SEASONAL DYNAMICS OF THE AMERICAN BURYING BEETLE (*Nicrophorus americanus*) IN EASTERN OKLAHOMA

By

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Title of Study: SEASONAL DYNAMICS OF THE AMERICAN BURYING BEETLE (*Nicrophorus americanus*) IN EASTERN OKLAHOMA

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Abstract: American Burying Beetle (ABB) (*Nicrophorus americanus*) populations have been in decline since the early 1900's, and much effort has been put into studying the survival of this now endangered species. Burying beetles (Coleoptera:Silphidae), which rely solely on carrion as both a reproductive and food resource, exclude most other competitors by burying small mammal and other vertebrate carcasses underground. Fertilized females may reproduce alone or in groups, but a carcass is usually buried by a male and female pair.

Small carrion are a short-lived, high-quality resource for many insects. The competition for this valuable resource is strong and has probably shaped many ecological, behavioral, and physiological traits of the associated insects. Not only do the burying beetles compete with other insects, they must also compete with vertebrate scavengers.

In southeastern Oklahoma, the ABB compete directly or indirectly with many other insect species. I completed 2273 trap-nights using above-ground pitfall traps that were placed in three separate areas within Pittsburg and Hughes counties in southeastern Oklahoma. After two years of sampling in this region, the four most abundant insect species trapped in conjunction with the ABB were the red-lined carrion beetle *Necrodes surinamensis*, the congener *Nicrophorus orbicollis*, the ridged carrion beetle *Oiceoptoma inaequale*, and the beetle *Euspilotus assimilis* from the Family Histeridae. Whole-season trap-catch data revealed significant overlap among these species and suggests that intraspecific competition may play an important role in local ABB persistence.

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CHAPTER I

INTRODUCTION

Nicrophorus americanus (American Burying Beetle (ABB)) is the largest species in its genus, is considered highly social, and exhibits extensive parental care (Lomolino et al. 1995). ABB populations have been in decline since the early 1900's, and much effort has been put into studying the survival of this now endangered species. Listed as critically endangered in 1989, the current known ABB range has been reduced from 35 U.S. states and three Canadian provinces, to only eight U.S. states (Bedick et al. 1999, USFWS 2014a).

Small carrion are a quickly depleted, high-quality resource for many insects (Hanski 1990, Koulianos and Schwarz 2000). Competition for this valuable resource is strong and has more than likely shaped many behavioral, ecological, and physiological traits of species that utilize carrion (Hanski 1990, Koulianos and Schwarz 2000). Burying beetles (Silphidae: *Nicrophorus* Fabricius), which rely solely on carrion as both a reproductive and food resource, exclude most other decomposer competitors by quickly burying small vertebrate carcasses underground (Pukowski 1933, Scott 1998, Koulianos and Schwarz 2000). This exclusion enables Silphids to thrive in a multitude of habitats provided carrion is readily available.

ABBs are considered strong interspecific competitors because of their size, but also regularly compete with other ABBs until a dominant single pair remains (Scott and Traniello 1989). In southeastern Oklahoma, little is known about the seasonal dynamics of insect species that utilize carrion as a resource. Results from previous studies in the region are based on limited seasonal sampling efforts but indicate that the most likely ABB competitors are the sexton beetle *Nicrophorus orbicollis* and the pustulated carrion beetle *Nicrophorus pustulatus*. Multi-year, season-long sampling that defines the temporal dynamics of insects that utilize fresh carrion will help identify the most likely competitors of ABBs in southeastern Oklahoma. The primary objective of my research was to document the seasonal activity of ABBs and the potential for competition from congeneric species.

CHAPTER II

REVIEW OF LITERATURE

Description and Biology of ABB

Physical Description. Nicrophorus americanus (American burying beetle (ABB)) is the largest of the *Nicrophorus* genus, as well as the largest member of the carrion beetle Family, Silphidae. Adults range in size from 25 to 45mm in length, with pronotum width ranging from 8 to 12mm (USFWS 2014a). ABBs are easily distinguished from other burying beetles by the large, orange maculation centered on the raised portion of their pronotum. The elytra are mainly black with two pair of scalloped orange maculations; one near mid-center and the other towards the tip of each elytron. Another large orange mark covers the frons (frontal head plate), and the clubbed sections of the clavate antenna are also orange. Tenerals (newly-emerged adults) tend to have more pliable, shiny elytra whereas older adults' elytra are more matte and dull in color which is likely due to the burrowing behavior exhibited by this beetle. Exact age is difficult to distinguish due to this behavior.

The sex of ABBs is easily distinguishable; males have large, square-like orange maculations on their clypeus (below the frons) whereas females have smaller, triangular-shaped markings. Females tend to be larger, but size is not necessarily diagnostic when identifying sex. Both ABB sexes are equipped with an impressive set of mandibles, which are necessary when rendering carrion for reproductive preparation and fending off competitors.

Behavior, Movement and Seasonal Biology. The ABB is a nocturnal species that lives for approximately one year. ABBs are most active from two to four hours after sunset, with no captures recorded immediately after sunrise (Walker and Hoback 2007, Bedick et al. 1999). During daylight hours, ABBs are assumed to bury themselves under detritus (Kozol, 1989). Adult ABB activity seems to decline in adverse weather conditions, such as heavy rain and strong winds (Bedick et al. 1999). Kozol et al. (1988) found that burying beetles were successfully trapped repeatedly on both rainy and windy nights, provided the temperature was above 59º F (15º C) on Block Island, Rhode Island.

Studies indicate that ABBs may move distances up to 29.19km within segments of their range (Bedick et al. 1999, Creighton and Schnell 1998, Jurzenski 2012, Jurzenski et al. 2011, Schnell et al. 1997-2006), and can be attracted to carrion at distances ranging from 0.25–10.0km over a six night period with an average flight distance of 1.23km per night. Creighton and Schnell (1998), and Peyton (1996) recaptured marked ABBs from as far away as 11.2km. Bedick *et al*. (2004) recaptured five ABBs from distances of 3–6km with an average nightly movement of 1km, and 85% of recaptures moving distances of 0.5km per night. However, in Nebraska Jurzenski *et al*. (2011) established the longest record of a 1-night movement by an ABB; 29.19km.

During September/October when night-time ambient temperatures drop below 60°F (15.5°C), ABBs are reported to initiate an inactive period (USFWS 2008). ABB's bury themselves as fully-sclerotized adults in the soil during these cooling early autumn periods for the duration of the winter, but habitat structure (i.e., woodland, grassland, grazed pastureland, etc.) does not appear to be a critical factor for over-winter survival rate in Oklahoma (Holloway and Schnell 1997). Overwintering adults become active during late-spring and produce a first generation that emerges in the summer. These teneral adults appear at peak numbers during the late summer, but it is unclear whether a second generation is produced in southeastern Oklahoma prior to overwintering (Kozol et al. 1988, Bedick et al. 2004, USFWS 1991).

ABB Habitat. The habitat preferences of ABBs have been studied extensively; possibly due to its listing as an endangered species. ABBs are considered habitat generalists, and can thrive in oak-hickory forests, grazed pasturelands, riparian zones, grasslands, and bottomlands found in Oklahoma, as well as in the coastal scrublands of Block Island, Rhode Island (Creighton et al. 1993). A study performed by Creighton *et al*. (1991) indicates that ABBs preferred grassland and oak-hickory forests in Oklahoma. In 1996, more than 300 ABBs were captured in Nebraska habitats consisting of grassland prairie, forest edge, and scrubland (Ratcliffe 1996).

Perhaps the most important factor that influences preparation of carrion for reproduction is the habitat's soil characteristics (Anderson 1982, Lomolino and Creighton 1996). Soil characteristics are important in determining how deep ABBs bury carrion and their success in establishing brood chambers. Although the burying depth of ABBs in Oklahoma has not been adequately studied, *Nicrophorus* species have been known to bury carcasses up to 20cm in laboratory studies (Anderson 1982) and recent field-based study results are consistent with the 20cm burial depth (Schnell et al. 2007). Others studies have shown that ABBs will bury carrion to depths up to 68cm (Hoback 2011).

While previous studies indicate that the ABB is a habitat generalist in terms of seeking food resources, it is likely more selective when it comes to burial sites needed for breeding. Although *N. tomentosus* and *N. defodiens* have been known to have limited reproductive success in arboreal settings (Lowe and Lauffe 2012), it is widely understood that ABBs bury carrion in the soil for reproduction, and soils that are too compact may limit the ability of ABBs to excavate a suitable brood chamber. Likewise, soils with a high sand percentage will not support the walls of the brood chamber and therefore also are not suitable for reproduction. Research on ABB habitat preferences indicates that adults were most active and carcasses were most apt to be buried in loose, loamy soils with high sand content and low clay content (Lomolino et al. 1995, Lomolino and Creighton 1996, Creighton et al. 1993). Level or gentle sloping topography (3% or less) and a well formed layer of organic litter at the ground surface are typical habitat of occupied by ABBs (USFWS 1991). Indeed, results from an experiment by Muths (1991) indicate that *N. orbicollis* preferred to bury carcasses in native soil that had been augmented with a 2:1 ratio of native (Riley County, KS) soils and bulk material in the form of clipped switchgrass (*Panicum virgatum*), over soils with a 5:1 ratio, or unadulterated native soil (Muths 1991).

Because of their sub-terrestrial activities, ABBs are subject to drowning, and soils that are saturated are unsuitable for brood chamber construction. Any of these aforementioned soil conditions that are considered unsuitable for carcass burial are thus unlikely suitable for reproductive habitats. Anderson (1982) suggested that, in general, male and female ABBs placed on carrion are more successful at establishing brood chambers in forested habitats due to the rich, loose soil characteristics. Lomolino and Creighton (1996) found reproductive success was higher in forest habitats verses grassland, because more carcasses were buried in the forested areas than the grassland habitat (Lomolino and Creighton 1996, Creighton et al. 1993). Carrion may be also more difficult to obtain and secure in grasslands due to the absence of a detritus layer and may be more difficult to bury due to the tendency of these soils to be more compact. However, of the carcasses buried in these two different habitats, numbers of larvae per brood did not appear to be influenced.

Holloway and Schnell (1997) observed positive correlations between the numbers of ABB captured and the biomass of small mammals and birds within a given range of where ABBs were found, regardless of the predominant vegetation structure. This suggests that habitat alone is not the key environmental factor for ABB occupation. Reproductive host availability also plays a role in ABB dynamics. Scavenging studies (performed by OSU Zoology department) indicate that the scavenge rate was higher in grasslands than in forested areas, suggesting that there may be less carrion available to ABBs in grasslands versus forests (Unpublished OSU Small Mammal Survey 2014).

Reproduction, Carcass Preparation, and Parental Care. While the ABBs life history requirements are similar to other *Nicrophorus spp.*, it is the largest burying beetle in North America and requires larger carrion sources to obtain maximum reproductive potential (i.e. maximum number of offspring) (USFWS 1991, Kozol et al. 1988, Trumbo 1992, Billman et al. 2014). ABBs preferred carrion sources for reproduction include dead birds and mammals weighing from 48.19 – 297.67 grams, with an optimum mass of 99.22 – 198.45grams (USFWS 1991).

Immediately upon emergence from their winter hibernation, overwintering ABBs begin searching for a mate and a suitable sized carcass for reproduction. *Nicrophorus* species are capable of locating a carcass between one and 48 hours of the host's death, but finding them in less than two days is more likely (Conley 1982, Ratcliffe 1996). Successful location of carrion depends upon a combination of factors including availability of suitable habitats for small vertebrates (Lomolino and Creighton 1996), density of competing scavengers (vertebrate and invertebrate), searching ability, reproductive status, and ambient temperature (Ratcliffe 1996, Wilson and Knollenberg 1984). Kozol *et al*. (1988) have shown that ABBs have no preference for avian verses mammalian carcasses, but once a carcass has been found, interspecific and intraspecific competition is likely until a single dominant pair claims the carcass (Scott and Traniello 1989). Being larger in size, ABBs are thought to out-compete other burying beetles (Kozol et al. 1988), and the successful couple will bury the carrion and begin to process it for reproduction.

