Distribution of Carrion Beetles (Coleoptera: Silphidae) in Different Geographic Regions of Virginia

Shana Margaret Beirne

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Richard D. Fell

Douglas G. Pfeiffer

Donald E. Mullins

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ABSTRACT

The distribution of beetles in the Family Silphidae has not been well studied in Virginia. The primary purpose of this study was to survey silphid beetles in a more systematic manner across different geographic regions of the state, with a special consideration for *Nicrophorus* species. The seasonal abundance and diversity of silphid beetles in Montgomery County, Virginia, was also examined. Baited pitfall traps were used to sample beetle distribution and abundance, and were placed in each of the five geographical regions of Virginia in the summers of 2007 and 2008. Traps were placed approximately one kilometer apart and were checked daily over a five day period for each of three sampling periods. A total of 4375 silphid beetles, consisting of 11 species in four genera, were collected in ten counties with beetles in the subfamily Silphinae being predominant. Within the Nicrophorinae, *Nicrophorus tomentosus* and *N. orbicollis* were dominant in 2007; whereas in the summer of 2008, *N. tomentosus* and *N. pustulatus* were the most commonly collected. Contingency analyses indicated that species abundance was associated with sampling period and geographic region. *Nicrophorus americanus* was not collected during either summer of surveying and only three *N. carolinus* were trapped in Suffolk County in the summer of 2008. For the Montgomery County survey, a total of 3276 beetles were found between the middle of April and the middle of October. The prevalent species within Nicrophorinae was *Nicrophorus tomentosus* and within the Silphinae it was *Necrophila americana*. Species abundance was associated with sampling period.

DEDICATION

I would like to dedicate this thesis to my parents, Mimi and Ob, and Dad; my fiancé, Eric; Eric's mom, Gloria; and the Entomology Department. If it were not for my parents, I never would have had the drive to finish what I had started in life. They always stood behind me, rooting me on, pushing me when I was slacking off, and helping me (emotionally and financially) whenever I needed it most. Without their support, I would not be where I am today. I would not even be in grad school if it were not for my fiancé, Eric. He helped me realize that no matter what, I needed to follow my dreams and that I should pursue my passion for insects. Eric has been my rock to lean on when I stopped believing in myself, and helped financially whenever possible. Gloria, who has a heart of gold, graciously accepted me into her family and always understood when I was too busy to come see her. If it were not for the extra push and the kick in the pants from the Entomology Department when I needed it the most, this never would have been completed.

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Chapter 1. Introduction

Beetles in the family Silphidae (Coleoptera) are known by several common names, which include carrion beetles, sexton beetles, and burying beetles. According to Peck (2001), there are 15 genera and about 175 species worldwide, with eight genera and 30 species in North America north of Mexico. There are presently two subfamilies in the Silphidae: Nicrophorinae and Silphinae. The Nicrophorinae are best known as "burying beetles" or "sexton beetles" because they inter a carcass as food for themselves and for their larvae. Parental behavior is also well known in this subfamily; this type of subsocial behavior is a rarity in the Coleoptera. The Silphinae do not bury the carcass, they either feed on the carcass above ground, or consume fly larvae associated with carrion and also do not exhibit any type of parental behavior.

Studies on diversity, habitat preferences, and seasonality have been conducted in many states of the United States on silphid beetles (Washington - Hatch and Rueter, Jr. (1934), New Jersey - Shubeck et al. (1981), Mississippi - Lago and Miller (1983), Kansas - Lingafelter (1995) and Rintoul et al. (2005), Nebraska - Ratcliffe (1996), Georgia - Uiyshen and Hanula (2004), Wisconsin - Katovich et al. (2005), and Ohio - Shea (2005)). Lingafelter (1995) and Katovich et al. (2005) found that silphid beetles tended to be generalists and do not prefer a specific terrestrial ecoregion. Some were found in open habitats and others in wooded areas. However, Ratcliffe (1995) noticed that traps placed in dense woods attracted fewer beetles.

Surveys for *Nicrophorus americanus* (Olivier) (the American burying beetle) have been conducted in various states as well, including (Nebraska - Ratcliffe (1992), Bedick et al. (1999), and Bedick et al. (2004); Oklahoma - Creighton et al. (1993) and Lomolino et al. (1995); Arkansas - Lomolino et al. (1995) and Carlton and Rothwein (1998); South Dakota - Backlund (1997); Massachusetts - Amaral et al. (1997) and Mckenna-Foster et al. (2005); Rhode Island -

Kozol et al. (1988) and Raithel et al. (2006); and Missouri - Barnhart et al. (2002)). This beetle is currently found in only nine states: Rhode Island, Oklahoma, Nebraska, Arkansas, South Dakota, Kansas, and Texas, where the beetle was discovered in surveys; and Ohio and Massachusetts where the beetle has been reintroduced. Very little research has been conducted on the distribution of silphid beetles in Virginia with very little effort directed to determining the presence or absence of the American burying beetle.

In order to gain a better understanding of the distribution of silphid beetles in Virginia, research was conducted for two summers (2007 and 2008) on silphid beetle distribution within the state. Two counties in each of the five geographic regions were surveyed: the Appalachian Plateau, the Valley and Ridge, the Blue Ridge Mountains, the Piedmont, and the Coastal Plain. Beetle populations were sampled through the use of baited pitfall traps. Traps were placed in open habitats as well as the forest's edge to exploit the habitat generalist. Traps were also placed in one area of Montgomery County and surveyed during the summer of 2008 to gain a better understanding of the variability of silphid beetle activity throughout the season.

Chapter 2. Coleoptera: Silphidae

Chapter 2.1 Background

There have been a number of studies on beetles in the Family Silphidae found in different areas of the world, but the major focus here will be on studies within North America. Some of the earliest studies were conducted by Blatchley (1910), Selous (1911), Jacques (1915), Fabre (1919), and Balduf (1935). Blatchley (1910) produced keys to carrion beetles of Indiana with extensive information on each species. Selous (1911) recounted his observations of various species of carrion beetles feeding on food sources which he witnessed for a few days in June. Jacques (1915) studied beetles that fed on dead fish in Cedar Point, OH. Fabre (1919) studied the behavior of burying beetles with regard to their burying rituals, and Balduf (1935) constructed an extensive life history of the Silphidae. Hatch (1927) extensively reported on species in the subfamily Silphinae in North America; including descriptions of the larvae, and also assembled an extensive key for the Silphidae with descriptions of each species. Headstrom (1977) compiled a small list of the carrion beetles in the United States, but only gave a description of each species with a general area of location. The most current key for the Silphidae, as well as most geographically comprehensive, has been provided by Anderson and Peck (1985). They not only described the carrion beetles of Canada and Alaska, but also provide a map where each species can be found in the United States.

Silphid beetles are very common throughout most, if not all, of North America and Canada. For example, Hatch and Rueter, Jr. (1934) listed the Silphidae of Washington, and provided a taxonomic key for identification. Shubeck et al. (1981) studied beetle species which were attracted to carrion in the Great Swamp National Wildlife Refuge, New Jersey; a study which included silphid species. Lago and Miller (1983) compiled records of silphids in

Mississippi, including the discovery of seven new species in the state. Studies of the Silphidae were also made in Kansas by Lingafelter (1995) and Rintoul et al. (2005). Lingafelter included information on habitat preference, as well as seasonality; while Rintoul et al. studied the diversity of silphids on the Konza Prairie Biological Station. In addition, Lingafelter gave an extensive description of Kansas' "physiography". Ratcliffe (1996) described the carrion beetles of Nebraska, giving descriptions on each subfamily, as well as each species. He described the ecosystems of Nebraska and the collection of the different silphid species. Seasonality and species of silphids were studied in northeastern Georgia by Uiyshen and Hanula (2004). Katovich et al. (2005) produced the first comprehensive survey of carrion beetles in Wisconsin; giving thorough family descriptions, collection locations, types of habitat, the carrion on which species were collected, and the type of trap utilized. Shea (2005) surveyed Cuyahoga County, Ohio, where he compared his findings from disturbed and undisturbed areas to determine relative carrion beetle abundance.

There are few references to the Silphidae of Virginia. Anderson and Peck (1985), listed silphid species found in Virginia; also the Entomology Insect Collection at Virginia Tech, the Natural History Museum in Martinsville, Virginia, and the Smithsonian Museum of Natural History hold specimens of the Silphidae collected in Virginia. Table 1 lists the species identified by Anderson and Peck and gives the number of species in each museum collection.

Table 1. Silphid beetle species listed as found in Virginia (Anderson and Peck 1985) or collected in Virginia. The table shows the number of specimens of each species in Virginia in the Virginia Tech Collection, the collection at the Virginia Natural History Museum in Martinsville, Virginia, and the collections at the Smithsonian Museum of Natural History, Washington, D.C.

Genus species	**Anderson/Peck**[1]	**# VT collection**	**# VA NHM**	**# Smithsonian**
Nicrophorus				
N. marginatus	+	1	18	15
N. tomentosus	+	32	132	42
N. orbicollis	+	10	307	133
N. sayi	+	4	45	5
N. defodiens	+	0	59	1
N. pustulatus	+	8	66	33
N. carolinus	+	0	1	0
N. americanus	+	1	1	12
N. spp.	-	47	2	0
Silpha[2]				
Silpha spp.	-	20	0	0
Necrodes				
N. surinamensis	+	31	40	27
Necrophila				
N. americana	+	26	81	41
Oiceoptoma				
O. inaequale	+	0	38	23
O. noveboracense	+	94	45	33

[1] Anderson and Peck (1985)
[2] This name was taken directly from the label. According to Anderson and Peck (1985), Silpha has been divided into numerous genera and is not used as a genus in North America.

Chapter 2.2 Evolution, Phylogeny, and Current Classification

Grimaldi and Engel (2005) stated that the oldest stem-group coleopteroid is from the Early Permian (280 Million Years Ago (mya)), but that true Coleoptera did not appear until the Triassic (230 mya). They further explained that the major diversity of Coleoptera appeared to have been achieved by the Late Jurassic (155 – 160 mya). Peck and Kaulbars (1987) confirmed that the Paleozoic record of beetle fossils was poor.

According to Grimaldi and Engel (2005), the earliest obvious relatives of beetles were cupedoids from the Early Permian (270 mya) of Chekarda in the Ural Mountains and the Czech Republic. These early "beetles" were extremely primitive and possessed few characteristics of true Coleoptera, and therefore were regarded as Protocoleoptera (Grimaldi and Engel, 2005).

They noted that five other families of very basal, cupedoid-like insects appeared in the Late Permian (260 – 255 mya) and were classified as Archecoleoptera. They also indicated that as the Permian ended, archecoleopterans became more common; one family persisted into the Triassic (250 mya), and another family even occurred until the Jurassic (200 mya).

By the Late Triassic (240 – 220 mya), beetles became more common, representing approximately 20% of the individual insects from insect deposits (Grimaldi and Engel, 2005). Triassic polyphagans included Staphylinidae. Grimaldi and Engel further stated that beetle diversity mushroomed in the Jurassic (200 mya), but was regionally biased to Europe and central Asia. According to Peck and Kaulbars (1987), there are no records of the Silphidae in Mesozoic fossils, but a beetle in the related Family Agyrtidae, *Mesecanus* (= *Mesagyrtes*) *communis* (Ponomarenko), was found near Novospassk, USSR in Jurassic deposits. Peck and Kaulbars assumed that the Silphidae probably arose in the early Mesozoic period, possibly in what would become the north temperate zone. Some lineages may have spread to the southern parts of

Pangea before the area separated from Laurasia as Gondwanaland. By the Late Jurassic (150 mya), Grimaldi and Engel (2005) noted that there was a dramatic diversification of terrestrial beetles. However, in the Early Cretaceous (140 mya) the beetles were more similar to ones from the Jurassic (200 mya) than to the beetles of the Late Cretaceous (100 - 70 mya), a change which was probably related to angiosperm radiation (Grimaldi and Engel, 2005). By the Late Cretaceous, an abundance of beetle species fed on angiosperms, a factor which contributed immensely to the beetle diversity of today (Grimaldi and Engel, 2005).

According to Peck and Kaulbars (1987), the only New World endemic genera of Silphidae are *Oxelytrum* and *Heterosilpha*. The *Oxelytrum* probably arose from an ancestor from the south temperate zone (Gondwanaland) and diversified when South America was isolated. Peck and Kaulbars noted that in this genus, only one species, *O. disciolle*, spread out of South America into Central America, Mexico, and south Texas sometime in the late Tertiary and/or Pleistocene. *Heterosilpha* may have originated from an unknown silphine ancestor in North America in the Mesozoic or Tertiary. These authors also noted that all other Nearctic genera of Silphidae also occur in at least the Palearctic or Oriental regions. Because the centers of diversity of all these genera are in the Old World, Peck and Kaulbars (1987) assumed that they arose there. It is likely that the Eurasian ancestral stocks of *Aclypea, Necrodes, Necrophila, Oiceoptoma,* and *Thanatophilus* crossed into North America at least once in Mesozoic or Tertiary via emergent lands in what is now the Bering Straits. Peck and Kaulbars also noted that the two silphine species common to Eurasia and North America (*Thanatophilus lapponicus* and *Aclypea opaca*) probably maintained gene flow across the Bering Bridge at times of low sea levels in the Pleistocene.

According to Peck and Kaulbars (1987), the genus *Nicrophorus* probably originated in the Old World. Reconstructed phylogenies for *Nicrophorus* spp. in the New World have been tentatively proposed and have placed into four species groups: the *orbicollis*, *defodiens*, *investigator* and *marginatus* groups.

The reconstructed phylogenies suggest that one species in the *orbicollis* group remained in northeastern North America and five other species evolved in Mexico, and Central and South America. *N. vespilloides* Herbst in the *defodiens* group is Holarctic and two species are Nearctic. Peck and Kaulbars (1987) also stated that in the *investigator* group, *N. investigator* Zetterstedt is Holarctic and four species are Nearctic or in Central America. In the *marginatus* group, four species are Nearctic. These findings led Peck and Kaulbars to conclude that there was at least one ancestral entry into the Nearctic in each of the *orbicollis*, *defodiens*, *investigator*, and *marginatus* groups and probably also for *N. americanus* and *N. pustulatus* Herschel. The two *Nicrophorus* species common to North America and Eurasia (*N. vespilloides*, and *N. investigator*) probably maintained gene flow across the Bering Bridge at times of low sea levels in Pleistocene time (Peck and Kaulbars, 1987).

Peck (2001) stated that two species of Silphidae have been introduced into the Nearctic from the Palearctic. *Dendroxena quadrimaculata* (Scopoli) was introduced intentionally into the northeastern United States for the control of gypsy moth (*Lymantria dispar*) larvae, but did not become established. The other species, *Silpha tristis* (Illiger), a scavenger on dead insects, was apparently accidentally introduced into southern California, and near Montreal, Quebec. This species seems to be established (Peck, 2001).

The Tree of Life web project (Anonymous 1) provides an extensive phylogenetic list of insects, including the beetles in the Family Silphidae found in North America. The Family

Silphidae are in the Order Coleoptera, Suborder Polyphaga, and Superfamily Staphylinoidea. The family is divided into two Subfamilies: Nicrophorinae and Silphinae. The Nicrophorinae contain one Genus *Nicrophorus*. The Silphinae contain 12 genera *Aclypea, Dendoxena, Diamesus, Heterosilpha, Heterotemna, Necrodes, Necrophila, Oiceoptoma, Oxelytrum, Ptomaphila, Silpha,* and *Thanatophilus*. The Tree of Life web project (Anonymous 1) also gives a detailed description on how to differentiate between the two subfamilies, Silphinae and Nicrophorinae. The antennae of both Silphinae and Nicrophorinae are 11 segmented, but nicrophorines have a greatly reduced pedicel that is fused to the scape making them appear to have a ten segmented antenna. Silphines lack a frontoclypeal (epistomal) suture. The larvae differ between the subfamilies as well with silphine larvae bearing a cluster of six stemmata on each side of the head, whereas nicrophorine larvae bear only a single stemma on each side.

The Nearctic species and genera (Tree of Life web project (Anonymous 1), Peck (2001), Peck and Kaulbars (1987), and Anderson and Peck (1985)) are shown in Table 2.

Peck (2001) stated that the Family Silphidae has historically included other taxa currently not regarded as silphids. Most notable among these are members of the Family Agyrtidae. Although still described by some specialists as silphids, they are no longer considered as closely related. The Silphidae are now restricted to the larger carrion and burying beetles. Several of the subfamilies or tribes were removed from the Silphidae and placed in either the Agyrtidae, the Leiodidae (e.g., Leptodirini and Estadiini), or Staphylinidae (e.g., Apateticinae, Trigonurinae, Microsilphinae). Following this reclassification, the silphids can be considered monophyletic and most closely allied to the Staphylinidae.

Table 2. Genera and species of the subfamilies of the Silphidae found in North America. (Tree of Life web project (Anonymous 1), Peck (2001), Peck and Kaulbars (1987), and Anderson and Peck (1985))

SUBFAMILY	GENUS	SPECIES
Nicrophorinae Kirby, 1837		
	Nicrophorus Fabricius	*N. americanus* Olivier
		N. carolinus (Linnaeus)
		N. defodiens Mannerheim
		N. guttula Motschulsky
		N. hybridus Hatch & Angell
		N. investigator Zetterstedt
		N. marginatus Fabricius
		N. mexicanus Matthews
		N. nigrita Mannerheim
		N. obscures Kirby
		N. orbicollis Say
		N. pustulatus Herschel
		N. sayi Laporte
		N. tomentosus Weber
		N. vespilloides Herbst
SUBFAMILY	**GENUS**	**SPECIES**
Silphinae Latreille, 1807		
	Aclypea Reitter	*A. bituberosa* (LeConte)
		A. opaca (Linnaeus)
	Heterosilpha Portevin	*H. aenescens* (Casey)
		H. ramosa (Say)
	Necrodes Leach	*N. surinamensis* (Fabricius)
	Necrophila Kirby & Spence	*N. americana* (Linnaeus)
	Oiceoptoma Leach	*O. inaequale* (Fabricius)
		O. noveboracense (Forster)
		O. rugulosum Portevin
	Oxelytrum Gistel	*O. discicolle* (Brulle)
	Thanatophilus Leach	*T. truncatus* (Say)
		T. lapponicus (Herbst)
		T. coloradensis (Wickham)
		T. sagax (Mannerheim)
		T. trituberculatus (Kirby)

Chapter 2.3 Life History

2.3.1 Behavior and Feeding

The life history of burying beetles in the genus *Nicrophorus* has been described by several researchers because they exhibit unique parental behavior (Fabre (1919), Milne and Milne (1944; 1976), Ratcliffe (1996), and Scott (1996; 1998)). A recent review by Scott (1998) focused on the biparental care and communal breeding. In general, the life cycle begins as adult beetles search out fresh carcasses to use for rearing young. Adult beetles find a carcass using odors detected by antennal receptors. After discovery the beetle must first determine if the animal is of acceptable size. In order to do this the beetle crawls underneath the carcass on its back and lifts the body with its legs. If the weight is acceptable, the beetle proceeds to examine the soil around the carcass, checking for soil softness. Moving the carcass can be done by a single beetle (which obviously takes more time), or it can be done with a partner of the opposite sex. The carcass needs to be buried quickly to ensure there are no competitors. Mating is usually delayed until after the carcass is buried. An adult beetle moves a carcass while underneath with its legs like a conveyor belt. If alone, the beetle has to move the carcass some distance and then leave to go loosen soil. If paired, one moves the carcass, while the other loosens the soil at the preferred site. When this is done in pairs they are able to take turns, and the work progresses more rapidly. After burying the carcass, the beetles mate. Occasionally the male will leave after mating, but he usually stays. Anderson and Peck (1985) reported that usually only one pair of adult beetles is associated with a carcass. More than one pair or even more than one species may be present initially. However, if more than one pair is present, fighting ensues until only one pair remains. This fighting usually takes place after the food source has been buried, and the beetles have emerged from underground.

