ABSTRACT

LASTRO, ELINA. Dung Beetles (Coleoptera: Scarabaeidae and Geotrupidae) in North Carolina Pasture Ecosystem (Under the direction of D. Wes Watson).

Dung beetles in families Scarabaeidae (subfamilies Aphodiinae, Scarabaeinae and Coprinae) and Geotrupidae (Geotrupinae) aid in the decomposition of dung providing many benefits to pasture and animal health. They improve the soil by burying nutrient-rich dung, and aerating and mixing the soil through tunneling activity. Dung beetles also compete with pestiferous flies and parasitic nematodes for dung resources. Recent trappings at two sites in North Carolina Piedmont and Coastal Plain regions revealed presence of 30 dung beetle species in cattle pastures.

A survey of dung beetles was conducted from May to October 2005 in 10 counties representing the three geographic regions of North Carolina, the Mountains, Piedmont and the Coastal Plain. Total of 1,863 specimens representing 15 species were collected from dung baited pitfall traps or directly from cattle dung. Most commonly collected species were *Aphodius pseudolividus* Olivier and *Onthophagus taurus* Schreber. Elevation, temperature and soil type were taken into consideration when rationalizing the presence of certain species in the different regions of North Carolina.

A study was conducted to evaluate benefits of *O. taurus* activity on soil nutrition and yield of two common North Carolina pasture grasses. Tunneling activity of *O. taurus* and dung burial for brood production elevated the levels of major plant nutrients P, K and N in three soil types (Piedmont clay, Coastal Plain sandy-loam and play sand) under laboratory conditions. *O. taurus* activity increased the yield of Sudangrass *Sorghum bicolor* (L.) and ryegrass *Lolium multiflorum* Lam. over the dung only treatment and control. Dung beetle presence improved ryegrass yield over the fertilizer treatment in Cecil red clay and play sand.

Methoprene, an insect growth regulator successfully reduced the horn fly [*Haematobia irritans* (L.)] numbers in an area-wide program in Nash Co., NC. Dung beetle trappings in the treatment area revealed no significant reduction in the populations of several common species compared to the insecticide free control. Laboratory bioassay determined the effect of methoprene on the fecundity, survival and size of the most common North Carolina dung beetle species *O. taurus*.

Keywords: dung beetles, North Carolina, horn fly, methoprene, nutrient cycling, ryegrass, Sudangrass.

DUNG BEETLES (COLEOPTERA: SCARABAEIDAE AND GEOTRUPIDAE) IN NORTH CAROLINA PASTURE ECOSYSTEM

by

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DEDICATION

Ovaj magistarski rad posvećujem svojim roditeljima Marku i Bernardi Laštro. Mama i tata hvala vam mnogo za svu vašu podršku i volim vas od svega srca.

I dedicate this work to my parents Marko and Bernarda Laštro. Mom and dad thank you so much for your support and I love you with all my heart.

BIOGRAPHY

Elina Lastro was born on August 5, 1981 to Marko and Bernarda Laštro in Sarajevo, Bosnia and Herzegovina. When she was seventeen she came to New York to visit her uncle Michael and aunt Elaine Lastro. Elina stayed in New York where she attended Fulton-Montgomery Community College. She received an Associates Degree in Science in 2001. In hopes of becoming a veterinarian she transferred to Cornell University where in 2003 she received a Bachelors Degree in Animal Science. While at Cornell University she volunteered in a Veterinary Entomology Laboratory where she became interested in entomology. That experience changed her career aspirations. Elina moved to Raleigh, North Carolina in 2003, where she worked on her Masters degree under supervision of Dr. D. Wes Watson.

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I. Literature Review

Natural History

Families Scarabaeidae and Geotrupidae in the order Coleoptera contain members commonly characterized as dung beetles and the subfamilies Scarabaeinae, Coprinae contain the true dung beetles. Other species of dung beetles are found in subfamilies Aphodiinae and Geotrupinae.

Dung beetles, as their name implies, feed on the feces of various animals. Larval mouthparts of these coprophagous insects are specialized for chewing solid or fibrous foods such as dung or carrion. In contrast, adults have mouthparts which allow them to feed only on dung liquids and smaller dung particles (Halffter and Mathews 1966). During feeding, these beetles use setael labral and labial pads to concentrate dung particles (Landin 1961, Hata and Edmonds 1983).

Most dung beetle species are generalists (euryphagy) although some feed on the feces of certain animal groups (stenophagy), whereas a limited number of dung beetles specialize on feces from only one species (intrinsic stenophagy). In North America most dung beetles prefer omnivore dung (especially swine), followed by the herbivore (cow, horse, sheep) and are least attracted to carnivore (dog) feces (Fincher et al. 1970). In India, feces preferences were as follows: cow > swine > human > horse > goat (Mittal and Bhati 1998). In France, out of 4,276 collected individuals representing 39 species, 2,750 beetles encompassing 13 species clearly preferred cattle over horse dung (Dormont et al. 2004).

Adults of some dung beetle species feed on other foods such as carrion, decaying plant matter, fruit, fungi, and occasionally other insects (Halffter and Matthews 1966).

Perhaps the most interesting occurrence of dung beetles is as the phoretic commensals on monkeys, kangaroos, sloths, and a few other animals. Other species have been found as endoparasites on humans, living in vertebrate nests and caves and in ant and termite nests, where they feed on excrement and debris. Kleptoparasitic behavior where some dung beetle species utilize dung collected by usually larger species has also been observed (Halffter and Matthews 1966, Davis 2000).

In finding food, dung beetles rely on olfactory and tactile stimuli. Comignan (1928) and Warnke (1934) found that if the antennae of scarab beetles were painted with lacquer they could not detect dung. The search for food is often carried out by flight, but some species rest with their antennae opened waiting for odors to direct them to food (Halffter and Matthews 1966). For Scarabaeinae, the final approach is made by walking whereas some *Phanaeus* species are skillful fliers and approach food in flight.

Depending on the genus, beetles will show different behaviors when manipulating dung. *Canthon* tends to either burrow into or under the dung or it will start making a ball. *Phanaeus* will either burrow under the dung or take away a part of it. *Onthophagus* species will immediately disappear under the dung pad to start digging tunnels and will not come out to the surface again. *Copris*, *Dichotomius* and *Ontherus* will dig on one side of the dung pad, leaving a characteristic pile of loose soil on that side.

Scarabaeinae and Geotrupinae behaviorally differ from Aphodiinae because they bury feces for larvae and for adults to feed on (Halffter and Matthews 1966). All tribes with the exception of Scarabaeini bury food directly under or near the food source. *Phanaeus*, *Onthophagus*, *Copris*, *Dichotomius* and a few Scarabaeinae species carry feces for considerable distances without rolling a ball. Remaining members of tribe Scarabaeinae form a ball out of dung before transporting it some distance where they bury it for larval and adult food. There is no precise record on the copulation of the dung beetles except for information on where and how long they copulate. In almost all dung beetles, there is male-female cooperation in brood-ball provisioning.

In addition to consumption, feces of various animals are used for construction of brood chambers. Nidification (nesting) behavior of dung beetles is complex and it differs among species, but it can be grouped into three major categories: paracoprid (tunneling), telecoprid (rolling) and endocoprid (dwelling) (Bornemissza 1976, Halffter and Edmonds 1982). Halffter and Matthews (1966) propose four groups of nidification behavior with some variation within.

