well as at a depth of 5 cm below the soil surface. We sealed a third temperature logger to the top of the exposed PVC pipe using clear packaging tape to capture air temperature readings. We replicated this logger station at all three study sites. We retrieved temperature data from the iButton loggers using the OneWireViewer software application by Java® (*v1.6*; Maxim Integrated Products, Inc., 2011).

2.4 | Data analysis

We used the car package (Fox & Weisberg, 2019) in R Statistical Software (*v4.2.2*; R Core Team, 2022) to create a logistic regression model to determine which factors contributed to the overwinter survival of *N. orbicollis* in this study. We included population, sex, and weight as the independent variables which may affect the outcome of the overwinter survival of the beetles. We assessed the models based on Akaike information criterion corrected for sample size (AICc) with the AICcmodavg package (Mazerolle, 2023) to determine the model of best fit. We made predictions using the best supported model and plotted them using ggplot2 (Wickham, et al., 2019). We created an additional logistic regression model using the car package (Fox & Weisberg, 2019) in R Statistical Software (*v4.2.2*; R Core Team, 2022) to determine if population contributed to the depth in which *N. orbicollis* buried overwinter. Likewise, we assessed the models based on Akaike information criterion corrected for sample size (AICc) with the AICcmodavg package (Mazerolle, 2023) to determine the model of best fit.

3 | RESULTS

A total of 39 (65%) *N. orbicollis* survived and 21 (35%) died overwinter. From the NY population, 25 (83%) survived and 5 (17%) died (Figure 1). From the RI population, 14 (47%) survived and 16 (53%) died (Figure 1). All beetles were found to be buried between 1 – 25 cm in a range of 0 – 28 cm. The greatest number of living beetles from the NY population (n = 11; 41%) were recovered between 6 – 10 cm below the soil surface (Figure 2). The greatest number of living beetles from the RI population recovered were equally distributed between 1 – 5 cm (n = 6; 11%) and 6 -10 cm (n = 6; 11%) (Figure 2). The logistic regression model created to determine if population contributed to burying depth resulted in the null model being the best-supported model (Table 1). Population had no significant effect on the depth to which *N. orbicollis* buried overwinter ($\chi^2 = 5.25$, df = 4, p = .263). All deceased beetles were recovered within 5 cm of the soil surface. The average weight of the surviving *N. orbicollis* recorded one day prior to the study was 0.37 g ± 0.01 (SE). The average weight of the same beetles at the end of the study was 0.38 g ± 0.01 (SE) (Figure 3).

Population was the best supported explanatory variable of the survival of the beetles according to model selection (Table 2). Population had a significant effect on overwinter survival when we ran the best-fitting model ($\chi^2 = 9.2045$, df = 1, $p < 0.01$). Predictions based on the population model indicate a greater rate of survival over winter for the NY population (Figure 4). All other top models (ΔAIC < 6.31) included the effect of population in addition to other variables (Mazerolle, 2023) (Table 1), though no other variables had significant effects (all $p > 0.05$).

The average daily air temperature from October 4, 2022 – March 24, 2023, was 0.3 °C ± 0.5 °C (SE) in a range from 17.6 °C to -21.0 °C (Figure 5). The average daily soil temperature at a depth

of 28 cm was 5.1 °C ± 0.2 °C (SE) in a range from 1.8 °C to 11.2 °C (Figure 4). Soil temperatures were recorded at a depth of 5 cm from January 22, 2023 - April 12, 2023, resulting in an average daily soil temperature of 2.0 °C ±0.1 °C (SE) in a range from 1.0 °C to 7.3 °C (Figure 5).

