

Native ant (*Formica rufa*, *Formica fusca*), *Nicrophorus* spp. interactions at small mammal carcass resources in the southern Rocky Mountains, Gunnison National Forest, Colorado.

Alexander Solis, Rosemary Smith

Abstract

Competition for carcass resources can be fierce with a broad range of taxa vying for control of the nutrient rich resource. Arthropod competition for carcasses is well studied. Flies, beetles, and ants are common carcass utilizers. The burying beetle (*Nicrophorus* spp.) is an obligate carrion breeder who has developed many methods of securing carcasses. Ants are opportunistic scavengers who would utilize many resource made available to them, including carcasses. Competition between the two taxa is not well understood, but invasive species *Solenopsis invicta* and native species of Florida, *Solenopsis geminata*, have been shown to have significant effect on *Nicrophorus* reproductive success. The purpose of this study is to investigate if native ants of the higher latitude and elevation of southern Rocky Mountains, Gunnison National forest, Colorado, have the same negative effect on *Nicrophorus* sequestration of carcass resource for reproduction. The study found the native ant species *Formica rufa* and *Formica fusca* had no effect on the burial of carcasses by *Nicrophorus*. These findings support previously established evidence of decreased competition for carcasses in higher elevations and latitudes.

Introduction

Carrion as a resource is often an overlooked subject in community ecology. Carcasses are a nutrient rich resource that is often spatially and temporally sensitive. Compared to the nutrients held within decomposing plant material, carrion possess greater amounts of macronutrients, such as nitrogen and phosphorus. (Swift et al. 1979;

Moore et al 2004). Due to the stochastic nature of carrion, organisms that utilize carcasses to feed or to reproduce must effectively locate and defend the carcass from other potential opportunists (Barton 2013).

A broad range of taxa utilize carcasses, from vertebrate scavengers, invertebrates, fungi, and microbes. These constituents of the carrion ecological community are the principle decomposers and distributors of the nutrients held within the carcasses, recycling them back into the ecosystem (Carter et al. 2007). Vertebrate scavengers are often second only to flies for arrival to a carcass site and maybe be responsible for the consumption of the majority of carrion (De Vault et al. 2003). Microbes and fungi are profoundly affected by carcass resource availability. Carter et al. (2008) found there to be a 400% increase in microbial biomass associated with *Rattus rattus* carcasses in tropical grasslands of Australia. The importance of microbial nutrient mediation and nutrient processing between trophic levels within an ecosystem is well recorded. (might need rephrasing) (Barton 2013) Arthropods tend to be the most species-rich and abundant organisms found at a carcass, other than microbes. (Braack 1987) Arthropods play a critical role in the decomposition process of carcasses and the recycling of nutrients back into the ecosystem (Parmenter and MacMahon 2009). Most studies investigating carcass community ecology found three or more arthropod taxa at each site, typically flies, beetles, and ants (Barton 2013).

For each species, an effective competitive strategy is necessary for the sequestration of ephemeral carcass resources. Of the estimated 75 species of *Nicrophorus* spp., the majority are found throughout the Northern hemisphere. This is most likely due to increased competition for carcasses from flies, ants, scavengers, and increased

decomposition rates in southern locales (Trumbo 1990). The burying beetle (*Nicrophorus* spp.) employs an array of behavioral strategies to secure carcasses, which are necessary for their reproductive success. These obligate carrion breeders are the only Coleopterans that participate in both brood rearing and bi-parental care (Milne and Milne 1976). Bi-parental care is considered an important factor to congeneric competition, but is not well understood for its importance to competition across taxa. Flies are the primary competitors of *Nicrophorus* for carcass resources. If a carcass is inundated with maggots *Nicrophorus* will abandon it. As an evolutionary response to this threat, *Nicrophorus* has developed a symbiotic relationship with phoretic mites that infest the beetle. When a beetle discovers a carcass, the phoretic mites living on the beetle will consume fly eggs that may be present on the carcass, effectively facilitating the beetle's reproductive success. Phoretic mites benefit in this relationship as the *Nicrophorus* beetle transports the mites from carcass site to carcass site, allowing it to breed and find new host beetles for its distribution. (transition) Microbes growing on the carcass have a negative impact on the fitness of *Nicrophorus* spp. offspring. The parent *Nicrophorus* will produce anal secretion that possess antimicrobial enzymes that reduce decomposition as well as protect the progeny from adverse effects of the microbes. Arce et al. (2012) found that larvae raised with resources coated with parent secreted lysozymes were twice as likely to survive. (transition) *Nicrophorus* has impressive ability to locate a carcass resource. Entomologist Frantisek Petruska found that upon removal from a carcass *Nicrophorus* was able to relocate the carcass from as far as 4 kilometers within 24 hours. This quick discovery is crucial to the success of carcass sequestration from other competitors. Despite extensive research into *Nicrophorus* behavior and competition for carcass

resource across taxa, there exists little literature on the impact of ants on *Nicrophorus*' obligate carcass breeding and even less on *Nicrophorus*' ability to combat ant activity on carcasses. Most ant are opportunist, utilizing any resource that becomes readily available. This includes small mammal carcasses, potentially employing high levels of recruitment to secure the resource. Scott et al (1987) found invasive fire ants to have a strong influence on *Nicrophorus* sequestration of carcass. The study further showed native ant *Solenopsis geminata* of Florida also affected *Nicrophorus* burial behavior in that southern locale. The focus of this study is to investigate whether native ants (*Formica rufa*, *Formica fusca*) of Gunnison National forest, Colorado, in the southern Rocky Mountains, have an influence on *Nicrophorus* burial success. *Nicrophorus* tends to compete better in montane environments where competition for carcass is less pronounced (Peck and Anderson 1985). Ant diversity and abundance are also known to decrease inversely with latitudinal and elevational gradients (Kusnezov 1957) which could improve *Nicrophorus*' ability to sequester carcasses through burial.

