

Out of Sight, Out of Mind: The Role of Carcass Burial and Maintenance in Reducing Competition in *Nicrophorus investigator*

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Abstract

Competition for ephemeral resources like carrion is intense among necrophagous insects, particularly burying beetles (*Nicrophorus* spp.), where reproductive success is limited by access to carcasses. Burial and post-burial maintenance behaviors are hypothesized to reduce carcass detection by competitors through the suppression of volatile organic compounds (VOCs). I investigated the relative importance of burial and maintenance in reducing discovery of small vertebrate carcasses by other carrion beetles. In a field study in a montane meadow in Colorado, I established can-based enclosures containing *Peromyscus maniculatus* carcasses under three treatments: surface (unburied), *N. investigator* pairs allowed to bury carcasses, but then removed to prevent further maintenance, and *-N. investigator* pairs allowed to bury carcasses and continue maintenance behaviors. Carcasses were protected from direct intrusion but exposed to visiting insects via screened funnel traps. Over two trials of daily monitoring (3 days each) and one trial of delayed monitoring (7 days), I recorded visitor identity, sex, and size, and measured burial depth and soil temperature. Surface and unburied carcasses had significantly higher discovery rates than buried carcasses ($\chi^2 = 7.83$, $p = 0.005$). Across all treatments, discovery proportions differed significantly (Fisher's exact test, $p = 0.011$), with maintained carcasses having the lowest detection. Mean visitor counts trended higher for surface carcasses, though differences

were not significant ($p = 0.096$). Burial depth did not significantly influence discovery ($p = 0.586$), indicating that even shallow burial reduced detection. These findings support the hypothesis that burial and maintenance function as effective exploitative competition strategies in *N. investigator*, likely mediated through VOC suppression. Such behaviors may contribute to priority effects that facilitate competitive coexistence. Future work should examine habitat-specific VOC dynamics and the individual contributions of maintenance behaviors.

Introduction

Competition for resources is a fundamental interaction that can shape ecological communities. Ecologists broadly sort competition into two distinct forms: exploitative and interference (Vance 1984). Exploitative competition is an indirect interaction where one organism's use of a resource deprives that resource from another. In contrast, interference competition is a direct form of competition where one organism physically prevents other organisms from utilizing a resource. Both forms of competition can occur within species (intraspecific) and between species (interspecific), and these dynamics can significantly alter species distributions. An example of this is Barred Owls outcompeting endemic northern spotted owls in the Pacific Northwest. Barred owls are generally larger, more aggressive, and more territorial. Due to these qualities in areas that barred owls occur they exclude northern spotted owls (Yackulic et al. 2014).

Beyond influencing distributions, competition can also affect trophic interactions and influence the structure and stability of food webs (Paine 1966). These interactions can be

especially pronounced in species that rely on rare or ephemeral resources like carrion or dung. In these circumstances, reproduction may be limited not by mating opportunities, but by access to the resource itself (Smith and Merrick 2001). Importantly, both exploitative and interference competition can lead to a range of outcomes such as competitive coexistence, extirpation, or local extinction (Chesson 2000).

To maintain competitive coexistence and sustain species diversity, communities must either reduce fitness differences between species or increase the strength of intraspecific competition relative to interspecific competition (Chesson 2000). These conditions can be met through a variety of mechanisms including spatial, temporal, and behavioral partitioning to limit competition over resources. Spatial partitioning reduces competition while allowing species to share the same habitat and utilize similar resources. This is observed in many taxa; however, one classic example is tree climbing bird species subdividing different regions of trees (MacArthur, Lara et al. 2015). Likewise, temporal partitioning is the portioning of resources at different times of the day, or year. This has been documented to reduce competition in both vertebrates and invertebrates, including *Nicrophorus* (Wilson et al. 1984; Gutman and Dayan 2005). Behavioral partitioning is another strategy species used to limit competition through adopting novel behaviors. An interesting example is observed in salt flat tiger beetles, which adopt unique thermoregulatory behaviors that allow for hunting at different times and in different microhabitats (Brosius and Higley 2013). Burying beetles (Order: Coleoptera, Family: Silphidae, Genus: *Nicrophorus*) employ many of these strategies, and are good model species to study competition, and competitive coexistence because they often co-occur with many congeners, and other necrophagous organisms (Scott 1998; Potticary et al. 2024).

Nicrophorus utilize carrion throughout much of their life cycle, relying on it for food and reproduction (Scott 1998; Potticary et al. 2024). *Nicrophorus* detect the volatile sulfur chemicals emitted by carcasses with their antennae and chemosensory organs on their legs, (Kalinová et al. 2009) and locate carcasses during searching flights. After discovering small vertebrate carcasses (primarily rodents) most species of *Nicrophorus* will bury and prepare them for their larvae. Various carcass preparation behaviors include moving carrion to a suitable burial site, burial, and then shaving fur, rounding the carcass, creating incisions, and secreting antimicrobial exudate (Potticary et al. 2024). The subsequent formation of a brood ball is necessary for the development of larvae and is their only source of nutrition until eclosion (Potticary et al., 2024). Because carrion is both limited and ephemeral, intraspecific and interspecific competition is frequent (Trumbo 1990; Scott 1990; Trumbo 1994). Carcass contests are well studied, and outcomes are determined by a variety of factors including habitat, nutrition, and size (Otronen 1988; Trumbo 1994; Vangenne et al. 2023).