4 | DISCUSSION

Although 65% of all *N. orbicollis* survived over the course of this study, a significant difference in the rate of survival was found between the NY and RI populations. A study by Gross et al. (2023) found that translocated populations have, on average, 64% lower performance than wild-resident populations related to movement, condition, growth, survival, and reproduction. The difference in overwinter survival between the NY and RI populations of *N. orbicollis* within this study was determined to be 43.4%. Although this study used the surrogate species, *N. orbicollis*, the results may be reassuring as an overwinter mark-recapture survey of translocated ABB from Block Island, RI to Nantucket Island, MA between 2007 and 2016 reported a recapture rate of 15% ± 4% (McKenna-Foster et al., 2016). The overwinter survival rate of the extant population of ABB on Block Island is not known. Therefore, although this study is relevant to the overwinter biology and translocation of *Nicrophorus* species, additional studies of the overwinter survival rate of ABB on Block Island would be valuable in understanding how ABB are likely to perform if translocated to NY. Through the determination of ABB overwinter survival rates on Block Island, the future assessment of translocated ABB throughout the northeastern continental US could be compared, allowing managers to prioritize reintroduction sites with the most suitable winter conditions.

Although soil conditions were not fully assessed in this study, both soil temperature and the depth at which beetles buried themselves were recorded. Similar studies by Hoback & Conley (2014) in Nebraska found correlation between mean soil temperatures and mean depth of bury by both *N. orbicollis* and *N. marginatus*, suggesting that beetles position themselves below the frostline in

soil to avoid freezing. The soil temperatures recorded at 5 cm and 28 cm below the soil surface in this study did not fall below freezing (0 °C) and the vast majority (76%) of surviving beetles were found at depths between 6 cm and 25 cm. The remaining 24% of surviving beetles were located at depths between 1 cm and 5 cm. As soil temperatures were not recorded at depths less than 5 cm, no frostline was determined in this study. However, as all deceased beetles were recovered at or near the surface (< 5 cm in depth) it is possible that soil temperatures may have sustained at or below freezing between the soil surface and 5 cm. The depth at which *N. orbicollis* was most often found in this study aligns more with the average depth (6 cm) at which ABB were found in a similar overwinter study in Arkansas (Schnell et al., 2008). A multiple year study in Nebraska determined the average depth of bury by *N. orbicollis* and *N. marginatus* ranged from 25.92 cm to 50.78 cm (Hoback & Conley, 2014). The depth to which beetles could bury in this study was limited by the bucket to 28 cm. However, as no beetles were located below 25 cm, we hypothesize that the 28 cm restriction did not impact their burying behavior.

It is unclear why some beetles would not bury themselves to avoid freezing. Hoback & Conley (2014) postulated that some beetles may have died prior to freezing due to the lack of food or desiccation as they could not escape from the study site. Research by Schnell et al. (2008), showed that overwinter survival of ABB in the southern range increased when ABB were provisioned with a rat carcass. This led to the provisioning of all *N. orbicollis* in this study to increase the likelihood of survival of both populations. Alternatively, Hoback & Conley (2014) determined that when air temperatures fell below freezing, burying beetles slowed their metabolic rates and remained below the soil surface without the need for a provisioned food source. As air temperatures within this study remained above freezing throughout the duration of the first month and soil temperatures below 5 cm remained above freezing, as well as the beetles being captive, we suspect that the provisions increased the survival of beetles in this study.

Although burying beetles are highly mobile insects (Raithel et al., 2006; Jurzenski et al. 2011) and ABB occurs in multiple habitat types throughout its current range (Kozol et al.,1988; Lomolino et al.,1995; Lomolino & Creighton, 1996; Creighton et al., 2009; Jurzenski et al., 2014), the forested habitat was kept consistent in this study based on the habitat in which the focal species, *N. orbicollis,* is most frequently captured (Anderson, 1982b; Scott, 1998; Trumbo & Bloch, 2002; Burke et al., 2020). Results from the Schnell et al. (2008) study found that ABB in grassland and woodland habitats had similar overwinter survival.

