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The Occurrence of the American Burying Beetle (*Nicrophorus americanus*) and Associated Silphid Beetle Community in South Dakota: Implications for Managed Relocation

William Wyatt Hoback [1,*], Daniel G. Snethen [2], Melissa Reed [1] and Michael C. Cavallaro [1]

[1] Department of Entomology and Plant Pathology, Oklahoma State University, Stillwater, OK 74078, USA; mleath@okstate.edu (M.R.); michael.cavallaro@okstate.edu (M.C.C.)
[2] Little Wound High School, Kyle, SD 57752, USA; silphidsnethen@hotmail.com
* Correspondence: whoback@okstate.edu

Abstract: The American burying beetle, *Nicrophorus americanus* Olivier (Coleoptera: Siliphidae), is a federally threatened species in the United States, occurring in less than 10% of its historic range. The continued monitoring of extant populations found in South Dakota, the northernmost edge of its confirmed range, is imperative to future conservation efforts, especially with the predicted loss of the species in southern regions because of climate change. Proposed strategies to preserve the species include the reintroduction or translocation of individuals from habitats that have become unsuitable. Beyond adequate habitat and carrion resource requirements, community-level silphid interactions may challenge these efforts because of competition. From 2018 to 2020, we used 80 carrion-baited pitfall traps per year to conduct two 5-day surveys in June and August. A total of 25,923 Silphidae belonging to 15 species were collected in 1200 trap nights. Cumulatively, 1150 *N. americanus* were captured and marked with 263 recaptures. Like past findings, *N. americanus* was concentrated in western Tripp County with limited occurrence in Gregory and Todd Counties, suggesting no expansion of their known range in the past decade. Generalized linear mixed-effects models indicated *N. americanus* abundance was significantly predicted by the co-occurrence of the carrion beetles *Oieceoptoma inaequale* F. and *Oiceoptoma noveboracense* Forster, whereas pitfall trap catches dominated by the burying beetle *Nicrophorus marginatus* F. had predictively less *N. americanus*. Collectively, these data provide insights into the existing, northernmost *N. americanus* population dynamics and silphid beetle communities. Concurrent with monitoring extant populations, the characterization of silphid communities that co-occur with *N. americanus* may provide much-needed information for managed relocation opportunities.

Keywords: climate change; Silphidae; conservation; burying beetle ecology

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Citation: Hoback, W.W.; Snethen, D.G.; Reed, M.; Cavallaro, M.C. The Occurrence of the American Burying Beetle (*Nicrophorus americanus*) and Associated Silphid Beetle Community in South Dakota: Implications for Managed Relocation. *Diversity* **2024**, *16*, 232. https://doi.org/10.3390/d16040232

Academic Editor: Mark C. Belk

Received: 23 February 2024
Revised: 6 April 2024
Accepted: 9 April 2024
Published: 13 April 2024

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1. Introduction

Climate change that alters abiotic environmental variables can negatively or positively influence insect population dynamics at the landscape level [1,2]. Range expansion and modified distribution patterns are well documented in insect species in response to the direct and indirect impacts of climate change [3,4]. For insect species specialists that are adapted to narrow thermal or moisture niches, a general shift northward and to higher elevations is likely to occur [5–8].

However, simple, uniform responses in distribution based solely on deviations in climatic gradients are unlikely. Multivariate biotic interactions, especially among co-occurring species, and species traits (i.e., resource use, reproductive capacity, and dispersal mechanisms) will further challenge the predictive power of changes to range projections [9]. Despite these challenges, biotic characterizations paired with population assessments are critical to future conservation and potential reintroduction efforts for species at risk of extinction from changing climates. The American burying beetle, *Nicrophorus americanus*

Oliver, is one such species that is facing predicted declines that may warrant the relocation of individuals.

Nicrophorus americanus is a member of the carrion beetle family Silphidae, a group of detritivores that recycle decaying materials from vertebrate carcasses back into the ecosystem [10]. Similar to other silphid beetles, *N. americanus* seeks a fresh carcass, which is used for feeding and rearing of offspring [10,11]. Because carrion is typically a limited resource, the discovery of a carcass is highly competitive and often occurs within two days but has been reported to occur as quickly as 35 min postmortem [12]. Usually, multiple individuals comprising several species discover the carcass and compete. Competition for a fresh carcass can lead to damage to beetles, including the loss of leg segments and antennae and even mortality [13]. As the largest carrion-feeding insect in North America, *N. americanus* generally secures carcasses that weigh between 50 and 200 g [14]. If the carcass has not been overtaken by fly larvae and is of appropriate size, only a single beetle pair will utilize the carcass [14,15]. Typically, this pair comprises the largest individuals of the largest species to find the carcass, with the other beetles either being driven away or killed by the victorious pair [16–19]. However, relatively few studies that sampled *N. americanus* also documented the entire silphid community, which is particularly important because competition with more numerous silphid species may limit its range [20].

Because of intense inter- and intra-specific competition, carrion beetles exhibit niche partitioning with species-specific seasonal and daily activity patterns [10,11]. *Nicrophorus americanus* is nocturnal, with activity occurring when nighttime temperatures are above 13 °C. Northern populations have a one-year life cycle, with overwintered adults emerging in late May, breeding in June, and producing offspring that emerge in August, forage, and then overwinter [13].

Although *N. americanus* has been recorded in at least 150 counties in 35 states, its distribution in the eastern and central United States declined from the 1920s to the 1960s, and it is currently only found at the peripheries of its former range [21]. Stable populations of *N. americanus* occur in Rhode Island, Nebraska, South Dakota, Oklahoma, Kansas, and Arkansas, while reintroductions in Massachusetts, Missouri, and Ohio make up the remaining range [22]. In 1983, *N. americanus* was included as an endangered species in the *Invertebrate Red Book* published by the International Union for the Conservation of Nature. In the United States, it was placed on the federal endangered species list in August 1989 (Federal Register 54:29652-55). Historical causes for the decline of this species are complex and include the loss of suitable habitat to agricultural and urban development, changes to bird and small mammal communities, increases in nighttime lighting, and pesticide use [20,23]. Perhaps the greatest threat to *N. americanus* in its remaining range is ongoing climate change, which could act as a synergist in combination with other stressors (Federal Register 85:65241-61). *Nicrophorus americanus* demonstrates a life history strategy that is susceptible to annual increases in temperature [22]. Although many insects develop faster at warmer temperatures, negative effects of increasing temperatures on *N. americanus* can include the mortality of adults from desiccation [13], impacts on carcass decomposition and failure of breeding [24], increased overwintering mortality from higher winter activity [25], and increased competition from other silphid beetles and flies [26–31].

Considering the broad geographic range formerly occupied by *N. americanus*, it is unlikely that vegetation or soil type were historically limiting. At its most northern known extant occurrence in South Dakota, an *N. americanus* habitat is characterized as both grassland prairie and wet meadow. Unlike other members of the *Nicrophorus* genus, no strong correlation with soil type or land use seems to exist [21,32].