Paracoprid beetles burrow tunnels under or near the food source. This behavior is present in most Coprinae and Geotrupidae. Padtern I of Halffter and Edmonds (1982) represents the most primitive nesting behavior. One or both parent beetles will dig a tunnel and form a sausage shaped brood mass at the end where a single egg is deposited. Sibling brood masses are separated by soil. Padterns II and III of Hallfter and Edmonds (1982) are more complex, but the beetles exhibiting this behavior are not as fecund. Brood balls are constructed in chambers created by parent beetles and more than one brood ball can be present in a chamber. Adult beetles exhibit parental brood care. For example, in genus *Copris* the female guards the brood chamber while cleaning and fixing the brood balls.

Endocoprid behavior (Padterns VI and VII of Halffter and Edmonds 1982) is present mostly in Aphodiinae and in some Coprinae. In this case the beetles do not build brood balls. They simply lay eggs in the food source or at the dung soil interface.

Adult telecoprid beetles take a portion of feces and form a ball. One or both parents roll the dung ball away from the food source, bury it in a shallow tunnel, and a female lays one egg in it. This is a padtern IV of Halffter and Edmonds (1982).

Other than a few exceptions most all dung beetles fall into one of these three categories. All Scarabaeidae and Geotrupidae have three larval stages and a pupal stage after which the adult emerges. However, after the eggs are laid, brood developmental time depends on the species as well as the environmental conditions (Halffter and Matthews 1966).

Benefits of Dung Beetles

The dietary habits of dung beetles play an important role in pasture sanitation. The national cattle census (dairy and beef cows, heifers, steers and bulls) estimates the population at 80,463,000 head (NCDA & CS 2005). The North Carolina Department of Agriculture and Consumer Services estimates the cattle population at 645,000 head for North Carolina (NCDA & CS 2005). Adult cattle deposit about 10 dung pads per day (Bornemissza 1960). Extrapolating from these data cattle produce about 804,630,000 dung pads per day in the USA and about 6,450,000 for North Carolina. The average dung pad covers approximately 0.1 m^2 of soil, (Bornemissza, 1960) which means that in North Carolina about 645,000,000 m^2 of pasture land is fouled by cattle dung every day or 235,425,000, 000 m^2 in the whole U.S. Dung pads cover the grass, preventing or slowing growth, and cattle tend to avoid grazing the area around dung pads leading to approximately 0.5 m^2 of unutilized or underutilized grass (Bornemissza 1960, Fincher 1981).

Slow and delayed degradation of accumulated dung renders the pasture unusable for grazing over long periods. Abundant dung beetle populations remove dung from the pasture rapidly and save producers about $0.38 billion otherwise lost to pasture fouling, reduced nutrient cycling, parasitism, and development of pest flies (Losey and Vaughn 2006).

The Australian Dung Beetle Project is often cited to illustrate the importance of dung beetles in pasture cleanup. The importation and production of cattle in Australia results in about 33 million tons of dung produced annually, and pasture fouling leads to about a 30% loss in underutilized pasture (Bornemissza 1960). In Africa, India and Mediterranean regions where cattle are indigenous, a variety of native dung beetle species swiftly removed dung from pastures. Unfortunately, dung beetle fauna in Australia were adapted to the pellet-like dung of native mammalian species. The importation of dung beetle species adapted to the large wet dung pads of cattle was undertaken (Bornemissza 1960).

The first Afro-Asian dung beetle imported into Australia was *Onthophagus gazella* Fabricius (Bornemissza 1976). In the first two years of the release *O. gazella* became established in a 400 km area, and by the seventh year *O. gazella* had a remarkable effect on the disappearance of dung pads all throughout the tropics, inland and areas south. During the ten-year project 23 more species of dung beetles were successfully released and established.

To reduce pasture fouling in the US, *O. gazella* was released at 5 sites in Texas from 1972 to 1975. Additional releases were conducted in Georgia, Arkansas and Mississippi. Since the releases were completed *O. gazella* also became established in Alabama, California, Oklahoma, Louisiana and most recently North Carolina (Blume and Aga 1978, Fincher et al. 1983, Hunter and Fincher 1985, Bertone et al. 2005). Rivera-Cervantes and

Garcia-Real (1991) reported collecting *O. gazella* in Guerrero, Mexico 1657 km south of the original release site in Texas, suggesting a dispersal rate of 90 km per year over 19 years.

Onthophagus taurus Schreber is a very common and successful dung beetle from the Middle East, Europe and North Africa. By 1974 this beetle was present in Florida where it has been accidentally introduced in 1971. Fincher and Woodruff (1975) later in 1974 reported collecting *O. taurus* in areas of Georgia and southeast Alabama. Further collections revealed presence of *O. taurus* in Mississippi, Louisiana, South Carolina and North Carolina (Fincher et al. 1983) as well as California and Missouri (Macrae and Penn 2001). *O. taurus* is the most common dung beetle in Piedmont and Coastal region of North Carolina making up over 60% of the total dung beetle fauna at these two sites (Bertone 2005).

In addition to removing dung from the soil surface, dung beetles contribute to pest reduction and nutrient cycling (Bornemisszza 1960, Fincher 1981, Bertone 2006). Dung beetles successfully compete for food resources with pest flies (Blume et al. 1973, Bornemissza 1970, Ridsdill-Smith 1993, Tyndale-Biscoe and Vogt 1996, Fay and Doube 1983, Doube and Moola 1988, Roth et al. 1988). Five major pestiferous flies on pastured cattle are of concern to producers because of their harmful effects, which often lead to production losses. These include the African buffalo fly (*Haematobia thirouxi potans* (Bezzi)), the Australian buffalo fly (*Haematobia irritans exigua* (de Meijere)), the bush fly (*Musca vetustissima* Walker), the face fly (*Musca autumnalis* De Geer) and the horn fly (*Haematobia irritans irritans* (Linnaeus)). Before dung beetle introduction, cattle feces on the Australian pastures took three months or longer to be disintegrated by termites and weathering (Ferrar 1975). To reduce breeding of pestiferous flies in the pasture, dung should be removed in four days or less. Dung beetles, while using the dung for food and reproduction, directly compete for resources with dung breeding flies making them a valuable asset in the fight against pasture flies (Blume et al. 1973, Bornemissza 1970, Ridsdill-Smith 1993, Tyndale-Biscoe and Vogt 1996, Fay and Doube 1983, Doube and Moola 1988, Roth et al 1988). By removing dung from the pasture, dung beetles also help reduce the number of gastrointestinal nematodes affecting pastured cattle (Bornemissza 1976, Fincher 1975, Bryan and Kerr 1989, Bryan 1973).

Dung beetles are actively engaged in nutrient cycling, improving soil tilth and moisture percolation (Bertone 2006, Bornemissza and Williams 1970, Bornemissza 1970, Yokoyama et al. 1991a, Yokoyama et al. 1991b). Dung beetle activity can improve yield and quality of various plants (Fincher et al. 1981, MacQueen and Beirne 1975, Bornemissza and Williams 1970, Kabir et al. 1985).

Although there are significant studies on dung beetles throughout the world, the study of these insects and their importance to North Carolina is relatively recent. Bertone (2005) conducted a study on the seasonality and abundance of dung beetles on two sites in NC. A portion of his studies concentrated on the role of dung beetles in nutrient cycling as well as the development of dung beetle compadible fly management plans. To gain more of an understanding of the importance of dung beetles in the pasture ecosystem, my effort is focused on field and laboratory studies evaluating a horn fly management plan reliant on the insect growth regulator methoprene for its compadibility with dung beetles. Furthermore, my studies have focused on the role of dung beetles in improved pasture health.