Methods and Materials

Study organisms

Nicrophorus species found in the study area include *N. investigator*, *Nicrophorus defodiens*, and *Nicrophorus guttula*. *N. defodiens* appear in less abundance than *N. investigator*, and *N. guttula* even more so. (Smith 2000) *Nicrophorus spp.* emerge from their over wintering in late June through July and are actively reproducing through August (Smith & Heese, 1995; Smith 2002). Carcasses used for reproduction are located using chemoreception. Upon discovery of a suitable carcass the *Nicrophorus* beetle will

release a pheromone to attract a mate. Pheromones released by the male burying beetle attracts both male and female beetles. (Muller and Eggert, 1987). This broadcasting can lead to increased intraspecific competition for the carcass resource. Competition between same sex beetles occurs often with the largest beetles asserting dominance over the carcass (Otronen 1988). The dominate pair of beetles will then participate in loose cooperative burial of the carcass. Only once the carcass is secured from other competitors do the beetles copulate. 12 hrs to 48 hrs after discovery of the carcass the female will oviposit, and approximately 56 hrs later the eggs will hatch. After 5-9 days the larvae will pupate. Duration of bi-parental care has been estimated to extend from 9- 16 days depending environmental factors, carcass size and species of beetle.

Study sites

This study was conducted in the vicinity of the Rocky Mountain Biological Laboratory, Gothic, Colorado (latitude 38° 57', sp. longitude 107° 00'; 2900 m elevation) in Gunnison National Forest. More specifically the sites of Deer creek trail, Gothic County Rd., and Judd Falls trail were used. Deer creek trail and Gothic County Rd sites were substantially less rocky than Judd falls and were classified as a fescue type community (Langenheim (1962).

Determining carcass utilization by ant taxa

To determine which ants of the region utilize carcass resources, 10 small mammal carcasses (*Peryomyscus spp.*) were set in three transects 30 meters apart. 5 of the carcasses sites were located in aspen understory and 5 in meadows at the deer creek trail site (Figure 1). Pitfall trap were used in conjunction with the carcasses. These were checked

every 24 hours during a 72-hour period. The ants captured in the pitfall traps were identified to assess ant species' utilization of carcass resources.

Determining carcass sequestration success of *Nicrophorus* based on Ant presence and density- Exp ver.1

To measure *Formica rufa* and *Formica fusca*'s effect on the reproductive success of *Nicrophorus*, an ant exclusion experiments was conducted using steel cans (15-cm diameter, 17-cm depth) buried approximately 14 cm deep, leaving a rim of 3 cm exposed above ground. 12 ant nests were located: six *F. rufa*, six *F. fusca*. A transect extended from the base of the ant nest up to 6 m away. Along the transect, two points were selected representing a near and far distance. For each species represented, 2 nests had distances of two and five m, one and three m, and four and six m. At each distance, two cans were buried one meter apart. Of the pair, one was selected as the exclusion and the other the control. The exposed rim of the exclusion can was coated in tangle foot tree tape to prevent ant entrance into the can. To assist ant access and exit of the can, a ramp of dirt on the exterior and interior of the can was created and maintained throughout the trial. Carcasses were placed at all cans at 8am on the first day of the 72-hour study period. Cans were checked every 3 hours from 8 am to 8 pm over the study period. Density of ants, species, whether *Nicrophorus* was present as well as the burial status were recorded.

Determining carcass sequestration success of *Nicrophorus* based on Ant presence and density- Exp ver. 2

This is the final iteration of my experimental design. It was conducted similarly to the previous experiment with slight changes to reduce interference by scavengers, and

intraspecific competition between *Nicrophorus*. The 12 sites previously mentioned were used for this experiment. Cans remained buried to the same specifications, but only one pair of cans were used per ant site. We determined distance to be arbitrary to the density of ants, therefore the closest pair of cans was used. Metal mesh screens were fixated on the top of the cans, small holes were cut into the tops of the control cans to permit ant access and exit. Wild caught *Nicrophorus* male and females were paired on site and placed into the cans midday of the first day of the study period. Cans were checked every 3 hours from 8 am to 8 pm over a 48 hour period. Ant density and burial status were recorded at every time interval.

Results

Taxa of Ants that Utilize Carcass Resources

Four genus of ants (*Camponotus*, *Formica*, *Myrmica*, and *Tapinoma*) were shown to utilize carcass resources in some fashion. *Formica fusca*, *Myrmica spp.*, *Formica rufa*, were found at carcasses the most frequently. Meadows also exhibited greater ant abundance than Aspen Understory. No vegetation type possessed all of the ants captured in the pitfall traps. *Camponotus spp.* was found exclusively in aspen understory while *Tapinoma sessile* was found only in the meadows of the study site, deer creek trail. *Formica fusca* was also absent from carcass sites found in the aspen understory, but found in the meadow. (Table 1)

Effect of Native Ant (*Formica spp.*) on *Nicrophorus* carcass sequestration, Exp ver. 1

The comparison of probabilities of burial success by *Nicrophorus* based on whether ants were present, in experiment ver. 1, showed there was not a strong effect between the two groups.