In South Dakota, museum specimens of *N. americanus* at South Dakota State University indicate that the species historically ranged from Brookings and Union Counties in the east and Haakon County in the west [33]. The species was rediscovered in 1995 in Tripp and Todd Counties, and population estimates conducted in 2007 suggested that a population exceeding 500 individuals existed in Tripp County [34]. The South Dakota population represents the most northern extent of the species' confirmed distribution. Climate change may generate new areas suitable for survival and reproduction of the species. Therefore, it is important to investigate potential *N. americanus* natural range expansion in these areas. Additionally, studies on the South Dakota *N. americanus* population and carrion beetle communities can inform conservation efforts in response to predicted losses of southern populations. This research aimed to (1) determine the current occurrence of *N. americanus* in South Dakota, (2) document population estimates within a priori prime *N. americanus* habitat, and (3) assess associations with silphid communities.

2. Materials and Methods

2.1. Carrion Beetle Sampling

From 2018 to 2020, we sampled for two weeks in June and two weeks in August using sets of 20 traps. Trap locations changed for each sample period in 2018 and 2019. Thus, 80 trap locations were assessed each year during peak activity for *N. americanus* in the northern region [35]. In 2020, trap locations were the same in June and August to assess reproduction and estimate population change.

Adult *N. americanus* and other carrion beetle species were sampled by use of a below-ground baited pitfall trap consisting of a five-gallon (18.9 L) plastic bucket (diameter 28.5 cm). Bedick et al. [36] found a five-gallon bucket to be the most appropriate sized pitfall trap when sampling for *N. americanus*. All buckets were washed using bleach and thoroughly rinsed before deployment. All buckets were buried in the ground, with approximately 4 to 5 cm of the bucket above ground level. Soil was then built up around the bucket, creating a gradient from ground level upwards to the bucket rim to limit the amount of water entering the buckets through runoff and splashing of water during rainfall events, as carrion beetles can drown very easily in even a small amount of water [37]. Approximately 5 to 8 cm of moist soil was placed in the bottom of the bucket. Extra substrate provides trapped carrion beetles more room to burrow into the soil, avoiding competitors, high temperatures, and desiccation. A square piece of plywood (37 cm by 37 cm) was supported by two sticks that were approximately 2.5 cm in thickness and placed on top of the trap. Plywood prevents the escape of trapped beetles and limits rainfall or debris from entering the bucket. Additional weight (soil plug) was then placed on top of the trap cover to reduce disturbance by vertebrate scavengers and to prevent the cover from being moved by wind [36].

All traps were baited with previously frozen laboratory rats (*Rattus norvegicus*) obtained from RodentPro.com. Rats were approximately 275 to 374 g and aged in airtight containers for 3 to 7 days, depending on environmental conditions, until they attained bloat and had a strong odor. All trapping used an open bait method where beetles have access to feed and obtain moisture from the carcass. Bait was replaced on day three or earlier if its condition degraded because of high temperatures or from feeding by large numbers of attracted insects. Attracted beetles fall to the bottom of the bucket, where the smooth sides prevent crawling out, and the board on top keeps them from being able to fly out [36].

All captured carrion beetles were identified to species, and *N. americanus* were sexed using methods by Bedick et al. [13]. Pronotal size of *N. americanus* was measured to the nearest mm using electronic calipers. During the first four days of each survey period, all captured *N. americanus* were marked using a cauterizer to obscure one of the four elytral maculations [38]. Captured *N. americanus* were released as quickly as possible into individual holes made in moist soil, approximately 50 m from the trap.

2.2. Site Selection

The 2018 and 2019 trapping was conducted to compare the extent of South Dakota range with previous reports [34]. In 2020, trapping was focused on assessing population numbers in the most densely occupied areas identified in the previous two years. Trap locations were selected by conducting a driving survey of available habitat in the target county. Although *N. americanus* is classified as a habitat generalist, replacement of grasslands with row crop agriculture and arid environments do not support its occurrence [21].

Extensive previous sampling in northern Nebraska and South Dakota led to development of criteria of likelihood to capture *N. americanus* based on visual characteristics of habitat. To ensure maximum likelihood of capturing *N. americanus*, we selected trap locations based on the following habitat criteria observed while driving on public roads. Prime habitat is most likely to capture *N. americanus*, and marginal habitats do not support the occurrence of the species.

5. Prime: Undeveloped wet meadows dotted with trees or forest areas with plenty of water available either by river, stream, or sub-irrigated soils. Little or no cropland visible.

4. Good: Grasslands which have low wetland meadows or grazed land and trees present. Sources of water are close by but may also have either some cropland or several sources of light pollution.

3. Fair: Savannah-type habitat interspersed with row crop agriculture. Agriculture located within two miles of either side of habitat appears suitable for *N. americanus*.

2. Marginal: Potential habitat restricted to one side of the road, predominately agriculture or dry, sandy upland areas that limit beetle occurrence because of desiccation.

1. Poor: Habitat is not typical low-lying grassland, or the area is dominated by row crop agriculture or has potential for large amounts of light pollution

All traps were placed in prime or good habitat and were placed a minimum of 1.6 km (1 mile) apart in public right of ways along roads or in wildlife management areas near roads. The predicted radius of the trap attraction is 800 m (0.5-mile), and each trapping event sampled 500 acres [39]. Traps were set on the first trap day before 1800 h and checked every subsequent morning by 1200 h for five consecutive days. Butler et al. [40] estimated that baited pitfall traps collect approximately 90% of present beetles over the five-day sampling period.

2.3. Hot Spot Analyses

In 2018, *N. americanus* were sampled in known areas of occurrence in Tripp and Todd Counties. In 2019, sampling occurred at the edges of known occurrences of *N. americanus* to establish the east–west distribution in South Dakota, with a limited number of control traps placed in Tripp County. Both the highest frequency of captures and the highest densities in 2018 and 2019 were observed in southern Tripp County. In 2020, focused sampling was conducted in Tripp County to identify areas that had the most *N. americanus*.

In total, 155 *N. americanus* sampling sites within Tripp County were compared during the years 2018 through 2020. The frequency of *N. americanus* captured per night at each trap site was spatially analyzed using the Getis-Ord Gi* statistic in ArcMap version 10.8 [41]. This approach compared the frequency of *N. americanus* captured per night at a trap site within the context of neighboring trap sites. For example, if the frequency of *N. americanus* is high at a trap site and the frequency of *N. americanus* for all that site's neighboring traps is also high, then all sites in the area with high frequency form a hot spot.

Getis-Ord Gi* analyses are as follows: (1) The Getis-Ord General G high/low clustering tool [41] was used to determine the optimal threshold distance within 100 m. (2) The spatial relationships among *N. americanus* trap sites within the study area were calculated to have a 6 km threshold using a fixed distance band. (3) Euclidian distance measures were implemented to complete the Getis-Ord Gi* analysis. The output from this analysis is a z-score for each *N. americanus* trap site. For statistically significant positive z-scores (greater than 1.645), the larger the z-score, the more concentrated the clustering of high values (hot spot). For statistically significant negative z-scores (less than −1.645), smaller z-scores represent more concentrated clustering of low values (cold spot). A z-score between 1.645 and −1.645 indicates no apparent spatial clustering of *N. americanus* trap sites.

The Kriging interpolation tool was implemented in ArcMap [41] using the z-scores calculated in the Getis-Ord Gi* analysis to generate the output surface. Kriging is an advanced geostatistical procedure that generates an estimated surface from a scattered set of points with z-scores. After conducting the hot spot analysis for all years, the analysis was reiterated for only 2020, which focused sampling on the most densely occupied area.