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II. Checklist of dung beetles (Coleoptera: Scarabaeidae and Geotrupidae) in North Carolina pastures

Abstract

A survey of dung beetles was conducted May – October 2005 in 10 counties representing the three geographic regions of North Carolina, the Coastal Plain, Piedmont and the Mountains. Total of 1,863 specimens representing 15 species were collected from dung baited pitfall traps or directly from cattle dung. The following species belonging to family Scarabaeidae were recorded: *Aphodius erraticus*(L.), *A. fimetarius* (L.), *A. haemorrhoidalis* (L.), *A. pseudolividus* Olivier, *A. rubeolus* Beauvois, *Ataenius erratus* Fall, *At. platensis* (Blanchard), *Onthophagus gazella* (Fabricius), *O. hecate hecate* Panzer, *O. oklahomensis* Brown, *O. pennsylvanicus* Harold, *O. taurus* Schreber, *Phaneus vindex* MacLeay, and *Canthon chalcite* Haldeman. *Geotrupes blackburnii blackburnii* Fabricius was the only species collected from family Geotrupidae. Most commonly collected species were *A. pseudolividus* and *O. taurus*. *A. pseudolividus* was not collected from Buncombe, Clay, nor Pender counties and *O. taurus* was not found in Rockingham Co. *A. rubeolus* specimens were recorded only from Chowan Co. Elevation, temperature, and soil type were taken into consideration when rationalizing the presence of certain species from different regions of North Carolina.

Keywords: Scarabaeidae, Geotrupidae, North Carolina, dung beetles

Introduction

Collections conducted in North America show the dung beetle assemblage of certain areas in U.S. and Canada. Extensive surveys have been conducted in Florida (Woodruff 1973), Georgia (Fincher 1975, Fincher 1979, Fincher and Woodruff 1979), Texas (Fincher et al. 1979, Howden and Howden 2001, Howden and Scholtz 1986, Nealis 1977), Minnesota (Cervenka and Moon 1991), North Carolina (Davis 1966, Bertone 2005), New Jersey (Price 2004) and Alberta, Canada (Floate and Gill 1998). Blume (1985) published a complete list of dung inhabiting insects and their distribution in America, North of Mexico.

Elevation plays an important role in dung beetle distribution. For example, Geotrupinae and Aphodiinae can live in the alpine zone and the distribution of some Aphodiinae species extends to higher elevations (Halffter and Matthews 1966). In contrast, the Scarabaeinae tend not to cross the 1,800 m alpine zones in Europe and North America. Depending on the part of the world Scarabaeinae will extend to different elevations. In Japan some *Onthophagus* species are not found above 1,300 m. In Africa and South America Scarabs are present at elevations ranging from 925 m to 4,400 m (Halffter and Matthews 1966).

Data compiled in North America clearly demonstrate a latitudinal distribution for certain genera. Of 17 species collected in Alberta, Canada, 14 belonged to genus *Aphodius*. The remaining three species belonged to Coprinae, Scarabaeinae and Geotrupidae. Introduced *Onthophagus nuchicornis* (L.) presented the highest percentage of the dung beetle fauna, but most remaining beetles were *Aphodius* species (Floate and Gill 1998).

More southern areas, such as Texas and North Carolina, are rich in Coprinae and Scarabaeinae. In Texas, the predominant species collected belonged to the genus *Onthophagus* (Howden and Howden 2001, Nealis 1977 and Howden and Scholtz 1986). For example, *O. pennsylvanicus* Harold represented 75% of the total number of beetles collected followed by *O. hecate hecate* Panzer (20%) (Nealis 1977). In 1985, 25% of collected dung beetles were *O. alluvius* Holden & Cartwright followed by *O. gazella* (Howden and Scholtz 1986). Howden and Howden (2001) collected 2,594 dung beetles from Texas and 75% were *O. alluvius*. Interestingly, native *O. alluvius* ended up out competing native *O. pennsylvanicus* and *O. h. hecate* as well as the imported *O. gazella*.

Blume (1985) reported the following species associated with cattle dung in North Carolina: *Canthon chalcites* Haldeman, *C. pilularius* (Linnaeus), *C. vigilans* LeConte, *C. (Boreocanthon) depressipennis* LeConte, *C. (Boreocanthon) probus* Germar, *C. (Glaphyrocanthon) viridis* (Beauvois), *Melanocanthon bispinatus* (Robinson), *Pseudocanthon perplexus* LeConte, *Onthophagus concinnus* LaPorte, *O. hecate hecate* Panzer, *O. oklahomensis* Brown, *O. pennsylvanicus* Harold, *O. taurus* Schreber, *O. tuberculifrons* Harold, *Phanaeus igneus* MacLeay, *P. vindex* MacLeay, *Dichotomius carolinus* Linnaeus, *Copris fricator* (Fabricius), *C. minutus* Drury, *Geotrupes blackburnii* (Fabricius), *G. egeriei* Germar, *G. splendidus* (Fabricius), *Aphodius bicolor* Say, *A. campestris* Blatchley, *A. distinctus* Muller, *A. fimetarius* Linnaeus, *A. granaries* Linnaeus, *A. haemorrhoidalis* Linnaeus, *A. lividus* Olivier, *A. lutulentus* Haldeman, *A. rubeolus* Beauvois, *A. rusicola* Melsheimer (as *A. ruricola*), *A. stercorosus* Melsheimer, *A. stupidus* Horn, *A. terminalis* Say, *A. vittatus* Say, *Ataenius abditus* (Haldeman), *A. apicalis* Hinton, *A. cylindricus* Horn, *A. imbricatus* (Melsheimer), *A. platensis* (Blanchard), *A. simulator* Harold, *A. spretulus* (Haldeman), *A. strigatus* (Say) (Table 1). *Aphodius erraticus* Linnaeus was later reported from North Carolina (Harpootlian 2001)

From March 2002 through September 2003, extensive dung beetle trapping was conducted in two counties, Wayne Co, located in the Coastal Plain and Rowan Co, located in the Piedmont of North Carolina (Bertone 2005). Thirty species belonging to eight genera were collected from both sites. Of these more than 90% were exotic dung beetles. In the coastal North Carolina region *O. taurus* comprised 73.4% of the total collection on the dairy unit and 45.4% on the beef unit (Table 2). *A. pseudolividus* was the second most abundant species. Similar data were collected in the Piedmont region where 66.4% of collected beetles were *O. taurus* followed by *Aphodius pseudolividus* Olivier (18.9%) (Table 3). Other species present in high numbers were *O. pennsylvanicus*, *O. gazella*, and *Aphodius erraticus*. Two new state records were *Aphodius prodromus* Brahm and *Onthophagus gazella* (Bertone 2005). *O. taurus* and *A. pseudolividus* were also the most abundant species in Nash Co., North Carolina located in the Coastal Plain (Table 4) (Bertone 2004, Chapter IV this thesis).

Factors such as climate, soil, and feces type all contribute to the dung beetle assemblage of a certain area (Halffter and Matthews 1966, Nealis 1977, Fincher 1973). Probably the most important factor is soil and depending on the species different soils are preferred. For instance *Onthophagus* species prefer sandy soils, *O. taurus* lives mostly in the sandy areas with sparse vegetation (Halffter and Matthews 1966). In South Texas 11 out of 16 species of Scarabaeinae and Coprinae preferred sandy to clay soils. This ultimately increases species fecundity since sandy soils make it easier to construct more tunnels (Nealis 1977).

Interestingly, Bertone et al. (2006) found in a laboratory study that Piedmont clay soil was most favorable for *O. taurus* and *O. gazella* brood production. In sandy-loam soil and play sand *O. taurus* produced significantly less brood and *O. gazella* produced no brood in play sand, a substrate lacking soil structure.

Fincher (1973) determined the affinity of four *Phanaeus* species for three different textural classes of soil. *P. vindex* MacLeay survival to the third larval instar was the highest (95%) in sandy clay loam; *P. torrens niger* d'Olsoufieff made brood balls only in sandy clay loam soil, while *P. igneus* MacLeay and *P. igneus floridanus* d'Olsoufieff did not construct any brood balls.