Once the carcass has been buried, the food source is then prepared by working the carrion into a ball, and removing the fur or feathers. Anal and oral secretions are spread over the body to hinder decomposition. The soil around the carcass is packed down and a small chamber is made by the female above the carcass in which to lay eggs. A conical depression is made in the prepared carcass beneath the egg chamber where regurgitated droplets of food are stored for the larvae. When the larvae hatch, they drop down onto the carcass. The adult female beetle stridulates to call the larvae to the prepared food where the adult transfers fluid from the pool to the larvae. Feeding duties may be shared by both parents. The parents continue to care for the larvae until they are ready to pupate, possibly going as far as preparing a pupal chamber for the mature larvae. When the larvae begin to pupate, the adults leave the nest chamber and seek out another carcass. (Milne and Milne 1976)

2.3.2 Development

Anderson and Peck (1985) noted that for *Nicrophorus* there are three larval instars and that complete development requires 20 – 31 days. The first instar completes development in about 12 hours, the second in about 24 hours, and the third from five to 15 days, depending on the species and conditions. The pupal stage lasts from 13 to 15 days. Anderson and Peck (1985) also summarized the less complex life cycle of the Silphinae. Adult beetles, upon finding a dead animal, will mate. The females then oviposit in soil around the carcass. Within two to seven days the larvae hatch, move to the carcass, and feed. There are three larval instars, the first requiring from three to seven days to complete development and the second and third requiring from three to 10 days. Pupation takes place in the soil and appears to last 14 to 21 days. Unlike *Nicrophorus*, these beetles appear to avoid competition with fly larvae at the carcass by waiting until the fly larvae have finished feeding. The beetle eggs hatch when the fly larvae are moving from the carcass to the soil in order to pupate. Larval development in the Silphinae is much slower than in *Nicrophorus*. Silphine adults are also occasionally found at dung and garbage, but it is unusual for them to breed there. *Nicrophorus* adults have also been observed feeding on dung or decaying fungi (Anderson and Peck 1985).

2.3.3 Feeding Preferences

Hatch (1957) noted that some species of *Silpha* have specialized on snails (subgenera *Ablattaria* and *Phosphuga*) and caterpillars (subgenus *Xylodrepa*), and that others are phytophagous, feeding on beets, spinach, and allied plants. Headstrom (1977) indicated that only a few species of carrion beetles, when pressed by hunger, become predaceous and attack living snails or other insects. A few species even occur in the nests of ants. Peck (2001) also noted that some silphid species are phytophagous and may be garden pests (*Aclypea*) and that others are predators of caterpillars or snails (*Dendroxena* in Europe). Ratcliffe (1996) indicated that a few silphids are found on dung or fungi, are phytophagous, or prey on fly larvae.

Chapter 2.4 American Burying Beetle

2.4.1 Historical and Current Range of *Nicrophorus americanus* Olivier

According to U.S. Fish and Wildlife (1991), Ratcliffe (1996), and Sikes and Raithel (2002), the American burying beetle (*Nicrophorus americanus* Olivier) was found throughout more than half of the United States from the east coast to the Midwest until the 1920's, and unfortunately this beetle species has declined tremendously, almost to extinction (Figure 1). The status of the American burying beetle was reviewed by U.S. Fish and Wildlife (1991) and Sikes and Raithel (2002). There are only nine known states where this beetle currently survives: Rhode Island, Oklahoma, Nebraska, Arkansas, South Dakota, Kansas, and Texas, where the beetle was discovered in surveys; Ohio (Ohio Department of Natural Resources, Anonymous 2) and Massachusetts (Roger Williams Park Zoo, Anonymous 3), where the beetle is continually trying to be reintroduced. The U.S. Fish and Wildlife Service (1991) stated in their Recovery Plan that there are several possible reasons for the decline of the American burying beetle. These included the extensive use of DDT in the 1950's and 60's, the introduction of a non-native, species-specific pathogen, the loss of suitable habitat, the decline of preferred food sources, and finally competition (since *N. americanus* is the largest of all the carrion beetles). The roll of DDT was dismissed because there had already been a massive decline in beetle populations before DDT was introduced. There was also no evidence for a new pathogen. U.S. Fish and Wildlife (1991) and Sikes and Raithel (2002) also stated that the loss of suitable habitat and acceptable food sources provided the most widely accepted reasons for the massive decline of this species. Since the American burying beetle requires carrion in a size range of 50 and 150 grams, passenger pigeons and the greater prairie chicken provided optimal size carcasses. Passenger pigeons numbered in the billions at the time, but unfortunately, both of these birds were eliminated by the middle of the 19th century. The wild turkey, various waterfowl, and shorebirds also provided acceptable weight carcasses, but apparently also suffered population declines in many areas. Limitations in available carcasses could also have increased interspecific competition between *N. americanus* and *N. orbicollis* Say. The two species are of similar size but *N. orbicollis* is more common. Lastly, competition with vertebrate scavengers has been stated as a possibility. Habitat fragmentation increases edge habitat, and could increase the contact of raccoons, foxes, opossums, and skunks with the beetles and newly discovered carcasses.

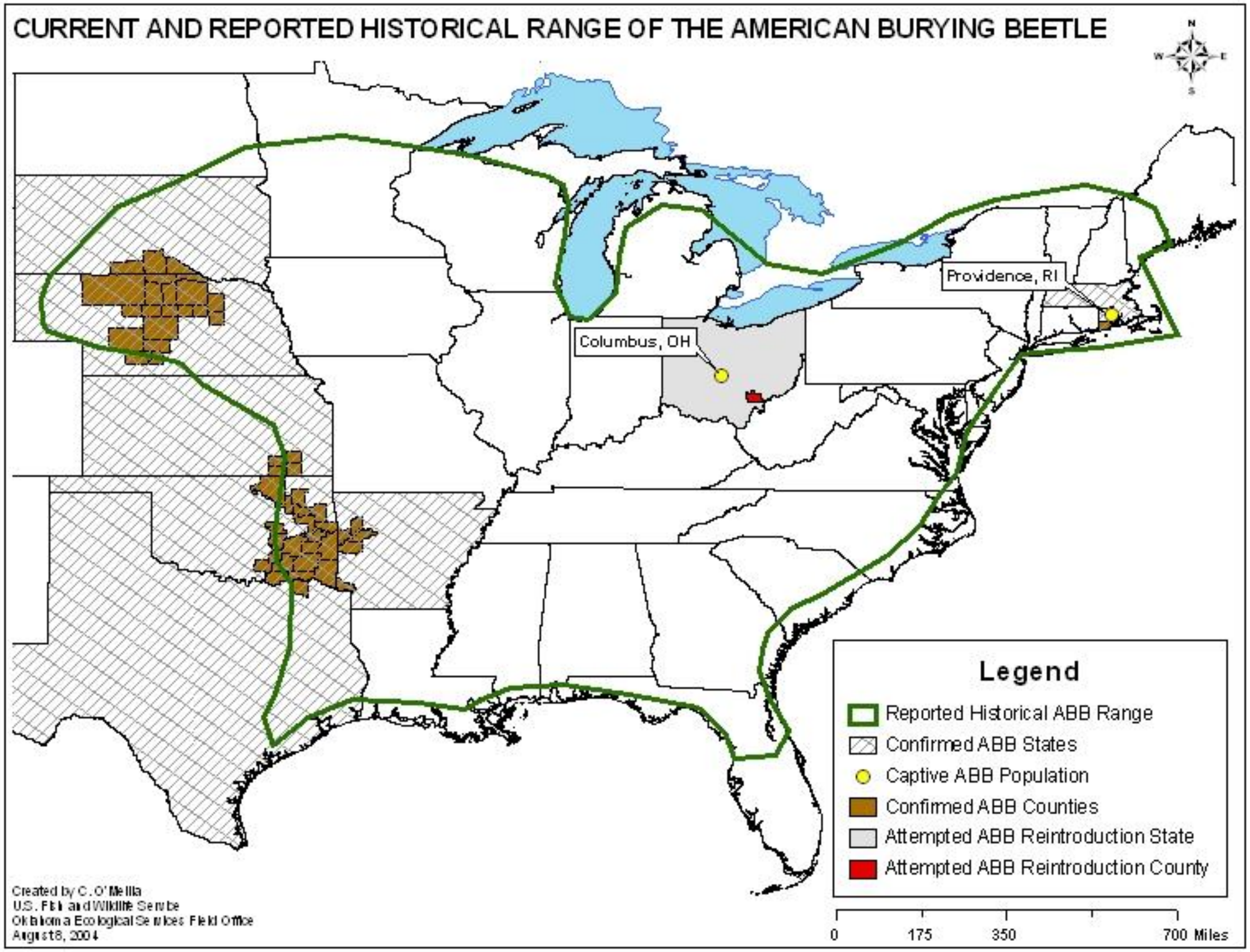


Figure 1. Current and reported historical range of the American burying beetle. (Map - US Fish and Wildlife Service, Oklahoma Ecological Services Field Office, August 8, 2004) (http://eol.org/pages/1044544/details)

2.4.2 American Burying Beetle Surveys

Sampling for the American burying beetle has been conducted by several researchers. Ratcliffe (1992), Bedick et al. (1999), and Bedick et al. (2004) researched the distribution and ecology of *N. americanus* in Nebraska, as well as implementing a new sampling protocol. Creighton et al. (1993) studied habitat preference of the American burying beetle in Oklahoma, and Lomolino et al. (1995) conducted field studies in Oklahoma and Arkansas to determine American burying beetle habitat preference. Backlund (1997) discussed new records of *N. americanus* in South Dakota, and Amaral et al. (1997) reviewed the reintroduction of the American burying beetle on Penikese Island, MA. Creighton et al. (1998) conducted a mark-recapture study to evaluate short-term movements of *N. americanus*, which would aid in devising plans for establishing new populations. Carlton and Rothwein (1998) researched the edge of the American burying beetle's range in Arkansas, and Kozol et al. (1988) studied the population of *N. americanus* on Block Island, RI. Barnhart et al. (2002) surveyed for American burying beetles in southwest Missouri. A survey and reintroduction of the American burying beetle in Nantucket, MA was conducted by Mckenna-Foster et al. (2005), and Raithel et al. (2006) studied the population trends and flight behavior of *N. americanus* on Block Island, RI.

The last dated American burying beetle collected in Virginia is located in the Virginia Tech collections, and was found in Blacksburg in August 1955.

Chapter 3. Survey of Silphid Beetles in Virginia, with Special Consideration for *Nicrophorus* Species.

Chapter 3.1 Introduction

Silphids are scavenger beetles that feed on small carrion. Within the Family Silphidae are the subfamilies Nicrophorinae and Silphinae. The Nicrophorinae, also known as carrion, burying, or sexton beetles, inter a carcass into loosened soil where a mated pair constructs a nest and cares for the young. Silphinae do not inter carcasses, lay their eggs next to the carrion, and do not exhibit any parental behavior.

Blatchley (1910) produced keys to carrion beetles of Indiana with extensive information on each species. Hatch (1927) discussed species in the subfamily Silphinae in North America, and provided descriptions of the larvae. Headstrom (1977) compiled a small list of the carrion beetles in the United States, but only gave a description of each species with a general area of location. Hatch (1957) assembled an extensive key for Silphidae with descriptions on each species. The most current and geographically comprehensive key for the Silphidae was published by Anderson and Peck (1985). They not only described the carrion beetles of Canada and Alaska, but also provided a small map where each species could be found in the United States.

Silphid beetles are very common throughout most, if not all, of North America and Canada. Ratcliffe (1996), for example, described the carrion beetles of Nebraska, giving descriptions on each subfamily, as well as each species. He described the ecosystems of Nebraska and the collection of the different silphid species. Shea (2005) surveyed in Cuyahoga County, Ohio, where he compared his findings from disturbed and undisturbed areas to determine relative beetle abundance. Lago and Miller (1983) compiled records of silphids in Mississippi, including the discovery of seven new species in the state. Shubeck et al. (1981)

studied carrion beetle species (including silphids) in the Great Swamp National Wildlife Refuge, New Jersey. Studies of the Silphidae were also made in Kansas by Lingafelter (1995), providing information on species habitat preference, as well as seasonality. He gave an extensive description of Kansas' "physiography" as well. Seasonality of silphids' species diversity was also studied in northeastern Georgia by Uiyshen and Hanula (2004). Katovich et al. (2005) produced the first comprehensive survey of carrion beetles in Wisconsin; giving thorough family descriptions, collection locations, types of habitat, the carrion on which species were collected, and the types of traps utilized for collection. Scott (1998) detailed the social behavior, especially the unique parental behavior.

Silphid beetles have, historically, been common in Virginia, but very little has been published on the silphid beetles of Virginia. A list of silphid species collected in Virginia is presented in Table 1 (Chapter 2). The list was compiled from specimens in the Virginia Tech, Virginia Museum of Natural History, and Smithsonian collections and contains genera and species number, including the species *Nicrophorus americanus*, thought to be extinct in Virginia.

Methods of surveying for silphids vary. Ratcliffe (1996) in Nebraska listed "baited pitfall traps, light traps, whole animal bait stations, and examination of road-killed animals" as collecting techniques. He used a 19 liter bucket for his pitfall traps. Comings (personal communication) used both 19 liter buckets in Rhode Island when surveying for the American burying beetle, and one-liter, wide-mouth jars for small traps set a few feet apart. Chicken, purchased in a local store was used as bait. Shea (2005) used two types of bait and different types of traps. The first trapping set-up used decayed pig carcasses placed either in dog cages, or a locked trailer. Mason jars containing anti-freeze were placed under the pigs in the dog cages and plastic trays under the carcass in the trailer. The second set-up used thawed chicks placed in mason jars with funnels covered by a wire gutter mesh. A net trap was placed above the jars, and baited with a chick in a shallow bowl covered by gutter mesh wire with a hole cut in the top. Shubeck et al. (1981), on the other hand, used 3.8 liter food cans concealed in a wooden box with wire mesh and a rain cover at the top. Fresh fish and chicken, and/or stale fish and chicken were combined as a bait. Lingafelter (1995) used baited pitfall traps in his survey work, using 500ml plastic cups or 350 ml glass jars with chicken hearts and gizzards as bait. He also used a black light, and the examination of "incidentally encountered dead vertebrates" for collecting silphids. Uiyshen and Hanula (2004) used cages that were covered with chicken wire on the sides and top but not on the side facing the ground. These cages were placed above a "collecting bucket" with chicken wrapped in cheesecloth dangling in the cage as bait. Anderson and Peck (1985) also suspended baits wrapped in cheesecloth, recommending fish, chicken legs, or chicken wings because of their ready availability and low cost. They used plastic ice cream containers or large tins for their traps, and secured the chicken wire over the trap with rocks. A board was placed on top of the rocks as a rain shield with a rock on top to keep it in place and prevent access by scavengers.

Previous studies in Virginia have utilized black lighting, pitfall traps and general insect traps for the collection of silphid beetles. Most of the specimens have come from general studies and no published studies specific to Virginia are available. The primary purpose of this study, therefore, was to survey silphid beetles in a more systematic manner across different geographic regions of the state to determine both species diversity and seasonal abundance. In addition, special consideration was given to beetles in the genus *Nicrophorus* which contains federally endangered species.

Chapter 3.2 Methods and Materials

3.2.1 Trap Placement and Data Collection

Six traps (except Accomack County, where there were only five traps) were placed in each of the five geographic regions of Virginia: Appalachian Plateau, Valley and Ridge, Blue Ridge Mountains, Piedmont, and Coastal Plain during the summers of 2007 and 2008 (Figure 2). The traps were set up in each region, each separated by approximately one kilometer. Seven and a half liter buckets were buried in the ground up to the lip. A 0.03 liter cup was used to hold the carrion, and a mesh screen was securely fastened around the top of the cup to keep the beetles from the carrion. The bait container was placed at the bottom of the bucket. All carrion used as bait was sealed in a Ziploc® baggie and allowed to "ripen" for three to five days. Mice were used as bait in the traps for the first visit to Wise County (May 20-26) in summer 2007, then mice and chicken were used together for the rest of summer 2007. The initial trip to Wise County did not produce any results, thus only chicken was used as bait for the traps in summer 2008. Chicken was chosen as bait due to its preferential use in a number of other recent studies (Shubeck et al. (1981), Anderson and Peck (1985), Lingafelter (1995), Uiyshen and Hanula (2004), and Comings (personal communication)); and it was readily available. A small amount of soil (< 1 inch) was placed at the bottom of the bucket to provide protection for the beetles if needed. A very moist sponge was also placed in the bucket to keep the beetles from dehydrating. For the first visit to Wise County, a top with a funnel in the middle was used to cover the bucket to minimize beetle escape; however, the tops were not used for the remaining counties or during the next summer. Chicken wire was tacked into the ground with tent stakes to keep out vertebrate scavengers and a board was propped up at a slant over the bucket to keep out rain.