Much of what is known about ABB overwinter survival is associated with the populations in the northern (Hoback & Conley, 2014) and southern (Schnell et al., 2008) limits of its range. While these studies provide insight into overwintering behaviors of burying beetles, including ABB, little is known about the overwinter survival rates of burying beetles in the northeastern US. Although survival rates may vary by species, the results of this study indicate that nearly half of the translocated *N. orbicollis* survived overwinter in NY. This may provide a starting point for modeling expected population growth rates of ABB released in Central NY and determining how many beetles should be part of the initial reintroduction. However, this result may be contingent upon multiple factors related to the habitat and climate into which they are released. Soil conditions need to be such that burying beetles can physically bury themselves to depths below the formation of any frostline (Hoback & Conely, 2014). As in this study and Schnell et al. (2008), if soil temperatures do not fall below freezing, the provisioning of carrion food resources may be appropriate to maintain survival rates similar to those we observed, as metabolic rates in ABB may not slow, forcing them to seek nutrients to subsist. Furthermore, as global temperatures continue to rise, the relationship between snowpack and ecological and biological functions should be considered (Monson et al., 2006; Zuckerberg & Pauli, 2018; Slatyer et al., 2022). Seasonal snowfall becomes an important insulating layer for many species which survive over winter in the subnivium or below ground (Block et al., 1987; Domisch et al., 2017; Gavazov et al.,

2017). The amount of snowfall and the duration of snowpack is expected to diminish in the Northeast as temperatures continue to rise (Chen et al., 2021). This decline may impact overwinter conditions and in turn the behaviors of burying beetles.

Many factors appear to influence the overwinter survival of burying beetles. Yet, much is still left to uncover about their overwinter ecology. Further studies examining the effects of a changing climate on the overwinter survival of burying beetles may provide insight into their behaviors during the winter season. Research related to the overwinter survival of ABB on Block Island would establish a rate of survival which may be applied in comparison to any reintroduced population of ABB throughout the Northeast. However, studies directly involving ABB can be difficult as they are a species of concern with a limited population. By providing relevant survival rates of a surrogate species from both an indigenous and translocated population, this study suggests that nearly half of an introduced population of burying beetles from Block Island could survive over the winter in NY.

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TABLES

Table 1. Akaike information criterion corrected for sample size (AICc), number of parameters (K), the difference between each model and the best (ΔAICc), model likelihood (L), and AICc weight (Wt) for values for the logistic regression models on the depth of bury of *Nicrophorus orbicollis* in forested sites at Greenwoods Conservancy, Hartwick, NY from October 2022 to April 2023. The best-supported model included the null model.

Models	K	AICc	ΔAICc	L	Wt
null	4	142.56	0.00	1.00	0.94
population	8	148.23	5.67	0.06	0.06

Table 2. Akaike information criterion corrected for sample size (AICc), number of parameters (K), the difference between each model and the best (ΔAICc), model likelihood (L), and AICc weight (Wt) for values for the logistic regression models on the overwinter survival of *Nicrophorus orbicollis* in forested sites at Greenwoods Conservancy, Hartwick, NY from October 2022 to April 2023. The best-supported model included the effect of population on survival.

Models	K	AICc	ΔAICc	L	Wt
population	2	72.7	0	1	0.35
population + sex	3	74.14	1.44	0.49	0.17
population * weight	4	74.23	1.53	0.46	0.16
population + weight	3	74.24	1.54	0.46	0.16
population + weight + sex	4	75.81	3.11	0.21	0.07
population * sex	4	76.44	3.74	0.15	0.05
weight	2	79.02	6.32	0.04	0.01
weight + sex	3	80.67	7.97	0.02	0.01
population * weight * sex	8	80.89	8.19	0.02	0.01
sex	2	81.24	8.54	0.01	0
null	2	85.65	12.95	0	0