2.4. Dominant Species

To characterize species interactions for limited ephemeral resources (i.e., carrion), the percentage of *Nicrophorus* species was examined at each trap location. Dominance was defined by a species exceeding 50% of the total *Nicrophorus* captured. Carrion beetles in the subfamily Silphinae use smaller carcasses for feeding but only reproduce on larger carcasses because adults do not provide parental care and larvae feed on both the carcass and developing fly maggots.

The percentage of *N. americanus* was calculated by dividing the number of *N. americanus* by the total of all *Nicrophorus* in a trap over the five-day period. Exclusive to the 2020 dataset, *N. americanus* percentages in June and August were compared to gain insights into the most likely areas of reproductive success.

2.5. Community Data Analyses

Nonparametric Spearman's rank correlation coefficients were used to estimate a rank-based measure of association between *N. americanus* and other silphid species collected in the same trap effort over five days (package "devtools", "Hmisc", "GGally"; https://cran.r-project.org (accessed on 6 June 2022)). A trap effort includes the cumulative total of beetles captured over the five trap nights at a single site from 2018 to 2020. This provided us with an a priori approach to explicitly test species associations in subsequent multivariate analyses. Moreover, non-metric multidimensional scaling (nMDS) was used to characterize the silphid community composition (package "vegan", "metaMDS") and provided a visual evaluation of silphids associated with *N. americanus* by trap counts (i.e., *N. americanus* [ABB] abundance categories: absent, 1–5, 6–19, >20). Unlike other ordination techniques, nMDS interpretation is not impeded by nonlinear relationships or nonnormal distributions and is preferred in ecological studies (Legendre and Legendre 1998). A rank order Bray–Curtis dissimilarity matrix was used to generate the nMDS plot, where pairwise distances intuitively build the final ordination, i.e., the closer the points, the more similar their silphid assemblage. Lastly, we built generalized linear mixed models (GLMMs) to determine the variance explained by the significant species relationships as identified by Spearman's rank correlation and visually confirmed by the nMDS. Data were analyzed using generalized linear mixed models (package "lme4"; [42]) with the response variable—total *N. americanus* abundance—inputted as count data using a negative binomial distribution. One model set was generated with combinations of eight silphid species identified by Spearman's rank correlation and nMDS. Using count data, the eight silphid species were considered fixed effect covariates (*Nicrophorus guttula*, *Nicrophorus marginatus*, *Nicrophorus pustulatus*, *Necroides surinamensis*, *Heterosilpha ramosa*, *Oiceoptoma inaequale*, *Oiceoptoma noveboracense*, and *Thanatophilus lapponicus*). All model iterations accounted for trap number ID and month sampled, each nested by year, respectively, as random effects. Continuous numeric variables were scaled and centered before running models. Normality of model residuals was evaluated using a Shapiro–Wilk test. The model fit distributions were evaluated using visual graphing tools (package "car") and further confirmed by a goodness-of-fit with a chi-square test based on residual deviance, which yielded a negative binomial distribution. Using the dredge function in package "MuMIn" [43], the top models were compared and ranked by corrected Akaike's Information Criterion (AICc) values. All silphid community analyses were computed in R version 3.4.1 [44].

2.6. Population Estimates

In 2020, mark–recapture data were used to estimate population size based on the Schnabel method [45]. The Schnabel method follows recapturing and marking of new individuals over a period of days to estimate the number of individuals in a closed population. Because traps were placed in the same locations in June and again in August, we used population estimates to assess changes in the populations.

3. Results

From 2018 to 2020, surveys were conducted using 240 baited pitfall traps with 5 trap nights per trap (1200 trap nights total). All sites sampled were rated as "prime" for occurrence of *N. americanus*. Cumulatively, a total of 25,923 silphid beetles were captured (Table 1). Because sampling in 2018 and 2019 was to establish South Dakota distribution and 2020 was to estimate populations in the best areas, we summarized captures by percentage across years. *Nicrophorus americanus* were captured in three of the five sampled counties, with the most positive traps occurring in Tripp County (Figure 1). Eight species of burying beetles (*Nicrophorus*) accounted for 76% of the Silphidae observed during this study. The most common species was *N. marginatus*, which is associated with grassland areas and accounted for 46.5% of the captures. *Nicrophorus americanus* accounted for 5.7% of the total captures and about 7% of the total *Nicrophorus* and was the third most common species. Across samples in areas with high numbers of *N. americanus*, the sex ratio was approximately 50:50 (Table 2). The size of *N. americanus* was consistently larger for males than females and was similar for males from 2018 to 2020; however, female size was significantly larger (t-test, p = 0.006) in 2020 compared to 2018 (Table 2).

Table 1. Total number of Silphidae belonging to 15 species during surveys in 5 South Dakota counties from 2018 to 2020.

Burying Beetle	Number	% of Total	% of Subfamily
Nicrophorus americanus	1479	5.71%	7.50%
Nicrophorus carolinus	492	1.90%	2.49%
Nicrophorus guttula	3984	15.37%	20.20%
Nicrophorus marginatus	12,053	46.50%	61.12%
Nicrophorus obscurus	424	1.64%	2.15%
Nicriophorus orbicollis	794	3.06%	4.03%
Nicrophorus pustulatus	137	0.53%	0.69%
Nicrophorus tomentosus	358	1.38%	1.82%
Carrion beetle			
Necrophila americana	1281	4.94%	20.65%
Necrodes surinamensis	1820	7.02%	29.35%
Heterosilpha ramosa	1230	4.74%	19.83%
Oiceoptoma inaequale	416	1.60%	6.71%
Oiceoptoma noveboracense	43	0.17%	0.69%
Thanatophilus lapponicus	1341	5.17%	21.62%
Thanatophilus truncatus	71	0.27%	1.14%
TOTAL	25,923		

Table 2. American burying beetle pronotal widths (mm) for 2018 and 2020 sampled in Tripp County, South Dakota.

2018			
Sex	**Mean**	**S.E.**	**N**
Male	10.06	0.06	215
Female	9.53	0.08	222
2020			
Sex	Mean	S.E.	N
Male	10.12	0.05	344
Female	9.93	0.06	365

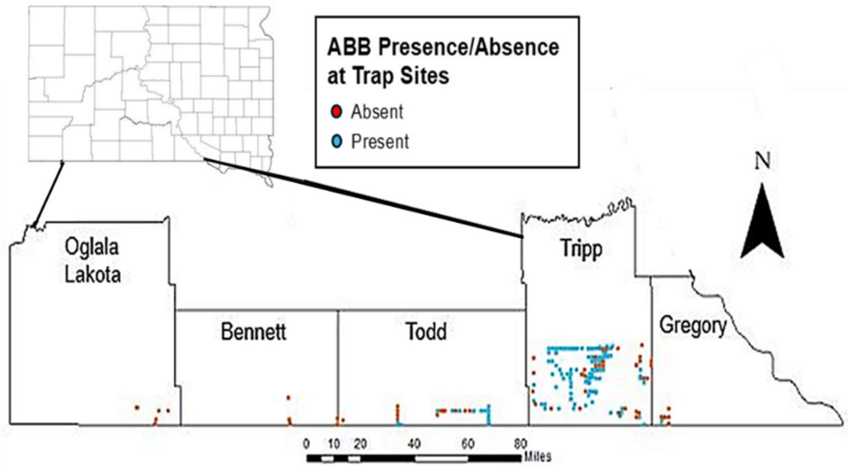

Figure 1. Counties sampled from 2018 to 2020 to determine presence of American burying beetles (ABB).