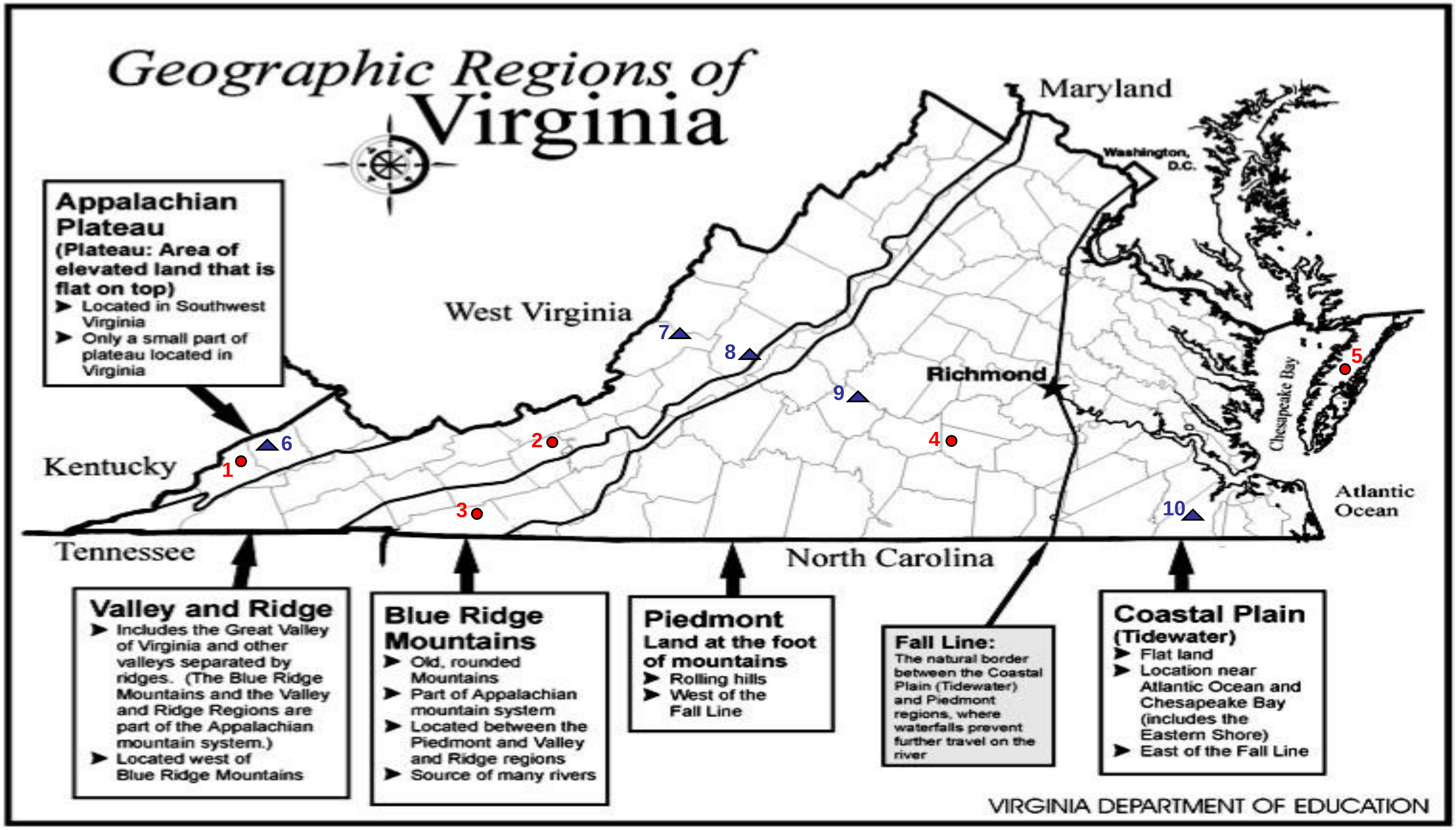


Figure 2. Locations in Virginia where silphid traps were set up in summers 2007 and 2008. Summer 2007, Traps 1 – 5, sites are labeled in Red Circles. Summer 2008, Traps 6 – 10, sites are labeled in Blue Triangles. Trap locations were: Trap 1 – Wise County; Trap 2 – Pulaski County; Trap 3 – Grayson County; Trap 4 – Nottoway County; Trap 5 – Accomack County; Trap 6 – Dickenson County; Trap 7 – Bath County; Trap 8 – Rockbridge County; Trap 9 –Appomattox County; Trap 10 – Suffolk County. (Virginia Department of Education - http://www.doe.virginia.gov/testing/sol/standards_docs/history_socialscience/index.shtml)


Figure 3. A survey site in Nottoway County in 2007 showing the set up of a baited pitfall trap.

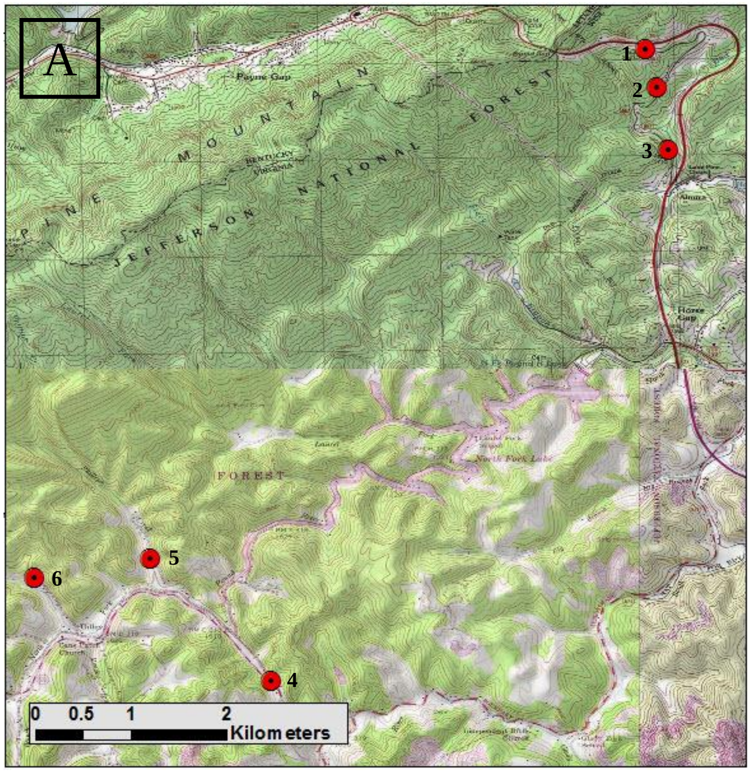
Photographs and GPS readings were taken at each of the trap sites during the summers of 2007 and 2008 (Figure 3). Traps were checked and the findings recorded every day for five days.

Silphids were either counted, identified, and released; or killed and identified in the lab. If they were identified in the field, they were released one kilometer or more from the traps. Any remains found in the sampling buckets were counted and included in the overall number of silphids found. The same area was sampled three times at different intervals during the summer to account for weather and seasonal differences in the activity of different beetle species. The trapping in each region was conducted in May/June (Early), then again in June/July (Mid), and finally in July/August (Late). Survey locations in each area were different for each of the two summers (Figures 4 - 8). Voucher specimens have been deposited into the Virginia Tech collection.

Most traps were placed at the edge of forested areas (in a field), although some traps were placed just inside the forest's edge (Wise County, Dickenson County, Rockbridge County, Bath County, and Appomattox County). A few traps were placed out in open fields (non-forested areas) where forest edge habitats were not available (Pulaski County). The elevation where traps were placed in Wise County ranged from approximately 500-700 meters, and Dickenson County was approximately 500-600 meters. The elevation where traps were placed in Pulaski County was approximately 600-650 meters, and Bath County was approximately 400-500 meters. In Grayson County, the elevation where traps were placed ranged from approximately 1150 meters at the entrance of Grayson Highlands State Park to approximately 1500 meters at the Visitor's Center; and in Rockbridge County the elevation where traps were placed was approximately 200-300 meters. In Nottoway County, the elevation where traps were placed was approximately

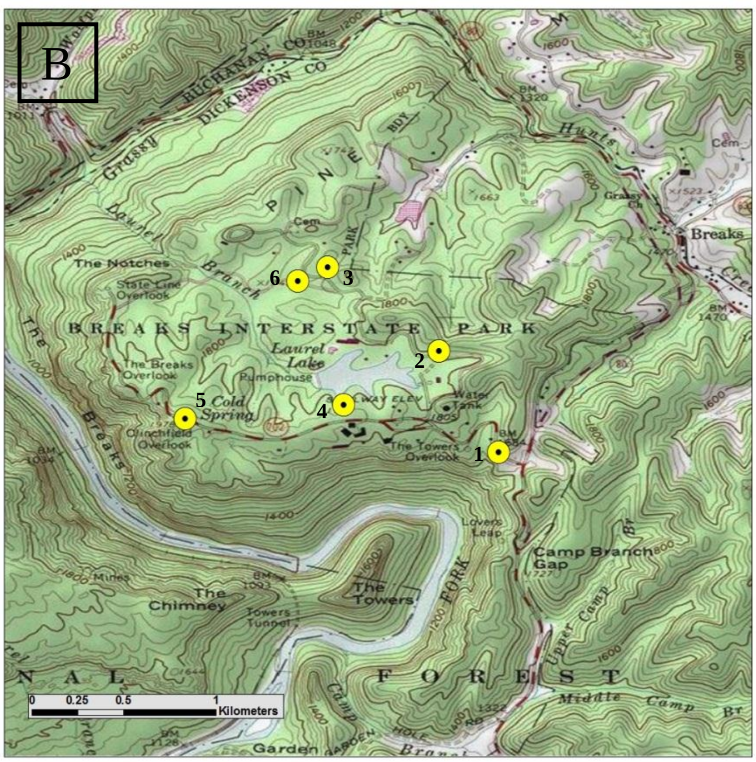
100 meters, and Appomattox County was approximately 200 meters. The elevation where traps were placed in Accomack County was approximately 5-10 meters, and in Suffolk County the elevation was also approximately 5-10 meters.

Silphid beetle diversity and seasonal abundance were also examined in Montgomery County, Virginia from April to October of 2008. Pitfall traps were placed in four locations; the Virginia Tech Moore Farm (Moore Farm) (Lat. 37.2180, Long -80.4652); the Virginia Tech Price’s Fork Research Facility (Price’s Fork) (Lat. 37.2132, Long. -80.4880); and two traps in Kentland Farm in Whitethorne (Kentland 1 (Lat. 37.2012, Long. -80.5936), and Kentland 2 (Lat. 37.1998, Long. -80.5915). Price’s Fork is a Virginia Tech research center that has an open field habitat. Moore Farm and Kentland are also Virginia Tech research farms that provided survey sites closer to a forest edge habitat (Kentland 1 was within the forest edge and Kentland 2 was next to an open field/forest edge). Traps were set up the same way that the statewide survey traps were set up, and checked on a weekly basis. Beetles were either collected for further identification or released approximately one kilometer from any traps. Beetles were first collected in the middle of April, 2008, and then on a weekly basis until the middle of October, 2008.



Latitude and Longitude:

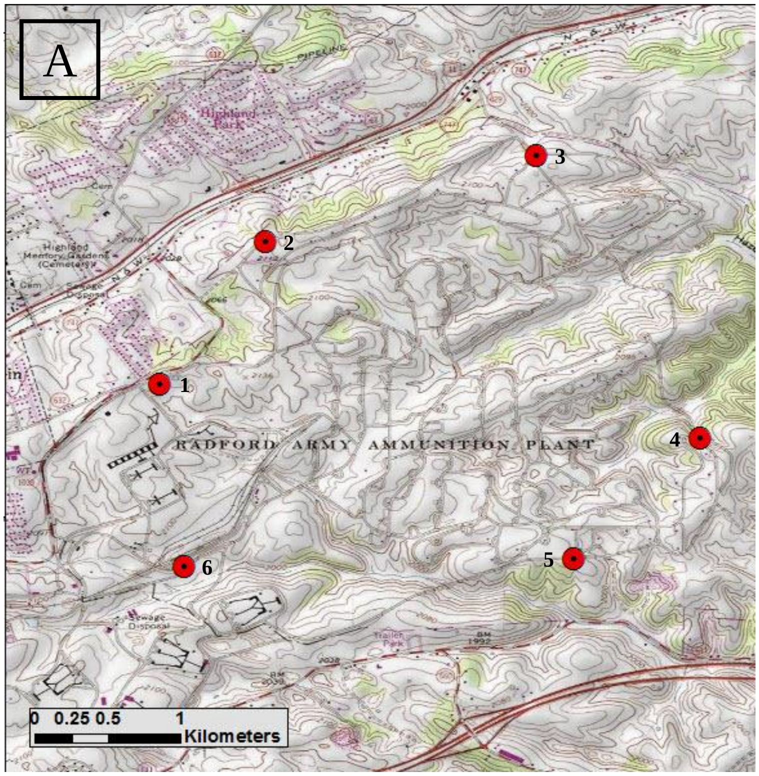
Trap 1: 37.0918, -82.3726
Trap 2: 37.0906, -82.3722
Trap 3: 37.0844, -82.3718
Trap 4: 37.0544, -82.3933
Trap 5: 37.0625, -82.4013
Trap 6: 37.0619, -82.4053



Latitude and Longitude:

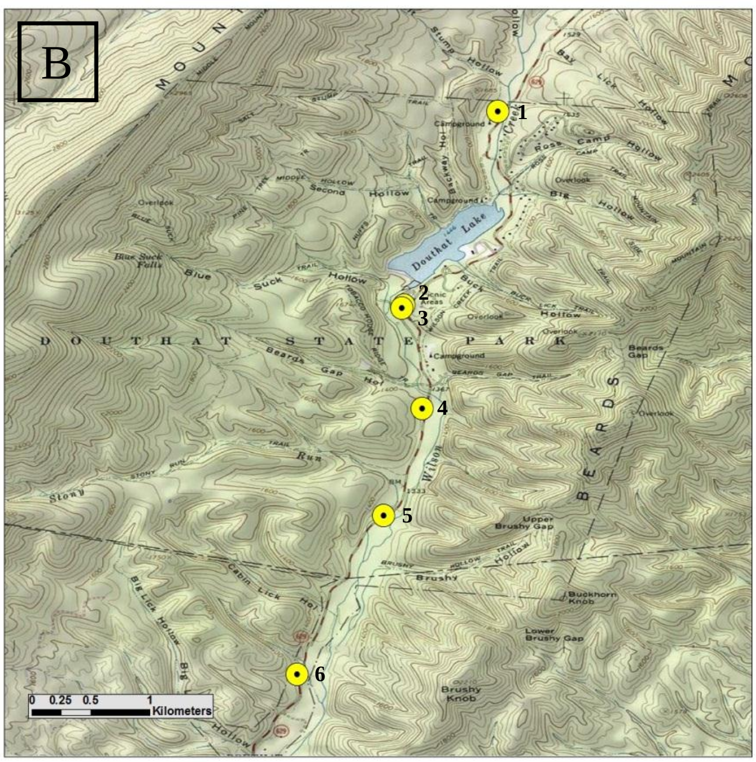
Trap 1: 37.1707, -82.1721
Trap 2: 37.1725, -82.1731
Trap 3: 37.1740, -82.1751
Trap 4: 37.1716, -82.1748
Trap 5: 37.1713, -82.1816
Trap 6: 37.1737, -82.1756

Figure 4. The location of baited pitfall traps in two counties in the Appalachian Plateau Region, a geographic region of Virginia. Figure 4A. Wise County (State Fig. 2) trap placement in summer 2007. Figure 4B. Dickenson County (State Fig. 2) trap placement in summer 2008.



Latitude and Longitude:

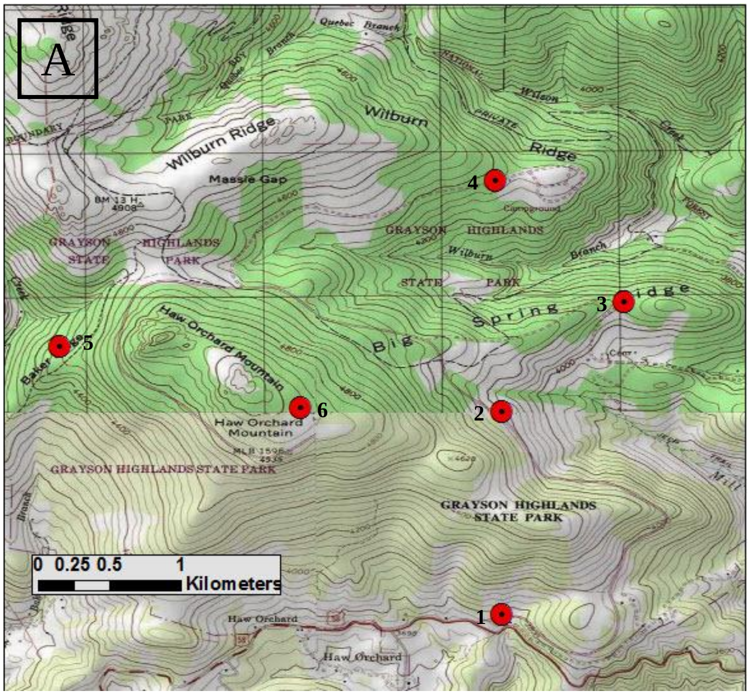
Trap 1: 37.0623, -80.4009
Trap 2: 37.0655, -80.3946
Trap 3: 37.0714, -80.3845
Trap 4: 37.0611, -80.3808
Trap 5: 37.0544, -80.3837
Trap 6: 37.0542, -80.4004



Latitude and Longitude:

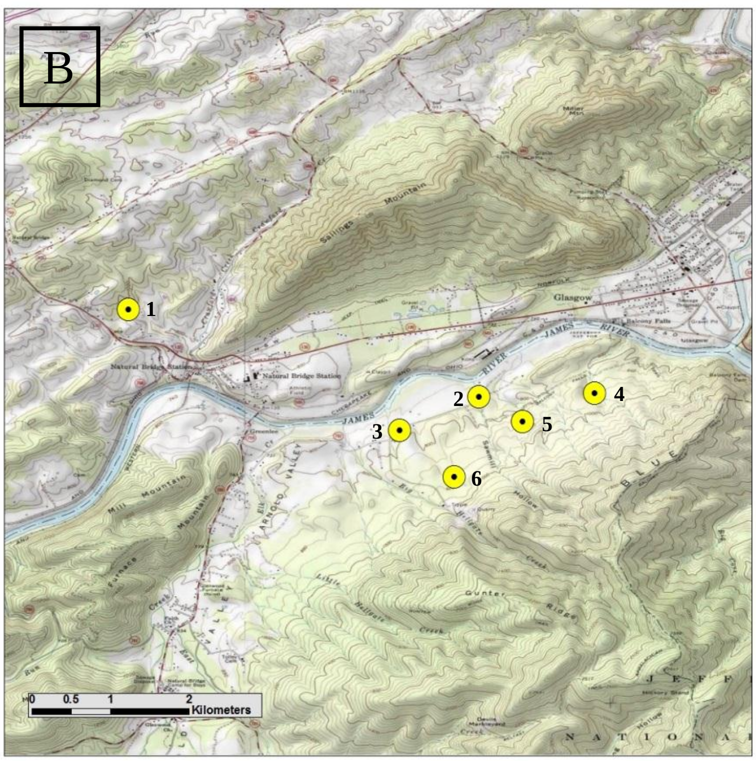
Trap 1: 37.5457, -79.4746
Trap 2: 37.5336, -794809
Trap 3: 37.5356, -79.4738
Trap 4: 37.5336, -79.4808
Trap 5: 37.5307, -79.4818
Trap 6: 37.5224, -79.4842

Figure 5. The location of baited pitfall traps in two counties in the Valley and Ridge Region, a geographic region of Virginia. Figure 5A. Pulaski County (State Fig. 2) trap placement in summer 2007. Figure 5B. Bath County (State Fig. 2) trap placement in summer 2008.