Due to carrion directly impacting fitness and reproductive success, burial is thought to be a key behavior in limiting competition. Burials allow smaller individuals to monopolize carcasses through the priority effect (Trumbo 2023). The priority effect is the competitive advantage afforded to early discoverers that arrive at and modify a resource first (Fukami 2015). In burying beetles, this advantage is conferred because burial has been shown to reduce the emission of the volatile sulfur chemicals which attract other carrion feeders (Kalinová et al. 2009). However, previous research on burial has shown mixed results across studies, either reducing arrivals entirely or only marginally (Scott 1990; Trumbo 1990). Factors affecting burial varies; however, microhabitat and soil type affect the rate and depth of burial (Scott 1990). If

carcasses are taken over by intruders, eggs and larvae are destroyed, demonstrating the significance of limiting discovery (Robertson 1993).

A second mechanism employed by *Nicrophorus* to reduce competition is post-burial maintenance (Trumbo and Sikes 2021). These behaviors include shaving and rounding a carcass as well as secreting antimicrobial exudate. Shaving is thought to reduce the emission of volatile sulfur chemicals emitted by hair (Dekeirsschieter et al. 2009). However, this removed hair often lines the burial chamber, and so the efficacy of this is questionable. Shaping the carcass into a ball is believed to lessen the cost of secreting exudate by reducing the surface area: volume of the carcass. Finally, *Nicrophorus* secrete an antimicrobial exudate that may also control the emission of volatile sulfur compounds (Körner et al. 2023). This raises an important question about which behavior - burial or post burial maintenance - is more important in decreasing carcass discovery by competitors.

To investigate burial and post-burial maintenance's influence on competition, I studied the locally abundant *Nicrophorus investigator* and the assembly of necrophagous organisms near the Rocky Mountain Biological Laboratory, located in the Upper East River Valley, Colorado, U.S.A. (39° N, 107°W). *N. investigator* is a species of burying beetle that occurs throughout the montane regions of western North America (Smith and Heese 1995). It co-occurs with several other *Nicrophorus* species, including *N. defodiens* and *N. guttula*, as well as other carrion beetles, primarily *Thanatophilus lapponica* and *Heterosilpha racemosa* (Rawinski and Smith 2021). *N. investigator* has shown a preference towards open, montane meadow habitats (Smith and Heese 1995). I tested the hypothesis that carcass discovery varies with burial and maintenance. I predicted that discovery would be highest for surface (unburied) carcasses, followed by buried

but not maintained carcasses, and the lowest discovery by buried carcasses maintained by adult *Nicrophorus*.

Methods

Nicrophorus and *Peromyscus*

I trapped > 100 wild *Nicrophorus investigator* using can traps (18cm deep, 15cm in diameter) baited with chicken legs and placed on trees or stakes to prevent interference from vertebrate scavengers. Captured beetles were separated by sex and kept in plastic bins with food (raw chicken) on a moistened paper towel until needed for the experiment (Smith and Merrick 2001).

For the rodent carcasses, I procured ~ 100 *Peromyscus maniculatus* carcasses salvaged from buildings at the RMBL under a Scientific Collection License from the State of Colorado Department of Natural Resources, Colorado Parks and Wildlife to Dr. Rosemary Smith #25TR0403). I weighed and sorted carcasses into two weight classes 16-18g and 20-22g and randomly assigned these to each treatment. Carcasses were kept frozen until use.

Experimental Design

I buried 15 cans across a montane meadow near the Rocky Mountain Biological Laboratory, located in the Upper East River Valley, Colorado, U.S.A. (39° N, 107°W) (Figure 1).



Figure 1: Map showing the Deer Creek field site (outlined in red) utilized for this experiment.

I buried large cans 20m apart to limit the effects of decreased competition that might occur by introducing carcasses to a relatively small area (Trumbo and Sikes 2021). I filled each can 2/3 of the way with soil taken from the immediate site (Smith and Merrick 2001). Each can had a wire screen cover to both contain the introduced beetle pair as well as to prevent intruders from contacting the carcass. Each can also had a secondary can placed over the top of the mesh with a securely attached screen funnel lid designed to capture any visiting insects that were attracted to the carcass (Figure 2) but exclude vertebrate scavengers and incidental visitors.



Figure 2: Image showing the trap design used to conduct this experiment. In the left most photo, the bottom can contained the carcass treatment and prevented any intrusions. The right photo shows the inside of the funnel can used to capture arriving competitors.

Three treatments were randomly applied to the cans: unburied carcass, beetle buried without maintenance, and beetle buried with maintenance. For the treatments involving beetle burial, I measured and then placed a randomly selected pair of *N. investigator* into cans and allowed them to bury. Within 24 hours after the burial, I removed the beetles in the no maintenance trial. In the unburied treatment, I placed a mouse carcass onto the surface of the soil (Scott 1998). If carcasses were not buried by beetles, they would be considered unburied. I checked each treatment every day for 3 days starting after the carcass was initially placed in the

can. All captured visitors were identified, counted, and released. Additionally, I sexed and measured the pronotum of all visiting *Nicrophorus*. I left cans for 3 days, which is the period where takeovers and intrusions are most likely (Robertson 1993; Trumbo 2002; Pastula et al. 2013; Vangenne et al. 2023). The experiment was repeated three times, after each trial randomly assigned the cans to a new treatment and repeated the experiment with fresh soil (Trumbo 2023). The third trial differed in that the treatment cans were only checked on Day 1 to apply the treatments and then again on Day 7 to collect intruders.