3.1. Hot Spot Analyses

The Getis-Ord Gi* hot spot analyses indicated the locations of hot spots with a significantly high frequency of *N. americanus* captured per night at each trap site and cold spots with a significantly low frequency of *N. americanus* captured per night at each trap site (Figure 2). For a large portion of the study area, comprising 96 trap sites, there was no significant clustering of captures, suggesting a relatively even and low frequency of individuals. We identified one statistically significant hot spot in the northwestern part of the study area that was comprised of 25 trap sites. In addition, we identified two statistically significant cold spots in the study area. One cold spot was located in the southwest corner of the study area and comprised five trap sites. The other cold spot, located in the eastern part of the study area, contained 19 trap sites. The distribution of cold spots helped to confirm the extant range of the species in South Dakota and was similar to the range found by Backlund et al. [34].

In 2020, population estimates were made for central (near the town of Clearfield) and eastern (near the town of McNeeley) areas of Tripp County using the five-day trap-and-recapture data for June and August (Figure 3). In June, the population estimate was 458 (range of 448–519) for McNeeley and 669 (range of 557–671) for Clearfield. Because each trap samples approximately 500 acres and is 90% efficient in capturing silphid beetles (21, 23), it is estimated that 0.07 *N. americanus*/acre occurred in June in the Clearfield area and 0.05 *N. americanus*/acre occurred in the McNeeley area. In August, the same areas had a population estimate of 308 (range of 284–311) for McNeeley and 553 (range of 527–628) for Clearfield. The estimated population in August included both teneral and senescent individuals, confirming that reproduction occurred.

3.2. Dominant Species

Analysis of the dominant *Nicrophorus* species across all dates and trap locations in 2018 and 2019 revealed a pattern of *N. carolinus* in the west, *N. orbicollis* in the east, and *N. marginatus* as the dominant species for most of the samples (Figure S1). The eastern part of Tripp County had 16 traps where *N. americanus* represented >50% of the *Nicrophorus* captured. These areas south of Winner, South Dakota, also were identified in the hot spot analyses (Figure 3).

In June 2020, *N. americanus* dominated captures at over half of the trap locations (25/40), suggesting strong success in overwintering and potentially indicating earlier activity than other *Nicrophorus* (Figure S2). In contrast, for the same trap locations sampled in August, *N. americanus* was only dominant at 6 locations, whereas *N. marginatus* was dominant at 29/40 (73%) of the locations (Figure S3).

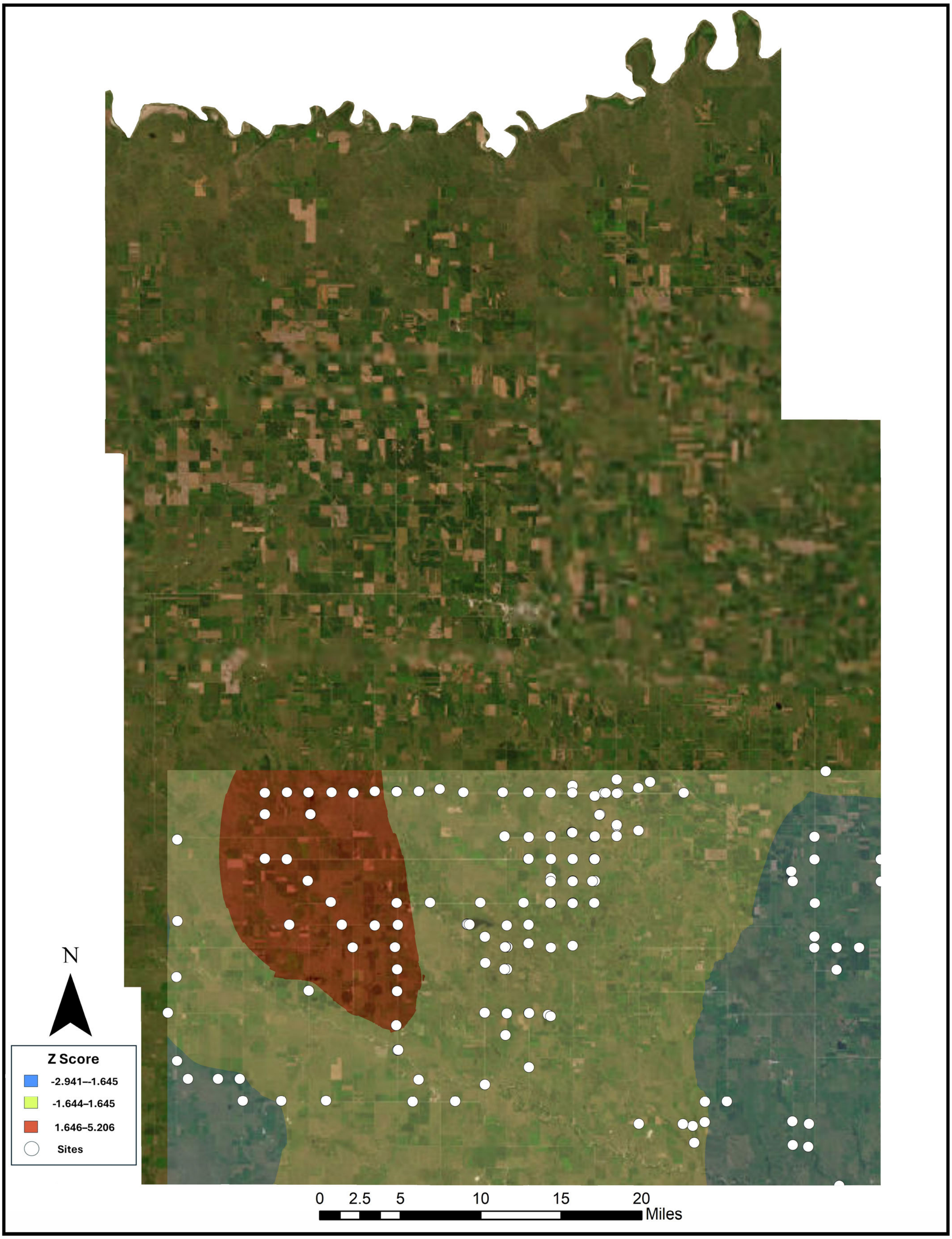

Figure 2. Hot spot analysis for the occurrence of American burying beetle in Tripp County, South Dakota, from 2018 to 2020. Red indicates traps with more likely occurrence (hot spots), and blue indicates traps with more likely absence of *N. americanus* (cold spots) among 155 trap locations.