Latitude and Longitude:

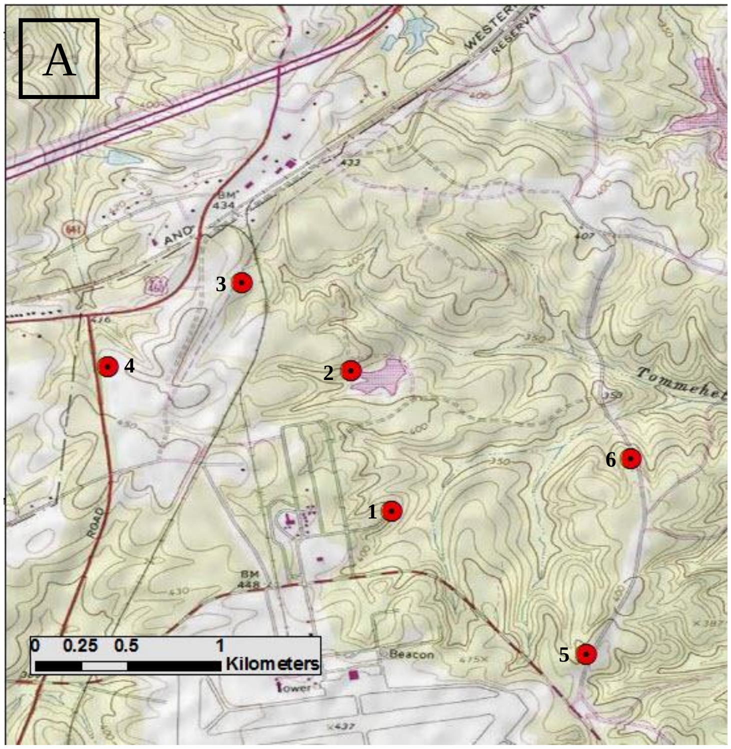
Trap 1: 36.3646, -81.2917
Trap 2: 36.3732, -81.2917
Trap 3: 36.3758, -81.2849
Trap 4: 36.3825, -81.2919
Trap 5: 36.3747, -81.3058
Trap 6: 36.3733, -81.3003



Latitude and Longitude:

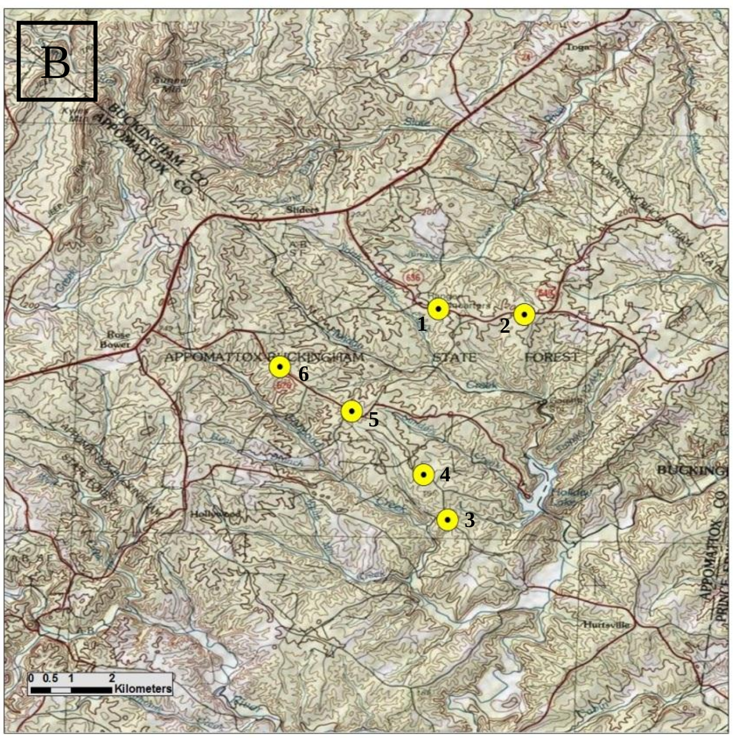
Trap 1: 37.3742, -79.3047
Trap 2: 37.3707, -79.2823
Trap 3: 37.3653, -79.2855
Trap 4: 37.3708, -79.2736
Trap 5: 37.3656, -79.2805
Trap 6: 37.3634, -79.2833

Figure 6. The location of baited pitfall traps in two counties in the Blue Ridge Mountains Region, a geographic region of Virginia. Figure 6A. Grayson County (State Fig. 2) trap placement in summer 2007. Figure 6B. Rockbridge County (State Fig. 2) trap placement in summer 2008.



Latitude and Longitude:

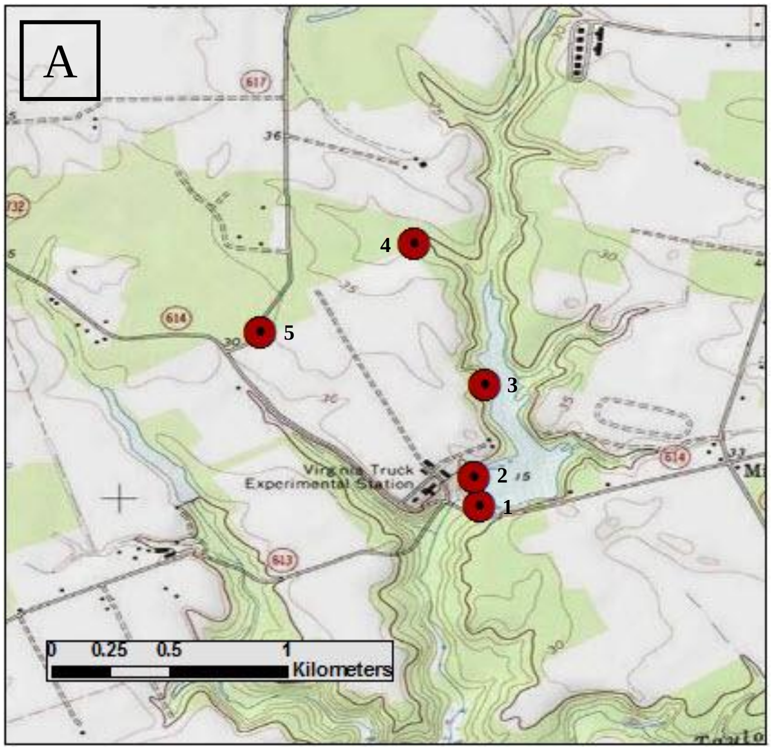
Trap 1: 37.0526, -77.5711
Trap 2: 37.0551, -77.5718
Trap 3: 37.0607, -77.5738
Trap 4: 37.0550, -77.5801
Trap 5: 37.0460, -77.5637
Trap 6: 37.0536, -77.5629



Latitude and Longitude:

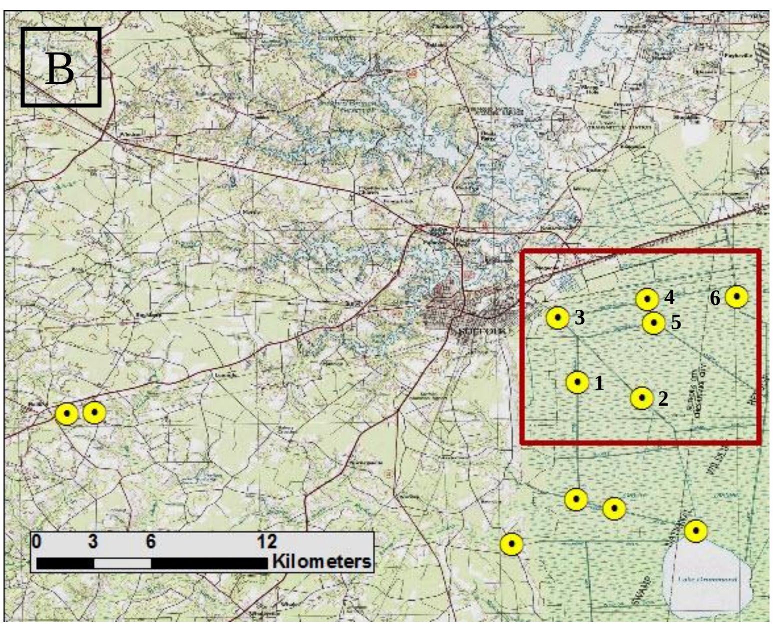
Trap 1: 37.2610, -78.3933
Trap 2: 37.2606, -78.3824
Trap 3: 37.2322, -78.3925
Trap 4: 37.2358, -78.3944
Trap 5: 37.2448, -78.4042
Trap 6: 37.2525, -78.4140

Figure 7. The location of baited pitfall traps in two counties in the Piedmont Region, a geographic region of Virginia. Figure 7A. Nottoway County (State Fig. 2) trap placement in summer 2007. Figure 7B. Appomattox County (State Fig. 2) trap placement in summer 2008.



Latitude and Longitude:

Trap 1: 37.3501, -75.4910
Trap 2: 37.3505, -75.4911
Trap 3: 37.3518, -75.4909
Trap 4: 37.3538, -75.4919
Trap 5: 37.3525, -75.4940



Latitude and Longitude:

Trap 1: 36.4146, -76.3144
Trap 2: 36.4118, -76.2955
Trap 3: 36.4335, -76.3218
Trap 4: 36.4405, -76.2945
Trap 5: 36.4327, -76.2934
Trap 6: 36.4411, -76.2715

Figure 8. The location of baited pitfall traps in two counties in the Coastal Plain Region, a geographic region of Virginia. Figure 8A. Accomack County (State Fig. 2) trap placement in summer 2007. Figure 8B. Suffolk County (State Fig. 2) trap placement in summer 2008. The traps in the red box are the original traps where samples were taken. Additional traps were placed (outside of the red box) to widen the search area to sample for *Nicrophorus carolinus* (Linnaeus) since only three were found.

3.2.2 Statistical Analysis of the Data

In order to analyze the data, Contingency Analyses were used for analyzing the data from the statewide survey and the Montgomery County sampling. When looking at the Contingency Tables (Appendix 1); the first number in each cell is the beetle count, the second number in each cell is the Column percent, and the third number is the Row percent. Chi-squared tests and Cochran-Mantel-Haenszel tests were used to test for significant association. The Chi-squared test determined if there was significant association between the two variables, and the Cochran-Mantel-Haenszel test makes an adjustment for the blocking factor. 'Beetle species' was compared with sampling period with geographic region as a blocking factor. 'Beetle species' was compared with region (or site in Montgomery Co.), with year as a blocking factor.

An additional test was conducted, a Correspondence Analysis, which showed any relationships the two variables may, or may not, have had. The results are presented as biplots. The red lines represent the variables and the blue dots represent the observations. The closeness of the lines and the angle formed by the lines indicate the degree of correlation between the variables – an acute angle indicates a positive correlation and an obtuse angle indicates a negative correlation between the variables. An angle of 0 or 180 degrees indicates a correlation of 1.0 or -1.0, respectively and an angle of 90 degrees represents a correlation of zero. The longer the vector is, the more variability relative to another vector. The distance between dots corresponds to their similarities in the observation profiles – observations with similar profiles will be closer together. A dot's distance from the origin (regardless of direction) shows the extremity of that observation's profile relative to the means of all the observations. (Greenacre (1993), Clausen (1998), and Manly (2004))

Chapter 3.3 Results

A total of 4375 silphid beetles were collected in 10[1] counties in Virginia during the summers of 2007 and 2008. The samples consisted of eleven species and four genera with beetles in the subfamily Silphinae being prevalent. Figures 9 - 13 show the species and the number of beetles collected at each trapping site for each summer. *Nicrophorus americanus* was not collected during either summer of surveying and only three *N. carolinus* were trapped in Suffolk County in the summer of 2008. Within the Nicrophorinae, *Nicrophorus tomentosus* Weber and *N. orbicollis* were dominant in 2007; whereas in the summer of 2008, *N. tomentosus* and *N. pustulatus* were most common. There were variations in the beetle species collected in each of the geographic regions of the Commonwealth during different times of the summer, as well as variations within the regions. There were more silphid beetles trapped in Pulaski County, in the Valley and Ridge Region Region, with *Nicrophorus marginatus* Fabricius being the most commonly collected species in the Nicrophorinae; but the second most common species was *Nicrophorus tomentosus*. The second highest number of beetles was trapped in Appomattox County in the Piedmont Region, with *Nicrophorus pustulatus* being the prevalent species in the Nicrophorinae, and *Nicrophorus orbicollis* being the second most common.

In the Montgomery County survey from mid-April to mid-October of 2008 (Figure 14), a total of 3276 beetles were trapped and the prevalent species within Nicrophorinae was *Nicrophorus tomentosus* (60 beetles) and within the Silphinae it was *Necrophila americana* (Linnaeus) (669 beetles). More beetles were trapped in June than in any other month totaling 602, September being the least successful with a total of 62 beetles trapped. *Necrophila americana* was trapped every month, while *O. noveboracense* (Forster), *O. inaequale*

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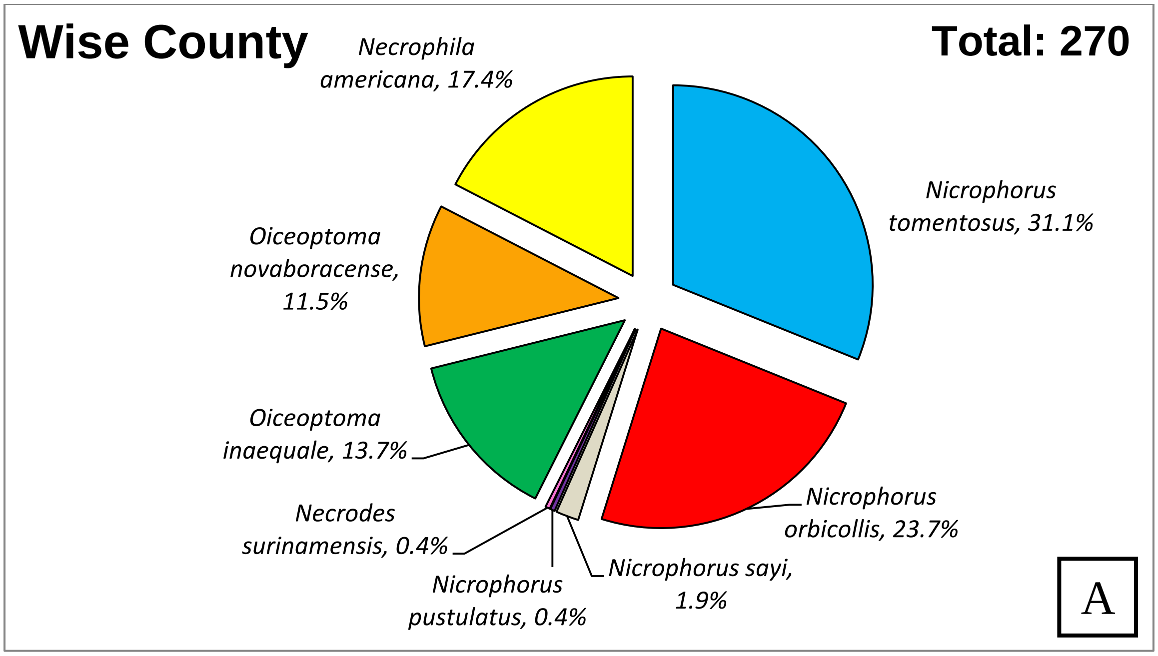
[1] It was not discovered that several traps were placed just over the county line until after GPS readings were examined. The main county is the only one noted, but in Bath County surveys, one trap went over the Allegheny County line and in Appomattox County, two traps went over the Buckingham County line.

(Fabricius), *Necrodes surinamensis* (Fabricius), *N. pustulatus* (which was the least trapped species with only 1 beetle), *N. orbicollis*, and *N. tomentosus* were only found during certain months.

3.3.1 Contingency Analysis of Species by Sampling Period (with Region as a Blocking Factor) for Commonwealth Surveys

The data for the Contingency Analysis in Figure 15 are shown in Appendix A. Contingency Table of Species by Period for the Commonwealth of Virginia. The Null Hypothesis, when comparing two variables, beetle species abundance and sampling period, is that the number of specimens of the beetle species collected is independent of (not associated with) sampling period. A Chi-Squared test indicated that there is a significant association between species abundance and period of sampling ($\chi^2 = 1868.26$; df = 20; $P < 0.0001$). To test whether the association of beetle species abundance and sampling period is influenced by region the Cochran-Mantel-Haenszel test was used. The Null Hypothesis is that beetle species and sampling period are mutually independent in the population sampled after controlling for region. The Cochran-Mantel-Haenszel test showed that after adjusting for region, there is a significant association between species and period ($\chi^2 = 1619.14$; df = 20; $P < 0.0001$).



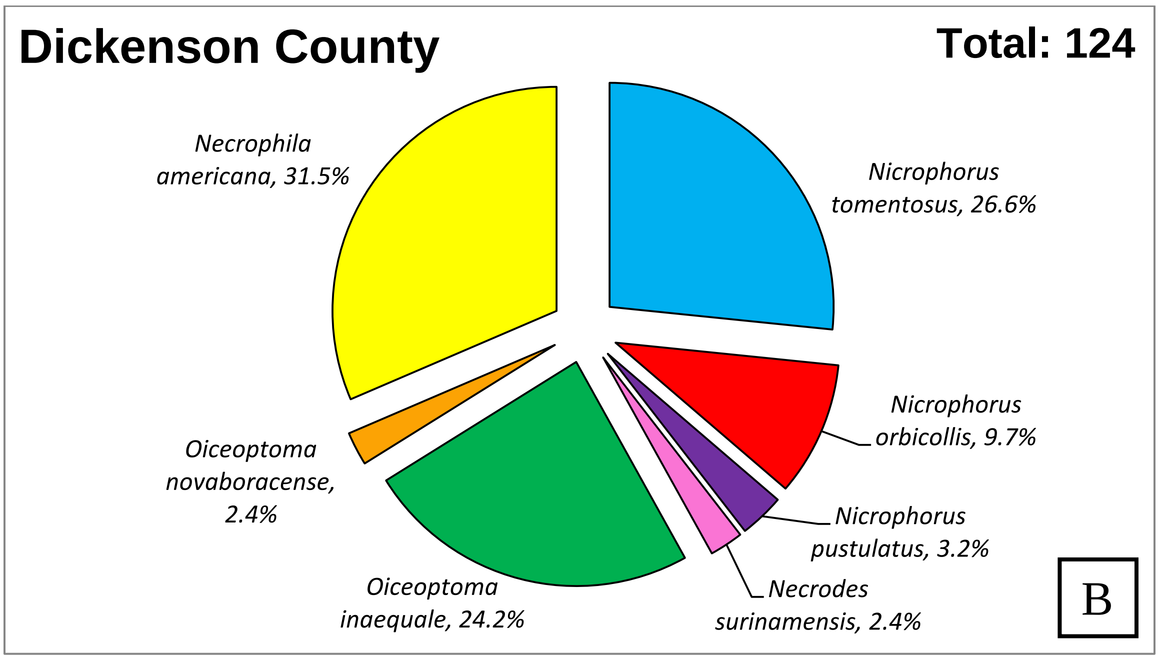
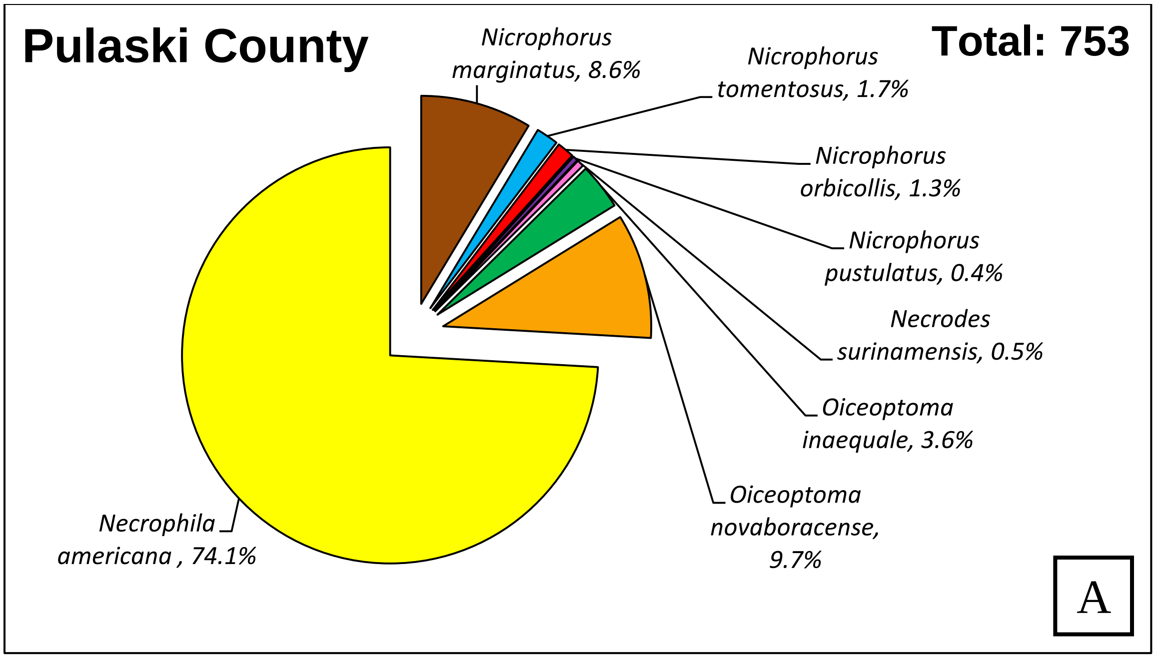


Figure 9. Trap catch results for the Appalachian Plateau Region of Virginia. Figure 9A. Silphid beetle results from baited pitfall traps in Wise County, VA for summer 2007. Figure 9B. Silphid beetle results from baited pitfall traps in Dickenson County, VA for summer 2008. Total refers to the number of beetles trapped during the three sampling periods.