Data Analysis

I analyzed the data using R version 4.4.1 (R Core Team, 2024). I combined the surface and unburied treatments into a single category and compared with the maintained and unmaintained treatments for differences in the proportion of discovery using a chi-square test of independence. The proportion of discovery across all treatments was compared using Fisher's exact test. Mean visitor counts were compared among treatments using a Kruskal–Wallis test. Burial depth was compared between discovered and undiscovered cans using a Mann–Whitney U test. Additionally, the probability of discovery was modeled as a function of mean burial depth using logistic regression.

Results

Table 1: Table showing the distribution of treatments at the conclusion of the experiment. Trial 1 (n=15) had one unsuccessful burial. Trial 2 (n=13) had 2 unsuccessful burials Trial 3 (n=17) had 2 unsuccessful burials. Two cans in trial 2 were destroyed by cows.

Treatment	Trial 1	Trial 2	Trial 3
Surface	5	5	5
Buried without maintenance	5	3	5
Buried With Maintenance	4	3	5
Unburied	1	2	2

For the combined Trial 1 and 2 surface and unburied treatments were combined, the proportion of discovered cans was significantly higher than the combined buried treatments (Chi-Square test of independence, X-squared = 7.8329, df = 1, p-value = 0.00513) (Figure 3).

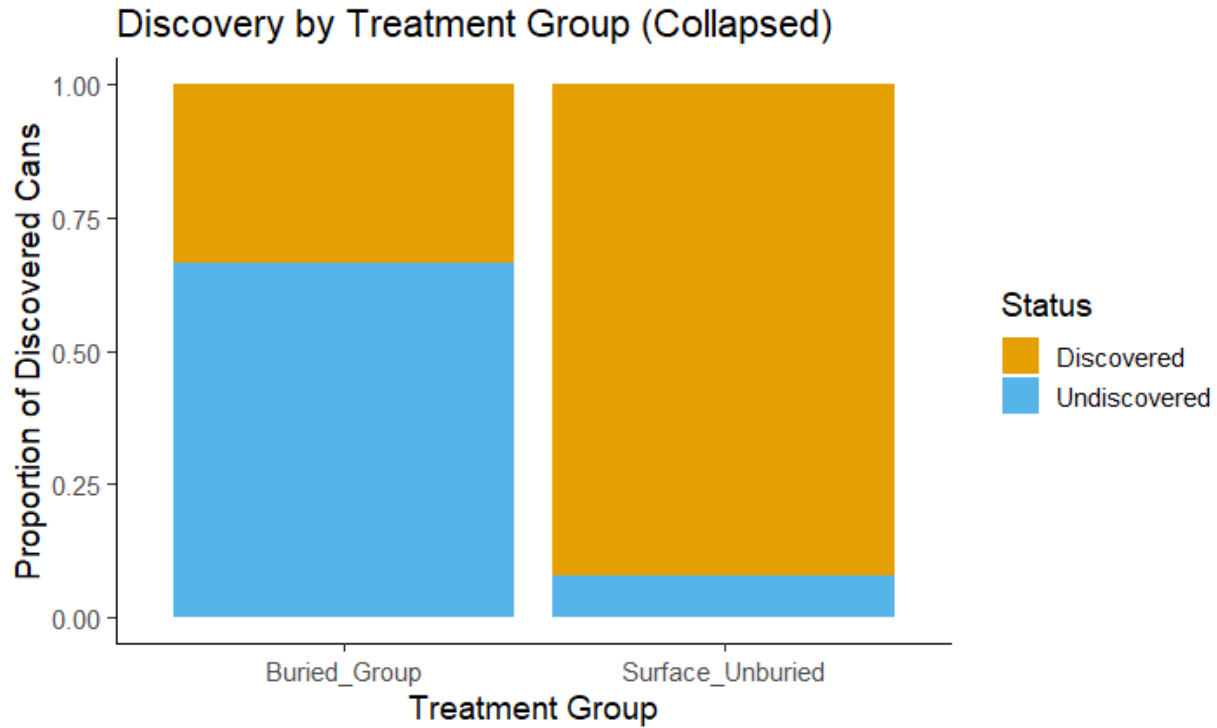


Figure 3: Proportion of discovered cans in the combined buried group (beetle-buried with and without maintenance) (n=14) and the combined surface group (surface and unburied treatments) (n=13).

Across all treatments, the proportion of discovered cans was significantly different based on treatment (Fishers Exact Test, $p = 0.011$) (Figure 4). Additionally, Pairwise Fisher's exact tests with bonferroni corrections revealed that the proportion of discovered cans in the combined Surface and Unburied group was significantly higher than in the Maintained group (Bonferroni-adjusted $p = 0.0096$), and was marginally significant from the No Maintenance group (Bonferroni adjusted $p = 0.0921$). No significant difference was found between the No Maintenance and Maintained groups (Bonferroni adjusted $p = 1.000$) (Figure 5).