FIGURES

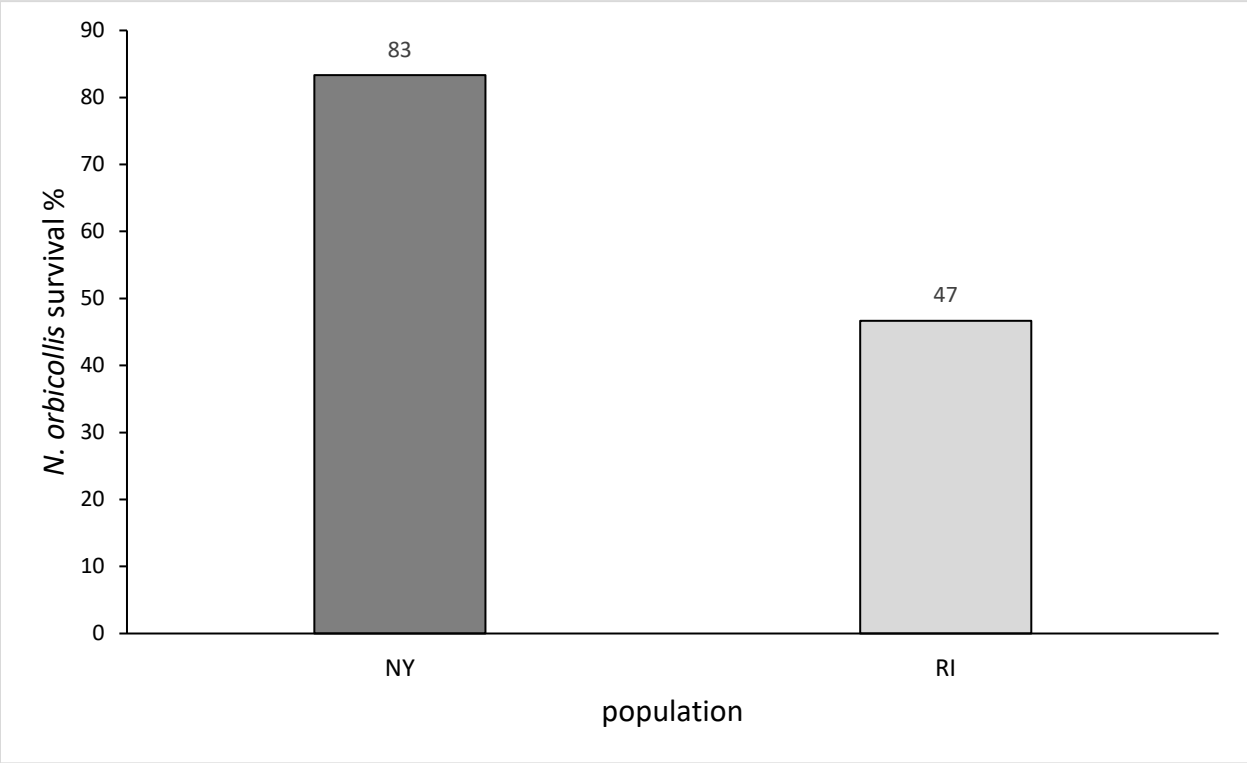

Figure 1. Over winter survival percentages of two *Nicrophorus orbicollis* populations (NY and RI) from October 2022 to April 2023 in forested sites at Greenwoods Conservancy, Hartwick, NY.