When ants were present the probability of burial by *Nicrophorus* was .21 compared to .26 when ants were excluded. (Figure 1)

The logistic regression analysis of showed no significant effect the average ant density had on the sequestration of carcasses by *Nicrophorus* with a p-value of 0.577. (figure 2) There was also no significant correlation between the maximum ant presence and burial success off *Nicrophorus*, exhibiting a p-value of 0.486. (figure 3)

Effect of Native Ant (*Formica spp.*) on *Nicrophorus* carcass sequestration, Exp ver. 2

In the experiment ver. 2, the probability of burial by *Nicrophorus* when ants were present was 0.85, while when ants were excluded the probability of burial was .89. (Figure 4)

The logistic regression analysis of the effect ant density has on burial success of *Nicrophorus* when intraspecific competition is controlled showed there was no significant relationship between burial failure and the average amount of ants at a carcass nor the maximum number of ants found at the carcass with p-values equal to 0.09273 and 0.0719 respectively. (Figure 5&6)

Discussion

The native ants *Formica Fusca* and *Formica rufa* did not show to have significant effect on the Carcass sequestration of *Nicrophorus*. The logistic regression model from version 1 of the experiment indicated that there is a more important factor that influence *Nicrophorus* burial success than ant presence. By making an informal comparison between the control of experiment ver. 1, which did not exclude any organism from the

carcass site, with the control of experiment 2, which excluded intraspecific *Nicrophorus* competition, we can begin to see a trend of the significance intrageneric/intraspecific competition affects burial success. With the exclusion of intrageneric/intraspecific competition, burial success of *Nicrophorus* went from 21% success rate to 85% success rate. During the experiment ver. 1 many carcasses were observed to have multiple *Nicrophorus* present, but the competitors on the carcass would consume the carcass rather than attempt to ward off rivals. The *Nicrophorus* would eat the carcass to the extent that it would no longer be suitable for burial. There is no current literature that has investigated intrageneric/intraspecific competition between *Nicrophorus* as a factor for carcass sequestration failure. (Figure 7) According to Fellers et al. (1982) ants are particularly adept at locating carcass resource than other scavengers, finding bait carcass within 36 minutes of placement with a median time of 3.75 minutes for rate of discovery. This would indicate that ants are likely to discover carcass before *Nicrophorus*, and removes the advantage of first arrival for *Nicrophorus*. Yet *Nicrophorus* is still not affected by ant presence. This may be due to how *Nicrophorus* intern carcasses and how ants approach carcass resources. Ants tend to stick to the surface of the carcass and focus their attention on the orifices of the carcass, such as the eyes, mouth, and anus, which provide the easiest access to the carcass interior. A mating pair of *Nicrophorus* insert themselves between the ground and the carcass and quickly excavate the dirt out from underneath the carcass in a radial fashion (Milne and Milne 1976). The carcass is engulfed by the dirt around it, usurping the carcass from ants. The beetle and the ant are separated by the carcass and do not interact directly. If the

beetle does expose itself to ants, the ants will attack and could potentially run off the beetle.

Other reason ants may have little effect on the sequestration of carcasses by *Nicrophorus* may be due to ant's intolerance to rainy conditions. Ants will have reduced recruitment while it is raining. Porter and Tschinkel (1987) found a 40% decrease in foraging behavior by fire ants, *Solenopsis invicta*. While *Nicrophorus* does not fly during inclement weather, if the beetle has already discovered a carcass it will continue the burial behavior unaffected by the weather (Merrick and Smith 2004). *Nicrophorus* will take this opportunity to bury the carcass unhindered by ant presence. While Scott et al. found that native ants of Florida have a significant effect on the reproductive success of *Nicrophorus* in that area. Native ants (*Formica rufa* and *Formica fusca*) of the southern Rocky Mountains in Gunnison National Forest, Colorado had no effect on the sequestration of carcasses by *Nicrophorus*. This further illustrates the distribution of *Nicrophorus* as a Northern hemispheric beetle or montane beetle. Less ant diversity and abundance in higher latitudes and elevations leads to more competitive success of *Nicrophorus spp.* interspecifically, while intraspecific/intrageneric competition continues to be of great influence.

While there was no significant effect of native ant presence on burial success, there are other aspects surrounding of ant, *Nicrophorus* relationships which are still not well understood. Other studies could use similar methods to investigate whether subterranean ants have an effect on brood failure of *Nicrophorus*, whether biparental care is an important factor to combating ant competition, or whether there exists

mutualism between *Nicrophorus* and ant species that remove fly eggs from carcasses, improving carcass quality.