In Nebraska, Bedick *et al*. (1999) found that ABBs reproduce only once per year. However, in a laboratory study, Lomolino and Creighton (1996) found that five of eight ABB pairs produced a second brood indicating that Oklahoma populations have the potential to produce two generations per year. Because the ABB is considered univoltine in most of its range and completes its lifecycle in one year, each year's population levels are largely dependent on the reproductive success of the year prior. This fluctuation is thought to be related to the "feast or famine" nature of the carrion resources on which they depend. Additionally, populations may be cyclic due to weather, disease, etc., with high abundance in one year, followed by a decline in numbers the next year. However, these short-term stochastic events are not believed to have catastrophic effects on robust populations (USFWS 2008).

Parental care in *Nicrophorus* is unique because both parents participate in the rearing of young (Scott 1989, Trumbo 1990). Brood care by at least one parent, usually the female, is critical for larval survival (Ratcliffe 1996). Fertilized females may reproduce alone or in groups, but a carcass is usually buried by a male and female pair. During burial, the pair strips the carcass of hair or feathers, likely destroying fly eggs and larvae. They then form the carcass into a brood ball using anal and oral secretions and store it in a small "crypt"; a brood chamber with stable walls of compressed soil. After burial is completed, which takes up to 24 hours (Wilson et al. 1984, Otronen 1988, Scott 1990, Koulianos and Schwarz 2000), the female lays its eggs in a chamber close to the brood ball. When the larvae hatch, they enter the crypt and begin to feed on the brood ball. The parents remain in the crypt for several days. They maintain the crypt, preserve the carcass with anal and oral secretions, defend the larvae against intruders, and then feed them (upon larval emergence) with predigested carrion. Brood sizes of ABBs can be greater than 25 larvae, but 12-18 is typical (Kozol 1990b). The reproductive time-frame from carrion burial to teneral adult emergence is anywhere from 48 to 65 days (Bedick et al. 1999, Kozol 1995, Ratcliffe 1996), and females are reproductively capable immediately upon emergence.

Historical data/population and distribution

ABB Endangered Species Status. The ABB was proposed for listing under the Endangered Species Act October 1988 (53 FR 39617) and designated as critically endangered

July 13, 1989 (54 FR 29652). Although the Final Recovery Plan was signed on September 27, 1991, critical conservation habitat has not been designated for the ABBs (USFWS 2014a). Due to the severity and unclear cause of ABB population decline, USFWS recovery protocol was focused on short-term improvement to describe the status of the species, rather than undertaking a broader range of actions and establishing clear criteria to bring about full species recovery. Therefore, criteria such as identifying three sustainable populations of 500 individuals were developed for downlisting, but not for recovery (USFWS 2014a, 1991, 2008). At that time, only two known disjunct populations inhabited the periphery of the species historical range of 35 states: four counties in Oklahoma and one small island (Block Island) off the coast of Rhode Island (USFWS 2008a).

Since the 1991 development of the Recovery Plan, other ABB populations have been discovered. Thus, the recovery objective of reducing or eliminating the immediate threat of extinction through discovery or establishment of new populations was met (USFWS 2008). Currently, at least four Environmental Protection Agency (EPA) Level III eco-regions contain natural ABB populations that are estimated at greater than 1,000 individuals (USFWS 2008). Extinction modeling results suggest that populations of greater than 1,000 ABBs can remain demographically viable without severe catastrophic events or carrying capacity (K) reductions through reduced carrion availability, loss of habitat, or habitat fragmentation (Amaral et al. 2005). The ABB remains endangered throughout its current range due to lack of populations in the Great Lakes and Southeast States, and remaining threats to existing populations (USFWS 2008).

ABB Historical Distribution. The historic geographic range of the ABB included over 150 counties in 35 U.S. states, which covered most of temperate eastern North America and along the southern borders of three eastern Canadian provinces (USFWS 1991, Peck and Kaulbars 1987). However, official records of ABB populations are inconsistent throughout this broad historical range (Figure 1).

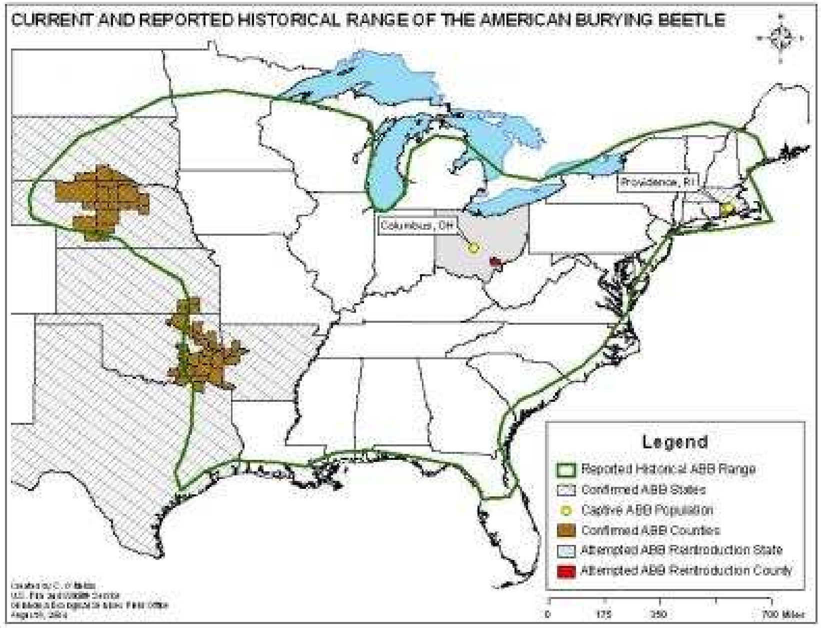

Figure 1. Historical Range of *Nicrophorus americanus* (USFWS)**.**

There are additional records from the Midwest region into the three Canadian provinces and in the northeastern United States and down to the Southeastern region (USFWS 1991), but is widely thought that the ABB disappeared from over 90 percent of its historical range during the 20th century (Lomolino et. al. 1995). The last known ABB specimens along the Atlantic seaboard, from New England to Florida, were collected in the 1940s near Long Island New York, Black Mountain North Carolina, Penikese Island Massachusetts, and Cambridge Maryland (USFWS 1991). In 1989, at the time of Endangered Species listing, known ABB populations were limited to Block Island, Rhode Island; and in Latimer County, Oklahoma. Survey efforts increased shortly thereafter, and the ABB was discovered in South Dakota, Nebraska and several other counties in Oklahoma.

Currently, the ABB is known to inhabit eight U.S. states: on Block Island off the coast of Rhode Island, Nantucket Island off coastal Massachusetts, eastern Oklahoma, western Arkansas (Carlton and Rothwein 1998), south-central and north-central Nebraska (Ratcliffe 1996, Bedick et al. 1999), southeastern Kansas (Sikes and Raithel 2002), south-central South Dakota (Backlund and Marrone 1995, Ratcliffe 1996), and northeast Texas (Godwin 2003). The ABBs in Missouri are a nonessential experimental population (under section 10(j) of the ESA) that was reintroduced in 2012. Most ABB populations are located on private land. Populations recently known to exist on public land including: Ouachita National Forest, Arkansas / Oklahoma; Ozark-St. Francis National Forests, Arkansas; Camp Gruber, Oklahoma; Fort Chaffee, Arkansas; Lake Eufaula, Oklahoma; Sequoyah National Wildlife Refuge, Oklahoma; James Collins Wildlife Management Area, Oklahoma; McAlester Army Ammunition Plant, Oklahoma; Block Island National Wildlife Refuge, Rhode Island; Valentine National Wildlife Refuge, Nebraska; and Camp Maxey, Texas (USFWS 2014a).

Confirmed Oklahoma ABB sightings or captures since 1992 occurred in the following counties: Atoka, Bryan, Cherokee, Choctaw, Coal, Craig, Creek, Haskell, Hughes, Johnston, Latimer, Le Flore, Marshall, Mayes, McCurtain, McIntosh, Muskogee, Okfuskee, Okmulgee, Osage, Pittsburg, Pontotoc, Pushmataha, Rogers, Seminole, Sequoyah, Tulsa, and Wagoner, and Washington (29 counties). Additional counties with ABB habitat and potential occurrence due the proximity to the above counties include: Adair, Carter, Delaware, Garvin, Kay, Lincoln, Love, McClain, Murray, Nowata, Ottawa, Pawnee, Payne, and Pottawatomie (Figure 2).

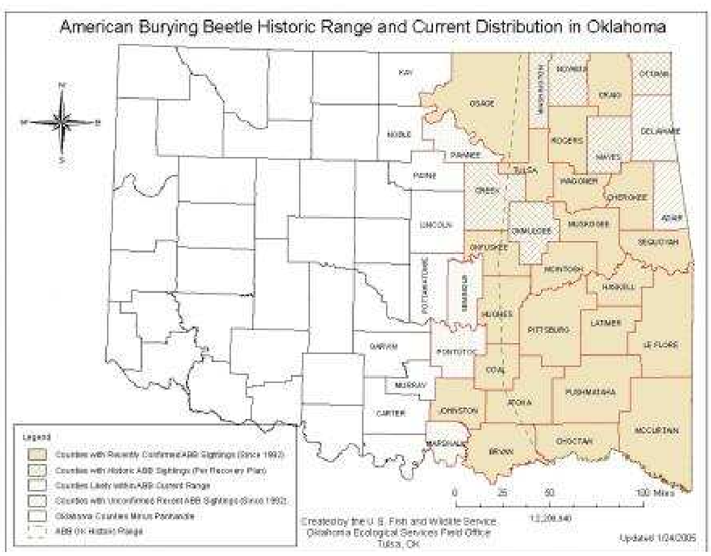

Figure 2. *Nicrophorus americanus* Distribution in Oklahoma (USFWS).

Numerous surveys have been conducted throughout eastern Oklahoma, western Arkansas, and northern Texas. Most of these were undertaken to determine whether ABBs inhabit areas anticipated to have soil disturbance actions slated for development projects and were sporadically performed without systematic or complete coverage across Oklahoma. Creighton *et al*. (1993) indicated that the population of ABBs at Camp Gruber, Oklahoma has been relatively constant since 1991 when annual surveys on the military installation were initiated. While numbers of ABBs have varied within this landscape annually, a self-sustaining population or metapopulation appears to exist (Schnell et al. 2005). In 2007, a total of 676 ABBs were captured in 1,305 trap nights at Camp Gruber; and in 2009, a total of 423 ABBs were captured at 59 trapping locations at Camp Gruber. Presently, it is known that eastern Oklahoma contains a sustained population of ABBs within their historical range (This thesis).

In 2010, reports from researchers at The Nature Conservancy's Tallgrass Prairie Preserve in Osage County, Oklahoma estimated a population of approximately 1,400 ABBs (USFWS 2014a). ABB populations at Camp Gruber and the Tallgrass Prairie Preserve are thought to represent high densities of ABBs. In Texas, ABB has been successfully captured at much lower numbers on Camp Maxey, Lamar County from 2004 - 2008, and a single ABB was documented at the Nature Conservancy's Lennox Woods, Red River County in 2004. No ABBs have been captured at Camp Maxey from 2009 - 2012, despite intensive sampling (Godwin and Minich 2005, USFWS 2008) (Figure 3).