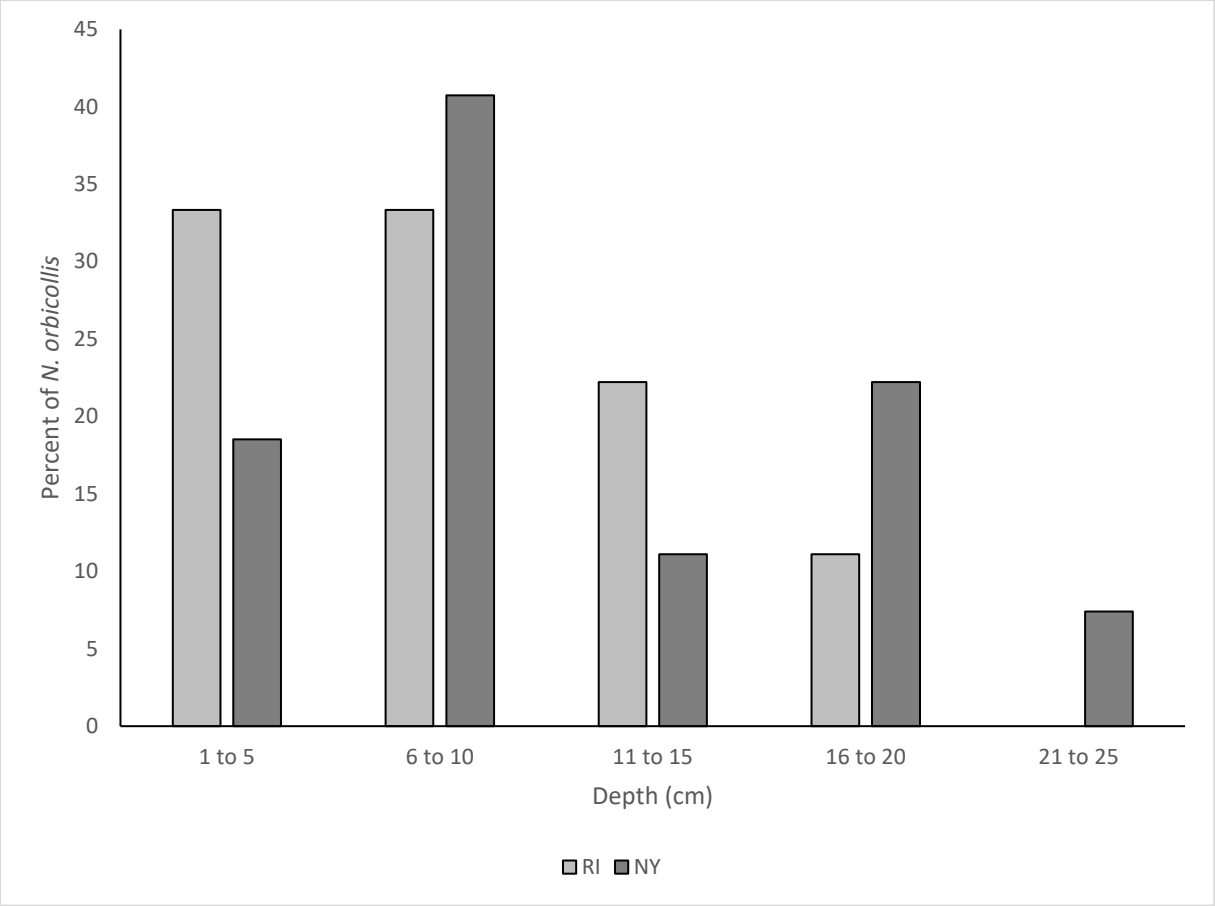

Figure 2. The percentage of *Nicrophorus orbicollis* from both RI and NY which survived over winter (October 2022 – April 2023) in forested sites at Greenwoods Conservancy in Hartwick, NY and the depth at which they were located in April 2023.