Since this was a novel experiment, there was substantial trial and error in methods and materials. While ver.2 of the experiment was able to reduce noise from unforeseen variables, significant improvements could still be made. Instead of perforated mesh as a means of ant access, vertical slits cut around the edge of the can could provide unimpeded access for ants, potentially increasing recruitment by ants to natural levels. Slits on the sides of the can would also require cans not to be buried as deep, which would allow more room between the mesh and can, causing less disruption when censusing the ant density of the cans. While introduction of mesh screens reduced scavenging by vertebrates, it was not completely nullified. Coarser mesh could be used, with a stronger method of securing the mesh than a rubber band, such as a wire fixture.

Acknowledgements

I would like to thank Dr. Rosemary Smith for her guidance, advice and teaching; Ryan Baker, Savannah Troy, and Ryan Meyers for manual labor; National Science Foundation for funding, and Rocky Mountain Biological Laboratory for giving me the opportunity to explore the field of ecological field research.

Citation

Arce, A. N., P. R. Johnston, P. T. Smiseth, and D. E. Rozen. "Mechanisms and fitness effects of antibacterial defences in a carrion beetle." *Journal of evolutionary biology* 25, no. 5 (2012): 930-937.

Braack, L. E. O. "Community dynamics of carrion-attendant arthropods in tropical African woodland." *Oecologia* 72, no. 3 (1987): 402-409.

Barton, Philip S., Saul A. Cunningham, David B. Lindenmayer, and Adrian D. Manning. "The role of carrion in maintaining biodiversity and ecological processes in terrestrial ecosystems." *Oecologia* 171, no. 4 (2013): 761-772.

- Carter, David O., David Yellowlees, and Mark Tibbett. "Cadaver decomposition in terrestrial ecosystems." *Naturwissenschaften* 94, no. 1 (2007): 12-24.
- Carter, David O., David Yellowlees, and Mark Tibbett. "Temperature affects microbial decomposition of cadavers (*Rattus rattus*) in contrasting soils." *Applied Soil Ecology* 40, no. 1 (2008): 129-137.
- DeVault, Travis L., Olin E. Rhodes Jr, and John A. Shivik. "Scavenging by vertebrates: behavioral, ecological, and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems." *Oikos* 102, no. 2 (2003): 225-234.
- Fellers, Gary M., and Joan H. Fellers. "Scavenging rates of invertebrates in an eastern deciduous forest." *American midland naturalist* (1982): 389-392.
- Kusnezov, N. "Numbers of species of ants in faunae of different latitudes." *Evolution* 11, no. 3 (1957): 298-299.
- Merrick, Melissa J., and Rosemary J. Smith. "Temperature regulation in burying beetles (*Nicrophorus* spp.: Coleoptera: Silphidae): effects of body size, morphology and environmental temperature." *Journal of Experimental Biology* 207, no. 5 (2004): 723-733.
- Milne, Lorus J., and Margery Milne. "The social behavior of burying beetles." *Scientific American* 235, no. 2 (1976): 84-89.
- Müller, J. K., and A. K. Eggert. "Effects of carrion-independent pheromone emission by male burying beetles (Silphidae: Necrophorus)." *Ethology* 76, no. 4 (1987): 297-304.
- Otronen, Merja. "The effect of body size on the outcome of fights in burying beetles (*Nicrophorus*)." In *Annales Zoologici Fennici*, pp. 191-201. Finnish Academy of Sciences, Societas Scientiarum Fennica, Societas pro Fauna et Flora Fennica and Societas Biologica Fennica Vanamo, 1988.
- Parmenter, Robert R., and James A. MacMahon. "Carrion decomposition and nutrient cycling in a semiarid shrub-steppe ecosystem." *Ecological Monographs* 79, no. 4 (2009): 637-661.
- Scott, Michelle P., James FA Traniello, and Isabelle A. Fetherston. "Competition for prey between ants and burying beetles (*Nicrophorus* spp): differences between northern and southern temperate sites." *Psyche: A Journal of Entomology* 94, no. 3-4 (1987): 325-332.
- Smith, Rosemary J., and Bryce Heese. "Carcass selection in a high altitude population of the burying beetle, *Nicrophorus investigator* (Silphidae)." *The Southwestern Naturalist* (1995): 50-55.
- Swift, Michael John, Oliver W. Heal, and Jonathan Michael Anderson. *Decomposition in terrestrial ecosystems*. Vol. 5. Univ of California Press, 1979.
- Trumbo, Stephen T. "Reproductive success, phenology and biogeography of burying beetles (Silphidae, *Nicrophorus*)." *American Midland Naturalist*(1990): 1-11.

Tables and Figures

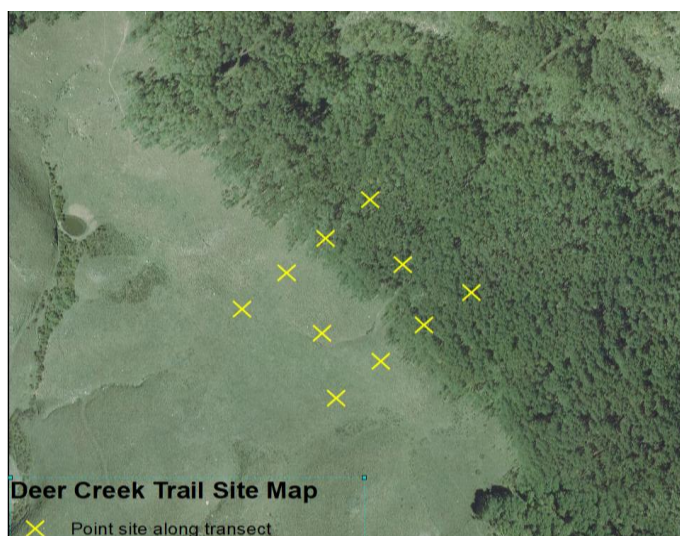


Figure 1. A map showing the transect points for the sites of carcass placement for determining which ant taxa utilize carcasses

Table 1. Carcass utilization by different ant taxa, in two vegetation types, in the southern Rocky Mountains, Gunnison National Forest, Colorado.