North Carolina is divided into three geographic regions: the Mountains to the west, centrally located Piedmont, and the eastern Coastal Plain. These three regions have different soil types and elevations. The Coastal Plain region occupies two fifths of North Carolina and has mostly sandy-loam soils and elevations lower than 200 m. Counties sampled in this region were Pender and Chowan Co.; Wayne Co. was also surveyed in 2002-2003 and Nash Co. in 2003 and 2004. The Piedmont plateau also occupies two fifths of the state and is dominated by red clay soils, with elevations range from 200 to 1,000 m. Counties sampled in this region were Catawba, Chatham, Rockingham, Union, and Wake; Rowan was also sampled by Bertone (2005) in 2002 to 2003. Mountain region elevation ranges between 1,000 m and 2,000 m; the predominant agricultural soils are clay-loam. Counties sampled in this region were Avery, Buncombe and Clay.

This survey was conducted to gain a general understanding of dung beetle presence and distribution relative to the extensive collections conducted by Bertone (2004) and

Bertone et al. (2005). Collections were made during the spring and summer months when beetles were most active.

Materials and Methods

Dung beetles were collected from Avery, Buncombe, Catawba, Chatham, Chowan, Clay, Pender, Rockingham, Union and Wake counties in North Carolina (Figure 1). These counties represent 10% of the 100 counties in NC. The survey was conducted between May and October 2005 with one collection date per county with the exception of Wake County with three collection dates (Table 5.). Dung was collected from beef and dairy cattle. Two methods were used to collect dung beetles. Dung-baited pitfall traps (see chapter IV for description) were placed in close proximity to cattle where they remained for 4 to 24 hours (Table 5). Number of traps varied between sites, but there were never less then ten traps per county (Table 5). Trapped dung beetles were placed in plastic zip-lock bags and brought to the laboratory where they were identified and counted. In addition to trapping, five randomly selected dung pads with evidence of dung beetle activity, i.e. presence of beetles or tunnels through the surface, were collected in plastic tubs and frozen at -18º C. Samples were thawed and washed through a sieve to extract the dung beetles, and species were identified and counted.

Results and Discussion

During the survey a total of 1,863 dung beetles representing 15 species were collected (Table 6). All of the collected species were previously recorded from North Carolina (Blume 1985) (Table 1). All species except *Aphodius haemorrhoidalis* have been previously collected during an 18-month period from Wayne Co., NC (Bertone 2005) (Table 2). *A. rubeolus*, *Ataenius erratus*, *Onthophagus gazella* and *O. oklahomensis* were not collected from Rowan Co., NC for the same trapping period (Bertone 2005) (Table 3). All species except *Canthon chalcites* were also collected from Nash Co., NC during the summer of 2003 (Bertone 2004) and 2004 (Chapter IV of this thesis) (Table 4). In this survey most commonly collected species were *Aphodius pseudolividus* Olivier (678 individuals) and *Onthophagus taurus* Schreber (518 individuals).

O. taurus was collected from all but one location, Rockingham Co, a northern county near the Virginia border where the traps were out for 5 hours on June 6, 2006 (Table 5). Absence of this exotic paracoprid species from Rockingham Co. is more likely a result of a short trapping period rather than climate since it was previously collected as far north as New Jersey (Price 2004) and New York (Hoebeke and Beucke 1997). *O. taurus* is active during warmer months in North Carolina (Bertone 2005). Temperatures at the time of the collection were cool with average daily temperature for May and June 17.5°C and 22.8°C, respectively. Elevation for Upper Piedmont Research Station is 262 m above sea level; *O. taurus* was subsequently collected from higher elevations in North Carolina.

O. gazella, an introduced paracoprid beetle, was collected from 3 counties: Pender, Union and Wake (Table 6). During the survey *O. gazella* was not collected at elevations above 208m. Pender Co. is located in the Coastal Plain region while Wake and Union counties are located in the Piedmont region (Figure 1). Data compiled by Bertone (2005) suggest that elevation may play a role in the distribution of *O. gazella*. No specimens were collected from Rowan Co. at 214 m while close to 4,000 individuals were trapped from Wayne Co. (elevation 24 m) and Nash Co. (elevation 48 m). *O. gazella* favored Cecil red clay over sandy-loam soils when depositing brood (Bertone 2006), but specimens were collected from both the Piedmont and Coastal Plain.

Three native *Onthophagus* species *O. h. hecate*, *O. pennsylvanicus* and *O. oklahomensis* were collected from all but two counties (Table 6). Although the traps were out for a 24-hour period which seemed to be sufficient in the previous trappings (Bertone 2004), collections in late September for Union Co. and early November for Clay Co. did not produce these species. *O. oklahomensis* and *O. pennsylvanicus* were collected mostly from March to early November and *O. h. hecate* was trapped later through November, December, and January (Bertone 2005). Temperature could be a reason for lack of presence of *O. h. hecate*. Average temperatures vary in different parts of North Carolina and it is usually 5.6º C cooler in the Mountain region and 5.6º C warmer in the Coastal Plain as compared to the central North Carolina (State Climate Office of NC). However, *O. h. hecate* has been collected from neighboring states west and north of NC including Tennessee, Kentucky and Virginia (Blume 1985), so it is likely that *O. h. hecate* was not collected because of restricted trapping effort on a single trapping date rather than the impact of low temperatures. According to Halffter and Matthews (1966) *O. oklahomensis* Brown, *O. pennsylvanicus* Harold, *O. taurus* Schreber prefer sandy soils. In North Carolina these species were found in areas with clay and sandy-loam soils, but the numbers were higher in the areas with sandy-loam soils. All three species were collected from Nash Co. from June to October 2003 and 2004 (Bertone 2004, Chapter IV of this thesis) (Table 4).

A. pseudolividus was the most commonly collected species. This exotic endocoprid beetle was not collected from Buncombe and Clay counties in the Mountains nor in Pender Co. in the Coastal Plain region (Figure 1, Table 6). The absence of *A. pseudolividus* from

Pender Co. site could be due to ivermectin use (Floate 1998) on the farm where collections were done. *A. pseudolividus* was previously collected from Wayne, Rowan, and Nash counties between March and early December (Bertone 2004, Bertone 2005, Chapter IV of this thesis) (Table 2, Table 3, Table 4). Absence of this species from the Mountains in early October is most likely a result of just one trapping date rather than lower temperatures.

Twenty three specimens of *A. rubeolus* were collected from Chowan Co. (Table 6). This native species was previously recorded in North Carolina (Blume 1985) (Table 1), and recently ten specimens were collected from Wayne Co., NC (Bertone 2005) (Table 2). *A. rubeolus* was found in the Coastal Plain region with characteristically lower elevations: Wayne Co. 24 m and Chowan Co. 6 m (Figure 1, Table 5).

Three other introduced endocoprid species were collected, *A. erraticus, A. fimetarius* and *A. haemorrhoidalis*. Bertone (2005) found *A. erraticus* to be active from March to early July. This species was collected from Chatham Co. in May and Rockingham Co. in early June in the current study (Table 6). Historically, *A. fimetarius* activity was during spring, early summer and late fall (Bertone 2005) and was collected in Rockingham Co. in a sample collected in early June. Few *A. haemorrhoidalis* were collected from Rowan Co. (Table 3) between April and early September (Bertone 2005) as well as Nash Co. (Table 4) during summer months (Bertone 2004, Chapter IV of this thesis). *A. haemorrhoidalis* was collected in July and August from Chowan and Catawba counties (Table 6). Interestingly one specimen was collected in early October from Clay Co. In a Swedish study *A. haemorrhoidalis* was collected primarily from traps in sandy areas (Vessby and Wiktelius 2003). Likewise, specimens collected from North Carolina predominantly came from areas with sandy-loam soils (Chowan Co. and Nash Co.).