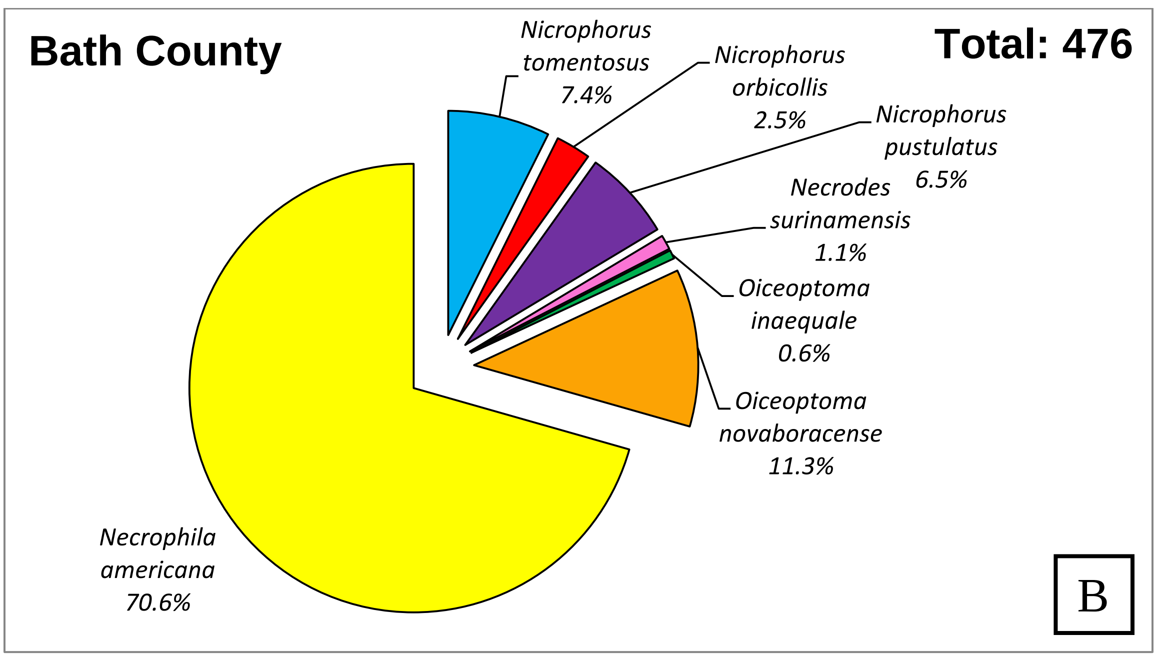
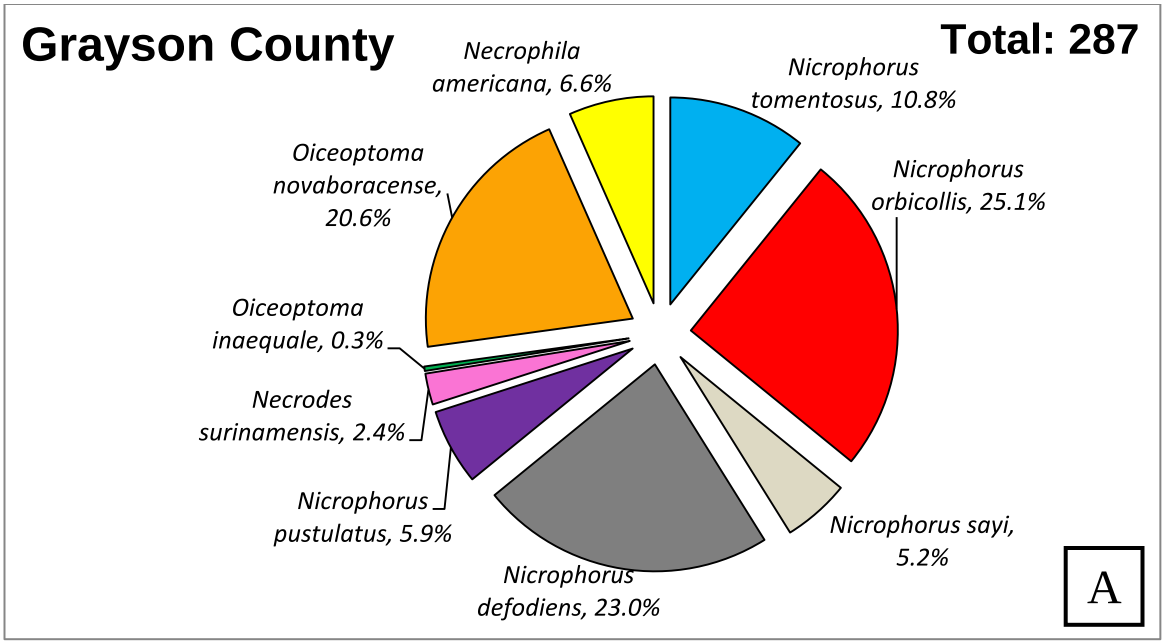


Figure 10. Trap catch results for the Valley and Ridge Region of Virginia. Figure 10A. Silphid beetle results from baited pitfall traps in Pulaski County, VA for summer 2007. Figure 10B. Silphid beetle results from baited pitfall traps in Bath County, VA for summer 2008. Total refers to the number of beetles trapped during the three sampling periods.



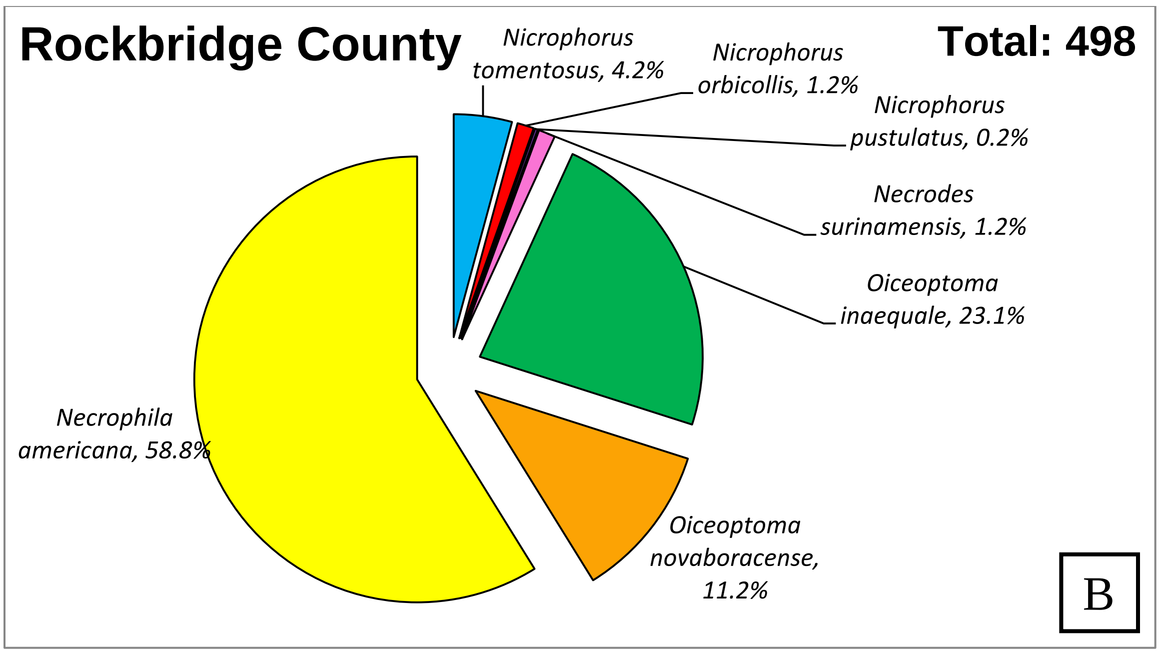
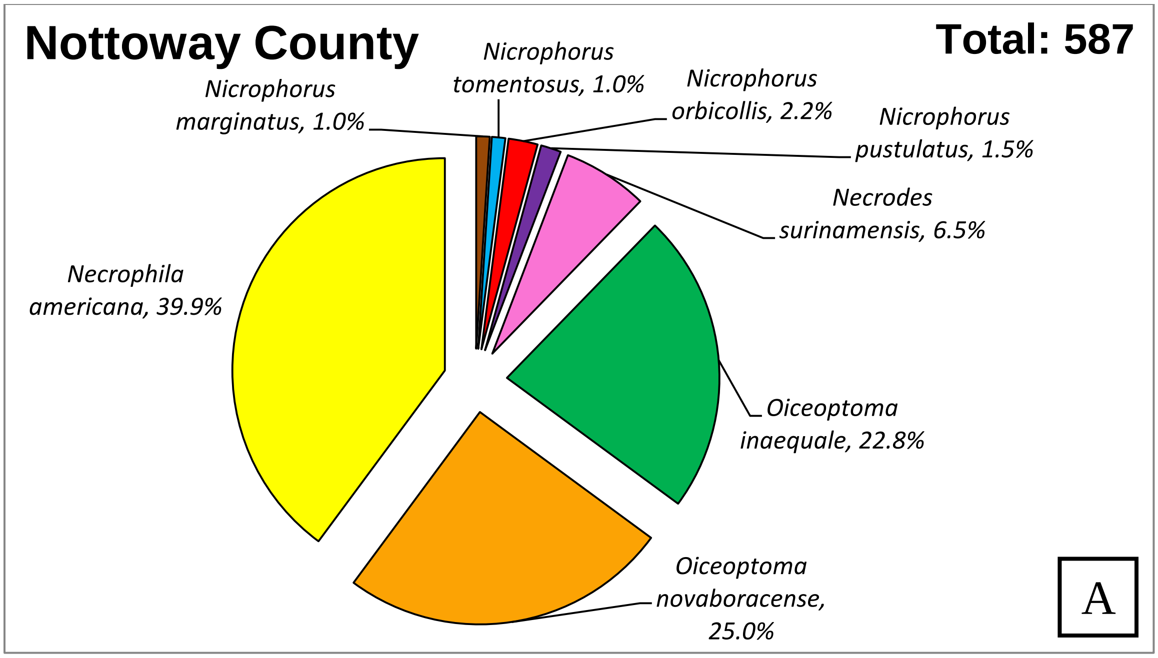


Figure 11. Trap catch results for the Blue Ridge Mountains Region of Virginia. Figure 11A. Silphid beetle results from baited pitfall traps in Grayson County, VA for summer 2007. Figure 11B. Silphid beetle results from baited pitfall traps in Rockbridge County, VA for summer 2008. Total refers to the number of beetles trapped during the three sampling periods.



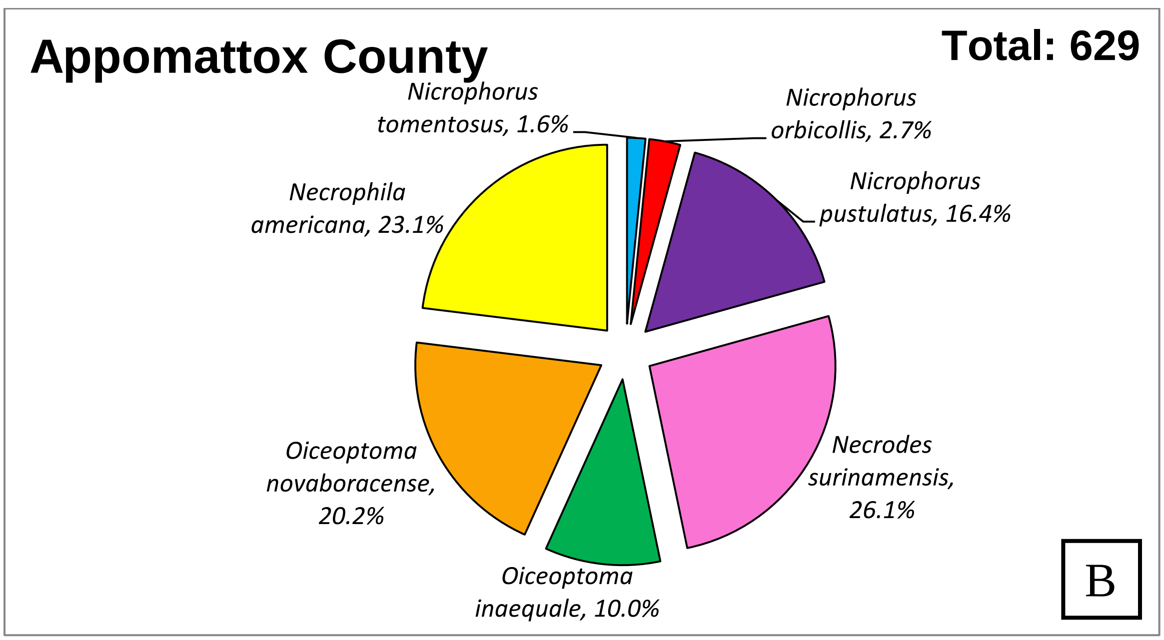
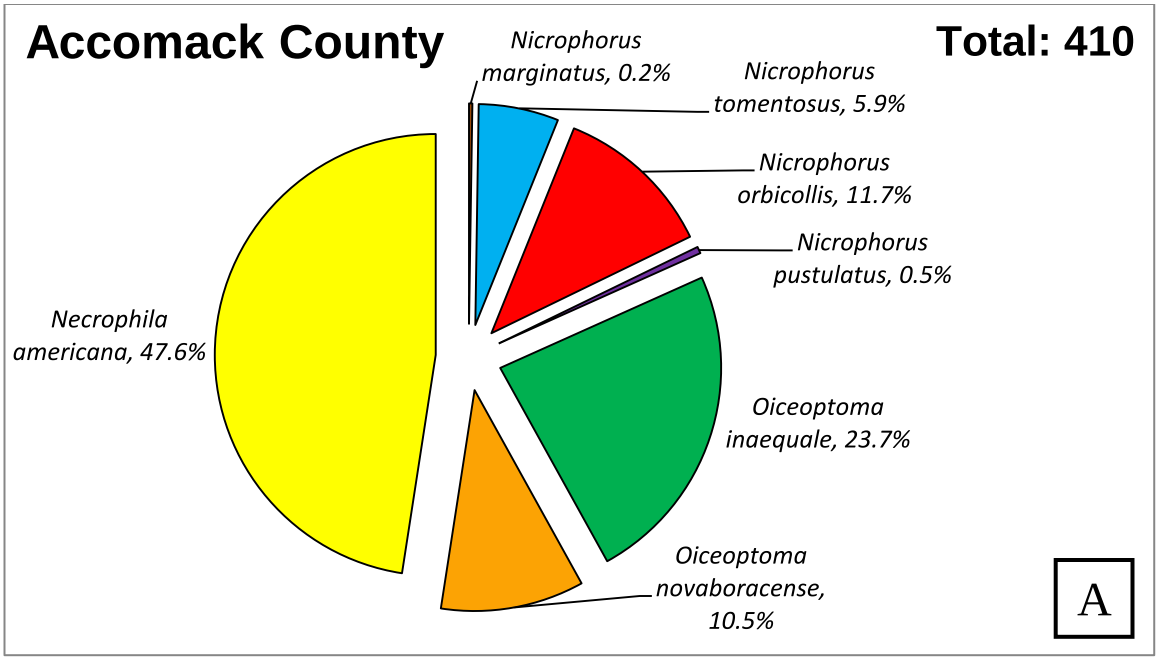


Figure 12. Trap catch results for the Piedmont Region of Virginia. Figure 12A. Silphid beetle results from baited pitfall traps in Nottoway County, VA for summer 2007. Figure 12B. Silphid beetle results from baited pitfall traps in Appomattox County, VA for summer 2008. Total refers to the number of beetles trapped during the three sampling periods.