Aspen Understory	# of each taxa censused
<i>Camponotus herculeanus</i>	1
<i>Camponotus modoc</i>	4
<i>Formica rufa</i>	2
<i>Myrmica spp.</i>	1

Meadow	# of each taxa censused
<i>Tapinoma Sessile</i>	5
<i>Formica fusca</i>	42
<i>Formica rufa</i>	13
<i>Myrmica spp.</i>	32

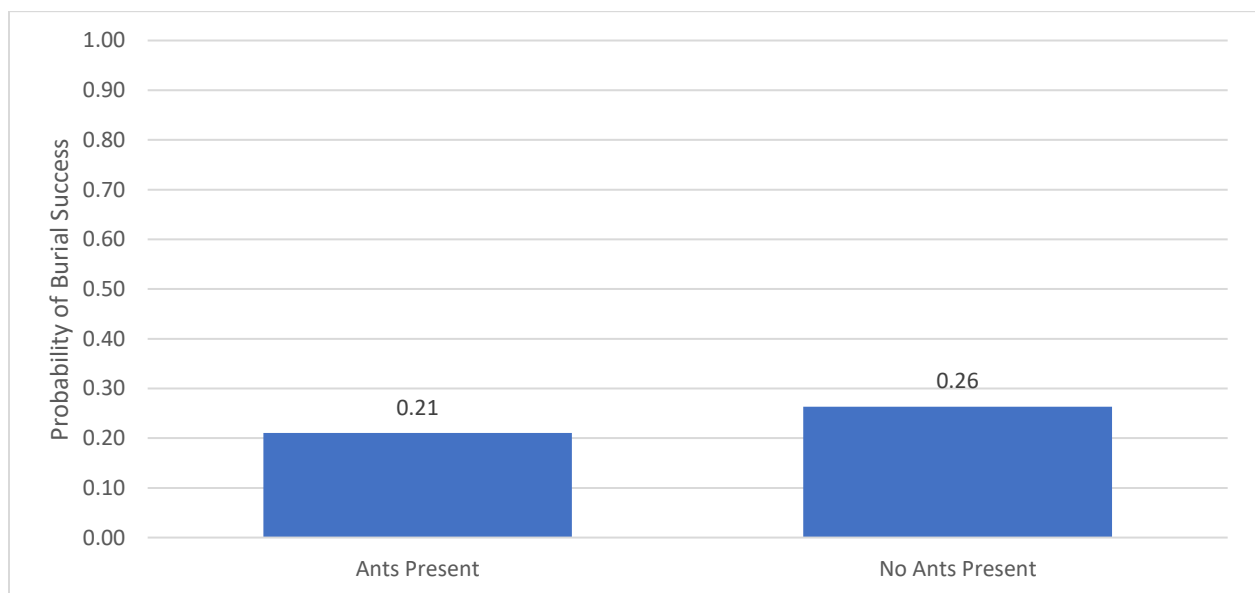


Figure 2. Probability of burial success by *Nicrophorus* based on presence of native ants- exp ver.1