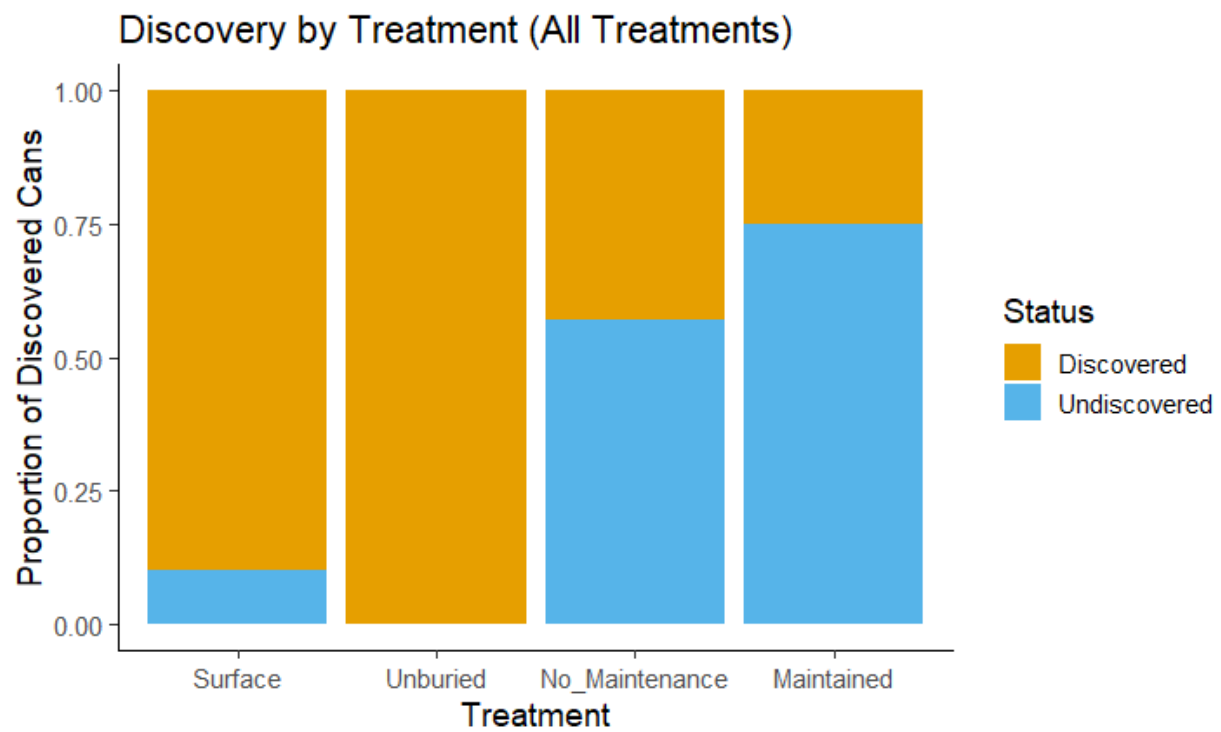


Figure 4: Proportion of discovered cans in all treatments (Surface, Unburied, No maintenance, and maintained).

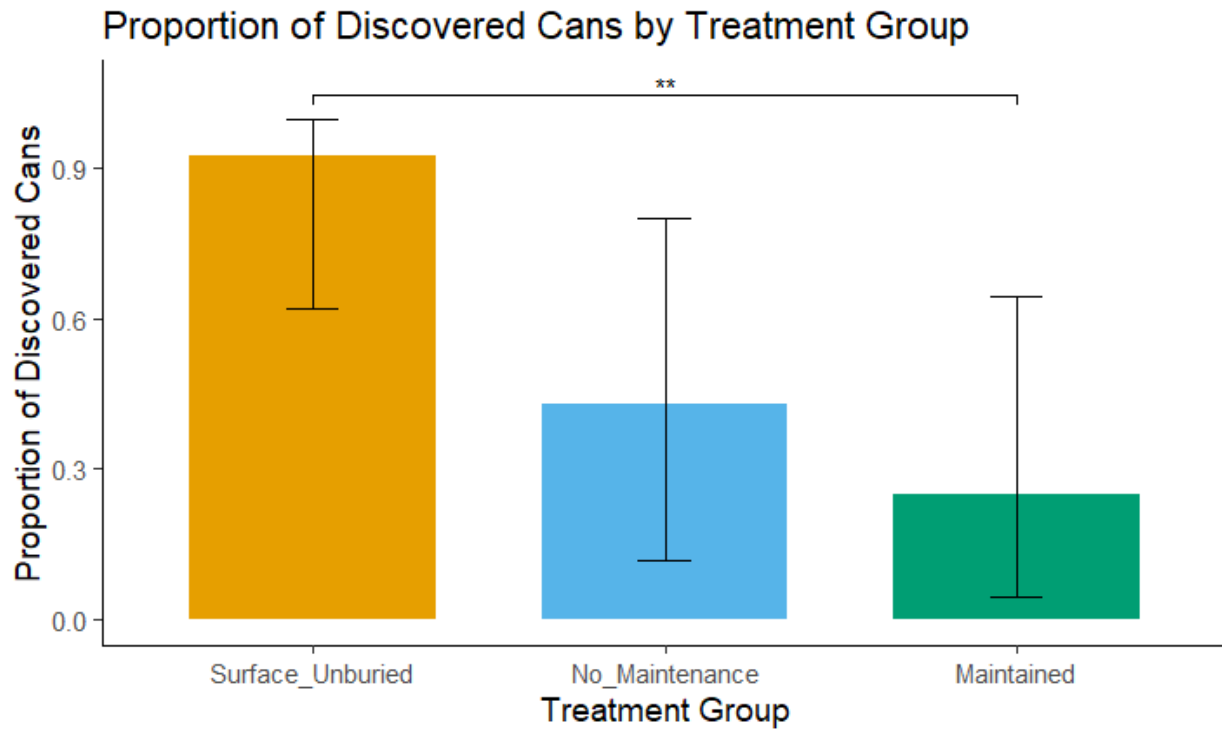


Figure 5: Proportion of discovered cans by treatment when surface and unburied treatments were combined. Bracket represents significant difference between discovery of surface unburied and maintained carcasses.