Greatest abundance of *At. erratus* was in Chowan Co. in July. It was also collected from Pender, Catawba and Clay counties. (Table 6) Previous collections showed this native endocoprid dung beetle to be most active between June and November (Bertone 2005). During this survey *Ataenius platensis* was collected only from Pender Co. in July (Table 6). It was previously collected in low numbers from Wayne Co. (Table 2) and Rowan Co. (Table 3) from April through October (Bertone 2005).

A single specimen of *C. chalcites* was recorded in Pender Co. (Table 6). Although this large native telecoprid species was recorded from North Carolina (Blume 1985) (Table 1), it was not collected in 2002-2003 collections (Bertone 2005).

P. vindex, a native paracoprid beetle, was previously trapped at Rowan and Wayne Co. but only 218 specimens were collected over 18 moths. Therefore it is not surprising that only seven individuals were collected from Pender Co. (July) with sandy-loam soils and one from Catawba Co. (August) where soil is Cecil red clay (Table 6, Figure 1). Fincher (1973) found that *P. vindex* preferred soils with higher clay content, but did make brood balls in sandy-loam as well.

G. b. blackburnii was the only trapped species from family Geotrupidae. This native species was collected between late September and late April from Wayne Co. (Table 2) and the only specimen from Rowan Co. was trapped in October (Table 3) (Bertone 2005), as well as from Nash Co. (Table 4) (Bertone 2004, Chapter IV of this thesis). Individuals collected in the current survey came from Pender, Avery and Union counties, representing all three geographic regions of NC.

Current survey indicates that *O. taurus*, the predominant species in Wayne, Rowan and Nash counties, is widespread throughout North Carolina. Importance of this species in pasture clean up, nutrient recycling and resource competition with horn flies iss discussed in the following chapters of this thesis. Presence of other species increases species richness and diversity and the resulting benefits are of great value to the farmers. Efforts should be made to conserve both native and introduced dung beetle species.

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Table 1. Dung beetle species previously collected from North Carolina as recorded by Blume (1985)

Canthon *chalcites* Haldeman	***Aphodius*** *bicolor* Say
C. pilularius (Linnaeus)	*A. campestris* Blatchley
C. vigilans LeConte	*A. distinctus* Muller
C. (Boreocanthon) depressipennis LeConte	*A. fimetarius* Linnaeus
C. (Boreocanthon) probus Germar	*A. granaries* Linnaeus
C. (Glaphyrocanthon) viridis (Beauvois)	*A. haemorrhoidalis* Linnaeus
Melanocanthon *bispinatus* (Robinson)	*A. lividus* Olivier
Pseudocanthon *perplexus* LeConte	*A. lutulentus* Haldeman
Onthophagus *concinnus* LaPorte	*A. rubeolus* Beauvois
O. hecate Panzer	*A. rusicola* Melsheimer (as *A. ruricola*)
O. oklahomensis Brown	*A. stercorosus* Melsheimer
O. pennsylvanicus Harold	*A. stupidus* Horn
O. taurus Schreber	*A. terminalis* Say
O. tuberculifrons Harold	*A. vittatus* Say
Phanaeus *igneus* MacLeay	***Ataenius*** *abditus* (Haldeman)
P. vindex MacLeay	*A. apicalis* Hinton
Dichotomius *carolinus* Linnaeus	*A. cylindricus* Horn
Copris *fricator* (Fabricius)	*A. imbricatus* (Melsheimer)
C. minutus Drury	*A. platensis* (Blanchard)
Geotrupes *blackburnii* (Fabricius)	*A. simulator* Harold
G. egeriei Germar	*A. spretulus* (Haldeman)
G. splendidus (Fabricius)	*A. strigatus* (Say)

Table 2. Species and number of dung beetles trapped from Goldsboro (Center for Environmental Farming Systems) Wayne Co., NC March 2002 – September 2003.

Aphodius *bicolor* Say	*A. platensis* (Blanchard)
A. campestris Blatchley	*A. simulator* Harold
A. distinctus Muller	***Canthon*** *pilularius* (Linnaeus)
A. erraticus Linnaeus	*C. vigilans* LeConte
A. fimetarius Linnaeus	***Copris*** *minutus* Drury
A. granarius Linnaeus	***Dichotomius*** *carolinus* Linnaeus
A.pseudolividus Olivier	***Geotrupes*** *b. blackburnii* (Fabricius)
A. lutulentus Haldeman	***Onthophagus*** *gazella* Fabricius
A. rubeolus Beauvois	*O. h. hecate* Panzer
A. rusicola Melsheimer	*O. oklahomensis* Brown
A. stupidus Horn	*O. pennsylvanicus* Harold
Ataenius *erratus* Fall	*O. taurus* Schreber
A. imbricatus (Melsheimer)	*O. tuberculifrons* Harold
A. miamii Cartwright	*Phanaeus vindex* MacLeay

Table 3. Species and number of dung beetles trapped from Salisbury (Piedmont Research Station), Rowan Co., NC March 2002 – September 2003.

A. distinctus Muller	***Ataenius** platensis* (Blanchard)
A. erraticus Linnaeus	***Copris** minutus* Drury
A. fimetarius Linnaeus	***Geotrupes** b. blackburnii* (Fabricius)
A. granarius Linnaeus	*O. h. hecate* Panzer
A. haemorrhoidalis Linnaeus	*O. pennsylvanicus* Harold
A. pseudolividus Olivier	*O. taurus* Schreber
A. prodromus Brahm	*Phanaeus vindex* MacLeay

Table 4. Species of dung beetles trapped from Nash Co., North Carolina during 2003 (Bertone 2004) and 2004 (Chapter IV of this thesis).

Aphodius *erraticus* Linnaeus	***Geotrupes*** *b. blackburnii* (Fabricius)
A. fimetarius Linnaeus	*G. splendidus* (Fabricius)
A. granarius Linnaeus	***Onthophagus*** *gazella* Fabricius
A. haemorrhoidalis Linnaeus	*O. h. hecate* Panzer
A. pseudolividus Olivier	*O. oklahomensis* Brown
Ataenius *erratus* Fall	*O. pennsylvanicus* Harold
A. platensis (Blanchard)	*O. taurus* Schreber
Ateuchus *histeroides* (Weber)	*O. tuberculifrons* Harold
Canthon *vigilans* LeConte	***Phanaeus*** *vindex* MacLeay
Dichotomius *carolinus* Linnaeus	