The isolated population of ABBs on Block Island off the coast of Rhode Island appears to be stable, as is the population in southern Tripp County, South Dakota. The Nebraska Loess Hills population was thought to be declining in 2006 and 2007, but that short-term decline was most likely caused by a drought and the subsequent effects on carrion availability. The population there has increased to perhaps tens of thousands in recent years following relief from the drought (W. Hoback, Oklahoma State University, pers. comm., September, 2014). Based on trapping efforts over the last two years in the Sandhills region in central Nebraska, many more ABBs occur in that population than previously thought. In 2010, over 1,000 ABBs were captured on and near USDA Project lands in Nebraska with relatively limited trapping events.

Population levels in Oklahoma and Arkansas can fluctuate biennially, but long term upward or downward trends can be troublesome to discern. ABB populations on Fort Chaffee in western Arkansas and Camp Gruber in eastern Oklahoma along with populations in Nebraska, all have populations at levels that are believed to be able to withstand the effects of stochastic weather events (USFWS 2008). Limited information is available on stability of small populations of ABBs elsewhere.

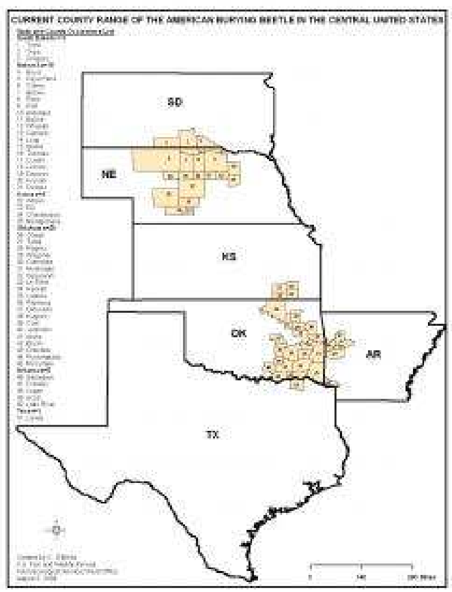

Figure 3. *Nicrophorus americanus* Range in South-central United States (USFWS)

Factors Associated with ABB Decline

Carrion Availability. The ABB requires fresh carrion in a particular size range, which is a finite resource in space and time. The ABB's scattered distribution and density, and their vulnerability to extinction are likely due to having this specific reproductive resource requirement (USFWS 2014a, Karr 1982, Pimm et al. 1988, Peck and Kaulbars 1987). Data available for ABB populations on Block Island, support the assertion that the primary mechanism for the species range-wide declines "lies in its dependence on carrion of a larger size class relative to that used by all other North American burying beetles, and that the optimum-sized carrion resource base has been reduced throughout the species range" (USFWS 1991). Since the middle of the 19th century, certain animal species in the ABB's preferred mass range have either been eliminated from North America or their numbers have been reduced over their historical range (USFWS 1991). This includes the passenger pigeon (*Ectopistes migratorius),* greater prairie-chicken (*Tympanchus cupido)* and wild turkey *(Meleagris gallopavo)*. At one time, the passenger pigeon was estimated to have been the most common bird in the world, with numbers ranging from 3 to 5 billion (Ellsworth and McComb 2003). There were once as many passenger pigeons within the estimated historical range of the ABB as there are numbers of all bird species currently overwintering in the United States. Wild turkeys and black-tailed prairie dogs (*Cynomys ludovicianus*) for example, occurred within the historical range of the ABB, and until recently, were extirpated from much of their former range or declined significantly. The wild turkey is currently on its way to recovering from this decline, but both of these animals at high densities may have supported ABB populations (Miller et al. 1990, USFWS 2008). During the westward expansion in North America, land use changes that fragmented native forests and grasslands created more edge habitats along with the removal of top-level carnivores such as the grey wolf (*Canis lupis*) and eastern cougar (*Puma concolor*). This extirpation and fragmentation resulted in the increase in meso-carnivore populations, which prey on small birds and mammals and compete directly with ABBs for carrion.

Habitat Changes. Schnell et al. (1997-2003, 1997-2006) reported that areas of high ABB concentration appeared to shift yearly throughout Fort Chaffee, Arkansas and Camp Gruber, Oklahoma, even though land use practices within each area stayed relatively constant (USFWS 2008). Losses associated with a one-time or short-term event are less likely to affect populations than longer-duration adverse events. Fragmentation of large contiguous habitats into smaller patches may increase species richness, but the species composition ultimately may change (Fujita et al. 2008). Forests and grassland fragmentation has been shown to cause a decrease of indigenous animal species and an increase in meso-carnivores that thrive in disturbed areas. The American crow (*Corvus brachyrhynchos),* raccoon (*Procyon lotor),* red fox (*Vulpus fulva),* opossum (*Didelphis virginiana),* striped skunk (*Mephitis mephitis),* coyotes (*Canis latrans),* and other opportunistic predators (Wilcove et al. 1986) are some of the meso-carnivores that displace indigenous species. Large habitat expanses that once contained high densities of indigenous animal species suitable to support ABB populations are now artificially fragmented, and may be causing increased competition for carrion resources among this “new” predator/scavenger community. Matthews (1995) experimentally placed carcasses in various habitats in Oklahoma where ABBs and *N. orbicollis* had been previously documented, then tracked the organisms that scavenged them. Of the carcasses, 83 percent were claimed by ants, flies, and vertebrate scavengers; about 11 percent were claimed by *N. orbicollis*, and only one was claimed by ABBs.

Competition Among Carrion Feeders. For most guilds (a group of organisms that exhibit similar habitat requirements and play a similar role within a community), the larger species tend to feed on larger prey, occupy more different types of habitats, dominate in competitive battles, and have larger home ranges. However, the larger species may be subject to exploitative competition (resource-limiting) from smaller species (USFWS 2014a, Ashmole 1968, Gittleman 1985, Hespenheide 1971, Rosenzweig 1968, Schoener and Gorman 1968, Vitt 2000, Werner 1974, Wilson 1975, and Zaret 1980). Larger prey are generally less abundant than smaller prey (Peters 1983, Brown and Maurer 1987, Damuth 1991, Lawton 1990, and Scharf at al. 2000) and larger guild member species require larger home ranges. Although weighing less than 2 grams, the ABB is nevertheless the largest member of a guild that specializes on vertebrate carcasses, an unpredictable and valuable resource (USFWS 2014a). Contrasting with other members of their guild, ABBs must persist over larger areas and a greater diversity of habitats to find suitable carrion for food and reproduction. Larger carcasses are more difficult to bury and are more energetically expensive than smaller ones (Creighton et al. 2007). While the ABB's large body size alone does not necessarily indicate endangerment, rarity and extinctions tend to be higher for the larger species within trophic levels or guilds (Vermeij et al. 2008, Diamond 1984, Martin and Klein 1984, Vrba 1984, Owen-Smith 1988, 1992).

Body size seems to be the most important factor for success in competitive battles between ABBs and congeners when securing carrion. Kozol *et al*. (1988) found that the largest individuals displace smaller burying beetles in a laboratory setting. ABBs have been recorded usurping a carcass that had been buried by another *Nicrophorus* species. However, environmental (and other) factors other than body size (e.g., ambient temperature or activity patterns) might also have some effect on the outcome of competition in general (Wilson and Fudge 1984). Trumbo (1992) showed that the potential for competition for carrion from other *Nicrophorus* congeners increased with carcass size, and Scott *et al*. (1987) saw similar results with carrion-feeding flies. Creighton *et al*. (2007) found that habitat fragmentation caused more scavenging by vertebrate species, a decreased availability of carcasses of the appropriate size, and increased competition between *Nicrophorus* species. It is expected that as ABB populations decline, the competitive struggles between ABBs and its sympatric congeners for sub-optimally sized carcasses would increase.

The ABBs most similar *Nicrophorus* relative is *N. orbicollis*. Although *N. orbicollis* is smaller in physical size, based on historical geographic range, similar ecological and physical tolerances (e.g., diurnality, overlapping breeding season), and phylogenetic information indicates these beetles may be each other's closest surviving relatives (Szalanski et al. 2000). Because of this similarity, they are likely each other's strongest congeneric competitors (Sikes and Raithel 2002), and interspecific competition may play a part in population assessment at the local level.

Typically, ABB surveys result in ten or more times more *N. orbicollis* than ABBs (Lomolino and Creighton 1996, Amaral et al. 1997, Carlton and Rothwein 1998). Kozol (1989) found that there was an 8:1 ratio of *N. orbicollis* to ABBs on Block Island, Rhode Island while Walker (1957) collected 19 times more *N. orbicollis* (175) than ABBs (9) where and when the ABBs were encountered in Tennessee. While the ABB is generally more successful in securing and preparing carcasses greater than 100 grams vs *N. orbicollis,* data suggest that *N. orbicollis* may be a formidable competitor for ABBs (Sikes and Raithel 2002) and may have actually increased in abundance in those areas where ABBs had been extirpated (USFWS 1991). In addition, *N. marginatus* may also be a competitor with ABBs, and this congener is on average slightly larger and utilizes larger carcasses for reproduction than *N. orbicollis.* In Nebraska and South Dakota, *N. marginatus* are typically more abundant than in Oklahoma (Backlund and Marrone 1997, Bedick et al. 1999).

Another threat to ABB success is brood parasitism after oviposition by other burying *Nicrophorus* species near ABB "owned" carcass (Trumbo 1992, 1994, Müller et al. 1998). *Nicrophorus pustulatus* is a known brood parasite of other burying beetles, but the effect on ABBs has not been studied extensively. Among locations where ABBs exist or could exist, documentation of the seasonal activity and abundance of important competitors would reveal critical periods of overlap where competition would be strongest. Detailed experiments would then reveal mechanisms during competitive outcomes between ABBs and other carrion beetles that overlap in space and time.

Describing intraspecific and interspecific interactions and the outcomes between generations requires both field and laboratory studies that adequately address the dynamics and mechanisms of competition at appropriate spatial scales. Because of their larger size, ABB is expected to successfully outcompete other *Nicrophorus* species for carrion of a particular size (size preferred by ABB) (Kozol et al. 1988), and interspecific competition should then have little impact on populations between generations. Therefore, based on our knowledge of ABB biology, intraspecific competition would be a significant factor influencing ABB populations from one generation to the next when preferred carrion numbers are limiting. No studies have been conducted that have adequately evaluated the outcomes of competition between ABBs or among *Nicrophorus* species between generations.

Estimating ABB Populations

Current USFWS ABB sampling methodologies are modified versions of those used in Kozol's (1989) assessment of the Block Island population, and procedures utilized in 1994 by Bedick et al. (2004) in central Nebraska. Both studies indicated that 5-gallon pitfall traps baited with natural carrion was the most efficient ABB trapping method. Sampling efficiency and individuals collected per unit of effort are the key issue when sampling most insects. However, when sampling endangered species, the key issue is minimizing injury and mortality. Current USFWS ABB trapping protocol states that for presence/absence surveys, trapping should continue for a minimum of five consecutive nights, and that each trap covers a 0.5 mile radius within the survey area (USFWS 2010). Trapping success is expressed as ABB per trap-night; i.e. the number of ABBs captured divided by the number of traps used, which will have been multiplied by the number of nights deployed (e.g. 24 ABB captured over 3 nights using 2 traps is 24 ÷ (3x2) = 4.00 trapping success or efficiency).

While ABBs are somewhat easy to capture, population estimates of ABBs are difficult to obtain. Although using pitfall traps is thought to be inherently inaccurate when determining populations of animals, a mark and re-capture technique may be useful for estimating ABB population size. The mark-recapture approach assumes that marked and unmarked ABBs are equally likely to be captured, and that a necessary number of the animals would be recaptured from one trapping event to the next. However, due to ability of the ABBs to move over wide distances, and the fact that they retreat underground for several weeks for reproduction, these assumptions may not apply (USFWS 2014a).