Table 2: Summary of the total number of visitors recorded for each treatment (Surface, Unburied, No Maintenance, Maintenance) across both trials. Values represent the sum of all visitors observed within each treatment–trial combination.

Trial	TRT	Total Visitors
1	M	19
1	NM	46
1	S	86
1	UB	38
2	M	6
2	NM	0
2	S	115
2	UB	65
3	M	0
3	NM	34
3	S	39
3	UB	9

Comparing the mean number of visitors per can revealed marginally significant difference (Kruskal-Wallis, $H = 6.347$, $df = 3$, $p = 0.096$), suggesting that surface and unburied cans received higher number of intruders on average (Figure 6).

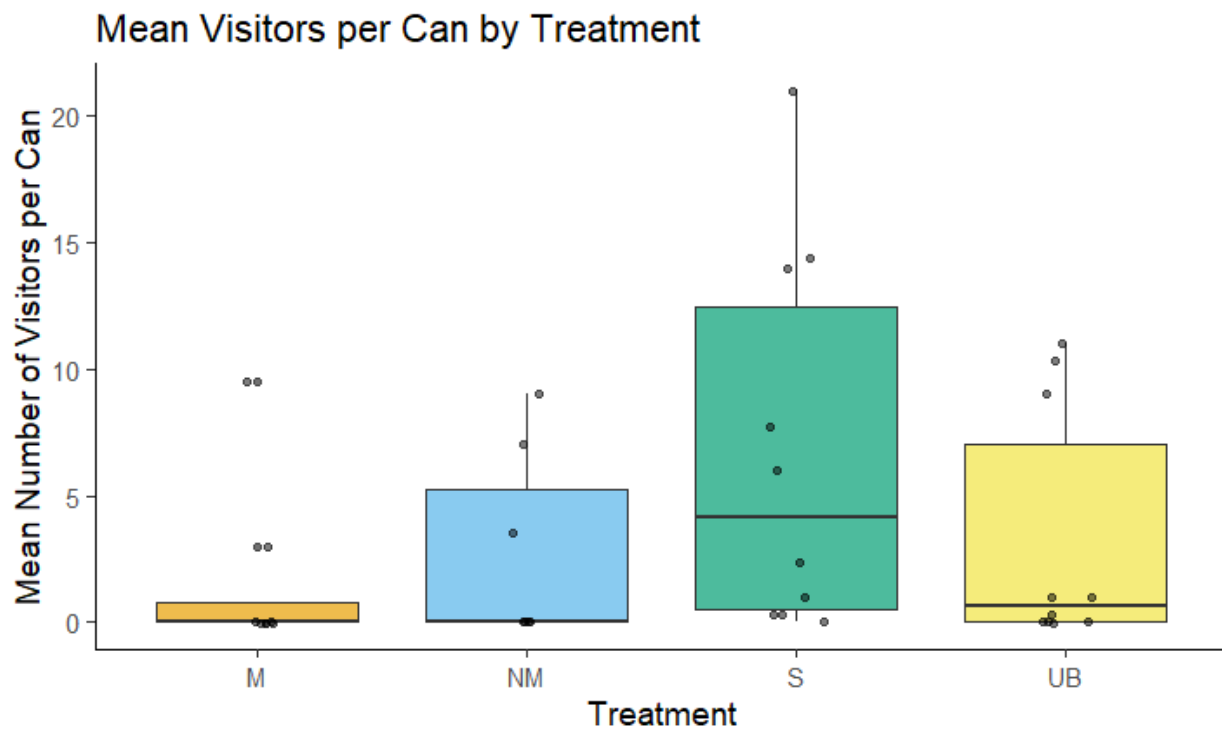


Figure 6: Graph showing mean number of visitors per can, per treatment (Maintained, No maintenance, Surface, and Unburied).

A Mann-Whitney U test revealed no significant difference in the mean burial depth of discovered and undiscovered cans (Mann Whitney U, $W = 81$, $p = 0.718$) (Figure x). Discovered cans had a mean burial depth of 3.48 cm ($n = 20$), while undiscovered cans had a mean burial depth of 4.10 cm ($n = 32$) (Figure 7).