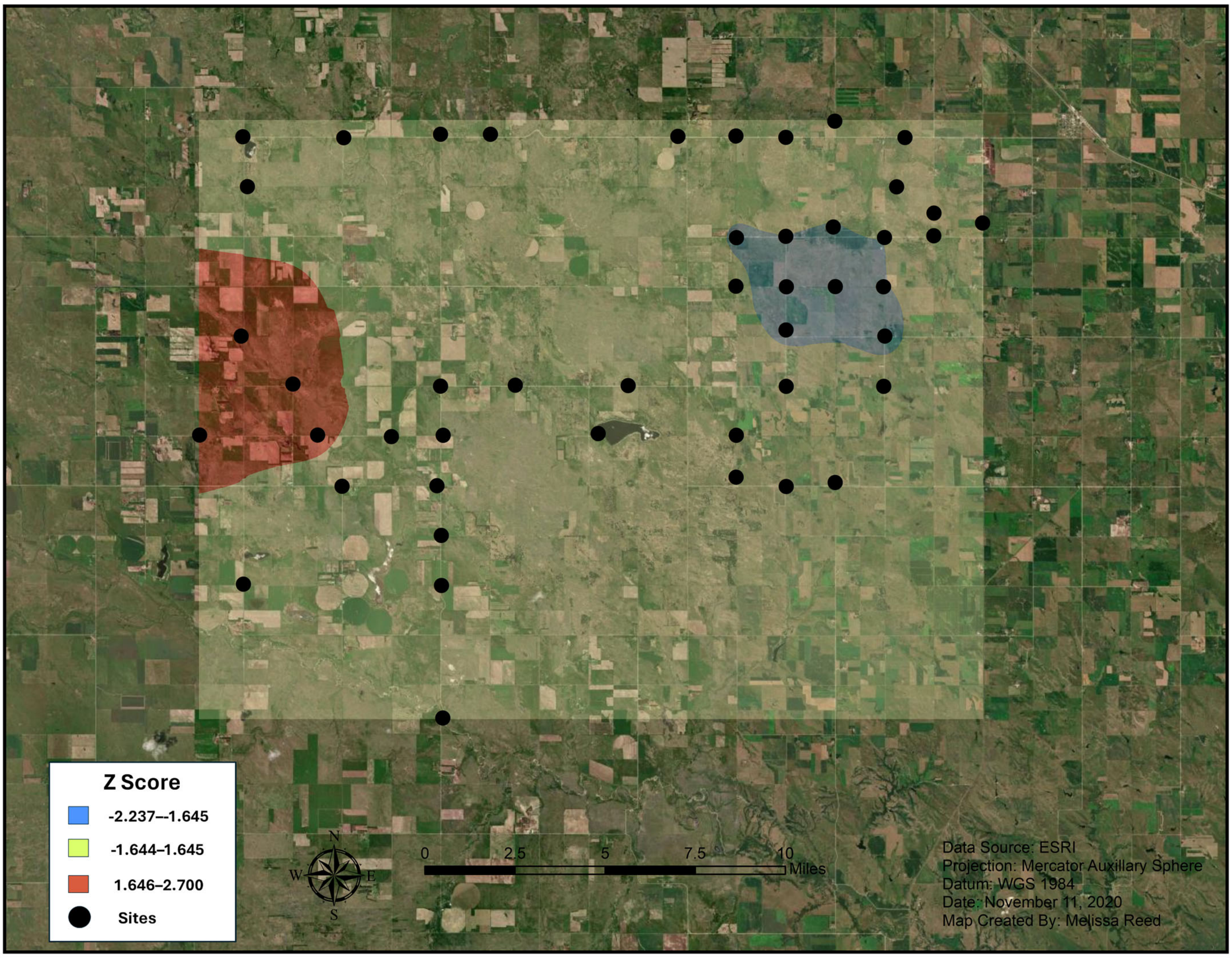

Figure 3. Hot spot analysis for occurrence of American burying beetle (ABB) in Tripp County, South Dakota, using only 2020 trap locations among 52 trap locations sampled in June and August. Red indicates traps with more likely occurrence (hot spots), and blue indicates traps with more likely absence of ABB (cold spots).

3.3. Community Data Analyses

Because trap locations varied among the years, a series of exploratory analyses were used to determine the relationship between *N. americanus* and other silphid beetle species. Seven silphid species displayed a significant positive correlation with *N. americanus* abundance (ranked by correlation coefficients): *N. guttula* (+0.3), *O. inaequale* (+0.3), *H. ramosa* (+0.3), *N. pustulatus* (+0.2), *T. lapponicus* (+0.2), *N. surinamensis* (+0.2), and *O. noveboracense* (+0.1). Five of the seven are carrion beetle species (Table 1). One silphid species showed a negative correlation, *N. marginatus*. The remaining species detected during surveys were not correlated with *N. americanus* abundance. See relationships among all silphid species captured from 2018 to 2020 (Figure 4).

To further characterize the silphid beetle community, non-metric multidimensional scaling (nMDS) plots were generated to provide a visual evaluation of the data (Figure 5). The nMDS reached a convergent solution after 17 iterations, and the three-dimensional solution had a stress level of 0.13. Stress levels from 0.1 to 0.2 are considered a quality representation of the reduced dimensionality and are interpretable [46]. Distinct patterns emerged among *N. americanus* abundance categories, and clear similarities from the Spearman's rank correlation were verified. Among the Nicrophorinae, *N. guttula*, *N. obscurus*, and *N. pustulatus* were positively associated with *N. americanus* abundance, and *H. ramosa*, *O. inaequale*, and *O. noveboracense* were the associated Silphinae. Interestingly, *N. orbicollis*, a forest specialist, strongly influenced the MDS1 (+0.44) and MDS2 (−0.55) range and represented the most distinct silphid separation among the sampled community, while *N. marginatus* was clearly isolated as the sole silphid associated with traps absent of *N. americanus* (Figure 5).