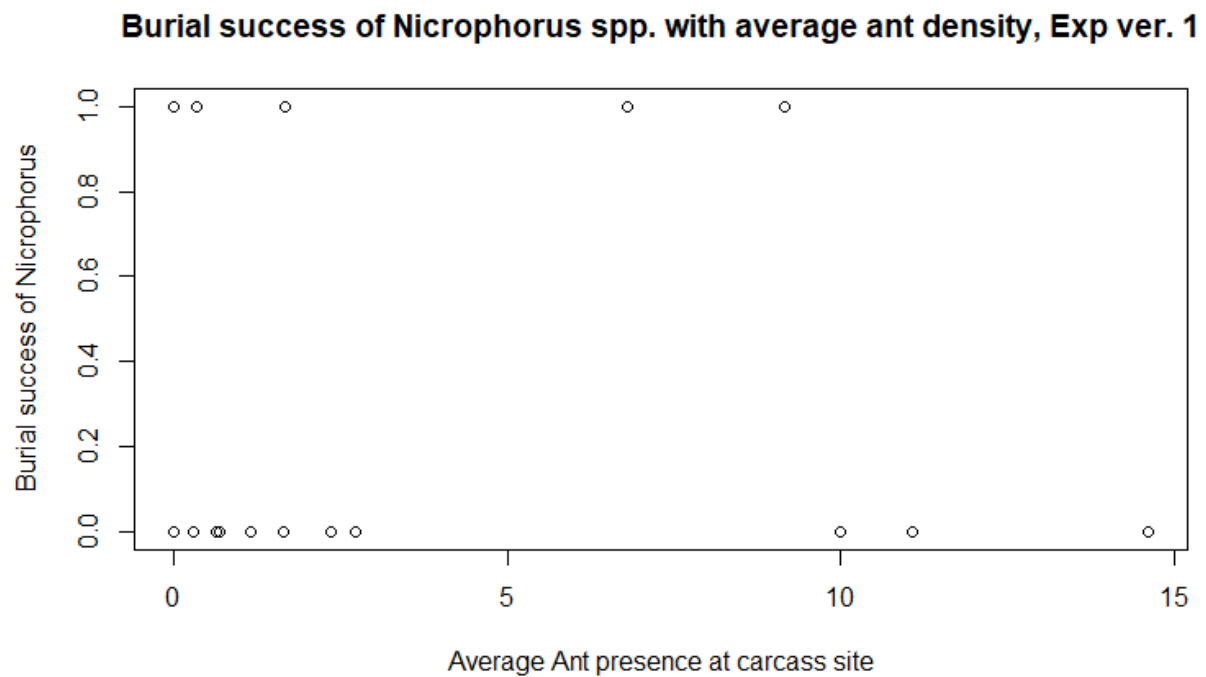


Figure 3. Logistic regression model of burial success of *Nicrophorus* spp. versus average ant density at carcass. 0=failure to bury, 1= successful burial. Effect of ant density on burial success by *Nicrophorus* spp. shown to be insignificant (P-value= 0.577).

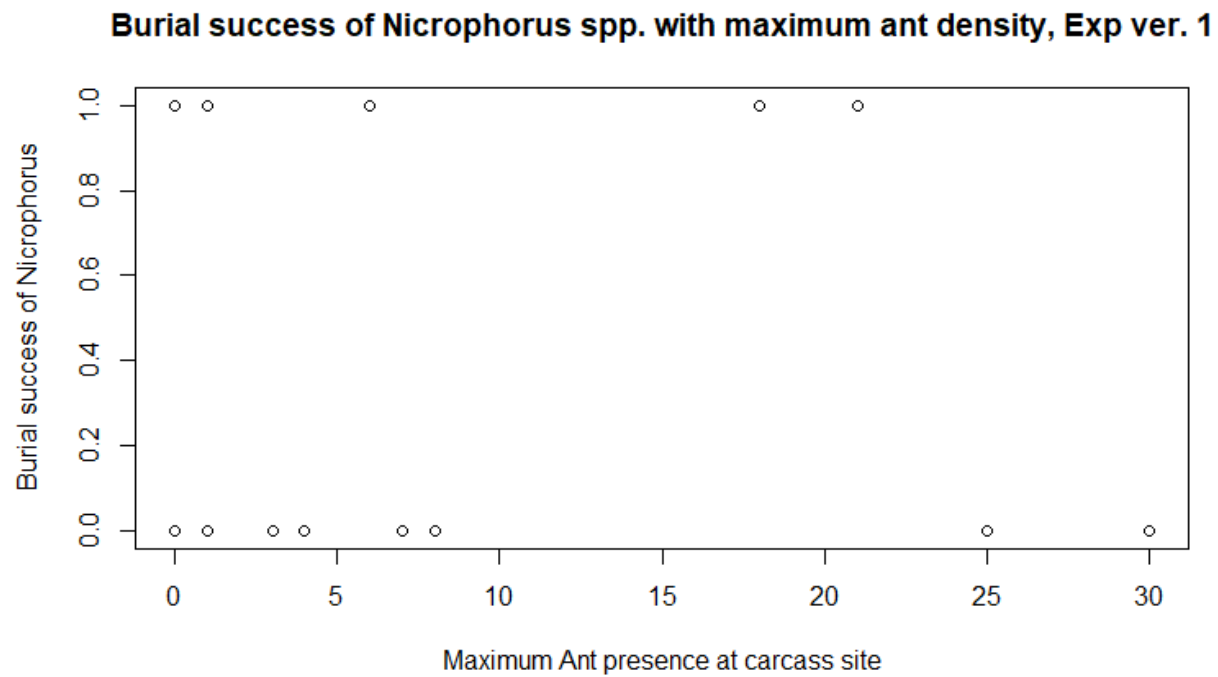


Figure 4. Logistic regression model of burial success of *Nicrophorus* spp. versus maximum ant density at carcass, using methods of exp. version 1. Binary response variables: 0=failure to bury, 1= successful burial. Effect of maximum ant density on burial success by *Nicrophorus* spp. shown to be insignificant (P-value= 0.486).