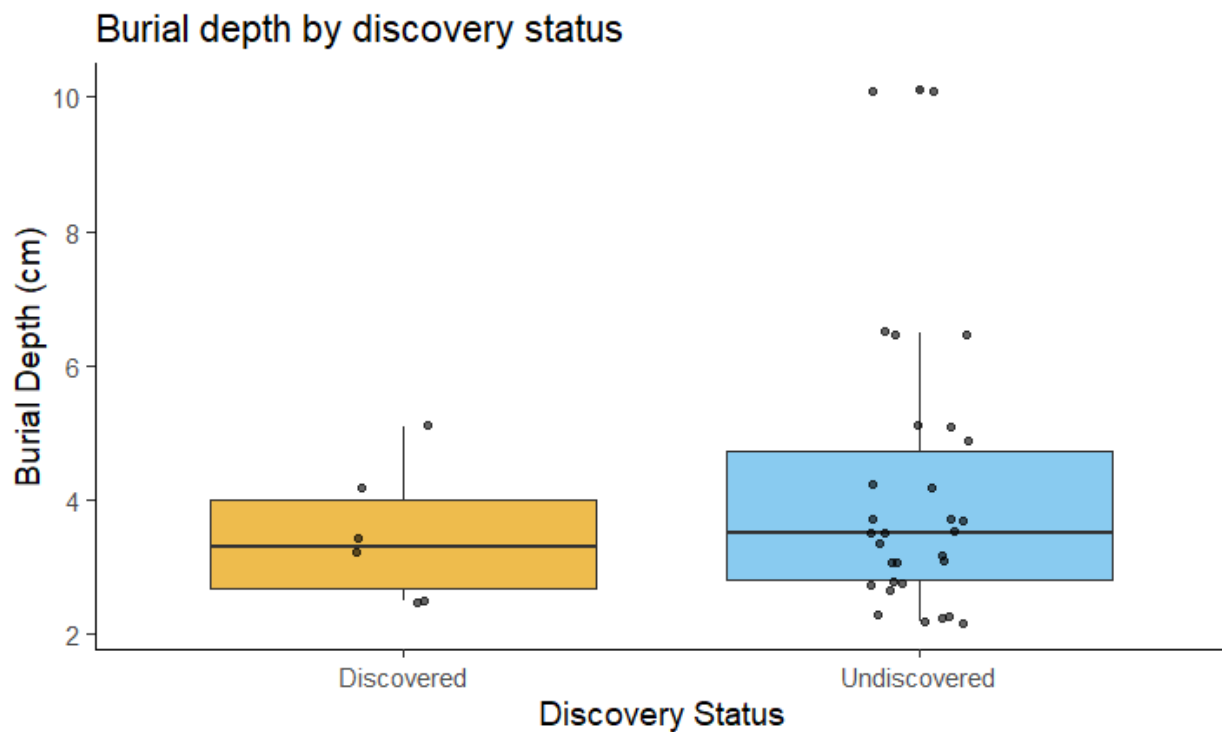


Figure 7: Mean burial depth of cans that were discovered vs. undiscovered. Points represent individual cans.

A logistic regression showed that mean burial depth was not a statistically significant predictor of discovery ($\beta = -0.1819$, OR = 0.834, 95% CI: 0.433–1.605, $p = 0.5863$) (Figure 8), although the negative slope indicates a trend for lower discovery with deeper burial.

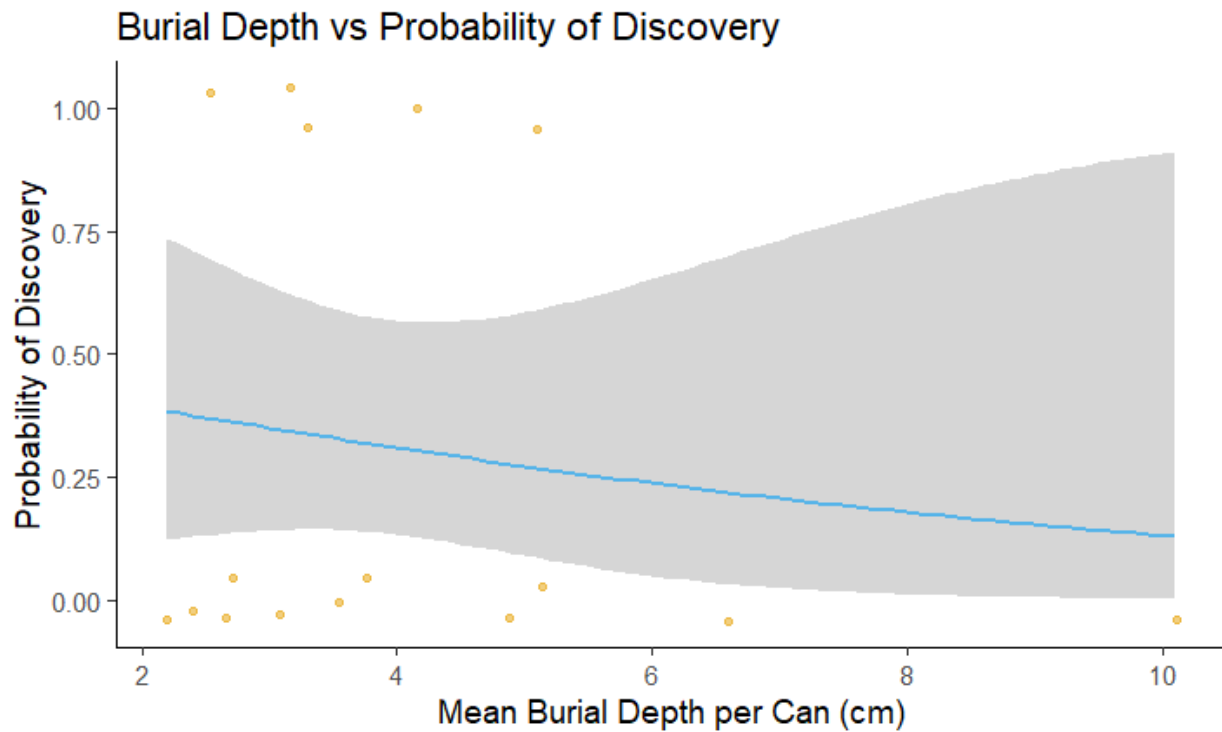


Figure 8: Relationship between mean burial depth per can and the probability of discovery. Points represent individual cans.

Discussion

This study looked at the role of burial and post burial maintenance in reducing competition over carcasses buried by *N. investigator*. Burial is a form of exploitative competition that significantly reduced the discovery of carcasses by other carrion beetles. Additionally, my

results support the predictions that continued maintenance of carcasses by adult *N. investigator* further reduces discovery of buried carcasses. On average the fewest number of competitors arrived on buried carcasses. Burial depth did not influence carcass discovery, suggesting that even shallow burial is effective at reducing discovery.