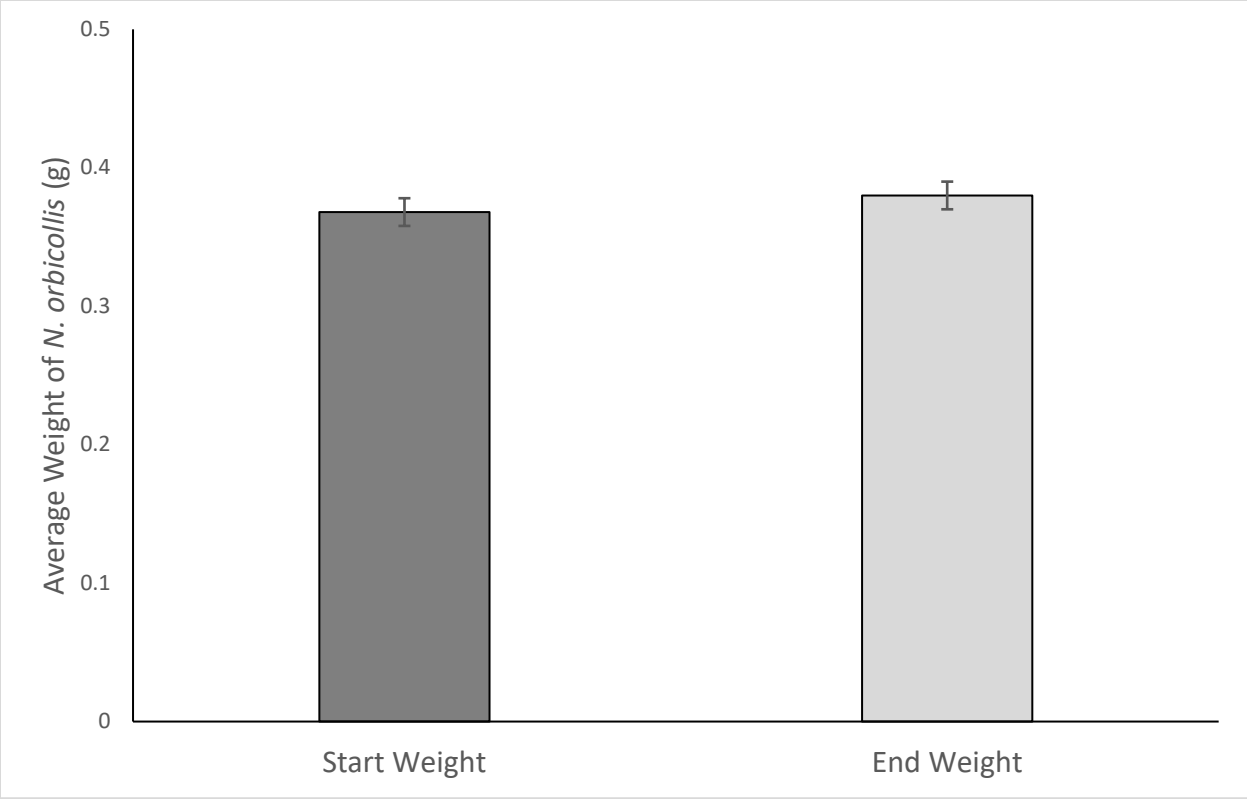

Figure 3. The average start and end weights (g) of all *Nicrophorus orbicollis* from two populations (NY and RI) which survived over winter in forested sites at Greenwoods Conservancy in Hartwick, NY from October 2022 until April 2023.