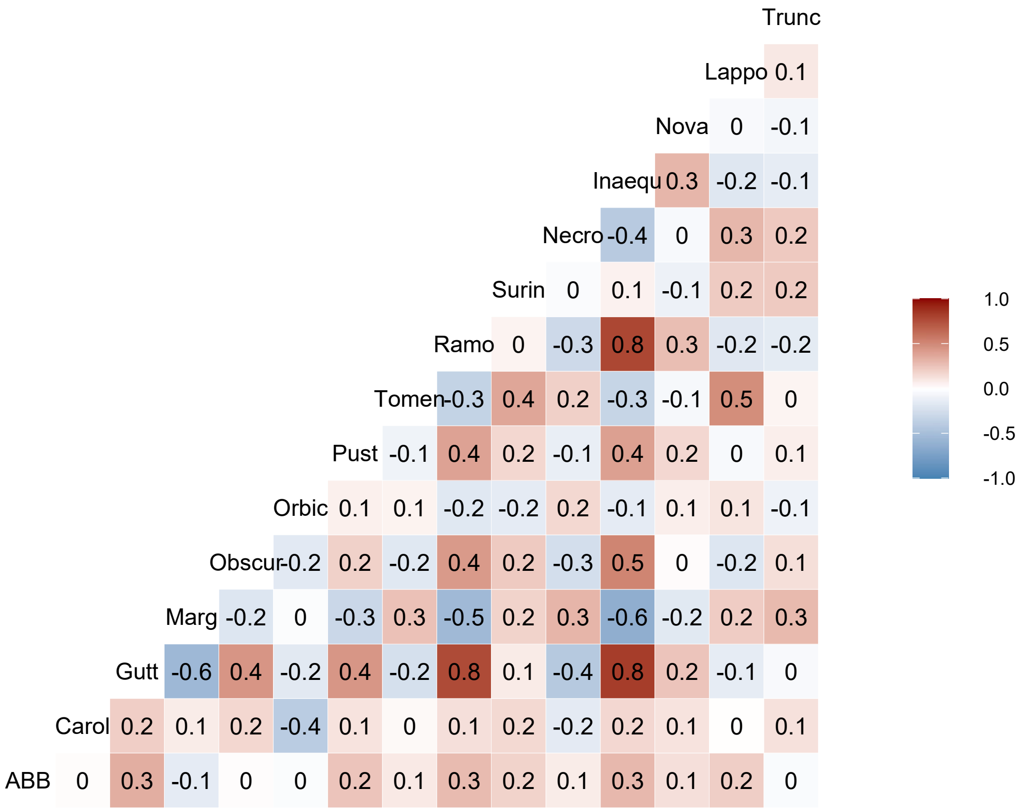

Figure 4. Spearman's rank correlation heat map for cumulative silphid beetle captures from 2018 to 2020 in South Dakota. (Species abbreviations: ABB, *Nicrophorus americanus*; Carol, *Nicrophorus carolinus*; Gutt, *Nicrophorus guttula*; Marg, *Nicrophorus marginatus*; Obscur, *Nicrophorus obscurus*; Orbic, *Nicriophorus orbicollis*; Pust, *Nicrophorus pustulatus*; Tomen, *Nicrophorus tomentosus*; Necro, *Necrophila americana*; Surin, *Necrodes surinamensis*; Ramo, *Heterosilpha ramose*; Inaequ, *Oiceoptoma inaequale*; Nova, *Oiceoptoma noveboracense*; Lappo, *Thanatophilus lapponicus*; Trunc, *Thanatophilus truncates*).

GLMMs were used to directly assess the relationship between *N. americanus* and silphid beetle species. The top model for *N. americanus* abundance included *O. inaequale* and *N. marginatus*, which explained 99% (adj. R^2) of the overall variation in the silphid species used in the global model. The abundance of *O. inaequale* displayed a positive relationship with greater *N. americanus* abundance (β ± S.E. = 0.032 ± 0.017, p = 0.06), whereas *N. marginatus* abundance had a significant negative influence on *N. americanus* abundance (β ± S.E. = −0.008 ± 0.001, $p < 0.001$). Interestingly, each of the top four model sets indicated that the presence of *N. marginatus* had a significant negative impact on *N. americanus* abundance. Conversely, both *Oiceoptoma* species were positively linked with *N. americanus* abundance (Table 3). Congruent responses among data analyses suggest evident community associations.

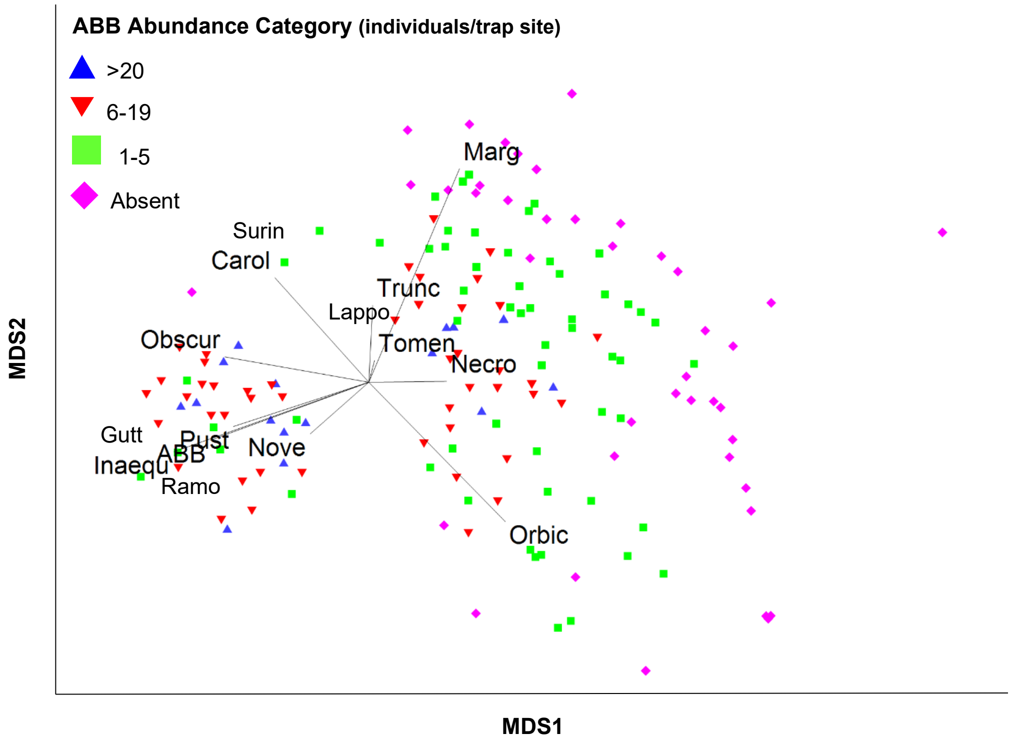

Figure 5. Non-metric multidimensional scaling (nMDS) plot of silphid species collected from 2018 to 2020, where trap sites are categorized by *N. americanus* abundance (Stress = 0.13). Species abbreviations are as follows: ABB, *Nicrophorus americanus*; Carol, *Nicrophorus carolinus*; Gutt, *Nicrophorus guttula*; Marg, *Nicrophorus marginatus*; Obscur, *Nicrophorus obscurus*; Orbic, *Nicriophorus orbicollis*; Pust, *Nicrophorus pustulatus*; Tomen, *Nicrophorus tomentosus*; Necro, *Necrophila americana*; Surin, *Necrodes surinamensis*; Ramo, *Heterosilpha ramosa*; Inaequ, *Oiceoptoma inaequale*; Nove, *Oiceoptoma noveboracense*; Lappo, *Thanatophilus lapponicus*; Trunc, *Thanatophilus truncatus*.

Table 3. Results from GLMM models (i.e., ranked AICc) assessing the associations between N. americanus and other silphid species collected from 2018 to 2020. Models were constructed to individually assess important species associations as identified by Spearman's rank correlations. Only the top models with an AICwt > 0.1 are presented.

***N. americanus* Abundance (Response Variable)** [a]	**Model Parameters** [b]			
	logLik	**AIC$_c$**	**ΔAIC$_c$**	**AIC$_{wt}$**
O. inaequale + *N. marginatus*	−648.98	1310.3	0	0.223
O. inaequale + *N. marginatus* + *O. noveboracense*	−649.31	1311.0	0.67	0.160
N. marginatus	−648.32	1311.1	0.80	0.150
O. inaequale + *N. marginatus* + *N. pustulatus*	−650.70	1311.7	1.33	0.115
Intercept-only (null)	−670.40	1349.0	38.63	<0.001

[a] Full (global) *N. americanus* model included fixed effects (count data). Random effects included trap number ID and month sampled, each nested by year, respectively. [b] Model parameters are listed by column: logLik (−2 × log-likelihood), corrected Akaike's Information Criterion (AICc), change in AIC$_c$ (ΔAIC$_c$), and model weights (AIC$_{wt}$).