The reduction in detection following burial is consistent with prior research showing that burial and maintenance behaviors such as shaving fur, rounding carcasses, and secreting antimicrobial exudate reduce the emission of volatile organic compounds (VOCs) (Potticary et al. 2024). These VOCs are vital cues used by searching adult burying beetles and other necrophagous organisms, and are the primary way that they detect carrion (Kalinova et al 2009). Experimental work altering the microbial community, and thus the emission of VOCs, shows significant reductions in detections (Trumbo & Steiger 2020). Similar research by Trumbo & Sikes (2021) showed that when carcasses prepared by *N. orbicollis* in laboratory settings were placed into the field, discovery rates by silphid beetles were 0%. Prepared carcasses by other, non-*Nicrophorus* silphids were discovered at much higher rates (Trumbo & Sikes 2021). It has also been demonstrated that feeding, and modification by non-*Nicrophorus* silphids attracts carrion beetles to carcasses (Ito & Hasegawa 2023). Thus, reducing discovery by other silphids by continued carcass maintenance behaviors by *Nicrophorus* may be a crucial adaptation in reducing the arrival of competitors.

The average number of Silphid visitors was not significantly affected by treatment. This could be explained by the number of carcasses that did not attract any visitors (22%) and the high variation in the number of arrivals (range 0-20). It is possible that once one silphid arrives this attracts others (Trumbo 1990), so that the counts are not measures of independent discovery of the carcass. More frequent checks of the cans and prompt removals of arrivals would reduce

this effect. In addition, carrion insect population density, weather conditions that affect the ability of beetles to engage in searching flights, and the impacts of weather on carcass decomposition rates and thus VOC emissions could all affect detection and arrivals. Long term research focusing on silphid arrivals has shown that it is extremely context dependent and fluctuates with year and season (Matuszewski & Mądra-Bielewicz 2021).

Burial depth did not influence the probability of discovery in this study. Neither did the mean burial depth vary between discovered and undiscovered carcasses. This contrasts with expected results that show deeper burials saw fewer carrion beetles (Shubeck 1985). The data do suggest that burial at any depth decreased the rate of detection. This difference could be explained by a variety of factors including the openness of montane as well as the moisture content and compactness of the soil (Dekeirsschieter et al. 2009). Burial depth seems to be a highly variable behavior within the genus, with some species of *Nicrophorus* only covering carcasses beneath the leaf litter while others bury at greater depths (Potticary et al. 2024). It would be interesting to find out if carcass maintenance behaviors alone would reduce discovery in shallowly buried carcasses.

These findings support the prediction that carcass burial and maintenance are important behaviors that reduce the detection of carcasses by other carrion beetles. Reducing discovery of this critical resource is an effective form of exploitative competition. This aligns with the concept of the priority effect, whereby early arrivals to a resource can modify it to their benefit (Fukami 2015). Additionally, the strength of burial as a form of exploitative competition may increase the relative strength of intraspecific competition between *N. investigator*. This could function as a “stabilizing force” promoting competitive coexistence as outlined by Chesson (2000).

Future work into the role of burial, and maintenance, as they relate to competition may expand the scope of this experiment into different habitat types such as the adjacent spruce and aspen forests where *Nicrophorus* and *Thanatophilus* are also found at carcasses but where climatic conditions are quite different from the open meadows. This would allow for a greater understanding of how the dispersal of VOCs is affected by habitats that differ in temperature, humidity, and openness/air flow. Future studies would also benefit from utilizing GCMS (Gas chromatography–mass spectrometry) by collecting samples under field conditions, rather than controlled laboratory settings. Additional studies that altered the duration of carcass maintenance at different stages would allow for a comparison of the effects of the individual steps of maintenance in sequence (i.e. burial, rounding, shaving, anti-microbial secretions) on reducing VOC emissions, carcass discovery, and competition. In addition, by manipulating the sexes present, the results would provide additional evidence for understanding the duration and extent of bi-parental investment during the reproductive cycle of the burying beetle.

References

- Brosius, T. R., & Higley, L. G. (2013). Behavioral niche partitioning in a sympatric tiger beetle assemblage and implications for the endangered Salt Creek tiger beetle. *PeerJ*, 1, e169.
- Cantu J 2024. The Fate of Burying Beetles and their Carcasses: Hardships, Competition and Environmental Factors. Student Paper.
- Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics*, 31, 343–366.
- Dekeirsschieter, J., Verheggen, F. J., Gohy, M., Hubrecht, F., Bourguignon, L., Lognay, G., & Haubruge, E. (2009). Cadaveric volatile organic compounds released by decaying pig carcasses (*Sus domesticus* L.) in different biotopes. *Forensic Science International*, 189, 46–53.

Fukami, T. (2015). Historical contingency in community assembly: Integrating niches, species pools, and priority effects. *Annual Review of Ecology, Evolution, and Systematics*, 46, 1–23.

Gutman, R., & Dayan, T. (2005). Temporal partitioning: An experiment with two species of spiny mice. *Ecology*, 86, 164–173.

Ito, M., Nishigaki, A., & Hasegawa, M. (2023). The effect of pioneer carrion beetles on the emission of volatile organic compounds and carrion insect community assembly. *Ecology and Evolution*, 13, e10818. <https://doi.org/10.1002/ece3.10818>

Kalinová, B., Podskalská, H., Růžička, J., & Hoskovec, M. (2009). Irresistible bouquet of death—how are burying beetles (Coleoptera: Silphidae: *Nicrophorus*) attracted by carcasses. *Naturwissenschaften*, 96, 889–899.