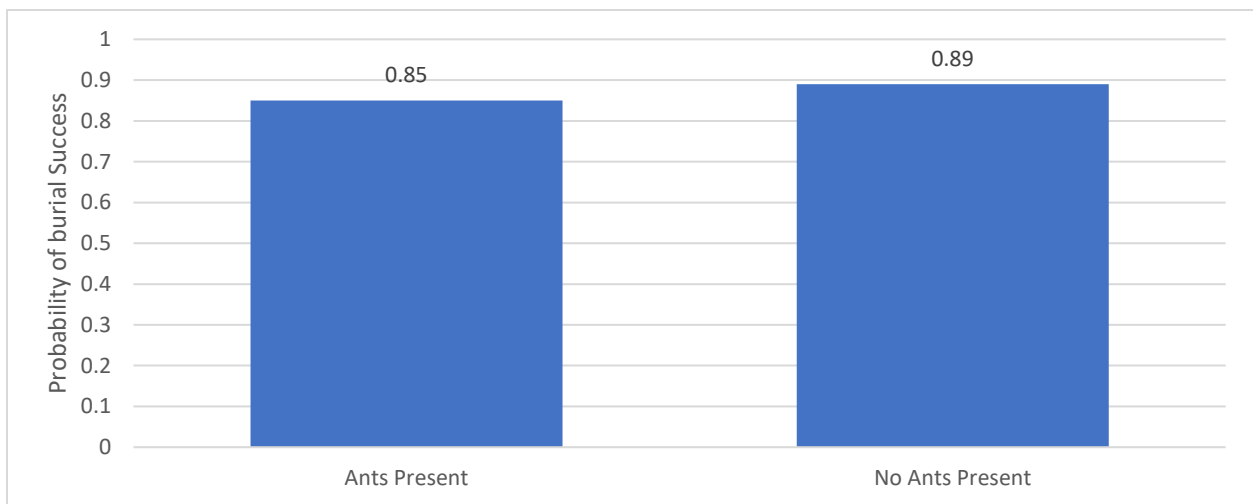


Figure 5. Probability of burial success by *Nicrophorus* based on presence of native ants- exp ver. 2

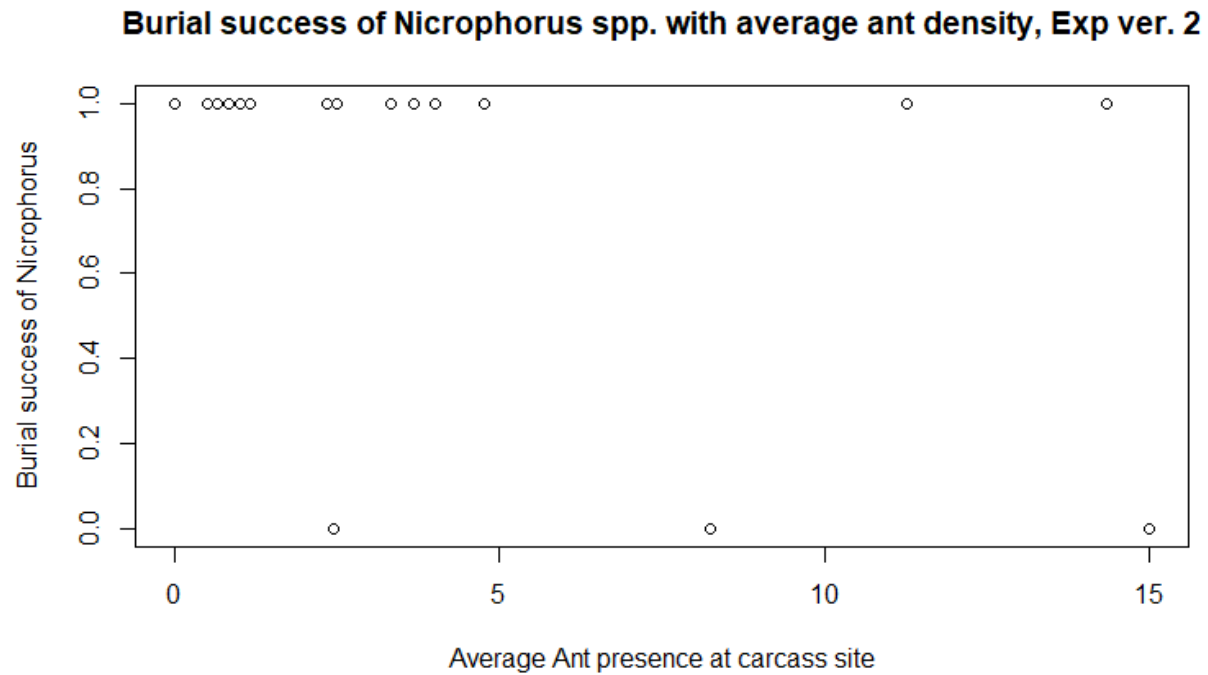


Figure 6. Logistic regression model of burial success of *Nicrophorus spp.* versus average ant density at carcass, using methods of exp. version 2. Binary response variables: 0=failure to bury, 1= successful burial. Effect of average ant density on burial success by *Nicrophorus spp.* shown to be insignificant (P-value= 0.09273).