False negative results are always a possible outcome of ABB trapping surveys. These false negatives are a clear indication of the inefficiencies associated with current sampling methodologies, but for low populations may also indicate a comparatively fast turnover rate in the (trappable) ABB population due to factors such as natural mortality rates, dispersal, and sub terrestrial reproductive activities (Creighton and Schnell 1998). Trap numbers and the relative distance between them may influence ABB capture (Bedick 2004), but it is currently unknown how trap deployment in space and time alters individual trap efficiency (Bedick et al. 2004).

Conservation Efforts for ABBs

It is unknown if extirpated ABB populations can successfully be re-established. Due to their ability to fly long distances in search for food, ABBs may disperse from a release area, making it difficult to establish a self-sustaining population. A reintroduction effort on Nantucket Island, Massachusetts, is still being evaluated and has not yet achieved the critical population size required for long-term existence. However, in 2011, trapping efficiency (ABBs per trap-night) at this location was greater than any year since 2006 (LoPresti et al. 2011). In 2011, a multi-year reintroduction effort was initiated in Ohio's Wayne National Forest; however, to date no ABBs have been recaptured. Another reintroduction effort implemented in Missouri in 2012 has shown successful reproduction of ABBs, though the population viability remains unknown.

Protection of large tracts of suitable native habitat appears to be the best practice for augmenting ABB conservation, since large areas of native habitat tend to support the highest known ABB populations (USFWS 2014a). Oklahoma's Tallgrass Prairie Preserve, and large military blocks of land such as Ft. Chaffee in Arkansas, Camp Gruber and the McAlester Army Ammunition Plant in Oklahoma support relatively large and sustained ABB populations.

Additional lands have been established at the Tall Grass Prairie Preserve through ABB mitigation funds and more ABB mitigation banks have been established in Oklahoma that should contribute to the recovery of the species (USFWS 2014a).

The USFWS has migrated from using bait-away stations, to capture and release efforts, and finally to the current protocol of presence/absence surveying and subsequent mitigation for those wishing to develop lands within known ABB habitat. In Oklahoma, bait away stations were used as a technique to remove ABBs from a given area prior to project soil disturbance without handling the ABBs or physically relocating them to another area (USFWS 2005). Capture and release methods were used (mainly as a research vehicle) and allowed developers to trap ABBs on land slated for disturbance and relocate them to protected areas with a known ABB presence. The USFWS now utilizes mitigation practices when developers opt to disturb lands within potential ABB habitat. A third-party presence/absence survey is implemented, and conservation acreage is established or “banked” if ABB’s are present. These conservation lands must meet strict guidelines and may be individual lands provided by the developer, conservation banks provided by entities other than the developer (bank sponsors), or third-party mitigation organizations. Bank sponsors generally have responsibility over larger tracts of conservation land and handle mitigations from multiple development projects, whereas third-party mitigation lands are used for a single project (USFWS 2014b).

Since becoming listed as an endangered species, ABB ecology, historical and present distributions, and habitat requirements have been studied extensively. Although current populations in Oklahoma appear to be stable or increasing, conservation efforts such as limiting ABB habitat fragmentation and utilizing practical land-use management could strengthen ABB populations within its current range.

CHAPTER III

METHODS AND MATERIALS

Study sites 2013-2014. Studies were performed at James Collins Wildlife Management Area (WMA) Blocker, Oklahoma, McAlester Army Ammunition Plant (McAAP) McAlester, Oklahoma, and private lands near Lamar, Oklahoma. GPS coordinates of individual trapping locations are shown in Table 1.

Table 1. ABB Trap #'s, Locations, at James Collins WMA, Lamar and McAAP, Oklahoma.

Site	Trap #	Lat	Long	Site	Trap #	Lat	Long	Site	Trap #	Lat	Long
James Collins	1	35.032217	-95.480550	Lamar	1	35.030479	-96.138361	MCAAP	1AC	34.811970	-96.004790
James Collins	2	35.036812	-95.476862	Lamar	2	35.030595	-96.129710	MCAAP	1BC	34.795330	-96.005180
James Collins	3	35.025755	-95.480278	Lamar	3	35.032148	-96.131147	MCAAP	2AC	34.774610	-95.963990
James Collins	4	35.033507	-95.485634	Lamar	4	35.029164	-96.132788	MCAAP	2BC	34.757240	-95.960530
James Collins	5	35.036576	-95.443617	Lamar	5	35.031680	-96.138980	MCAAP	3AC	34.822310	-95.945460
James Collins	6	35.011643	-95.455631	Lamar	6	35.025800	-96.134900	MCAAP	3BC	34.806090	-95.941900
James Collins	7	35.005564	-95.492831	Lamar	7	35.031350	-96.131830	McAAP	R1	34.805879	-95.875586
James Collins	8	35.027382	-95.518868	Lamar	8	35.020590	-96.128220	McAAP	R2	34.785877	-95.885500
James Collins	9	35.030888	-95.453474	Lamar	9	35.038910	-96.140360	McAAP	R3	34.781022	-95.914467
James Collins	10	35.017941	-95.484454	Lamar	10	35.039140	-96.135410	McAAP	R4	34.755868	-96.013551
James Collins	11	35.028942	-95.494363	Lamar	E1	35.026150	-96.123860	McAAP	R5	34.863562	-95.972767
James Collins	12	35.032479	-95.372438	Lamar	E2	35.023800	-96.123360	McAAP	R6	34.877089	-95.941755
James Collins	13	34.985448	-95.475997	Lamar	ENE1	35.027115	-96.124409	McAAP	R7	34.816176	-95.969285
James Collins	14	35.002346	-95.599004	Lamar	ENE2	35.025432	-96.123729	McAAP	R8	34.853438	-95.853680
James Collins	15	35.005290	-95.490830	Lamar	NNE1	35.028741	-96.124992	McAAP	R9	34.842500	-95.942778
James Collins	16	35.003910	-95.491500	Lamar	NNE2	35.028741	-96.124992	McAAP	R10	34.828611	-95.901111
James Collins	17	35.003991	-95.493168	Lamar	S1	35.023140	-96.126950	McAAP	R11	34.879722	-95.957500
James Collins	18	35.007137	-95.492277	Lamar	S2	35.022320	-96.124740	McAAP	R12	34.811667	-95.978333
								McAAP	R13	34.857354	-95.899241

Traps within these locations were deployed at least 0.5 miles (~800 meters) apart according to USFWS protocols (USFWS 2010). Sampling/trapping events consisted of consecutive three-day periods during the spring/summer/fall, with four to five days in between events. At James Collins WMA, eighteen traps were deployed in 2013 and the three most efficient traps sites from 2013 were redeployed in 2014 (Table 1, Figures 4 and 5; traps 7, 17, and 18). In 2013, there were 98 three-day trapping events and 90 three-day events in 2014. At the Lamar site (Table 1, Figure 6), eighteen traps were deployed in 2013 and trap locations 1, 4, 5, and 7 were redeployed in 2014 for this study. There were 90 three-day events in 2013 and eight three-day events in 2014. At the McAAP site, nineteen traps were deployed in 2013 for 28 three-day events, and again in 2014 for 89 three-day trapping events (Table 1, Figure 7).

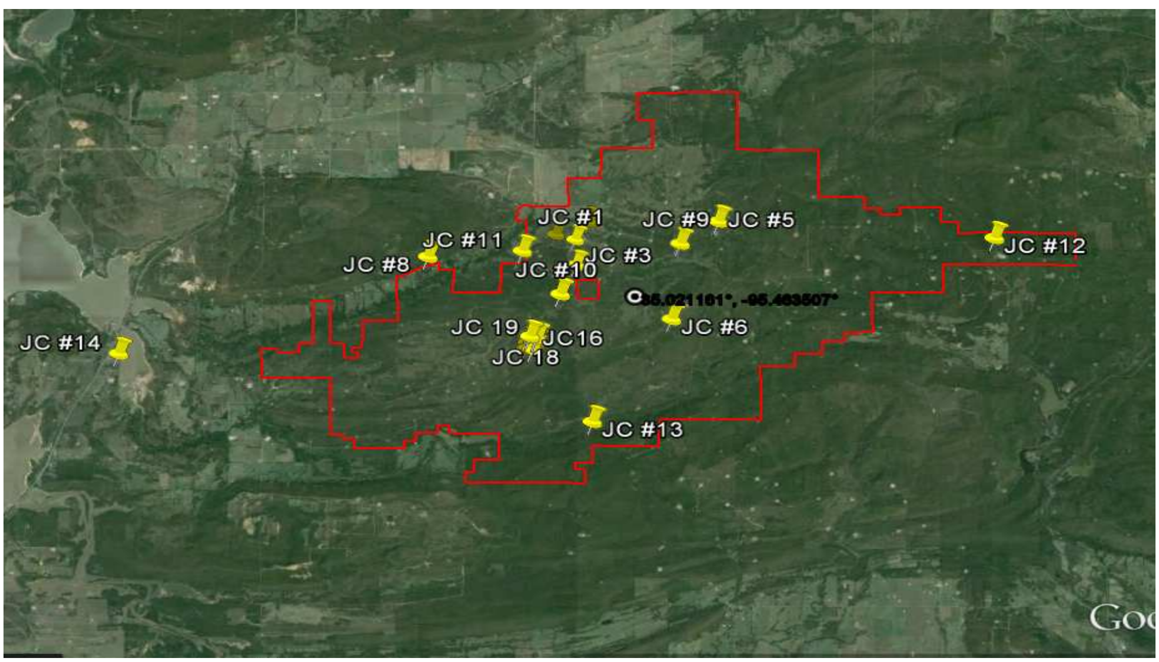

Figure 4. 2013 – 2014 ABB trap locations at James Collins WMA, Oklahoma (Google Earth).

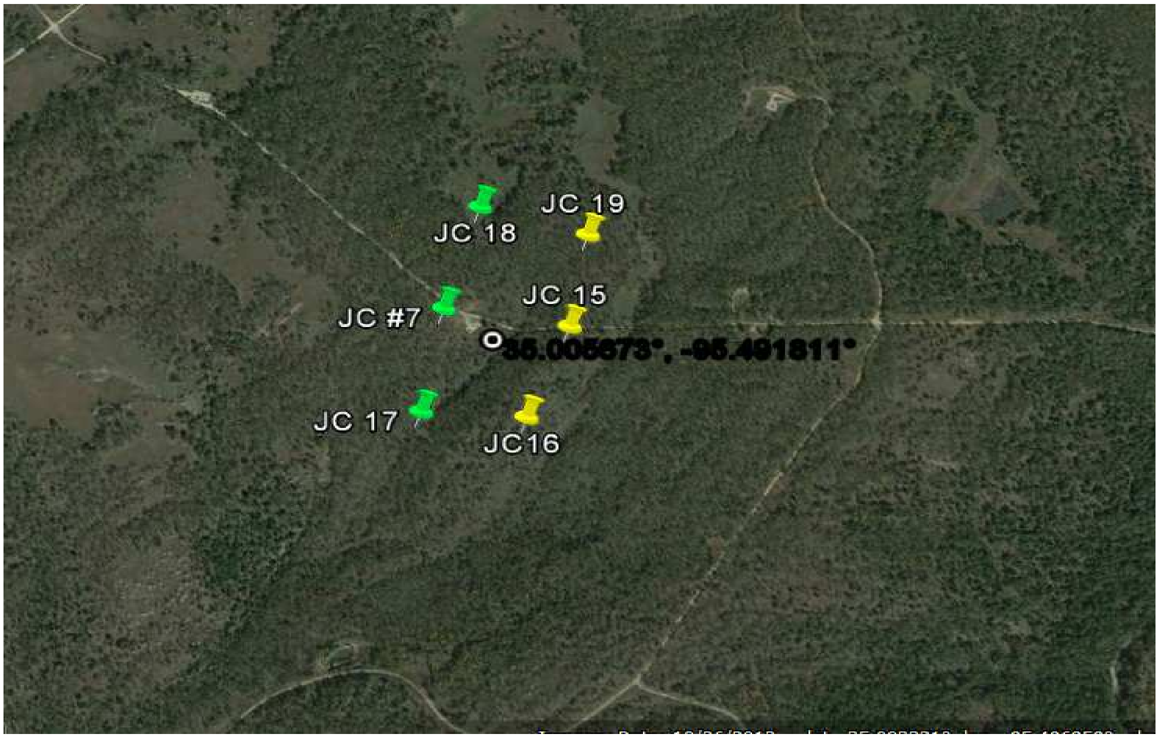

Figure 5. 2014 ABB trap locations at James Collins WMA, Oklahoma (Google Earth).