4. Discussion

4.1. *Nicrophorus americanus* Range and Abundance

Surveys from 2018 to 2020 revealed that *N. americanus* continue to occur in South Dakota and are concentrated in Tripp County. Surveys of an additional four counties detected a low number of *N. americanus* at a few sites in Todd and Gregory Counties. From these data compared to previous studies, the distribution and range of *N. americanus* has not expanded in South Dakota [33,34]. Northern and western ranges appear to be limited by soil type [21,38]. Additionally, in the north and east, where soils could support *N. americanus*, the conversion to row crop agriculture [32] and associated changes to the carrion base appear to prevent occurrence [21]. Other climatic factors, including precipitation and overwintering ground temperature, may also limit more northern occurrences of *N. americanus* in South Dakota [47].

Because *N. americanus* produce an average of 15 offspring per brood [48] and have a single generation per year, the August capture rate is anticipated to be higher. Schnabel population estimates of *N. americanus* in the areas of highest occurrence revealed an estimate of about 1000 individuals in June. Surprisingly, the August population estimates were lower at both locations, overall, totaling about 850 individuals. The Schnabel estimate uses multiple recaptures across days to extend the Petersen method to a series of samples in which individuals caught at each sample are first examined for marks, then unmarked individuals are marked, and all individuals are released. Marking occurs on each of the sampling days, but only a single type of mark is used. Using the Peterson method, Backlund et al. [34] reported a doubling in population between June and August. This difference may be explained by climate factors, including variation in precipitation, nighttime temperatures, or shifts in activity patterns associated with warmer average temperatures or more variation in precipitation [49]. The weekly or bi-weekly monitoring of a population [29,49] and population sampling after emergence from overwintering and again after breeding in more areas would be valuable for documenting shifts and interpreting population stability.

Hotspot analyses reveal that *N. americanus* is concentrated in Tripp County, supporting previous findings by Backlund and Morone [33] and Backlund et al. [34]. The results of previous and current survey efforts indicated that central Tripp County supported more than 500 *N. americanus* in an area of about 20,000 acres. Despite documenting a self-sustaining population in South Dakota, *N. americanus* is not widespread, and numbers recorded per trap night are concerning. The highest observed capture in an individual trap during this survey was 23 individuals. Further, only 10 traps out of 240 (4%) traps captured 10 or more individual *N. americanus* in a trap night. In contrast, 662 trap nights captured zero *N. americanus* (44.8%) despite only placing traps in habitats visually rated as prime or good for the likelihood of *N. americanus* occurrence.

4.2. Nicrophorus americanus and Silphid Community Composition

Silphids constitute an ecologically diverse component of the carrion-dependent insect community and have attracted the interest of community ecologists for decades. Collections throughout North America provided seasonal and regional taxonomic distributions and descriptions of co-occurring species [10,29,31,50–54]. Carrion is a highly contested resource, and to minimize costly interactions [13], co-occurring siliphids will occupy distinct habitats [29], modify diel activity [55], and seasonally target reproduction on preferred carcass sizes [18,31]. Temporal and spatial tactics to limit interspecific competition are important for ephemeral resources like carrion [11,56]. However, there is still seasonal and preferred carcass-size overlap among the collective silphid community in most regions, where resource partitioning is further influenced by biotic and abiotic gradients [31,49,54].

Competition, activity patterns, and niche partitioning among closely related *Nicrophorus* recently revealed the effects of temperatures on seasonal activity, allowing the coexistence of *Nicrophorus* [28,30,31]. In warming climates, shifts in activity patterns increase overlap among these closely related species [49]. Additionally, in the study of the montane species, *Nicrophorus nepalensis* revealed that populations at different elevations relied on thermal tolerance and reproductive photoperiodism to shape breeding phenology. The authors of this study concluded that these adaptations would be lost as beetles attempt to breed at warmer temperatures [57]. Diversity of the carrion community in the Colorado Mountains was also shown to be most diverse at intermediate elevations, with temperature and understory vegetation differences affecting both diversity and the availability of carrion and influencing numbers of individuals of a species [28]. Climate change is likely to increase competitive interactions among these groups as their lifecycles and habitat utilization are changed by abiotic conditions. Recent studies reported on a carrion beetle community across seasons [29] and provided details of circadian period activity [27]. Because the day-active *N. marginatus* adjusts activity with temperatures [58], assessing these communities with ongoing climate change may record behavioral plasticity or better predict losses of species with temperature change. It will be particularly important to assess carrion beetle communities in southern ranges where *N. americanus* is expected to be lost within the next decades [23].

Although carrion beetle communities include both members of the subfamily Silphinae, which use large carcasses, feed on fly larvae, and do not exhibit parental care [14], and Necrophorinae, the burying beetles, which bury and prepare small carcasses underground, few studies examined these interactions. Competition among closely related species could also serve as a potential factor in losses of *N. americanus* across their range [20]. However, relatively few studies reported other species of *Nicrophorus* associated with *N. americanus* [26], and even fewer reported on the entire carrion beetle community [29,59]. Conley et al. [60] describe a potential Silphinae/Nicrophorinae interaction between *N. marginatus* and the largest Silphinae, *N. surinamensis*, suggesting direct competition in grassland habitats. However, most Silphinae likely avoid direct, sustained competition by exploiting medium to large carcasses with larvae feeding on decaying material and maggots after hatching from the surrounding soil [61].

By examining the entire silphid community, we found two significant species interactions with *N. americanus* among siliphids collected in South Dakota from prime *N. americanus* habitat: a positive association with *Oiceoptoma* spp. (Silphinae) and a negative association with *N. marginatus* (Nicrophorinae). Previous surveys found *Oiceoptoma* spp. in a variety of habitats, depending on the locality [29,61]. For example, *Oiceoptoma noveboracense* was found to be four times more likely to be sampled in woodland habitats in the Kansas Flint Hills [29], whereas a similar study conducted in southern Ontario, Canada, did not determine a distinct habitat preference [61]. As a habitat generalist, *N. americanus* can be found in woodlands, wet meadows, and prairie habitats [35]. In South Dakota, *N. americanus* were collected near sub-irrigated meadows that were used for ranching and hay production. *Oiceoptoma* spp. co-occurrence with *N. americanus* may be an artifact as habitat generalists. It is also important to acknowledge that *O. inaequale* and *O. noveboracense* represented 1.60% and 0.17% of the total silphids collected over the study period, respectively. This should contextualize their relative importance.

Different competitive pressures are exerted among co-occurring Silphinae and Nicrophorinae species. However, differing life history strategies serve to minimize competition intensity [61]. For all data combined from 2018 to 2019, most traps were dominated by *N. marginatus*, a day-active grassland generalist, constituting 46.5% of the total. This is a substantial disparity from the next most abundant species, *N. guttula*, at 15.4%. Tripp County, South Dakota, is dominated by grasslands. In another study conducted in western Michigan, a high abundance of *N. marginatus* occurred in fields of >25 ha, but traps placed 10 m into forests collected none [62]. This suggests that *N. marginatus* may be unable to disperse across woodlands and may relate to *N. americanus*, being unable to naturally colonize otherwise suitable habitats separated by unsuitable conditions.