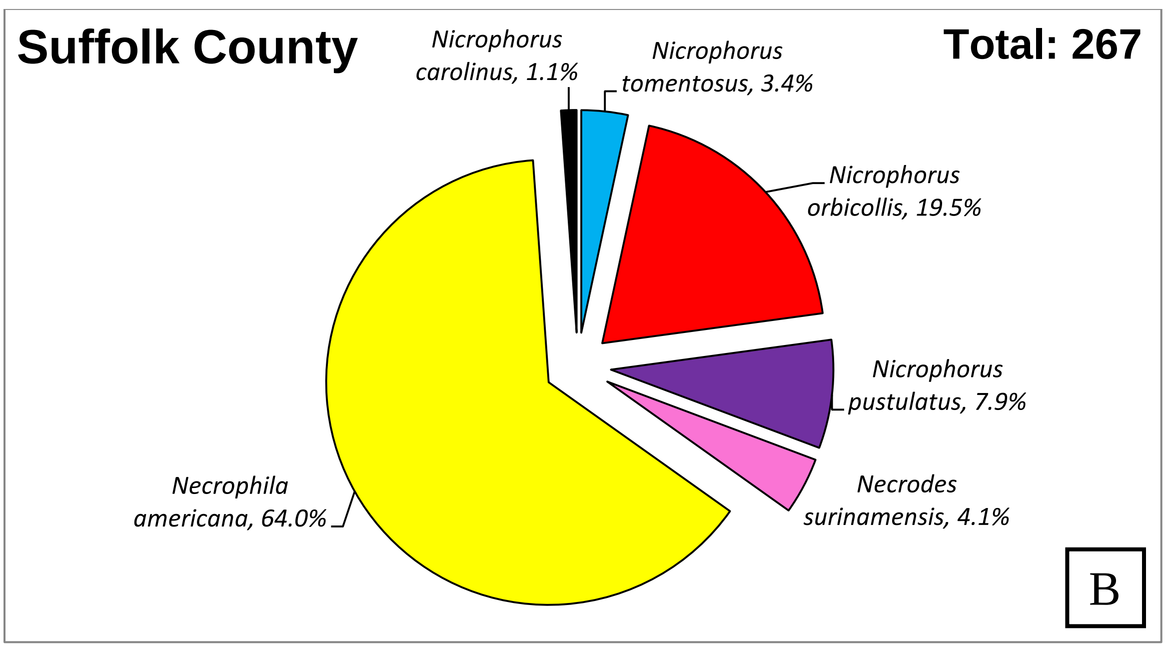
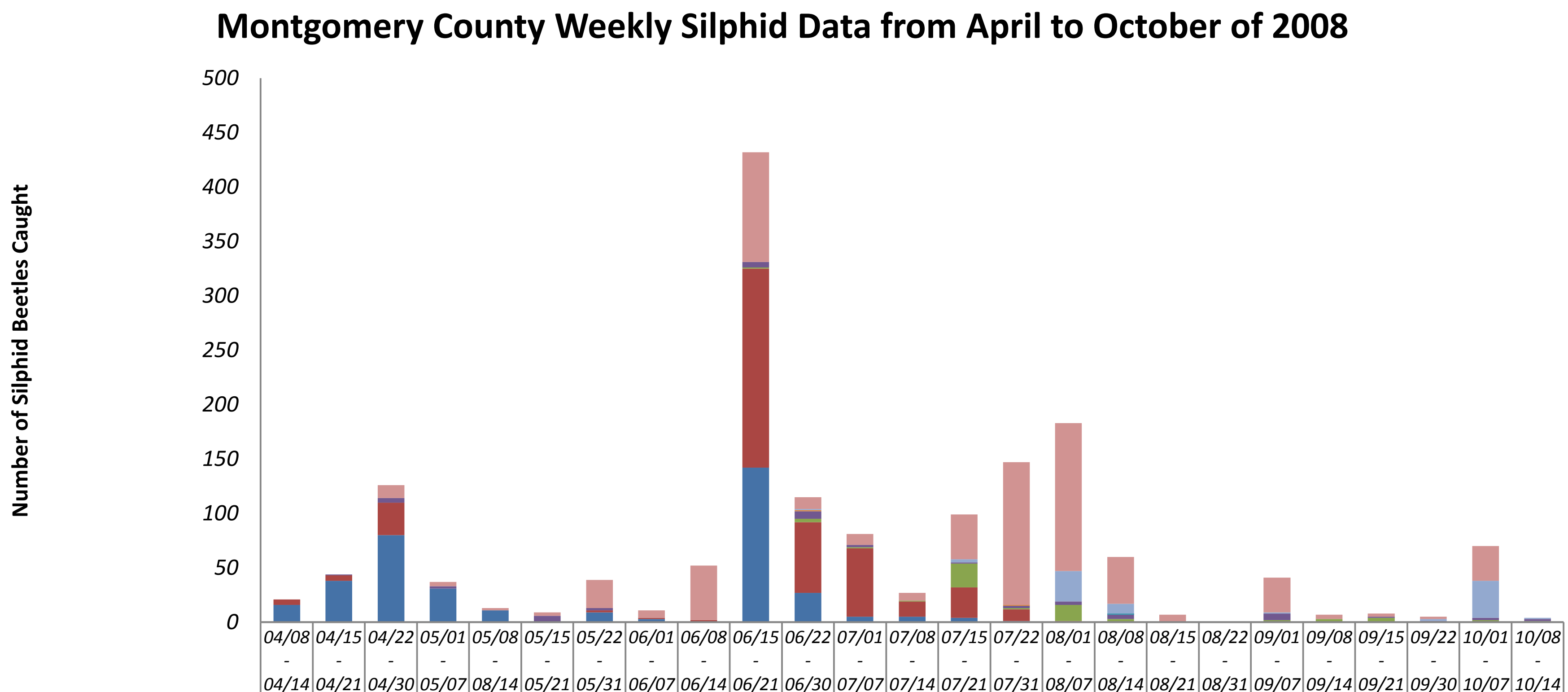


Figure 13. Trap catch results for the Coastal Plain Region of Virginia. Figure 13A. Silphid beetle results from baited pitfall traps in Accomack County, VA for summer 2007. Figure 13B. Silphid beetle results from baited pitfall traps in Suffolk County, VA for summer 2008. Total refers to the number of beetles trapped during the three sampling periods.



	04/08 - 04/14	04/15 - 04/21	04/22 - 04/30	05/01 - 05/07	05/08 - 08/14	05/15 - 05/21	05/22 - 05/31	06/01 - 06/07	06/08 - 06/14	06/15 - 06/21	06/22 - 06/30	07/01 - 07/07	07/08 - 07/14	07/15 - 07/21	07/22 - 07/31	08/01 - 08/07	08/08 - 08/14	08/15 - 08/21	08/22 - 08/31	09/01 - 09/07	09/08 - 09/14	09/15 - 09/21	09/22 - 09/30	10/01 - 10/07	10/08 - 10/14
Necrophila americana	0	0	12	4	2	3	26	7	50	101	11	10	7	41	131	136	43	7	0	32	4	3	2	32	0
Necrodes surinamensis	0	0	0	0	0	0	0	0	0	0	1	0	0	3	0	28	9	0	0	1	0	0	2	34	1
Nicrophorus marginatus	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Nicrophorus pustulatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Nicrophorus orbicollis	0	1	4	2	0	6	2	0	0	5	7	2	0	1	2	3	4	0	0	6	0	1	1	2	2
Nicrophorus tomentosus	0	0	0	0	0	0	0	0	0	1	3	1	1	22	1	15	3	0	0	2	3	4	0	2	1
Oiceoptoma novaboracense	5	5	30	0	0	0	2	1	2	183	65	63	14	28	11	1	0	0	0	0	0	0	0	0	0
Oiceoptoma inaequale	16	38	80	31	11	0	9	3	0	142	27	5	5	4	1	0	0	0	0	0	0	0	0	0	0

Figure 14. Montgomery County, Virginia, silphid trap data from mid-April 2008 to mid-October 2008.

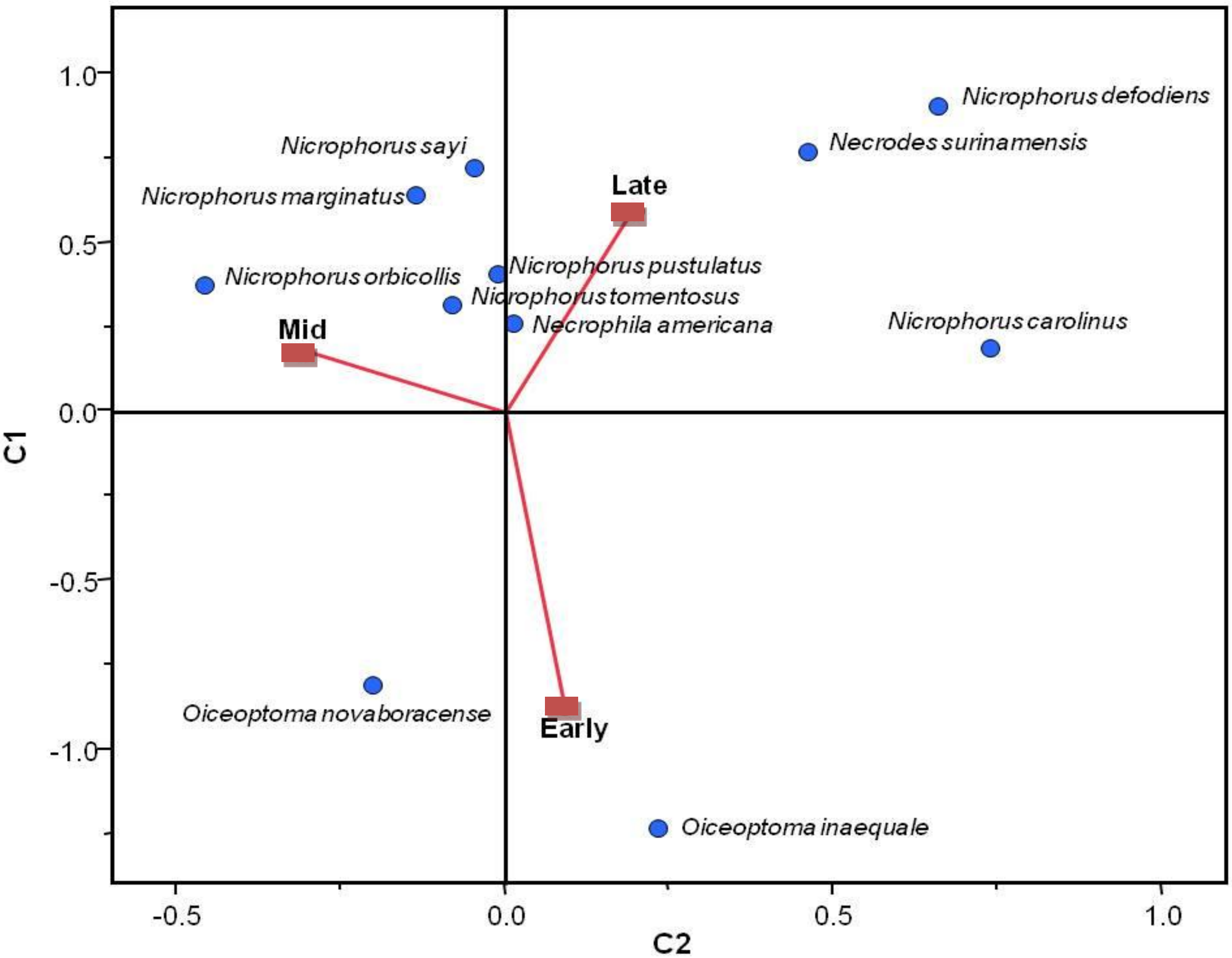


Figure 15. Correspondence Analysis showing the relationship between period (red lines) and species (blue dots) from silphid beetle surveys in the Commonwealth of Virginia during three different sampling periods in 2007 and 2008. Early is May/June, Mid is June/July, and Late is July/August. C1 = Correspondence Dimension 1; C2 = Correspondence Dimension 2

Figure 15 shows the correspondence analysis for the silphid beetles collected during three different seasonal sampling times in Virginia. The top half of the graph represents species occurrence during the Mid and Late periods, while the bottom half of the graph shows species that occurred mainly during the Early period. There appears to be little or no correlation between Mid and Late sampling periods with respect to the species and their abundances; however, there appears to be a negative correlation between the Early and Mid, and similarly between Early and Late. The longer vector of the Early period indicates greater variability in abundances compared to Mid and Late periods. Since *N. pustulatus, N. tomentosus,* and *N. americana* have similar column profiles (See Contingency Table – Appendix A. Contingency Table of Species by Period for the Commonwealth of Virginia), they are located closer together on the biplot.

3.3.2 Contingency Analysis of Species by Geographic Region (with Year as a Blocking Factor) for Commonwealth Surveys

The data for the Contingency Analysis in Figure 16 are shown in Appendix B. Contingency Table of Species by Region for the Commonwealth of Virginia. The Null Hypothesis, when comparing the two variables, beetle species abundance and region of sampling, is that the number of specimens of the beetle species collected is independent of (not associated with) the region of sampling. A Chi-Squared test indicated that there is a significant association between species and region of sampling ($\chi^2 = 2387.07$; df = 40; $P < 0.0001$). To test whether the association of beetle species abundance and region of sampling is influenced by sampling period the Cochran-Mantel-Haenszel test was used. The Null Hypothesis is that beetle species and region of sampling are mutually independent in the population sampled after controlling for sampling period. The Cochran-Mantel-Haenszel test showed that after adjusting for sampling period, there is a significant association between species and region of sampling ($\chi^2 = 2498.02$; df = 40; $P < 0.0001$).

In Figure 16, the beetle species appear to separate into three groups based on the five geographic regions: these are (1) Piedmont, (2) Blue Ridge Mountains and Appalachian Plateau, and (3) Coastal Plain and Valley and Ridge. The acute angles indicate that there is a positive correlation between the species abundance in Blue Ridge Mountains and Appalachian Plateau, and also between Coastal Plain and Valley and Ridge regions. Alternately, Piedmont tends to be negatively correlated with the other 4 regions, as shown by the obtuse angles, and even a strong negative correlation between Piedmont and Coastal Plain (as seen with the 180 degree angle). The longer vectors of Piedmont and Appalachian Plateau indicate greater variability in abundances compared with Blue Ridge Mountains, Coastal Plain, and Valley and Ridge. The closeness of the points (blue) to the region point (red) indicates that species occurred predominantly in that region. *Nicrophorus carolinus* is associated predominantly with the Coastal Plain region. Since *N. orbicollis* and *N. tomentosus* have similar column profiles (See Contingency Table – Appendix B. Contingency Table of Species by Region for the Commonwealth of Virginia), they are located closer together on the biplot.

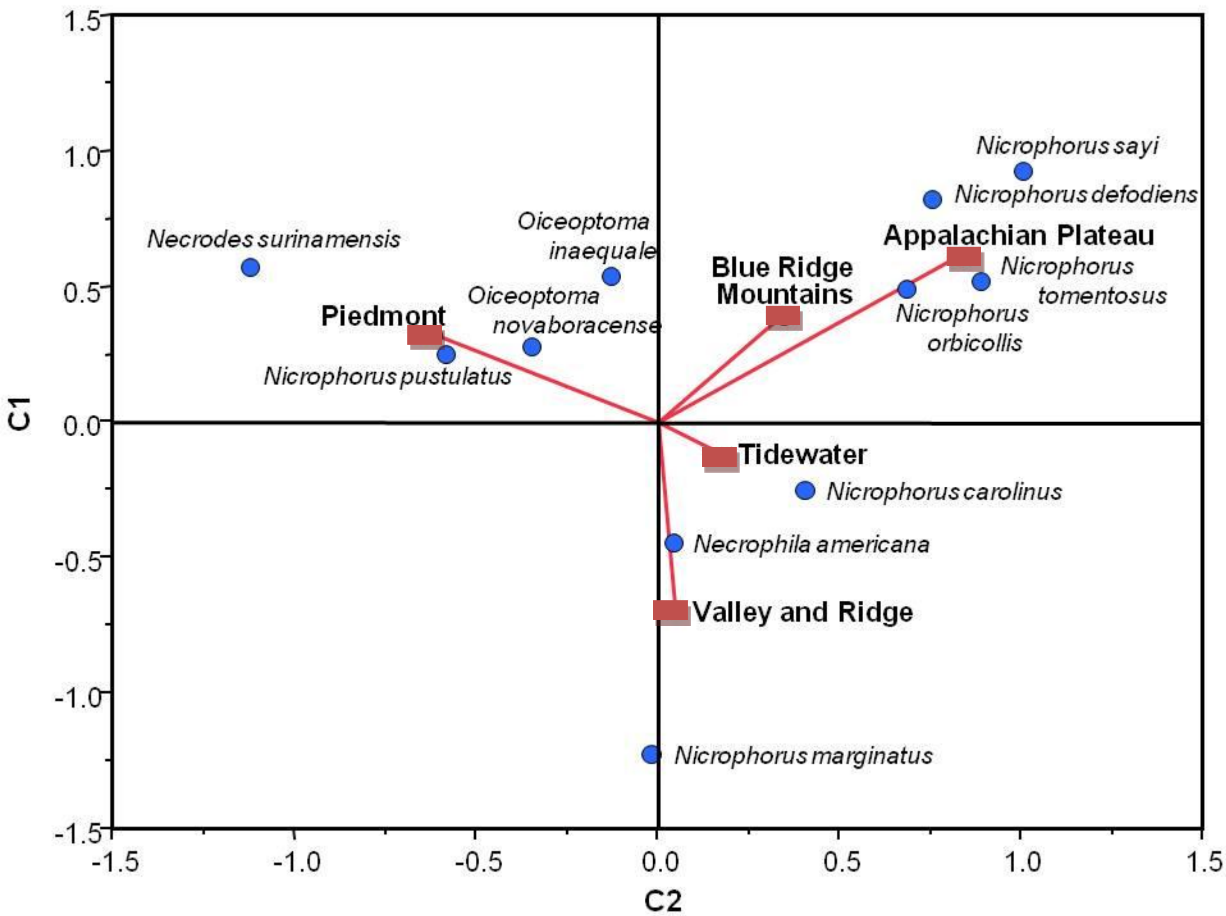


Figure 16. Correspondence Analysis showing the relationship between region (red lines) and species (blue circles) from silphid beetle surveys conducted in the Commonwealth of Virginia during three different periods in 2007 and 2008. C1 = Correspondence Dimension 1; C2 = Correspondence Dimension 2

3.3.3 Contingency Analysis of Species by Site

The data for the Contingency Analysis in Figure 17 are shown in Appendix C. Contingency Table of Species by Period for Montgomery County, VA. The Null Hypothesis, when comparing the two variables, beetle species abundance and sampling site, is that the number of specimens of the beetle species collected is independent of (not associated with) sampling site. The Chi-Squared test indicated that there is significant association between species and site ($\chi^2 = 34.35$; df = 21; $P < 0.0001$).

Figure 17 shows little or no correlation between Moore Farm and Kentland 2 with respect to the species and their abundances; however, there appears to be a positive correlation between Price's Fork and Moore Farm. Also, there appears to be a negative correlation between Price's Fork and Kentland 1, Price's Fork and Kentland 2, Kentland 1 and Kentland 2, and Kentland 1 and Moore Farm. The top half of the figure represents species occurrence at Kentland 1 and Kentland 2, while the bottom half of the figure shows species that occurred mainly at Price's Fork and Moore Farm. The longer vector of Price's Fork indicates greater variability in abundances compared to Kentland 1, Kentland 2, and Moore's Farm. Since *N. tomentosus,* and *O. noveboracense* have similar column profiles (See Contingency Table – Appendix C. Contingency Table of Species by Period for Montgomery County, VA), they are located closer together on the biplot.