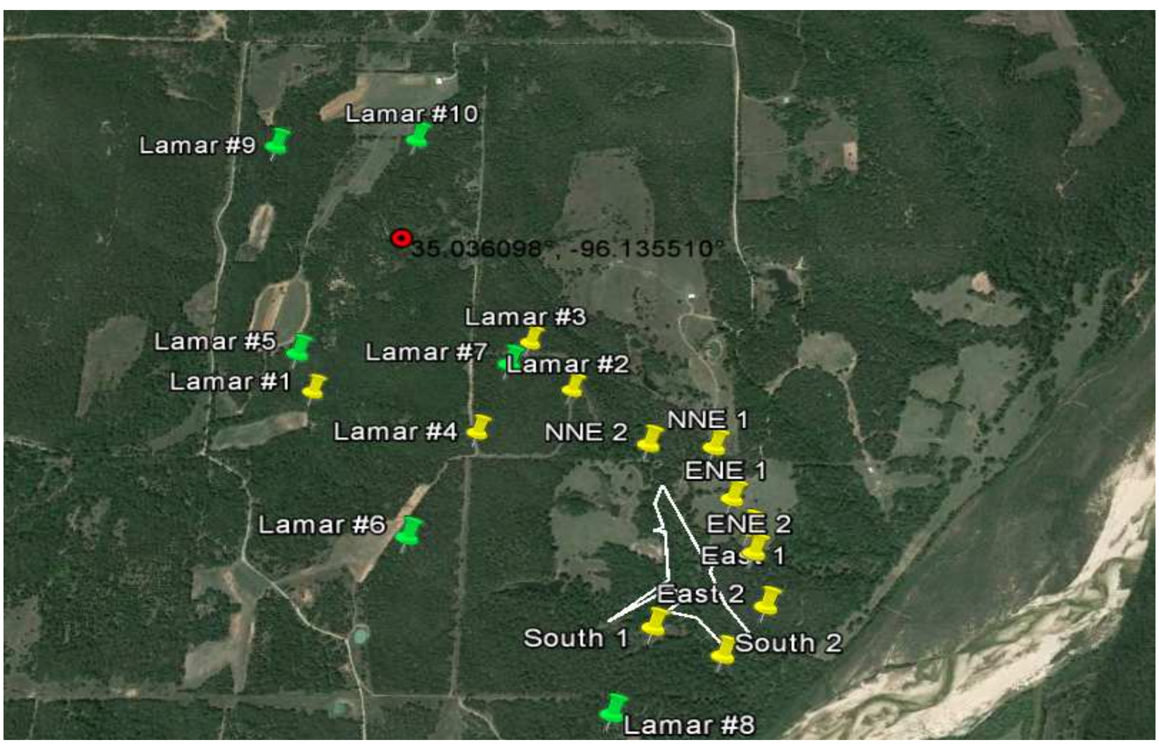

Figure 6. 2013 – 2014 ABB Trap Locations at Lamar, Oklahoma (Google Earth).

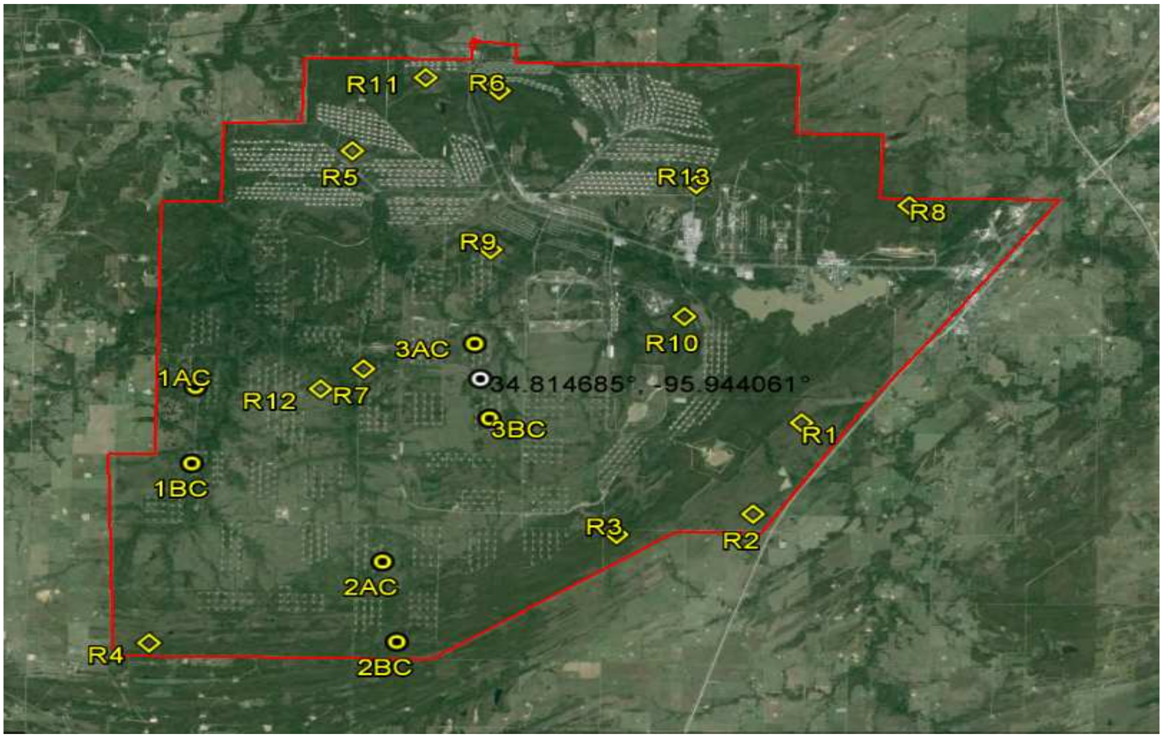

Figure 7. 2013 – 2014 ABB Trap Locations at McAAP McAlester, Oklahoma (Google Earth).

Trapping ABBs. ABB traps were similar to those used by Kozol (1989) and consisted of a camouflage five-gallon bucket, recessed plywood cover with a centered 6" opening, a 6" funnel secured beneath the 6" opening, two $^{5}/_{16}$" by 5" j-bolts, two fender washers, two $^{5}/_{16}$" wing nuts, and a rain shield spaced 1in to 2" above the 6" entry opening (Figure 8). The bucket contained approximately 32 $^{1}/_{16}$" holes drilled to allow for scent dispersal, and 16 $^{1}/_{16}$" holes drilled in the bottom to allow for rainwater drainage. Each trap was baited using a covered Gladware™ 25 oz. container holding a 100-200g rat (*Rattus spp*.) that had been allowed to partially decompose for three days prior to use. Rats were supplied by Big Cheese Rodents ™. The bait container had approximately 20 $^{1}/_{16}$" holes to allow for scent dispersal. A 15cm to 20cm layer of moist soil or peat was placed in the bucket (under the bait) to allow captured ABB (and other insects) to burrow.

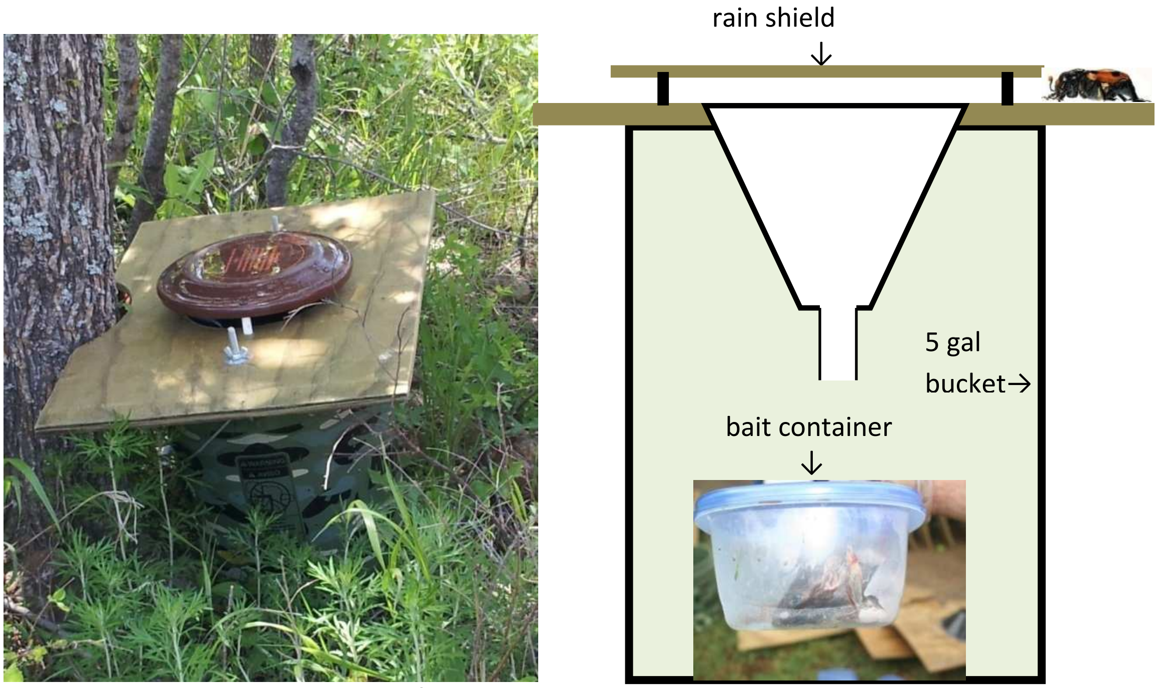

Figure 8. ABB Trap Deployed (left) and Trap Construction Depiction (right).

Baited ABB traps were deployed one day prior to each three-day trapping event. Upon initial deployment, GPS coordinates (NAD83) were determined using Garmin Rino 130™ or eTrex10™ handheld units at individual locations. Traps were secured to available sturdy vegetation using two 1m to 1.5m lengths of 6 gauge wires, and placed 0.3m to 0.5m above the ground to discourage ant infestation. Traps were monitored daily between 5:00am and 10:00am to document 24hr beetle captures, and to release live ABBS in an effort to prevent mortality from excessive heat accumulation in traps (USFWS 2005). Ant-infested traps were redeployed close to existing locations and suspended 1m – 2m above ground using overhanging vegetation.