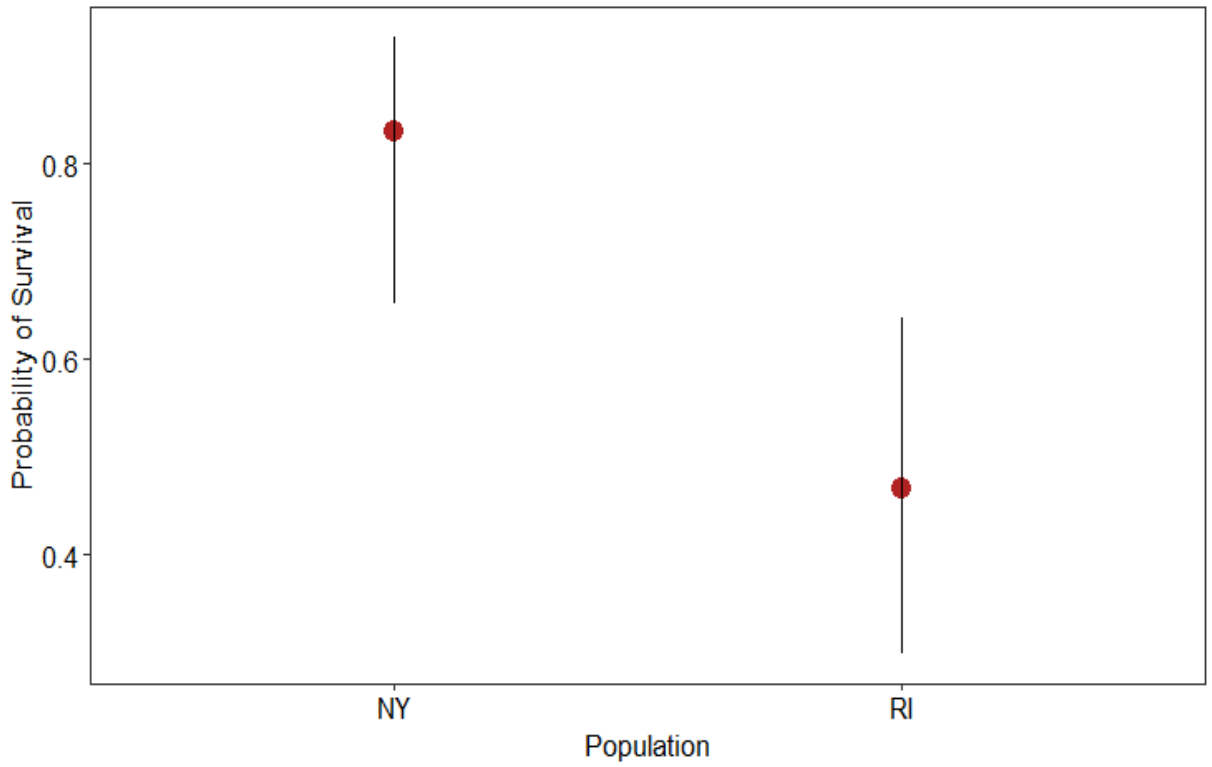

Figure 4. The probability of overwinter survival at Greenwoods Conservancy, Hartwick, NY for *Nicrophorus orbicollis* either local to the study site (NY) or translocated from Block Island, Rhode Island (RI).

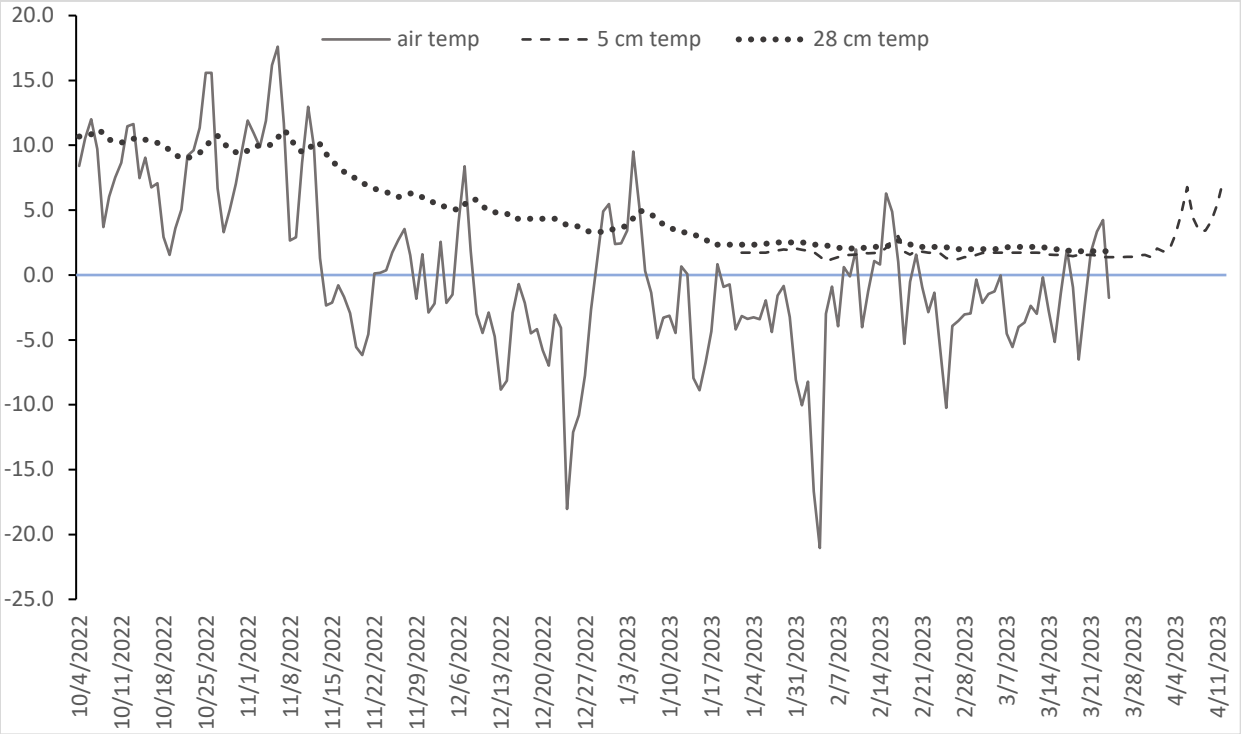

Figure 5. The daily average air temperature (°C) and soil temperatures (°C) recorded from October 4, 2022, until April 11, 2023, among three forested sites at Greenwoods Conservancy in Hartwick, NY. Soil temperatures were recorded at depths of 5 cm and 28 cm.