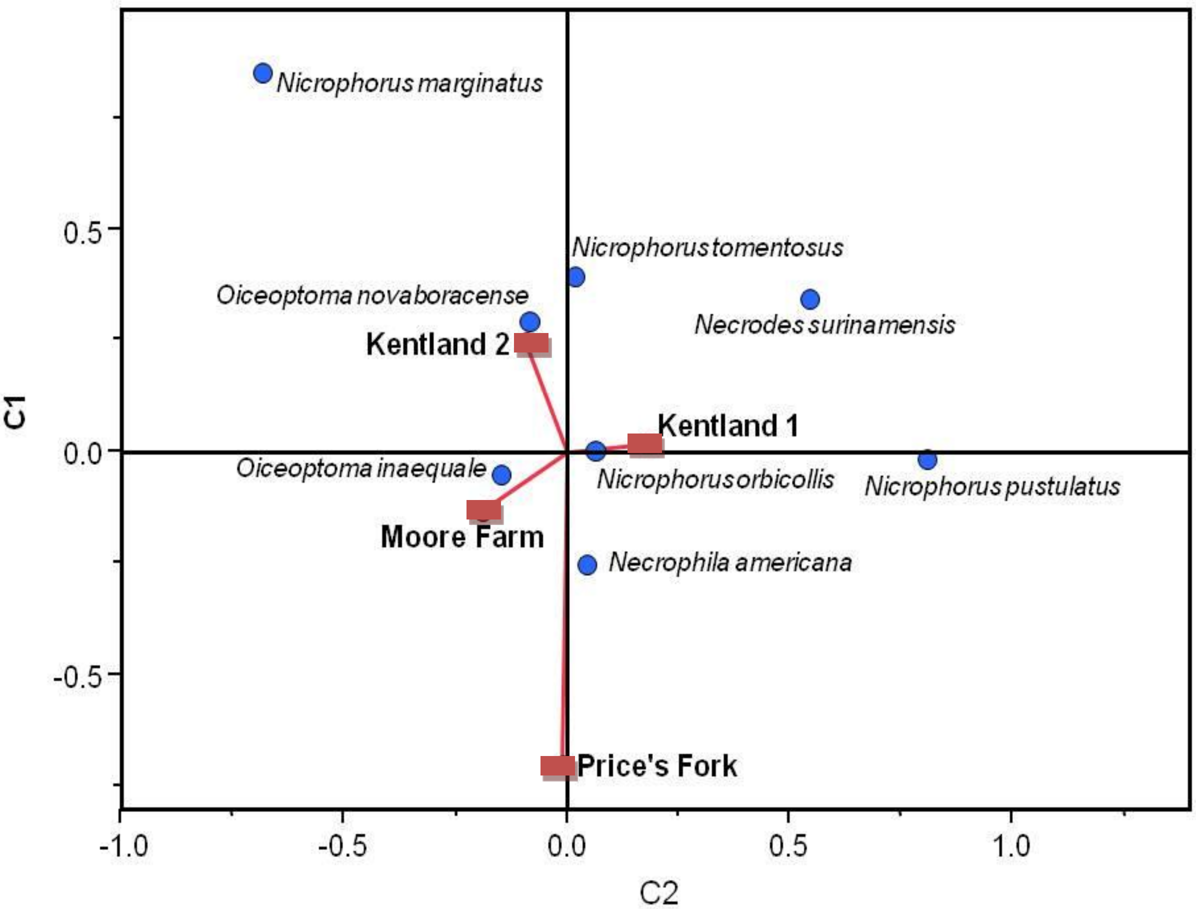


Figure 17. Correspondence Analysis showing the relationship between site (red lines) and species (blue circles) from silphid beetle surveys conducted in Montgomery County, VA from mid-April to mid-October. C1 = Correspondence Dimension 1; C2 = Correspondence Dimension 2

3.3.4 Contingency Analysis of Species by Period (with Site as a Blocking Factor) for Montgomery County Survey

The data for the Contingency Analysis in Figure 18 are shown in Appendix D. Contingency Table of Species by Month for Montgomery County, VA. The Null Hypothesis, when comparing the two variables, beetle species abundance and sampling period, is that the number of specimens of the beetle species collected is independent of (not associated with) sampling period. A Chi-Squared test indicated that there is a significant association between species and period of sampling ($\chi^2 = 191.49$; df = 14; $P < 0.0001$). To test whether the association of beetle species abundance and sampling period is influenced by sampling site the Cochran-Mantel-Haenszel test was used. The Null Hypothesis is that beetle species and sampling period are mutually independent in the population sampled after controlling for sampling site. The Cochran-Mantel-Haenszel test showed that after adjusting for sampling site, there is a significant association between species and period ($\chi^2 = 184.49$; df = 14; $P < 0.0001$).

In Figure 18, there appears to be a negative correlation between the sampling periods Early and Mid season, Early and Late season, and Mid and Late season. The top half of the figure represents species occurrence during the Late period, while the bottom half of the figure shows species that occurred mainly during the Early and Mid periods. The longer vector of the Early period indicates greater variability in abundances compared to Mid and Late periods. Since *N. tomentosus* and *N. americana* have similar column profiles (See Contingency Table – Appendix D. Contingency Table of Species by Month for Montgomery County, VA), they are located closer together on the biplot.

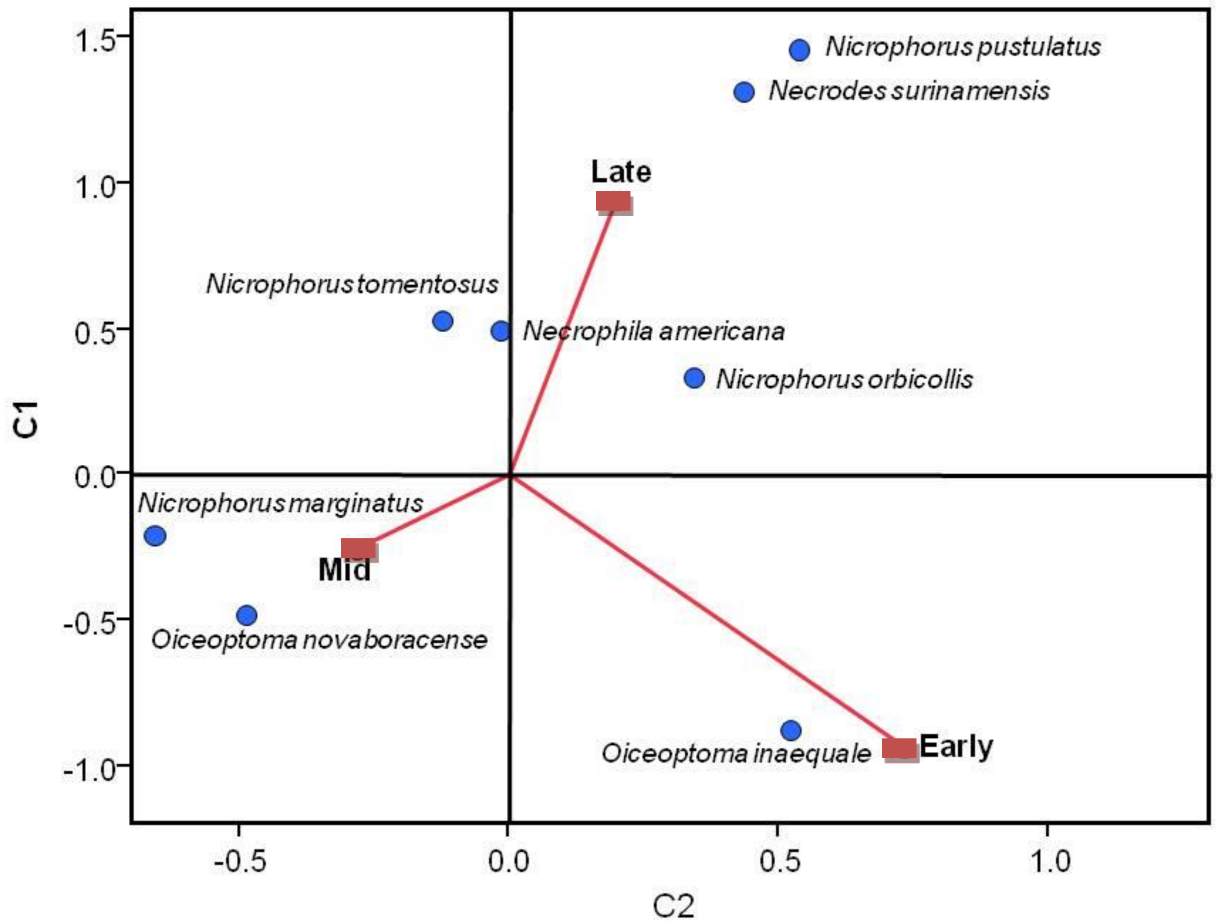


Figure 18. Correspondence Analysis showing the relationship between period (red lines) and species (blue circles) from silphid beetle surveys conducted in Montgomery County, VA from mid-April to mid-October. Early = April, May; Mid = June, July; Late = August, September, October. C1 = Correspondence Dimension 1; C2 = Correspondence Dimension 2

3.3.5 Contingency Analysis of Species by Month (with Site as a Blocking Factor) for Montgomery County Survey

The data for the Contingency Analysis in Figure 19 are shown in Appendix E. Contingency Table of Species by Site for Montgomery County, VA. The Null Hypothesis, when comparing the two variables, beetle species abundance and month sampled, is that the number of specimens of the beetle species collected is independent of (not associated with) month sampled. The Chi-Squared test indicated that there is a significant association between species and the month ($\chi^2 = 259.41$; df = 42; $P < 0.0001$). To test whether the association of beetle species abundance and month sampled is influenced by sampling site the Cochran-Mantel-Haenszel test was used. The Null Hypothesis is that beetle species and month sampled are mutually independent in the population sampled after controlling for sampling site. The Cochran-Mantel-Haenszel test showed that after adjusting for site, there is a significant association between species and the month sampled ($\chi^2 = 231.89$; df = 42; $P < 0.0001$).

Figure 19 shows positive correlation between all months that have acute angles associated with them (April and May), negative correlation between all months that have obtuse angles associated with them (April and August), and little to no correlation between any months that have an angle of 90 degrees (April and October). The top half of the figure represents species occurrence during the months of July, August, September, and October; while the bottom half of the figure shows species that occurred mainly during the months of April, May, and June. The longer vector of April, May, and October indicates greater variability in abundances compared to June, July, August, and September. Since *N. marginatus* and *O. noveboracense* have similar column profiles (See Contingency Table – Appendix E. Contingency Table of Species by Site for Montgomery County, VA), they are located closer together on the biplot.

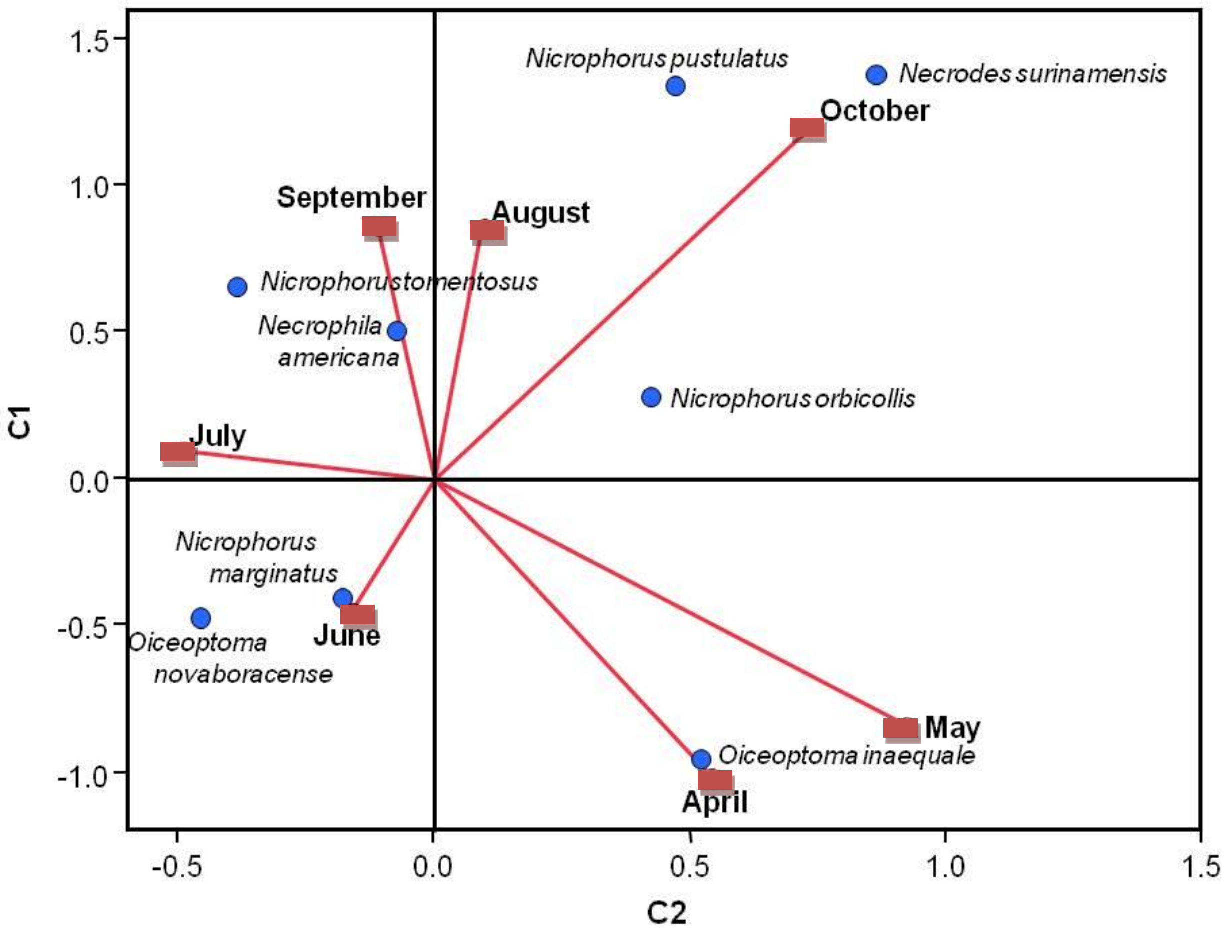


Figure 19. Correspondence Analysis showing the relationship between month (red lines) and species (blue circles) from silphid beetle surveys conducted in Montgomery County, VA from mid-April to mid-October. C1 = Correspondence Dimension 1; C2 = Correspondence Dimension 2

Chapter 3.4 Discussion

There were a total of 4375 silphid beetles captured in ten counties of Virginia during the summers of 2007 and 2008, with 11 species in four genera identified. Beetles in the subfamily Silphinae were more commonly collected than those in the Nicrophorinae. The dominant species was *N. americana* in both summers, with beetles in the genus *Oiceoptoma* being the second most frequently collected beetles in the traps. *Nicrophorus* species in general were less commonly collected, with *N. tomentosus* and *N. orbicollis* being prevalent in the summer of 2007, and *N. tomentosus* and *N. pustulatus* being the most frequently trapped species in the summer of 2008. In similar studies in Ohio, Shea (2005) stated that *O. noveboracense* was the dominant species collected. In New Jersey, Shubeck, et al. (1981) also reported that *O. noveboracense* was the most prevalent species collected, with *N. americana* the second most common. Most reports from Kansas (Lingafelter 1995) and Georgia (Ulyshen and Hanula 2004), on the other hand, indicated *O. inaequale* was more common with *N. americana* being the second most frequently collected species. There could be many reasons for not finding silphids during the first week of surveying in Wise County in the summer 2007. Surveying commenced in May, which may have been too early for silphids in that area to be active. The initial use of mice may also have not been as effective as the chicken due to the strong odor of decay associated with the ripened chicken. Since tops with funnels were initially used, it may have reduced scent dispersal from the bucket. Adjustments were made by getting rid of the tops and funnels, and surveying stayed the same the rest of the summer of 2007 and all of the summer of 2008.

Nicrophorus americanus was not found at any time during survey periods, supporting the belief that the species is extinct in Virginia. *Nicrophorus carolinus* was only collected in one county in the summer of 2008. Further surveys need to be conducted to determine the status of this species in Virginia. Anderson and Peck (1985) and Peck and Kaulbars (1987) reported that *N. carolinus* is widespread throughout the United States, from central states south to Texas and Arizona, as well as most of the southeastern states, but it is unclear whether they are in Virginia. Before this study, there was only one documented specimen found in Virginia and it is housed in the collection at the Virginia Natural History Museum in Martinsville, Virginia. Anderson and Peck (1985) stated that *N. defodiens* Mannerheim is also widespread throughout the United States, but tends to be more concentrated in the northwestern, north central and northeastern states. Interestingly this species was only collected at higher elevations in one county in Virginia in 2007.   Anderson and Peck (1985) also stated that *N. marginatus* is found throughout the majority of the United States and all of Virginia. This species was only found in two counties – Pulaski County (where it was the most common silphid found) and Appomattox (where only one specimen was found). The trapping results for the other *Nicrophorus* species suggested that the distributions of these beetles in Virginia may be more limited than originally believed, but further studies are needed. In addition to silphids, a number of ants, roaches, a large number of histerids, staphylinids, dung beetles, hide beetles, and dermestids (larvae and adults) were found in the baited pitfall traps throughout both summers.

According to the data, there appeared to be little or no correlation between Mid and Late sampling periods with respect to the species and their abundances. However, there appeared to be a negative correlation between Early and Mid period samples, and similarly between Early and Late period samples. There was greater variability in species abundances in the Early period compared to Mid and Late periods. There was a positive correlation between the species abundance in the Blue Ridge Mountains and Appalachian Plateau, but this finding was not unexpected since both regions have higher elevations. Surprisingly there was also a positive correlation between the species abundance between the Tidewater and Valley and Ridge regions. Since *N. marginatus* was found in both regions, this could partially explain the positive correlation, in spite of the differences between the two regions. The negative correlation between Piedmont and the other four geographic regions (Figure 16) is more difficult to explain, but could result from a number of factors such as differences in land use patterns.

In Montgomery County, 3276 total beetles were trapped from mid-April to mid-October of 2008. The prevalent species within Nicrophorinae was *Nicrophorus tomentosus* (60 beetles) and within the Silphinae it was *Necrophila americana* (669 beetles). More beetles were trapped in June than in any other month with a total of 602, September being the lowest with a total of 62 beetles trapped. *Necrophila americana* was trapped every month, while *O. noveboracense, O. inaequale, Necrodes surinamensis*, *N. pustulatus* (which was the least trapped species with only 1 beetle), *N. orbicollis*, and *N. tomentosus* were only found during certain months.

Analyses were conducted to compare species abundance by sampling site. The biplot showed little or no correlation between Moore Farm and Kentland 2 with respect to the species and their abundances. However, there appeared to be a positive correlation between Price's Fork and Moore Farm; and a negative correlation between Price's Fork and Kentland 1, Price's Fork and Kentland 2, Kentland 1 and Kentland 2, and Kentland 1 and Moore Farm. It was interesting that Kentland 1 and Kentland 2 were negatively correlated, since they were in the same general area. Kentland 1 was within the forest edge and Kentland 2 was next to an open field/forest edge, but they were at the same elevation. The biplot also indicated there was greater variability in species abundances in Price's Fork compared to Kentland 1, Kentland 2, and Moore's Farm. There was a significant association between species and sampling site, therefore a closer look was taken to compare species abundance by sampling period, with sampling site as a blocking factor. According to these data there appeared to be a negative correlation between the sampling periods Early and Mid, Early and Late, and Mid and Late; a similar pattern to the statewide data. The analysis of species abundance by months sampled, with sampling site as a blocking factor, supported the findings from the period sampling. The data showed there were positive correlations between early months such as April and May, negative correlation between months like April and August, and little to no correlation between months such as April and October. The figure also showed that the months of April, May, and October indicated greater variability in species abundances compared to the months of June, July, August, and September.

Additional surveys are needed to get a better understanding of the distribution and abundance of *N. carolinus, N. defodiens, and N. marginatus* abundances and the possible existence of *N. americanus* in Virginia. Inquiries should also be made into the feasibility of reintroducing the American burying beetle to the Commonwealth of Virginia, a species that was at one time common within the state.

Chapter 4. Summary

Silphid (carrion, sexton, or burying) beetles are known worldwide, and according to Peck (2001), there are eight genera and 30 species in North America north of Mexico. With two subfamilies in the Silphidae: Nicrophorinae and Silphinae - Nicrophorinae is best known for interring the carcass and parental behavior, while Silphinae is not associated with either behavior.

There have been numerous studies conducted in many states in the United States on the distribution and behavior of silphid beetles (Washington - Hatch and Rueter, Jr. (1934), New Jersey - Shubeck et al. (1981), Mississippi - Lago and Miller (1983), Kansas - Lingafelter (1995) and Rintoul et al. (2005), Nebraska - Ratcliffe (1996), Georgia - Uiyshen and Hanula (2004), Wisconsin - Katovich et al. (2005), and Ohio - Shea (2005)). However, little research has been conducted in Virginia, especially in regard to *Nicrophorus americanus* (American burying beetle).