Sample processing. At each morning of the three days after traps were deployed, captured ABBs were counted, sexed, aged (teneral or adult) according to maculation coloration and condition, and pronotum width was measured using a Kobalt™ 0.5ft metric and SAE calipers (accuracy=0.025mm). All ABBs were marked with bee tags and released according to USFWS guidelines (USFWS 2010). *Nicrophorus* congeners were identified on site, counted and measured (pronotum width - in mm). All other insects were placed in a solution of ~80% ethanol (ETOH) and glycerin, identified to species, and counted for each 24hr period. Voucher specimens (all insects except ABBs) were deposited in the K.C. Emerson Entomology Museum, Department of Entomology and Plant Pathology, Oklahoma State University, Stillwater, Oklahoma.

Data Summary and Analysis. At each location and for each three-day sampling event, average count/trap-night was calculated for each *Nicrophorus* species. Trap-night data were then plotted over time at each location for each year to graphically represent overlap in seasonal activity of competing species.

At locations/years where season-long data were collected (James Collins WMA 2013, 2014; Lamar 2013; McAAP 2014), data were further analyzed to investigate relationships between captures of overwintering adult *Nicrophorus* species caught in the spring (A) and captures of the teneral adults (T) throughout the remainder of the season. Since no definitive second generation was confirmed, all summer/fall *Nicrophorus* species data points were included as tenerals (T). Because *Nicrophorus* species are highly mobile within sub-populations (Bedick et al. 1999, Creighton and Schnell 1998, Jurzenski 2012, Jurzenski at al. 2011, Schnell et al. 1997-2006), individual data points (trap-night averages from three-night events) within locations are considered independent within the spring and summer. But, locations are likely representative of a sub-population and therefore investigating relationships between A and T is appropriate.

Analysis (PROC CORR, SAS® 2014) is based on a limited dataset and centered around captures associated with the presumed dominant competitor, ABBs (Kozol et al. 1988). This preliminary analysis focuses on relationships for ABB trap captures between generations and factors that might be associated with changes. Several questions were addressed:

Question 1 – Is there a relationship between “A” counts of *N. americanus* trap captures and “T” counts of *N. americanus* trap captures?

Question 2 – Is there a relationship between “A” counts of *N. americanus* trap captures and “T” counts of other *Nicrophorus* trap captures?

Question 3 – Is there a relationship between “A” counts of other *Nicrophorus* trap captures and “T” counts of *N. americanus* trap captures?

Question 4 – Is there a relationship between “A” counts of other *Nicrophorus* trap captures and “T” counts of other *Nicrophorus* trap captures?

Question 5 – Is there a relationship between “A” ratios of ABB/*Nicrophorus* species trap counts and “T” ratios of ABB/*Nicrophorus* species trap counts?

CHAPTER IV

RESULTS AND DISCUSSION

***Nicrophorus* Relative Abundance and Seasonal Trends**.

During 2013, a relatively high number of *Nicrophorus* beetles were captured among all locations in 648 trap-nights; *N. americanus* captures totaled 364 individuals, *N. orbicollis* captures totaled 849, *N. pustulatus* captures totaled 106, and *N. tomentosus* captures totaled 224. Other species captured included three additional members of the Family Silphidae *Oiceoptoma inaequale* (920), *Necrodes surinamensis* (888), and *Necrophila Americana* (138), *Euspilotus assimilis* (Histeridae, 469), *Creophilus maxillosus* (Staphylinidae, 385), and *Dermestes caninus* (Dermestidae, 92). Overall, trap capture totals during 2014 were similar/lower and may have been reduced by a reduced number of trap nights (405). *Nicrophorus americanus* (231), *N. orbicollis* (277), *N. pustulatus* (245), and *N. tomentosus* (66); *O. inaequale* (192), *N. surinamensis* (1353), *N. Americana* (31), *E. assimilis* (Histeridae, 356), *C. maxillosus* (Staphylinidae, 314), and *D. caninus* (Dermestidae, 445) remained relatively abundant among locations. Clearly, traps were effective at attracting insects that utilize carrion.

Although high numbers of burying beetles (Silphidae) in Oklahoma were expected, overall capture rates varied from previous trapping studies in the region. Lomolino and Creighton (1996) conducted ABB surveys in eastern and central Oklahoma from 1991 through 1994 and documented an overall capture rate (individuals per trap-night) of 0.05 for *N. americanus*, 1.14 for *N. orbicollis*, 0.25 for *N. tomentosus*, and 0.02 for *N. pustulatus* (Table 2). Carlton and

Rothwein (1998) conducted surveys in eastern Oklahoma and western Arkansas with an overall nightly capture rate of 0.02 and 0.02 in for *N. americanus* in 1994 and 1996, respectively. They also documented a nightly capture rate of; 1.06 (1994) and 0.17 (1996) for *N. orbicollis*, a nightly capture rate of 0.19 (1994) and 0.20 (1996) for *N. tomentosus*, and a nightly capture rate of 0.14 (1994) and 0.03 (1996) for *N. pustulatus* (Table 2).

Nightly capture rates in 2013 during my study were 0.56 for *N. americanus*; 1.31 for *N. orbicollis,* 0.35 for *N. tomentosus*, and 0.16 for *N. pustulatus.* In 2014, nightly capture rates *for N. americanus* were 0.57, 0.68 for *N. orbicollis*, 0.16 for *N. tomentosus*, and 0.61 for *N. pustulatus*. These relatively high numbers are likely representative of local populations and not based on recaptures of the same individual. Indeed, the recapture rate of marked individuals (ABBs) was only ~11% for all *N. americanus* collected over the two year period (K. Risser 2014 unpublished data).

Comparing overall average capture rates for *Nicrophorus* species can be misleading because averages are calculated over separate activity periods, multiple generations, and multiple trap locations. However, this metric is considered a useful measure of relative abundance for a geographic area (USFWS 2010). Comparisons among surveys also depend on consistent trapping protocols and may be compromised by failure to account for variables such as quality and amount of bait used, disturbed traps, differences in trap design, local weather patterns, and inadequate sample size (Carlton and Rothwein 1998). This trapping approach was quite similar to those of Lomolino and Creighton (1996) and Carlton and Rothwein (1998). However, these other studies did not have multi-year season-long data to include in capture rate calculations which would likely reduce nightly averages because intensive trapping is conducted during low and high activity periods. Although ABB congener nightly capture rates appear similar among both current and previous surveys, the surveys for this study indicate that ABB relative abundance is much higher (Table 2) than previous surveys and may reflect an overall increase in local population density in this region of the U.S.

Table 2. Silphidae capture rates (C/R) for previous surveys (Lomolino and Creighton 1996, Lomolino *et al*. 1995, Carlton and Rothwein 1998, Ferrari 2013, 2014) conducted in eastern Oklahoma/western Arkansas.

Study	Year(s)	C/R - *N. americanus*	C/R - *N. orbicollis*	C/R - *N. tomentosus*	C/R - *N. pustulatus*
Lomolino & Creighton	1991-1994	0.05	1.14	0.26	0.02
Lomolino *et al*.[1]	1992	0.16	0.17	<0.01	<0.01
Lomolino *et al*.[2]	1992	0.10	1.19	0.03	0.01
Carlton & Rothwein	1994	0.02	1.06	0.19	0.14
Carlton & Rothwein	1996	0.02	0.17	0.16	0.03
Ferrari[3]	2013	0.18	0.37	0.40	0.02
Ferrari[4]	2013	0.86	2.59	0.37	0.33
Ferrari[5]	2014	0.51	0.38	0.10	0.48
Ferrari[6]	2014	0.60	0.76	0.21	0.65

[1]Fort Chaffee AR, [2]Camp Gruber Ok, [3]James Collins WMA OK 2013, [4]Lamar OK 2013, [5]James Collins WMA OK 2014, [6]McAAP OK 2014.

At the locations I surveyed, overwintering adult ABBs appeared during May and June; first generation teneral ABBs began to emerge in late June/early July, and there was evidence of a second generation that appeared active from August into early September (Figures 9, 10, 11 and 14). My seasonal surveys appeared to substantiate Lomolino and Creighton's (1996) laboratory studies that indicated a second brood of ABBs is possible in Oklahoma. The impact of a second generation on long-term persistence is unknown, but based on the absence of ABB throughout much of the southern US, it is doubtful that warmer climates and multiple generations favor persistence of this species (Godwin and Minich 2005).

James Collins WMA is considered a suitable habitat for sustained *Nicrophorus* populations and during 2012 was approved as a relocation site for ABBs by USFWS (A. Barstow, 2012 personal communication). Vegetation habitat is mainly oak-hickory forests and un-grazed grasslands. Although soil characteristics are mainly stony loam and are not typically ideal for ABB habitat, ABB population levels appeared to be stable. James Collins WMA in 2013 (Figure 9) totaled 53 individuals over 98 trapping nights with an overall capture efficiency (individuals/trap/day) of 0.54 (± 0.14 SE). Capture rates varied among other *Nicrophorus* species: *N. orbicollis* captures totaled 110 with an overall capture efficiency of 1.12 (± 0.29 SE), *N. pustulatus* captures totaled 7 with an overall capture efficiency of 0.07 (± 0.03 SE); *N. tomentosus* captures totaled 118 with an overall capture efficiency of 0.40 (± 0.14 SE). ABB captures at James Collins WMA in 2014 (Figure 10) were similar to 2013 and totaled 57 individuals, but over 37 trapping events the overall capture efficiency increased to 1.54 (±0.43 SE). *Nicrophorus orbicollis* captures totaled 42 with an overall capture efficiency of 1.14 (± 0.35 SE), *N. pustulatus* captures totaled 53 with an overall capture efficiency of 1.43 (± 0.43 SE), and *N. tomentosus* captures totaled 11 with an overall capture efficiency of 0.30 (± 0.11 SE).

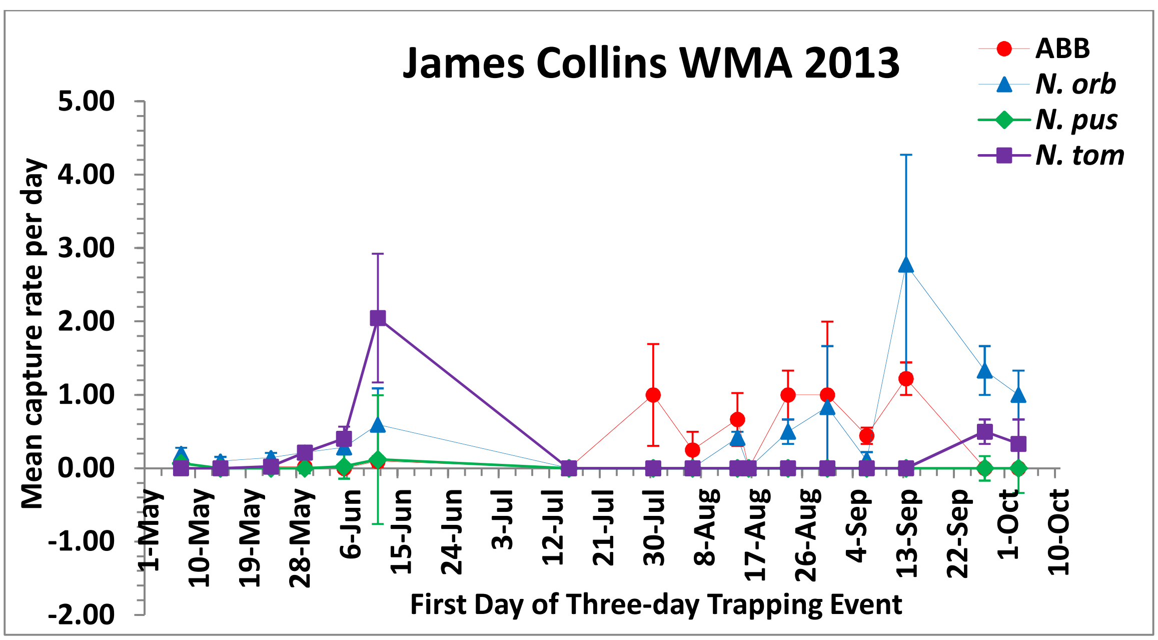

Figure 9. 2013 Mean seasonal capture rates (per day ±SE) of *N. americanus*, *N. orbicollis*, *N. pustulatus*, and *N. tomentosus* at James Collins WMA, Oklahoma.