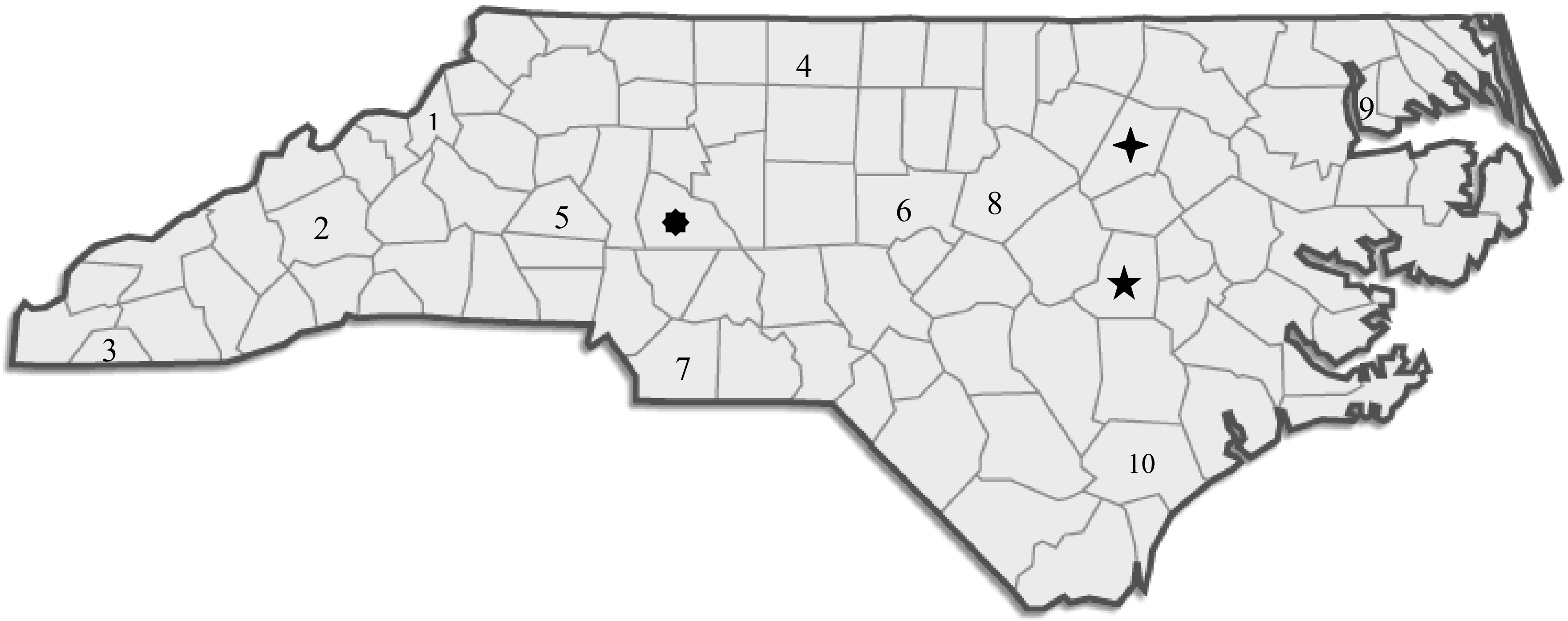

Figure 1. Map of North Carolina with outlined counties. 2005 survey counties: Mountain Region: 1. Avery, 2. Buncombe, 3. Clay; Piedmont Region: Rowan, 4. Rockingham, 5. Catawba, 6. Chatham, 7. Union, 8. Wake; Coastal Plain: Nash, Wayne, 9. Chowan, 10. Pender.

✹= Rowan and ★= Wayne which were monitored by Bertone et al. (2005), and ✦= Nash monitored by Bertone (2004) and in chapter IV of this thesis.

Table 5. List of counties, number of traps, time period that the traps were out, type of cattle present in the pastures with dates when beetles were collected.

County	Date	Elevation (m)	Number of traps	Time period (hrs)	Cattle type
Chatham	05/26/05	188	15	5	Dairy
Rockingham	06/06/05	262	20	5	Beef
Wake	07/07/05	117	10	24	Beef
Chowan	07/13/05	6	22	5	Beef
Pender	07/22/05	6	20	6	Dairy
Wake	08/06/05	117	5	24	Beef
Avery	08/11/05	1144	10	16	Beef
Catawba	08/11/05	295	20	24	Beef and Dairy
Wake	08/28/05	117	10	24	Beef
Union	09/23/05	207	20	4	Beef
Buncombe	10/01/05	661	15	24	Beef
Clay	10/01/05	580	15	20	Dairy

Table 6. List of dung beetle species with the list of counties, elevation, and dates when they were collected.

County	**Date**	**Elevation (m)**	*Aphodius erraticus*	*Aphodius fimetarius*	*Aphodius haemorrhoidalis*	*Aphodius pseudolividus*	*Aphodius rubeolus*	*Ateanius erratus*	*Ataenius platensis*	*Geotrupes b. blackburnii*	*Onthophagus gazella*	*Onthophagus hecate*	*Onthophagus oklahomensis*	*Onthophagus pennsylvanicus*	*Onthophagus taurus*	*Phanaeus vindex*	*Canthon chalcites*	**County totals**
Chatham	05/26/05	188	4	-	-	4	-	-	-	-	-	7	-	-	40	-	-	**55**
Rockingham	06/06/05	262	4	2	-	153	-	-	-	-	-	8	35	1	-	-	-	**203**
Wake	07/07/05	117	-	-	-	1	-	-	-	-	-	-	-	-	87	-	-	**88**
Chowan	07/13/05	6	-	-	8	390	23	208	-	-	-	51	26	101	59	-	-	**866**
Pender	07/22/05	6	-	-	-	-	-	14	20	4	8	61	-	1	5	7	1	**121**
Wake	08/06/05	117	-	-	-	3	-	-	-	-	1	-	1	-	2	-	-	**7**
Avery	08/11/05	1144	-	-	-	10	-	-	-	3	-	-	1	-	65	-	-	**79**
Catawba	08/11/05	295	-	-	1	23	-	1	-	-	-	12	13	1	188	1	-	**240**
Wake	08/28/05	117	-	-	-	4	-	-	-	-	-	-	-	-	26	-	-	**30**
Union	09/23/05	207	-	-	-	90	-	-	-	11	5	-	-	-	37	-	-	**143**
Buncombe	10/01/05	661	-	-	-	-	-	-	-	-	-	1	-	-	6	-	-	**7**
Clay	10/01/05	580	-	-	9	-	-	12	-	-	-	-	-	-	3	-	-	**24**
Species total			**8**	**2**	**18**	**678**	**23**	**235**	**20**	**18**	**14**	**140**	**76**	**104**	**518**	**8**	**1**	**1863**

IV. Impact of *Onthophagus taurus* (Coleoptera: Scarabaeidae) activity on soil richness and plant yield

Abstract

Benefits of the most common North Carolina dung beetle *Onthophagus taurus* Schreber on soil richness and plant yield were studied. The experiment was designed to mimic a rotational pasture grazing system. Three types of soil were used: North Carolina Piedmont Cecil red clay, Coastal Plain sandy-loam and play sand as a nuitrient deficient control. Yields of the warm season grass *Sorghum bicolor* (L.) and a cool season grass *Lolium multiflorum* Lam. grown in the three soil types with and without dung beetles were examined. Treatments included: dung plus (+) five pairs of *O. taurus*, dung only, fertilizer, and an untreated control. Soil analyses were performed to measure the amount of P, K, and N in the underlying soil for all treatments.

O. taurus activity significantly increased the yield of Sudangrass and ryegrass over the dung-only treatment and the control. Ryegrass yield was increased by dung beetle activity over the fertilizer treatment as well, except in sandy-loam soil. Dung beetle activity increased the amount of phosphorus, potassium, and total nitrogen (NH_4 and NO_3) measured in all three soils over the dung-only treatment and the untreated control. Ammonium-nitrate fertilizer significantly increased NH_4 and NO_3 over the other treatments.

Keywords: *Onthophagus taurus*, dung beetles, nutrient recycling, ryegrass, Sudangrass.

Introduction

The feeding and reproductive habits of dung beetles play an important role in the pasture ecosystem. Dung beetles are actively engaged in nutrient cycling, improved soil tilth and moisture percolation (Bornemisszza and Williams 1970, Bornemisszza 1970, Yokoyama et al. 1991a, Yokoyama et al. 1991b). Dung beetles remove feces from the pasture surface, making more grass available for forage. Lastly, dung beetles have an indirect impact on flies by reducing fly breeding habitat, i.e. feces (Fincher 1990). As environmental stewards, cattle producers recognize the benefits of dung beetles and the importance of a healthy pasture ecosystem.