Keller, M. L., D. R. Howard & C. L. Hall. 2021. The thermal ecology of burying beetles: Temperature influences reproduction and daily activity in *Nicrophorus marginatus*. *Ecological Entomology* 46(6):1266–1272.

Körner, M., Steiger, S., & Shukla, S. P. (2023). Microbial management as a driver of parental care and family aggregations in carrion feeding insects. *Frontiers in Ecology and Evolution*, 11, 1252876.

Lara, C., Pérez, B., Castillo-Guevara, C., & Serrano-Meneses, M. A. (2015). Niche partitioning among three tree-climbing bird species in subtropical mountain forest sites with different human disturbance. *Zoological Studies*, 54, 28.

Matuszewski, S., Małdra-Bielewicz, A. Heat production in a feeding matrix formed on carrion by communally breeding beetles. *Front Zool* 18, 5 (2021). <https://doi.org/10.1186/s12983-020-00385-7>

Otronen, M. (1988). The effect of body size on the outcome of fights in burying beetles (*Nicrophorus*). *Annales Zoologici Fennici*, 25(2), 191–201.

Paine, R. T. (1966). Food web complexity and species diversity. *The American Naturalist*, 100, 65–75.

Pastula EC, Merritt RW. Insect arrival pattern and succession on buried carrion in Michigan. *J Med Entomol*. 2013 Mar;50(2):432-9.

Potticary, A. L., Belk, M. C., Creighton, J. C., Ito, M., Kilner, R., Komdeur, J., Royle, N. J., Rubenstein, D. R., Schrader, M., Shen, S., Sikes, D. S., Smiseth, P. T., Smith, R., Steiger, S.,

Trumbo, S. T., & Moore, A. J. (2024). Revisiting the ecology and evolution of burying beetle behavior (Staphylinidae: Silphinae). *Ecology and Evolution*, 14, e70175.

Rawinski, A., & Smith, R. (n.d.). Abundance and elevational range shifts of three species of burying beetle in Gunnison County, Colorado and importance of stridulation during reproduction in burying beetles.

Robertson, I. C. (1993). Nest intrusions, infanticide, and parental care in the burying beetle, *Nicrophorus orbicollis* (Coleoptera: Silphidae). *Journal of Zoology*, 231, 583–593.

Scott, M. P. (1990). Brood guarding and the evolution of male parental care in burying beetles. *Behavioral Ecology and Sociobiology*, 26, 31–39.

Scott, M. P. (1998). The ecology and behavior of burying beetles. *Annual Review of Entomology*, 43, 595–618.

Shubeck, P. P. (1985). Orientation of carrion beetles to carrion buried under shallow layers of sand (Coleoptera: Silphidae). *Entomological News*, 96, 163–166

Smith, R. J., & Heese, B. (n.d.). Carcass selection in a high-altitude population of the burying beetle, *Nicrophorus investigator* (Silphidae).

Smith, R. J., M. Bonilla, C. Calahan, and J. Mann. 2000. Comparison of reproductive success of in-situ burial versus the use of abandoned burrows for carcass interment by *Nicrophorus investigator* (Coleoptera: Silphidae). *Journal of the Kansas Entomological Society* 73:148–154. <http://www.jstor.org/stable/25085959>.

Smith, R. J., & Merrick, M. J. (2001). Resource availability and population dynamics of *Nicrophorus investigator*, an obligate carrion breeder. *Ecological Entomology*, 26, 173–180.

Trumbo, S. T. (1990). Interference competition among burying beetles (Silphidae, *Nicrophorus*). *Ecological Entomology*, 15, 347–355.

Trumbo, S. T. (1994). Interspecific competition, brood parasitism, and the evolution of biparental cooperation in burying beetles. *Oikos*, 69, 241–249.

Trumbo, S. T., & Bloch, P. L. (2002). Competition between *Nicrophorus orbicollis* and *N. defodiens*: Resource Locating Efficiency and Temporal Partitioning. *Northeastern Naturalist*, 9(1), 13–26.

Trumbo, S. T., & Steiger, S. (2020). Finding a fresh carcass: bacterially derived volatiles and burying beetle search success. *Chemoecology*. doi:10.1007/s00049-020-00318-0

Trumbo, S. T. (2023). Moving the corpse to hide the evidence: Horizontal as well as vertical movement is important when burying beetles cache a carcass. *Journal of Insect Behavior*, 36, 11–19.

Trumbo, S. T., & Sikes, D. S. (2021). Resource concealment and the evolution of parental care in burying beetles. *Journal of Zoology*, 315, 175–182.

Vance, R. R. (1984). Interference Competition and the Coexistence of Two Competitors on a Single Limiting Resource. *Ecology*, 65(5), 1349–1357.

Vangenne YD, Sheppard B, Martin PR. 2023. Behavioral dominance interactions between two species of burying beetles (*Nicrophorus orbicollis* and *Nicrophorus pustulatus*) PeerJ 11:e16090

Wilson, D. S., Knollenberg, W. G., & Fudge, J. (1984). Species packing and temperature-dependent competition among burying beetles (Silphidae, *Nicrophorus*). *Ecological Entomology*, 9, 205–216.

Yackulic, C. B., Reid, J., Nichols, J. D., Hines, J. E., Davis, R., & Forsman, E. (2014). The roles of competition and habitat in the dynamics of populations and species distributions. *Ecology*, 95, 265–279.