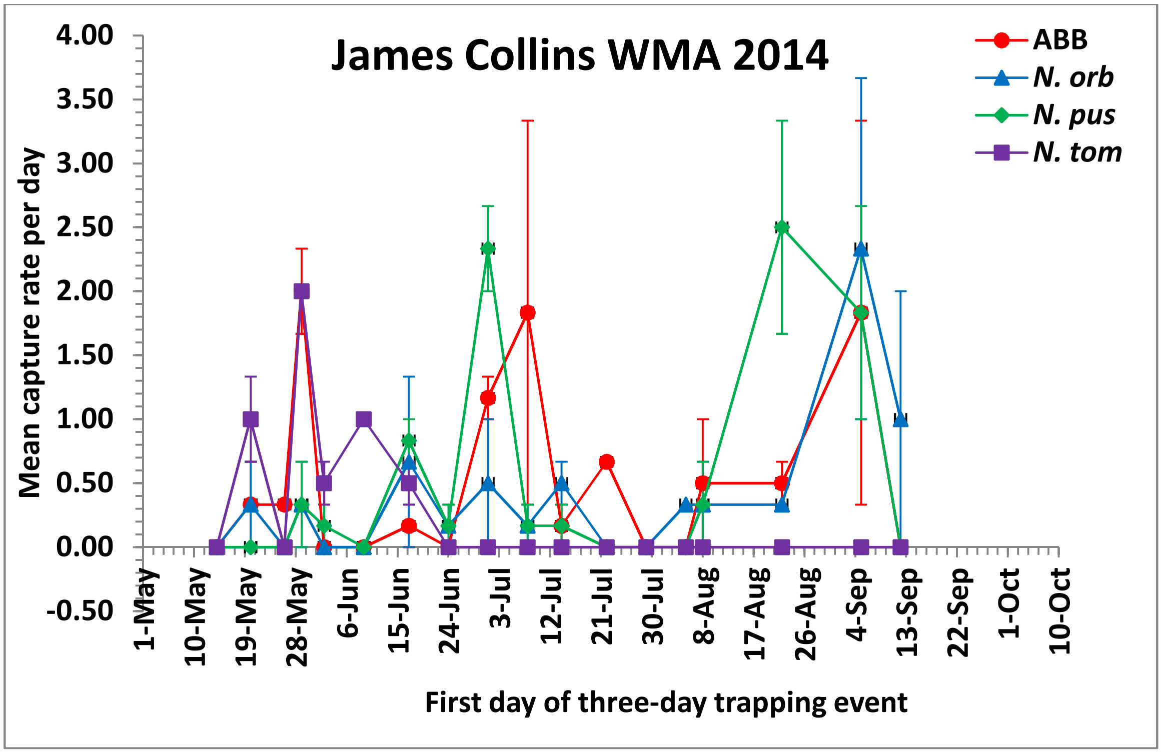

Figure 10. 2014 Mean seasonal capture rates (per day ±SE) of *N. americanus*, *N. orbicollis*, *N. pustulatus*, and *N. tomentosus* at James Collins WMA, Oklahoma.

The Lamar site habitat is mainly oak-hickory forests with rich sandy loam soils, and is considered an optimal site for long-term persistence of *Nicrophorus* species. Indeed, ABB captures at the Lamar site in 2013 (Figure 11) totaled 233 individuals over 90 trapping events with an overall capture efficiency of 2.59 (±0.41 SE). *Nicrophorus orbicollis* captures were particularly high and totaled 700 with an overall capture efficiency of 7.78 (± 1.73 SE). The other *Nicrophorus* species were also quite abundant in traps: *N. pustulatus* captures totaled 90 with an overall capture efficiency of 1.00 (± 0.20 SE), and *N. tomentosus* captures totaled 101 with an overall capture efficiency of 1.12 (± 0.24 SE).

Very few samples were taken at the Lamar site in 2014 (Figure 12) and ABB totals were limited to 15 individuals over 8 trapping events with an overall capture efficiency of 1.86 (±1.13 SE). *Nicrophorus orbicollis* overall capture efficiency remained high in 2014 at 4.13 (± 0.83 SE; 33 captures). During 2014, Captures of *N. pustulatus* totaled 19 with an overall capture efficiency of 2.38 (± 0.63 SE), and no *N. tomentosus* were captured at this site in 2014. Mean seasonal capture rates of aforementioned *Nicrophorus* species (per day) are shown in Figure 12.

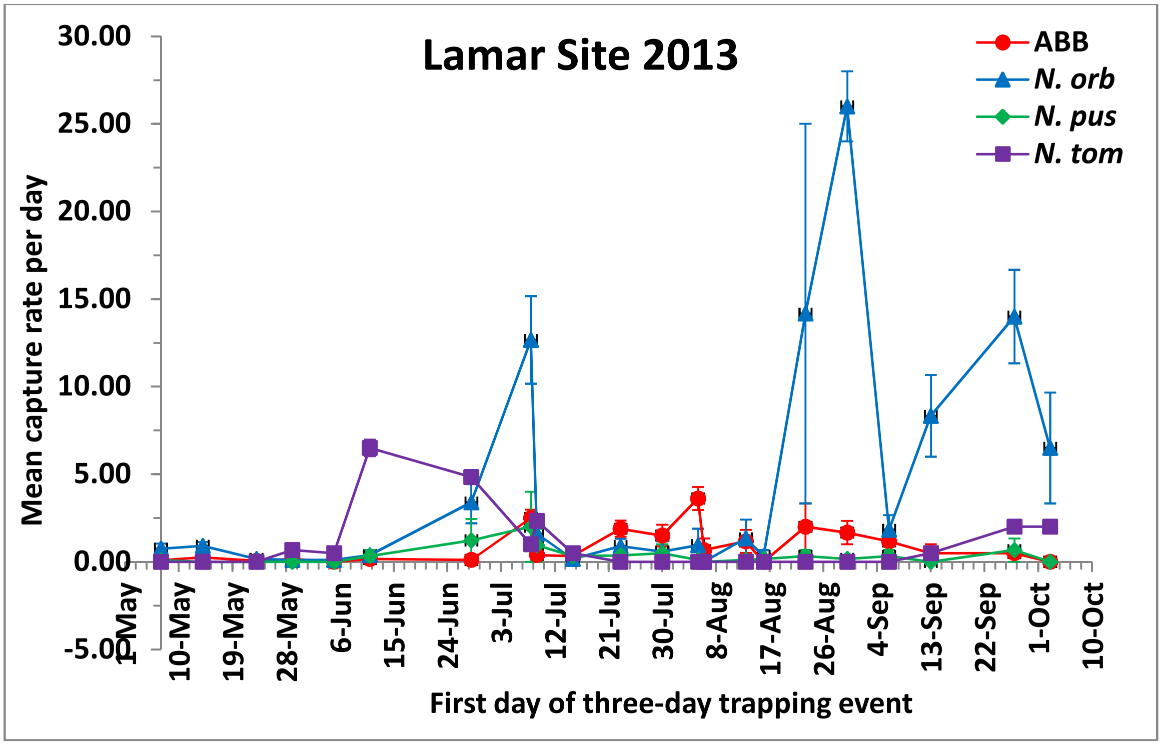

Figure 11. 2013 Mean seasonal capture rates (per day ±SE) of *N. americanus*, *N. orbicollis*, *N. pustulatus*, and *N. tomentosus* at Lamar, Oklahoma.

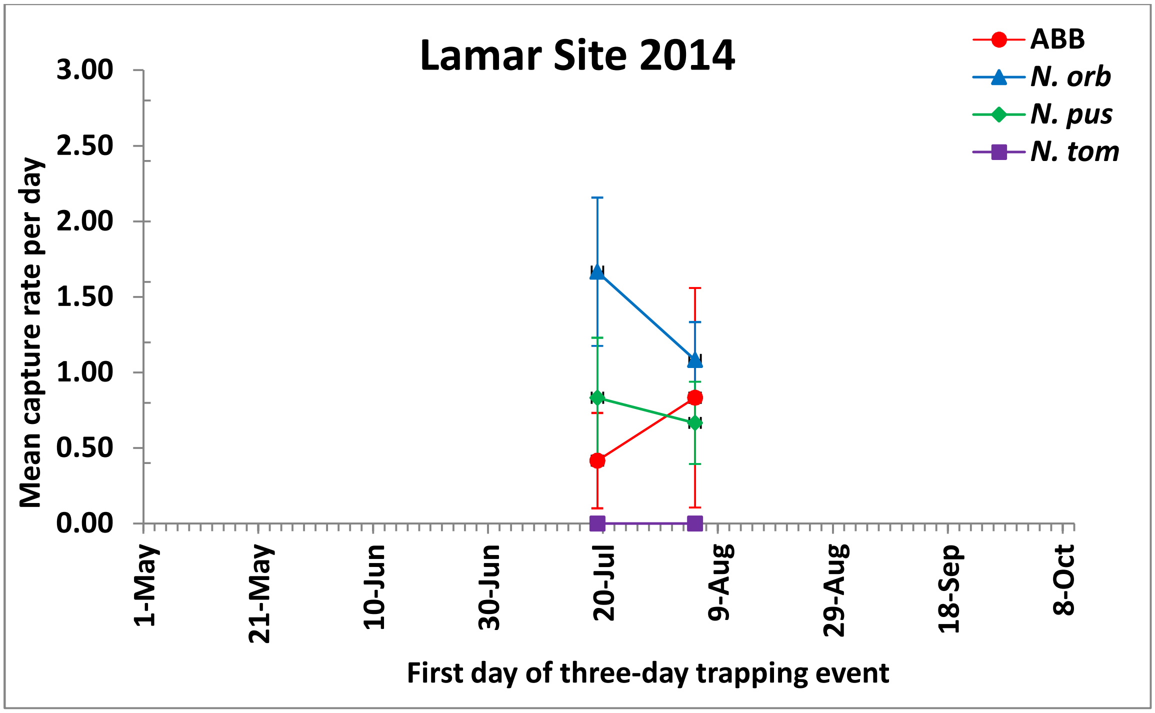

Figure 12. 2014 Mean seasonal capture rates (per day ±SE) of *N. americanus*, *N. orbicollis*, *N. pustulatus*, and *N. tomentosus* at Lamar, Oklahoma.

The McAAP site is a relatively undisturbed combination of oak-hickory forest and un-grazed grassland habitat with fine sandy-loam soils, and was considered an optimal site for long-term persistence of *Nicrophorus* species. A limited number of samples were taken at McAAP in 2013 (Figure 13) and ABB totals were limited to 78 individuals over 28 trapping events, but the overall capture efficiency was quite high at 2.79 (±0.64 SE). McAAP is a relatively undisturbed habitat and ideal for ABB, but not necessarily for other *Nicrophorous* species. In 2013, *N. orbicollis* captures totaled 39 with an overall capture efficiency of 1.39 (± 0.62 SE), whereas *N. pustulatus* captures totaled 9 with an overall capture efficiency of 0.32 (± 0.15 SE) and *N. tomentosus* captures totaled 5 with an overall capture efficiency of 0.18 (± 0.15 SE).