The amount of dung buried by coprophagus beetles is governed by many factors, including the number of dung beetles present, type of dung, age of dung, size of beetles, and soil type. The presence of specialized dung beetles for the target feces type is necessary for a timely dung removal. For instance, in North Queensland, Australia before the introduction of exotic dung beetles it took 3 to 12 months for cattle dung to disintegrate (Ferrar 1975, Gillard 1967). The rate of feces removal was increased when dung beetles specialized to feed on dung of domesticated animals were introduced.

The size of dung beetles governs the rate of dung burial (Horgan 2001, Lindquist 1933, Mittal 1993). In Kansas, larger *Pinotus carolinus* (L.) buried an average 48.5 grams of cattle feces, where smaller *Phanaeus* spp. averaged 9.62 grams of feces buried (Lindquist 1933). The smallest beetle observed, *Copris tullius* Oliver, deposited an average of 7.26 grams of feces beneath the soil surface. Brood balls of *Onthophagus hecate hecate* Panzer and *O. pennsylvanicus* Harold found under feces droppings averaged 0.26 and 0.11 grams in weight, respectively. When plotted, the amount of dung buried was directly related to the mean body size of a female in different species (Horgan 2001). Smaller species deposit feces at a much slower rate. Intuitively, smaller dung beetles are less efficient in pasture sanitation, unless present in very high numbers.

Succession and composition of dung beetle species may be affected by aging feces in tropical environments (Mittal and Vadhera 1998). Dung beetles in the *Drepanocerus* genera were present in feces aged 0 to 4 days during the May dry season and up to 8 days during the August wet season. The authors suggest that older and dryer dung is less suited to habitation by *Drepanocerus* beetles.

Other factors affecting the amount of dung removed by dung beetles are soil type (Fincher 1973, Horgan 2001), soil moisture (Barkhouse 1986), climate (Halffter and Matthews 1966, Holter 1979), vegetation type (Halffter and Matthews 1966), and cattle diet (Dadour and Cook 1996). Dung beetle *Onthophagus binodis* Thunberg produced significantly higher number of brood masses, hence buried more feces when presented with pasture-fed cattle feces compared to grain-fed cattle dung (Dadour and Cook 1996).

Lindquist (1933) noted that the seasonal presence of dung beetles is correlated to the amount of feces removed. Fresh burrows of *P. carolinus* were present from early May to late October, with numbers declining toward the end. Similarly, freshly made burrows of *Copris tullius* Olivier and two *Phanaeus* spp. were observed from early May and again in mid to late October, with barely any burrowing being done during hot and dry mid-summer weather.

One benefit of dung beetles in the pasture ecosystem is the incorporation of nitrogen from the cattle feces back into the soil (Gillard, 1967). About 80% of nitrogen in feces is lost by volatilization, but when dung beetles are present losses are reduced to 5 to 15%. Gillard

(1967) measured the average amount of nitrogen in the area of the fecal pad with beetles present to be 380 kg/ha, and without beetles 85 kg/ha.

Fincher et al. (1981) studied the effects of dung beetles on the yield and quality of coastal Bermuda grass. Dry matter yields for a dung (+) beetles treatment was 7,791 kg/ha compared to 6,364 kg/ha for feces-only treatment, and 8,305 kg/ha for the 224 kg nitrogen fertilizer treatment. Dry matter yield for coastal Bermuda grass overseeded with wheat had an average of 3,509 kg/ha with dung beetles present, compared to 3,217 kg/ha for dung only treatment, and 2,807 kg/ha for the fertilizer treatment. In a third experiment the highest yield and crude protein of Bermuda grass was correlated to beetle density (Fincher et al. 1981).

In a comparative study on the effects of dung beetle activity, unburied dung and fertilizer, beardless wheat grass yields and crude protein were significantly greater as a result of beetle activity, but less than fertilizer treatments with two different rates of nitrogen (MacQueen and Beirne 1975). Both fertilizer treatments had the highest percent nitrogen content in the plant tops. All of the treatments had higher yield and crude protein content than the control. However, the experiment indicated that there is a possible negative impact of surplus nitrogen on the overwintering young beardless wheat grass, and dung beetles may have an added benefit (MacQueen and Beirne 1975). For instance, dung beetle activity lowered acid detergent fiber of grass indicating that beetles prevented N surplus and improved nutritional value (Bang 2005).

In Australia, dung mechanically mixed into soil (37 g/pot), and the activity of *Onthophagus australis* Guer (31.3 g/pot), significantly increased Japanese millet yields above dung placed on the surface (17.3 g/pot) and the control (13.7 g/pot) (Bornemissza and Williams 1970). Similar results were obtained with the root yields. Total uptake of nitrogen, sulphur, and phosphorus was greatest from the plants grown on soils mechanically mixed with feces followed by dung + beetles. The lowest uptake was from the control, followed by the surface dung-only treatment.

In a study of the growth response of wheat plants, ten pairs of *Onthophagus spp.* and ten pairs of *Aphodius spp.* added to 400 g of cow feces increased the plant height, number of leaves and grains, and grain weight, over the treatments containing only dung, dung removed from the soil surface after 9 days, dung mixed in with soil manually, fertilizer mixed in with soil, and soil alone (Kabir et al. 1985). Dung beetles also increased the amount of nitrogen, sulfur, phosphorus, and potassium in the soil over the dung only and fertilizer treatments.

Digonthophagus gazella (sic. *Onthophagus gazella*) prevented loss of at least 140 g of ammonia per kg of cow feces, equaling 57 million kg of ammonia per year in the US alone (Harris et al. 1980). Similarly, the presence of *O. gazella* increased the yield and amount of N and P in savannah grass, *Brachiaria decumbens* Staph., over the untreated control, but not the fertilizer treatment (Behling Miranda et al. 2000).

Many benefits of dung beetles such as fly and nematode control, improvement of yield and quality of pasture grasses, soil enrichment by nutrient recycling and aeration, pasture sanitation, call for increased efforts in dung beetle conservation.

North Carolina cattle pastures are characteristically marginal lands less suited to growing higher valued commodity crops. Seasonal extremes in temperature and precipitation require farmers to adjust the pasture grass composition to maximize yields through planting annuals. Two common North Carolina pasture grasses are the warm season Sudangrass, *Sorghum bicolor* (L.), and the cool season ryegrass, *Lolium multiflorum* Lam.

The objective of this study was to determine the impact of the most abundant dung beetle species in North Carolina, *O. taurus* activity, on the yield of two common North Carolina pasture grasses and in three different soil types: Piedmont Cecil red clay, sandy-loam commonly found in eastern North Carolina, and play sand, which was used as a nutrient deficient control.

Materials and Methods

Soils used in this study were Cecil red clay, sandy-loam, and play sand as a nutrient deficient control. Cecil red clay was collected from the Lake Wheeler Field Experiment Station, North Carolina State University (NCSU), Raleigh, NC. A prepared sandy-loam soil was purchased from American Soil and Mulch, Inc. Morrisville, NC. The play sand was purchased from a local home improvement store. Fresh cattle dung was collected from the Center for Environmental Farming Systems (CEFS), Goldsboro, NC. Dung was frozen at -20^{o}C to kill any dung-dwelling arthropods present in the dung. Dung was thawed for 24 hours before the start of an experiment and manually homogenized. Adult *O. taurus* were live trapped from CEFS and NCSU using a dung-baited pitfall trap described by Bertone (2005). Collected live beetles were separated by sex and kept in 2-liter ice cream containers with a commercial potting soil (Black Kow, Black Gold Compost Co., P.O. Box 190, Oxford FL) before use in the experiment. Ammonium nitrate (Ammon-Nite 34-0-0, Air Products, Pensacola FL) was used as a fertilizer applied at label rate equivalents. The two common North Carolina pasture grasses used were a warm season Sudangrass and a cool season ryegrass. Sudangrass seed was obtained from Kaufman Seed, Ashdown AR, 71822.