Two counties in each of the five geographic regions in Virginia were surveyed in the summers of 2007 and 2008: Wise County and Dickenson County (Appalachian Plateau), Pulaski County and Rockbridge County (Valley and Ridge), Grayson County and Bath County (Blue Ridge Mountains), Nottoway County and Appomattox County (Piedmont), and Accomack County and Suffolk County (Coastal Plain). Eleven species and four genera were trapped in the two summers. Traps were also placed in one area of Montgomery County and left there from April until October in 2008 in order to survey the variability of silphid beetles throughout the active season in one area.

A total of 4375 silphid beetles were found during the summers of 2007 and 2008, consisting of four genera and 11 species. In the Montgomery County survey from April to

October of 2008, a total of 3276 beetles were trapped with four genera and eight species collected.

Species diversity and seasonal abundance of beetles in the Family Silphidae is, in fact, similar for the different geographic regions of Virginia. Contingency analyses were conducted to analyze the data from the statewide and the Montgomery County surveys. Silphid beetle abundance was compared with sampling period with geographic region as a blocking factor, and silphid beetle abundance was also compared with region (or site in Montgomery Co.), with year as a blocking factor. Chi-squared tests and Cochran-Mantel-Haenszel tests (for blocking factor) were used to test for significant association, and there was significant association in all tests conducted. Finally, correspondence analyses were used to show graphically the relationships between variables. Montgomery County analysis showed that, like the statewide analysis, there appeared to be a negative correlation between all sampling periods (Early, Mid, and Late).

REFERENCES:

Amaral, M., A. Kozol, and T. French. 1997. Conservation status and reintroduction of the endangered American burying beetle. Northeast. Nat. 4: 121-132.

Anderson, R.S. and S.B. Peck. 1985. The carrion beetles of Canada and Alaska. The insects and arachnids of Canada, Part 13. Coleoptera: Silphidae and Agyrtidae. Canadian Government Publishing Centre Supply and Services Canada. Ottawa, Canada. 1-121.

Anonymous 1. Tree of Life Web Project. 1995. Arthropoda. Version 01 January 1995 (temporary). http://tolweb.org/tree/. Accessed October 15, 2007.

Anonymous 2. Ohio Department of Natural Resources. American burying beetle. http://www.dnr.state.oh.us/Home/wild_resourcessubhomepage/ResearchandSurveys/WildlifePop WildlifePopulationStatus/AmericanBuryingBeetle/tabid/19233/Default.aspx. Accessed December 9, 2012.

Anonymous 3. Roger Williams Park Zoo. American burying beetle repopulation project. http://www.rwpzoo.org/143/american-burying-beetle-repopulation-project. Accessed December 9, 2012.

Backlund, D. C. 1997. New records of the endangered American burying beetle, *Nicrophorus americanus* Olivier, (Coleoptera: Silphidae) in South Dakota. Coleop. Bull. 51: 53-58.

Balduf, W. V. 1969 (1935 Repr.). The bionomics of entomophagous Coleoptera, 6. Silphidae. Carrion Beetles. E.W. Classey. Hampton, Middlesex. 1: 68-75.

Barnhart, M. C. and R. Brown. 2002. A survey for American burying beetles in Southwest Missouri. http://courses.missouristate.edu/ChrisBarnhart/Documents/pdf_files/ Barnhart%20and%20Brown%202002.pdf. 1-12. Accessed December 9, 2012.

Bedick, J. C., B. C. Ratcliffe, W. W. Hoback and L. G. Higley. 1999. Distribution, ecology, and population dynamics of the American burying beetle [*Nicrophorus americanus* Olivier (Coleoptera, Silphidae)] in south-central Nebraska, USA. J. Insect Conserv. 3: 171-181.

Bedick, J. C., B. C. Ratcliffe and L. G. Higley. 2004. A new sampling protocol for the endangered American burying beetle, *Nicrophorus americanus* Olivier (Coleoptera: Silphidae). Coleop. Bull. 58: 57-70.

Blatchley, W.S. (1910). Family VIII. Silphidae. An illustrated descriptive catalogue of the Coleoptera or beetles known to occur in Indiana. The Nature Publishing Co. Indianapolis, IN. 272-277.

Carlton, C.E. and F. Rothwein. 1998. The endangered American burying beetle, *Nicrophorus americanus* Olivier, at the edge of its range in Arkansas (Coleoptera: Silphidae). Coleop. Bull. 52: 179-185.

Clausen, S. 1998. Applied Correspondence Analysis. An Introduction. Sage Publications, Inc. CA., USA. 69 pp.

Creighton, J. C., C. C. Vaughn, and B. R. Chapman. 1993. Habitat preference of the endangered American burying beetle (*Nicrophorus americanus*) in Oklahoma. Southwest. Nat. 38: 275-276.

Creighton, J. C. and G. D. Schnell. 1998. Short-term movement patterns of the endangered American burying beetle *Nicrophorus americanus*. Biol. Conserv. 86: 281-287.

Fabre, J. 1924. The glow-worm and other beetles (Alexander Teixeira De Mattos, Trans.). New York: Dodd, Mead and Company. (Original work published 1919). XI-XII: 294-351

Grayson, K. 2008. Personal communication by e-mail on August 11, 2008.

Greenacre, M.J. 1993. Correspondence Analysis in Practice. Academic Press, Ltd., CA., USA. 195 pp.

Grimaldi, D. and M. S. Engel. 2005. Coleoptera and Strepsiptera. Evolution of insects. Cambridge University Press. New York. 10: 357-366.

Hatch, M. H. 1927. Studies on the Silphinae. J. N.Y. Entomol. Soc. 35: 331-370.

Hatch, M. H. 1957. The beetles of the Pacific Northwest: Part II Staphyliniformia. University of Washington Press. Seattle. 16: 5-16.

Hatch, M. H. and W. Rueter, Jr. 1934. Coleoptera of Washington: Silphidae. University of Washington Publications in Biology. Washington. 1: 151-161.

Headstrom, R. 1977. The beetles of America. A.S. Barnes and Co., Inc. New Jersey. 104-108.

Jaques, H.E. 1915. The fish feeding Coleoptera of Cedar Point. Ohio Nat. J. Sci. 15: 525-528.

Katovich, K., N.L. Kriska, A.H. Williams, and D.K. Young. 2005. Carrion beetles (Coleoptera: Silphidae) of Wisconsin. Great Lakes Entomol. 38: 30-41.

Kozol, A. J., M. P. Scott, and J. F. A. Traniello. 1988. The American burying beetle, *Nicrophorus americanus*: Studies on the natural history of a declining species. Psyche. 95: 167-176.

Lago, P.K. and P.R. Miller. 1983. Records of Mississippi Silphidae [sic] [Coleoptera] with a key to the species known to occur in the state. J. Miss. Acad. Sci. 28: 83-87.

Limolino, M. V., J. C. Creighton, G. D. Schnell, and D. L. Certain. 1995. Ecology and conservation of the endangered American burying beetle (*Nicrophorus americanus*). Conserv. Biol. 9: 605-614.

Lingafelter, S.W. 1995. Diversity, habitat preferences, and seasonality of Kansas carrion beetles (Coleoptera: Silphidae). J. Kans. Entomol. Soc. 68: 214-223.

Manly, B.F.J. 2004. Multivariate Statistical Methods. A Primer. 3rd Ed. Chapman and Hall/CRC, Boca Raton, FL. 214 pp.

Mckenna-Foster, A., W. T. Maple, and R. S. Kennedy. 2005. American burying beetle (*Nicrophorus americanus*) survey and reintroduction on Nantucket 2005. http://www.stlzoo.org/downloads/NantucketMAFinalReport.pdf. 1-14. Accessed April 2008.

Milne, L. J. and M. J. Milne. 1944. Note on the behavior of burying beetles (*Nicrophorus Spp*.). J. N.Y. Entomol. Soc. 52: 311-327.

Milne, L. J. and M. J. Milne. 1976. The social behavior of burying beetles. Sci. Am. 235: 84-89.

Newton, A. and S. B. Peck. 1975. Baited pitfall traps for beetles. Coleop. Bull. 29: 45-46.

Peck, S.B. 2001. Family 21. Silphidae. American Beetles. CRC Press. Boca Raton, FL. 1: 268-271.

Peck, S. and M. M. Kaulbars. 1987. A synopsis of the distribution and bionomics of the carrion beetles (Coleoptera: Silphidae) of the conterminous United States. Proc. Entomol. Soc. Ont. 118: 47-81.

Raithel, C. J., H. S. Ginsberg, and M. L. Prospero. 2006. Population trends and flight behavior of the American burying beetle, *Nicrophorus americanus* (Coleoptera: Silphidae), on Block Island, RI. J. Insect Conserv. 10: 317-322.

Ratcliffe, B.C. 1996. The carrion beetles (Coleoptera: Silphidae) of Nebraska. Bull. Univ. Neb. State Mus. 13: 1-100.

Rintoul, D.A., L.M. Krueger, C. Woodard, and J.E. Throne. 2005. Carrion beetles (Coleoptera: Silphidae) of the Konza Prairie Biological Station. J. Kans. Entomol. Soc. 78: 124-133.

Scott, M. P. 1996. Communal breeding in burying beetles. Am. Sci. 84: 376-382.

Scott, M. P. 1998. The ecology and behavior of burying beetles. Annu. Rev. Entomol. 43: 595-618.

Selous, C.F. 1911. A preliminary note on the so-called carrion-feeding Coleoptera. Entomol. Month. Mag. 2: 86-89.

Shea, J. 2005. A survey of the Coleoptera associated with carrion at sites with varying disturbances Cuyahoga County, Ohio. Ohio J. Sci. 105: 17-20.

Shubeck, P.P., N.M. Downie, R.L. Wenzel, and S.B. Peck. 1981. Species composition and seasonal abundance of carrion beetles in an oak-beech forest in the Great Swamp National Wildlife Refuge (N.J.). Entomol. News. 92: 7-16.

Sikes, D. S. and C. J. Raithel. 2002. A review of hypotheses of decline of the endangered American burying beetle (Silphidae: *Nicrophorus americanus* Olivier). J. Insect Conserv. 6: 103-113.

Smith, G., S.T. Trumbo, D.S. Sikes, M.P. Scott, and R.L. Smith. 2007. Host shift by the burying beetle, *Nicrophorus pustulatus*, a parasitoid of snake eggs. J. Evol. Biol. 20: 2389-2399.

Steele, B.F. 1927. Notes on the feeding habits of carrion beetles. J. N.Y. Entomol. Soc. 35: 77-81.

U.S. Fish and Wildlife Service. 1991. American Burying Beetle (*Nicrophorus americanus*) Recovery Plan. Newton Corner, Massachusetts. 80 pp.

Ulyshen, M.D. and J.L. Hanula. 2004. Diversity and seasonal activity of carrion beetles (Coleoptera: Silphidae) in northeastern Georgia. J. Entomol. Sci. 39: 460-463.

APPENDIX A. CONTINGENCY TABLE OF SPECIES BY PERIOD FOR THE COMMONWEALTH OF VIRGINIA

Count Col % Row %	*N. carolinus*	*N. defodiens*	*N. marginatus*	*N. orbicollis*	*N. pustulatus*	*N. sayi*	*N. tomentosus*	*Necrodes surinamensis*	*Necrophila americana*	*O. inaequale*	*O. noveboracense*	Total
Early	1 33.33 0.07	0 0.00 0.00	1 1.39 0.07	30 9.23 2.16	28 14.51 2.01	0 0.00 0.00	44 15.38 3.17	8 3.51 0.58	420 20.32 30.22	478 89.85 34.39	380 65.40 27.34	1390
Mid	0 0.00 0.00	7 10.61 0.50	32 44.44 2.27	184 56.62 13.05	70 36.27 4.96	9 40.91 0.64	112 39.16 7.94	42 18.42 2.98	705 34.11 50.00	53 9.96 3.76	196 33.73 13.90	1410
Late	2 66.67 0.13	59 89.39 3.75	39 54.17 2.48	111 34.15 7.05	95 49.22 6.03	13 59.09 0.83	130 45.45 8.25	178 78.07 11.30	942 45.57 59.81	1 0.19 0.06	5 0.86 0.32	1575
Total	3	66	72	325	193	22	286	228	2067	532	581	4375

Appendix A. Surveys of silphid beetles from the Summers of 2007 and 2008. The first number in each cell is the actual number of beetles found. The second number in each cell is the percent of the Column Total. The third number in each cell is the percent of the Row Total.

APPENDIX B. CONTINGENCY TABLE OF SPECIES BY REGION FOR THE COMMONWEALTH OF VIRGINIA

Count Col % Row %	*N. carolinus*	*N. defodiens*	*N. marginatus*	*N. orbicollis*	*N. pustulatus*	*N. sayi*	*N. tomentosus*	*Necrodes surinamensis*	*Necrophila americana*	*O. inaequale*	*O. noveboracense*	Total
Appalachian Plateau	0 0.00 0.00	0 0.00 0.00	0 0.00 0.00	87 26.77 20.96	6 3.11 1.45	5 22.73 1.20	127 44.41 30.60	4 1.75 0.96	86 4.16 20.72	66 12.41 15.90	34 5.85 8.19	415
Blue Ridge Mountains	0 0.00 0.00	66 100.00 8.99	0 0.00 0.00	93 28.62 12.67	22 11.40 3.00	17 77.27 2.32	52 18.18 7.08	7 3.07 0.95	242 11.71 32.97	117 21.99 15.94	118 20.31 16.08	734
Piedmont	0 0.00 0.00	0 0.00 0.00	6 8.33 0.48	34 10.46 2.72	110 56.99 8.79	0 0.00 0.00	27 9.44 2.16	197 86.40 15.75	371 17.95 29.66	231 43.42 18.47	275 47.33 21.98	1251
Tidewater	3 100.00 0.43	0 0.00 0.00	1 1.39 0.14	90 27.69 13.01	21 10.88 3.03	0 0.00 0.00	32 11.19 4.62	11 4.82 1.59	394 19.06 56.94	97 18.23 14.02	43 7.40 6.21	692
Valley and Ridge	0 0.00 0.00	0 0.00 0.00	65 90.28 5.07	21 6.46 1.64	34 17.62 2.65	0 0.00 0.00	48 16.78 3.74	9 3.95 0.70	974 47.12 75.92	21 3.95 1.64	111 19.10 8.65	1283
Total	3	66	72	325	193	22	286	228	2067	532	581	4375

Appendix B. Surveys of silphid beetles from the Summers of 2007 and 2008. The first number in each cell is the actual number of beetles found. The second number in each cell is the percent of the Column Total. The third number in each cell is the percent of the Row Total.

APPENDIX C. CONTINGENCY TABLE OF SPECIES BY PERIOD FOR MONTGOMERY COUNTY, VA

Count Col % Row %	*Necrodes surinamensis*	*Necrophila americana*	*Nicrophorus marginatus*	*Nicrophorus orbicollis*	*Nicrophorus pustulatus*	*Nicrophorus tomentosus*	*Oiceoptoma inaequale*	*Oiceoptoma noveboracense*	Total
Early	0 0.00 0.00	5 3.80 10.71	0 0.00 0.00	2 17.23 4.59	0 0.00 0.00	0 0.00 0.00	32 46.97 65.82	9 10.20 18.88	49
Mid	1 7.78 0.73	64 46.03 32.73	0 90.16 0.17	4 33.82 2.27	0 0.00 0.00	8 49.89 3.94	36 53.03 18.72	81 88.85 41.43	195
Late	17 92.22 16.55	69 50.17 68.43	0 9.84 0.04	6 48.96 6.31	0 100.00 0.23	8 50.11 7.59	0 0.00 0.00	1 0.96 0.85	101
Total	18	138	0	13	0	15	69	91	345

Appendix C. Survey of silphid beetles from the Summers of 2007 and 2008. The first number in each cell is the actual number of beetles found. The second number in each cell is the percent of the Column Total. The third number in each cell is the percent of the Row Total.

APPENDIX D. CONTINGENCY TABLE OF SPECIES BY MONTH FOR MONTGOMERY COUNTY, VA

Count Col % Row %	*Necrodes surinamensis*	*Necrophila americana*	*Nicrophorus marginatus*	*Nicrophorus orbicollis*	*Nicrophorus pustulatus*	*Nicrophorus tomentosus*	*Oiceoptoma inaequale*	*Oiceoptoma noveboracense*	Total
April	0 0.00 0.00	3 1.99 8.33	0 0.00 0.00	1 3.83 1.52	0 0.00 0.00	0 0.00 0.00	21 30.95 64.39	9 9.37 25.76	33
May	0 0.00 0.00	3 1.81 15.63	0 0.00 0.00	2 13.40 10.94	0 0.00 0.00	0 0.00 0.00	11 16.02 68.75	1 0.83 4.69	16
June	1 3.66 0.54	32 22.90 25.54	0 90.16 0.27	4 28.07 2.96	0 0.00 0.00	2 10.85 1.34	33 47.57 26.34	53 58.80 43.01	124
July	1 4.12 1.06	32 23.14 45.39	0 0.00 0.00	1 5.74 1.06	0 0.00 0.00	6 39.05 8.51	4 5.46 5.32	27 30.04 38.65	71
August	8 43.59 11.00	55 39.77 76.25	0 0.00 0.00	4 30.11 5.45	0 84.60 0.28	4 27.33 5.82	0 0.00 0.00	1 0.96 1.20	72
September	1 2.75 7.14	3 2.17 42.86	0 0.00 0.00	1 7.66 14.29	0 0.00 0.00	3 16.27 35.71	0 0.00 0.00	0 0.00 0.00	7
October	8 45.88 37.49	11 8.24 51.13	0 9.84 0.16	1 11.19 6.56	0 15.40 0.16	1 6.51 4.49	0 0.00 0.00	0 0.00 0.00	22
Total	18	138	0	13	0	15	69	91	345

Appendix D. Survey of silphid beetles from the Summers of 2007 and 2008. The first number in each cell is the actual number of beetles found. The second number in each cell is the percent of the Column Total. The third number in each cell is the percent of the Row Total.

APPENDIX E. CONTINGENCY TABLE OF SPECIES BY SITE FOR MONTGOMERY COUNTY, VA

Count Col % Row %	*Necrodes surinamensis*	*Necrophila americana*	*Nicrophorus marginatus*	*Nicrophorus orbicollis*	*Nicrophorus pustulatus*	*Nicrophorus tomentosus*	*Oiceoptoma inaequale*	*Oiceoptoma novaboracense*	Total
Kentland 1	12 65.75 8.83	56 40.77 41.59	0 0.00 0.00	6 43.13 4.16	0 84.60 0.15	5 34.82 3.95	22 31.55 15.98	34 37.89 25.35	136
Kentland 2	6 30.95 5.27	31 22.16 28.65	0 90.16 0.31	4 28.20 3.44	0 0.00 0.00	9 55.31 7.95	23 33.50 21.50	35 38.77 32.88	107
Moore Farm	1 3.30 0.81	32 23.18 43.16	0 9.84 0.05	3 21.40 3.76	0 15.40 0.05	1 3.80 0.79	17 24.76 22.89	21 23.34 28.50	74
Price's Fork	0 0.00 0.00	19 13.89 68.39	0 0.00 0.00	1 7.27 3.38	0 0.00 0.00	1 6.07 3.32	7 10.19 24.91	0 0.00 0.00	28
Total	18	138	0	13	0	15	69	91	345

Appendix E. Survey of silphid beetles from the Summers of 2007 and 2008. The first number in each cell is the actual number of beetles found. The second number in each cell is the percent of the Column Total. The third number in each cell is the percent of the Row Total.