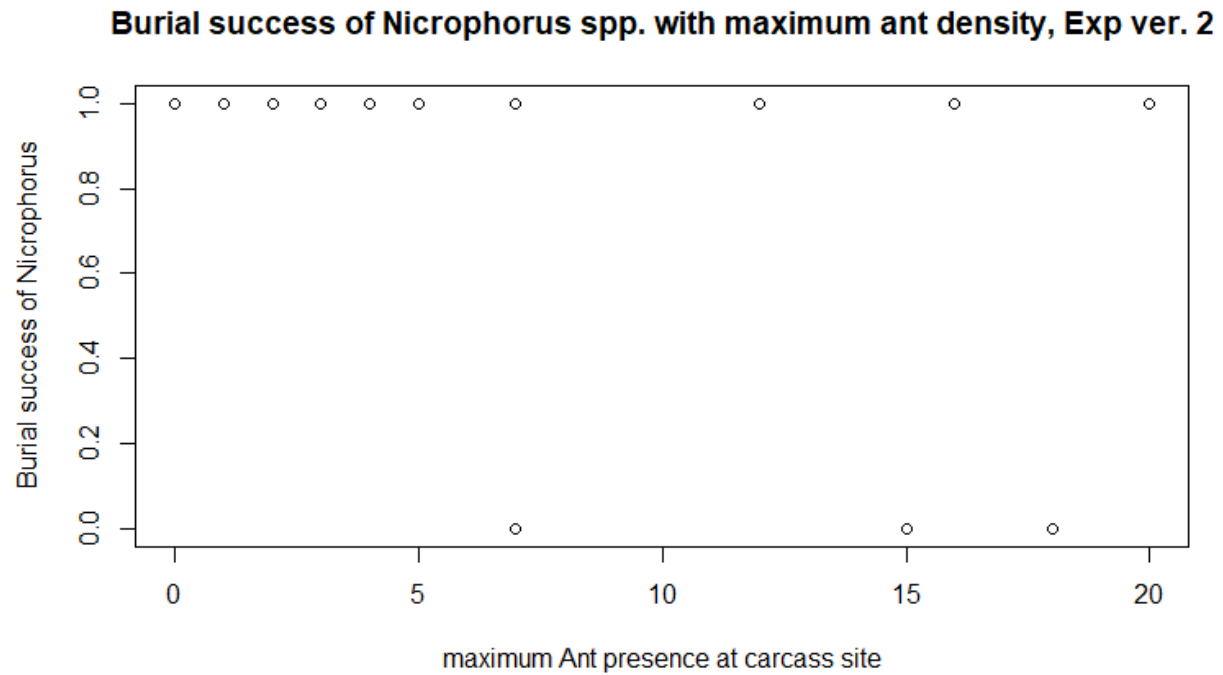


Figure 7. Logistic regression model of burial success of *Nicrophorus* spp. versus maximum ant density at carcass, using methods of exp. version 2. Binary response variables: 0=failure to bury, 1= successful burial. Effect of maximum ant density on burial success by *Nicrophorus* spp. shown to be insignificant (P-value= 0.0719).

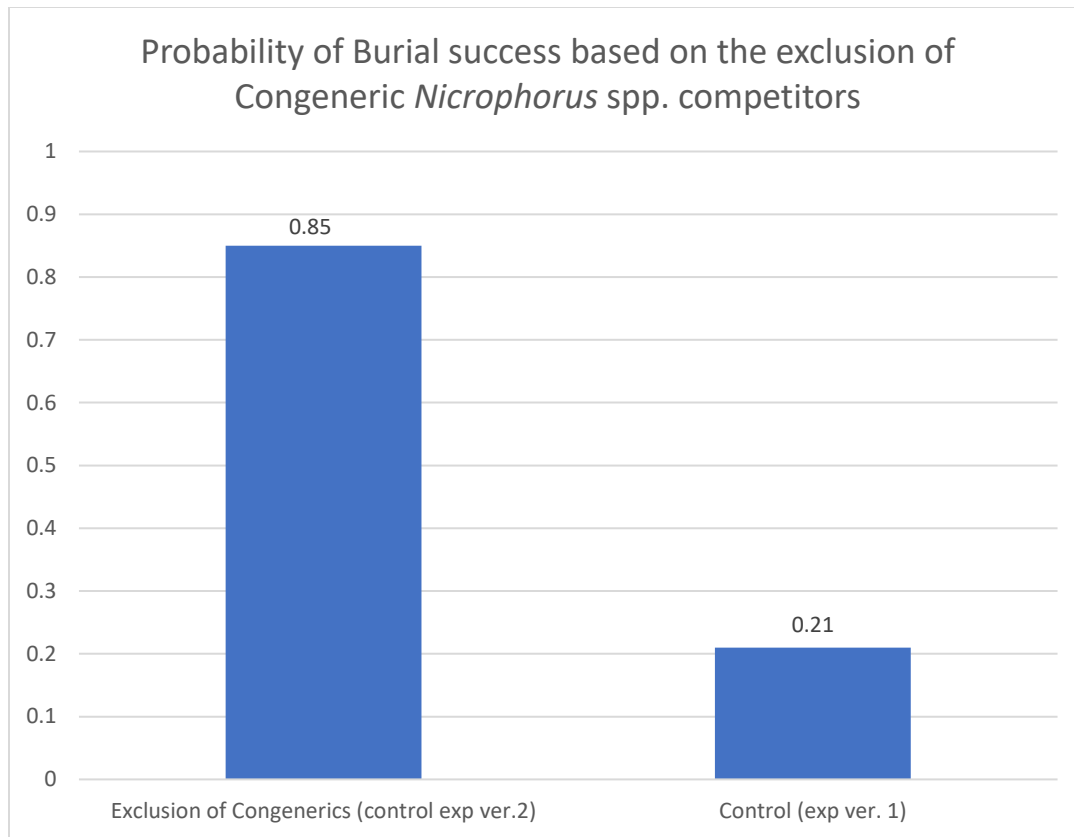


Figure 8. An informal comparison of the controls of experiment version 1 and version 2. Control of version 2 excluded congeneric competition between *Nicrophorus* spp. The difference in burial success when congeneric competitors are excluded illustrate this as an important factor to burial success in *Nicrophorus* spp.