Western traps (Figure S2) had the highest percentage of *N. carolinus*, a species that is adapted to drier, sandier soils. Conversely, the easternmost traps were dominated by *N. orbicollis*, a nocturnal species that occurs in association with trees. These results are not unexpected, as Bishop et al. [32] identified similar habitat associations among *Nicrophorus*. All species of *Nicrophorus* overwinter as adults and reproduce during the summer months. The average brood size for *Nicrophurus* is 15 offspring, but smaller species, such as *N. marginatus* and *N. orbicollis*, utilize smaller carcasses [10], which are more common.

One of the most surprising findings was the shift in dominant species between June and August at the same trap locations. *Nicrophorus americanus* is the largest North American silphid and generally has smaller populations than other *Nicrophorus*. However, in June, it was the dominant species in 62% of trap locations.

There are several potential factors that could explain this dominance, including greater success at overwintering in northern climates and earlier activity because of the ability to warm flight muscles. Additionally, other species may avoid traps with *N. americanus* during its main breeding period. Future research should examine these results as they may play a role in explaining *N. americanus* persistence in some parts of its former range.

The reversal of dominance trends in August also should be further researched. It is likely that more *N. marginatus* are generated each year because of the larger number of small carcasses available. In August, most *Nicrophourus* should be seeking carcasses as food rather than as a breeding resource prior to overwintering as new adults [13]. Although *N. marginatus* may compete with *N. americanus*, larger beetles usually win the competition for breeding resources. The five traps with *N. americanus* dominance may still be important to identify overwintering habitats. If beetles move to specific locations later in the season, they would be expected to be captured more frequently near those locations.

The continued presence of *N. americanus* in South Dakota and elsewhere is likely influenced by many factors, including land use changes that also affect vertebrates that serve as carrion sources. In addition, remaining *N. americanus* likely face competition from other carrion beetles and are affected by climate change. In 2019, South Dakota experienced record-breaking rainfall in the spring and summer, which is likely to have reduced *N. americanus* numbers by flooding brood balls. In addition, climate warming may affect overwintering beetles by causing them to expend food resources before the environment is suitable for foraging activity.

4.3. Implications for Reintroduction and Translocation

Collectively, only 3% of reintroduction efforts for improved conservation outcomes focused on invertebrates. Among the beetles of conservation concern, the reintroduction of *N. americanus* has been attempted the most [63,64]. At their core, reintroductions intentionally insert a new species into a preexisting ecological network and result in the reconfiguration of species interactions [65]. Assessing co-occurring species interactions and their supplemental indication of a successful reintroduction effort is not an entirely novel concept. For example, specific plant species associations were found to be positive or negative indicators of the localized success after reintroducing the federally threatened golden paintbrush, *Castilleja levisecta*, to new suitable habitat [66].

Predictive models can guide species reintroduction efforts. At the same time, data, including the complexity of habitat suitability, dispersal processes, population dynamics, and interspecies interactions, can further optimize the decision-making process [67]. The latter is rarely considered due to the data requirements, i.e., intensive surveys of the existing community in a suitable range.

The only surviving natural population of *N. americanus* in eastern North America occurs on Block Island, off the coast of Rhode Island [68,69]. This population was used to create a captive breeding program and reintroduce *N. americanus* to islands on the east coast [70]. Reintroduction efforts for *N. americanus* occurred on Nantucket and Penikese Islands, off the coast of Massachusetts, in Ohio, Missouri [70], and in New York. Efforts on Pekinese Island resulted in the establishment and persistence of very low numbers with natural carrion [69]. The best-studied and most successful reintroduction occurred on Nantucket Island, where *N. americanus* established themselves and successfully bred. However, when supplements to the population and carrion sources were ceased, the population declined drastically, leading Mckenna-Foster et al. [68] to suggest that persistence was limited by the availability of the right-sized carrion.

The longest-running program, and one of the most successful to date, is on Nantucket Island. Nantucket Island is relatively isolated, 40 km south of Cape Cod. The criteria that made it a viable reintroduction site include (1) a historical presence of ABBs, (2) an assumed relative abundance of possible vertebrate carrion (primarily birds), (3) a lack of mammalian scavengers and predators, (4) a large area of protected land, and (5) a favorable bio-political climate with multiple organizations willing to partner on the project (pers. comm. Christopher Raithel).

5. Conclusions

It is important to continue monitoring visually suitable habitats using consistent methods to detect changes in population and population structure (size, sex ratio). In addition, the protection of large tracts of land is necessary to conserve *N. americanus*. These tracts of land need to be associated with sandy soils and rangeland to support *N. americanus*. Although the total area occupied by *N. americanus* represents almost 960,000 acres, in this study, the occurrence of *N. americanus* was estimated to be about 0.07 beetles per acre in the hotspot for occurrence, similar to data reported for high-density areas of the Nebraska Sandhills [35]. Almost half the traps placed in visually favorable habitats resulted in the capture of zero *N. americanus* in a trap night. Based on these results, it appears that *N. americanus* has not expanded its range in South Dakota and that the number of acres supporting the species is less than was previously estimated [70]. Surveys throughout South Dakota may provide inferential locations for *N. americanus* reintroductions based on the existing carrion beetle community.

Here, we propose the presence/absence of regionally identified indicator species in the most suitable habitats (i.e., prime *N. americanus* habitat) could be inferentially considered an artifact of existing competition dynamics among silphids and should be explicitly tested. Future managed relocation efforts should not only utilize this approach but also consider the entire silphid community when surveying to assess post-reintroduction success. Reintroduction scenarios are high-stakes conservation interventions and create an opportunity for valuable data collection.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d16040232/s1, Figure S1: Traps with all Nicrophorus for a five day period between 2018–2020 where American burying beetles (N = 36/240 trap locations) were the dominant Nicrophorus (>50% of captures). Figure S2: Distribution of dominant (>50% of captured Nicrophorus) species for traps sampled in June 2020. Figure S3: Distribution of dominant (>50% of captured Nicrophorus) species for traps sampled in August 2020.

Author Contributions: Conceptualization, W.W.H. and D.G.S.; methodology, W.W.H., D.G.S. and M.R.; software M.C.C. and M.R.; validation, M.R. and M.C.C.; formal analysis, M.R., W.W.H. and M.C.C.; investigation, D.G.S. and W.W.H.; resources, W.W.H.; data curation, M.C.C. and M.R.; writing—original draft preparation, W.W.H. and D.G.S.; writing—review and editing, M.C.C., M.R., W.W.H. and D.G.S.; visualization, M.C.C. and M.R.; supervision, W.W.H.; project administration, W.W.H.; funding acquisition, W.W.H. All authors have read and agreed to the published version of the manuscript.

Funding: Funding was provided by a grant to WW Hoback from the USFWS office in Pierre, South Dakota, with additional support from Hatch Project accession No. 1019561 from the USDA National Institute of Food and Agriculture.

Institutional Review Board Statement: Not applicable.

Data Availability Statement: The data presented in this study are available on request from the corresponding author due to the protected status of *Nicrophorus americanus*.

Acknowledgments: No external parties influenced the experimental design, objectives, or results of the present study. The authors thank Rafael Hayashida and Lauren Osborn for valuable comments on an earlier draft of this work.

Conflicts of Interest: The authors declare no conflict of interest.

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