During 2014 (Figure 14), more traps were deployed throughout the year and ABB captures at McAAP were higher at 159 individuals over 89 trapping events and an overall capture efficiency (individuals per three-day event) of 1.79 (±0.31 SE). Inclusion of additional trap nights with low ABB numbers lowered efficiency calculations, however, McAAP is clearly a suitable habitat for this endangered species. In 2014 at McAAP, other *Nicrophorus* species totals were higher: *N. orbicollis* captures totaled 202 with an overall capture efficiency of 2.27 (± 0.45 SE), *N. pustulatus* captures totaled 173 with an overall capture efficiency of 1.94 (± 0.35 SE), and *N. tomentosus* captures totaled 55 with an overall capture efficiency of 0.62 (± 0.25 SE).

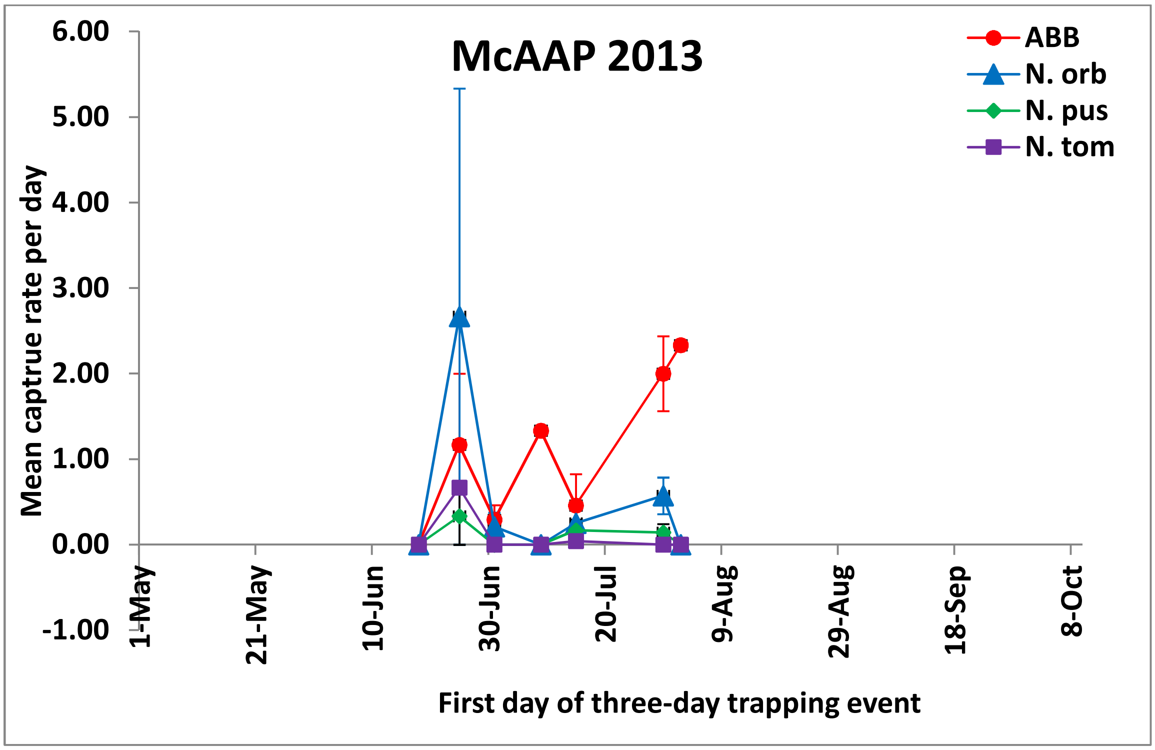

Figure 13. 2013 Mean seasonal capture rates (per day ±SE) of *N. americanus*, *N. orbicollis*, *N. pustulatus*, and *N. tomentosus* at McAAP McAlester, Oklahoma.

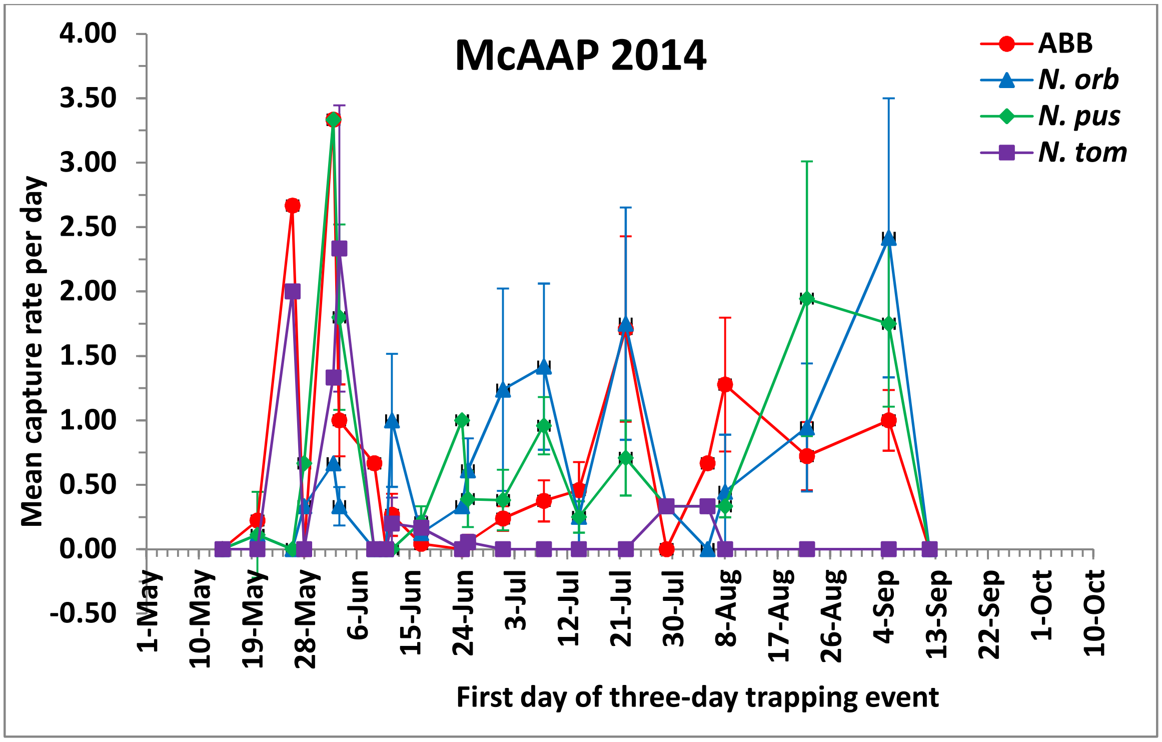

Figure 14. 2014 Mean seasonal capture rates (per day ±SE) of *N. americanus*, *N. orbicollis*, *N. pustulatus*, and *N. tomentosus* at McAAP McAlester, Oklahoma.

Potential for Competition among *Nicrophorus* Species.

The seasonal dynamics of *Nicrophorus* species provide information on their biology for this region but also on the potential for interspecific competition for reproductive resources. ABB activity in early summer (late May – early June) is a result of overwintering adults emerging from hibernation and searching for reproductive resources. First generation teneral ABBs appear in late June/early July, and the apparent second generation appears during August-early September. Among *Nicrophorus* species, *N. tomentosus* was the most active/abundant at all sites in May and early June, with an additional periods of reduced activity in late summer/early fall (Figures 9 and 11). The early season overlap between overwintering ABB and *N. tomentosus* indicate the potential for significant competition for reproductive resources, however, relatively high ratios of ABB:*N. tomentosus* tenerals during late summer/early fall indicate that competition during spring had little effect on ABB populations.

Though the seasonal data are highly variable, suggestive overlaps among *N. americanus*, *N. orbicollis* and *N. pustulatus* trap catches indicate the potential for competitive interaction providing resources are limited. Data from the Lamar site during 2013 provide the most compelling evidence of a potential competitive interaction among these species. The very large population of overwintering *N. orbicollis* is followed by an even larger populations of teneral adults (Figure 11), while teneral populations of ABB and *N. pustulatus* remain disproportionately low compared with other locations/years (See other Figures).

Correlation analysis provided interesting but preliminary interpretations of relationships between overwintering and teneral populations (Table 3). The strongest relationships observed approached significance (P ~0.05) indicates that 1) a higher count of overwintering other *Nicrophorus* species was positively correlated with 1st generation (teneral) adult ABB counts, 2) a higher count of overwintering other *Nicrophorus* species was positively correlated with 1st generation (teneral) other *Nicrophorus* counts, and a higher ratio of ABB/*Nicrophorus* species trap counts was negatively correlated with ratios of ABB/*Nicrophorus* species trap counts. The two positive correlations suggest that teneral counts of other *Nicrophorus* species are not negatively influenced by competition among overwinter individuals (including ABB). This conclusion is to be expected, especially when other *Nicrophorus* species are able to utilize a wide range of carrion size (Kozol et al. 1988) which ultimately reduces direct competition.

The negative correlation between generations for ABB/*Nicrophorus* species trap count ratios, however, suggests that overwintering ABBs are interacting/competing in the spring and this competition has an influence on teneral populations. A weak and non-significant negative relationship for ABB counts between generations supports this idea. ABBs compete for a particular carrion size range and are considered the dominant competitor, and this negative relationship could reflect significant intraspecific competition from emerging overwintering ABBs for limited resources. That is, provided resources are limited, intraspecific competition is a predominant factor influencing ABB populations from one generation to the next. These conclusions are speculative, because seasonal data can only reveal overlap and correlations among *Nicrophorus* species that are competing for carrion resources. Quantifying intraspecific and interspecific competitive interactions among these species, however, will require detailed field and laboratory experiments that pit individuals/mating pairs against each other as resources become limited.

Table 3. Pearson correlation coefficients between ABB/other *Nicrophorus* counts of overwintering (A) and tenerals (T) for James Collins WMA, Lamar, and McAAP, Oklahoma, 2013, 2014.

Correlation	***n***	***r***	***P***
ABB Count (A) vs ABB Count (T)	4	-0.292	0.708
ABB Count (A) vs Others Count (T)	4	-0.163	0.838
Others Count (A) vs ABB Count (T)	4	0.973	0.027
Others Count (A) vs Others Count (T)	4	0.929	0.071
ABB/Nicrophorus Count ratio (A) vs ABB /Nicrophorus Count ratio (T)	4	-0.949	0.051

CHAPTER V

CONCLUSION

The endangered American burying beetle and other carrion-utilizing insects were captured in eastern Oklahoma during 2013 and 2014 using a USFW approved bait-trapping technique similar to the approach described by Kozol (1989). Three locations were surveyed with known ABB activity, and trap deployment locations were chosen to include a variety of habitats including oak-hickory forests and un-grazed grasslands with deep loamy soils.

Current *N. americanus* populations in Oklahoma appear to be relatively consistent from year to year based on average capture rates of 0.18 and 0.86 in 2013, and 0.51 and 0.60 in 2014. These ABB capture rates are higher than those reported by Lomolino and Creighton (1996) and Carlton and Rothwein (1998) (0.05 and 0.02) and could be due to conservation efforts by USFWS which promoted practical soil disturbance stewardship and effective land-use management. Season-long survey data from several locations/years suggested that a second generation of ABBs are emerging during late summer/early fall.

Results from all sites indicate that there are relatively high populations of congeneric species (*N. orbicollis*, *N. tomentosus*, and *N. pustulatus*) that occur in conjunction with ABBs, and that *N. orbicollis* is most likely the ABBs strongest competitor. However, based on the capture of overwintering and teneral adults at each location, ABBs were clearly able to find and secure carrion for reproductive resources. Documenting whether competition from congeners is influencing short-term and long-term ABB populations will require (1) more intensive monitoring over a longer period of time, and (2) competition studies (lab and field) that pit ABBs against *Nicrophorus* congeners to quantify factors that lead to successful processing of carrion for reproduction.

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