Ryegrass seed was purchased from a local home & garden store (Supplier: Johnston Seed Co., Ashburn, GA).

Soils were placed in 3.8-liter black flower pots with the drain holes screened to prevent soil loss. Pots were manually raised to about 10 cm above the ground and dropped ~ 5 times to compact the soil. Potted soils were saturated with water and left to drain overnight. The following day treatments were distributed. The control treatment consisted of untreated soil. The second treatment consisted of 250 g of cattle feces placed on the soil surface. Treatment number three consisted of 250 g of cattle dung being placed on the soil surface together with five pairs of male and female *O. taurus*. The last treatment was 2.64 g of ammonium nitrate fertilizer distributed on the soil surface.

All pots were covered with window screen held in place by rubber bands. After 10 days feces and beetles were removed from the pots. Soil samples were taken from the pots with a soil probe (Oakfield LS Model, Great Lakes IPM, Vestaburg, MI) and each 300cc soil sample was placed in cardboard soil sample boxes (NC Department of Agriculture) to air dry. After the soil samples were taken, the potted soils were gently pressed to fill the probe holes and each pot watered with 250 ml of tap water. Soil was analyzed for the primary nutrients phosphorus (P), potassium (K) and nitrogen (N) at the Analytical Services Laboratory, Department of Soil Sciences, NCSU. Mehlich III analysis determined the amount of potassium (K) and phosphorus (P) present in soil under different treatments (Mehlich 1984a). Soil extractions done by 1 molar KCl (Keeney and Nelson 1987) were used to determine the amount of nitrogen present in soil under different treatments by use of LACHAT Quickchem automatic flow injection ion analyzer (LACHAT Instruments, Milwaukee, WI).

Sudangrass seed was added to each pot (8 grams). Grass was watered every other day with 250 ml of water until the end of 40 days when it was cut about 7cm in length above the soil surface to simulate cattle grazing (Figure 1). Grass cuttings were placed in labeled envelopes, weighed and air dried for 20 days. The second treatment was applied after the first cutting. Dung and beetles were removed after 10 days and the soils sampled. After 40 days, the grass was cut the second time to simulate a second grazing event. Grass was weighed and data recorded. The cool season ryegrass was not planted until after the second treatment was distributed. The ryegrass (planted at a rate of 2 grams per pot) was grown and harvested in the same manner as Sudangrass, with another treatment preceding the second grass cutting. Sudangrass and ryegrass were grown in separate pots.

Data were analyzed using analysis of variance in SAS 8.2 for comparing the beetle treatments and non-beetle treatments (ANOVA, PROC GLM, SAS Institute 2001). Treatment means were separated using Tukey's Studentized Range Test ($\alpha = 0.05$). A square root transformation was performed to all raw data to normalize the distribution. Statistical analysis of soil nutrients was performed in the same manner. Interactions for soil by treatment, replicate by soil by treatment, and cutting by soil by treatment were included in the analysis.

Results and Discussion

Soil analysis: Primary Nutrients

This experiment focused on the changes in primary nutrients resulting from the treatment of clay, sandy-loam and play sand with bovine feces or the combination of bovine feces and dung beetles. A third group of untreated soils were used to provide a baseline for treatment comparisons. The presence of dung beetles significantly ($P < 0.05$) increased phosphorus in all but two cases: the first dung application for sandy-loam and the second application on play sand (Table 1).

Beetle incorporation of dung significantly increased K levels relative to dung only and the control, regardless of test soil ($P < 0.05$) (Table 1). The dung only and the dung + beetles treatments were significantly greater than the control ($P < 0.05$). However, soil differences were not significant between dung and dung + beetles following the 1^{st} and 2^{nd} application (Table 1).

Increases in ammonia (NH_4) in the dung and dung + beetles treatments were significantly greater ($P < 0.05$) than the control in the combined application and the first application, regardless of soil type (Table 2). NH_4 increased significantly in the dung + beetles treatment relative to the control in the first and second application. The dung only treatment was not significantly different from the control in the second treatment application (Table 2). NH_4 in the soils was significantly different for the sandy-loam and play sand for the 1^{st} and 2^{nd} applications (Table 2). NH_4 did not significantly differ for clay soils in either 1^{st} or 2^{nd} application. These results indicate that dung beetle activity conserves NH_4 and reduces losses to volatilization. In a prior study, loss of ammonia (NH_4) from cow dung was reduced, but not significantly by *O. gazella* activity as compared to dung alone (Harris et al. 1980). Still, a total of 57 kg of ammonia per year could be coserved by beetle activity (Harris et al. 1980).

Dung beetle activity increased detectable NO_3 in all but two occasions (Table 2). The presence of *O. taurus* increased NO_3 in clay soils but no increase was observed in sandy-loam soil after the first application or when data for both applications were combined. After the second treatment application, increases of NO_3 were detectable in all three soils with a significant increase ($P < 0.05$) in play sand. As expected, the fertilizer treatment significantly increased NO_3 and NH_4 in all three soil types. Because the fertilizer treatment was superior to other treatments, it was necessary to exclude it from the analysis to allow for normalization of the data (Tables 2, 3, 7, 8, 9, 10, and 11). I combined detectable NH_4 and NO_3 from the analysis to quantify total N available for plant uptake. There was a significant ($P < 0.05$) increase in total N for 8 replicates (Sudangrass and ryegrass pots combined) with *O. taurus* in play sand following the first treatment application (Table 3). In the clay and sandy-loam treatments, low levels of both NH_4 and NO_3 may be attributed to N volatility (Havlin et al. 1999, Brady and Weil 1996).

A pair of *O. taurus* beetles buries on average 36.8 g of dung (Hunt and Simmons 2002). Typically five pairs of beetles, as used in this study, would bury 184 g of the dung presented to them. Depending on soil, *O. taurus* may have buried less dung in sand and sandy-loam than in clay (Bertone 2006, Fincher 1973). Nevertheless, the observed increase in primary nutrients P and K indicates that a few beetles can significantly improve nutrient cycling.

<u>Soil nutrients and grass crop.</u>

Changes in primary nutrients in the soil were effected by grass type (Table 4, Table 5, and Table 6). Analysis of soils in Sudangrass pots indicated significantly higher P and K than ryegrass. Regardless of crop differences, dung + beetles increased nutrients in the test soils.

Phosphorus was significantly ($P < 0.05$) higher in all dung + *O. taurus* treatments for all three soil types and after all three treatment applications in the ryegrass cultivated pots as compared to dung only treatment and control (Table 4). Overall means had the same trend with dung + *O. taurus* treatment being significantly ($P < 0.05$) higher than dung only and the control treatment. Furthermore, the dung-only treatment was significantly higher than the control.

A similar trend was observed in the soils with Sudangrass cover (Table 5). Even though the differences were not significant ($P > 0.05$), in all cases dung beetles increased the amount of P as compared to untreated and dung only-soils. In all cases the dung + *O. taurus* treatment was significantly ($P < 0.05$) higher than the control treatment (Table 6).

Phosphorus in plants has several functions (Havlin et al. 1999). The most essential role is in energy storage and transfer (ADP and ATP). Phosphorus is also an important constituent of nucleic acids, coenzymes, nucleotides, phosphoproteins, phospholipids, and sugar phosphates. A sufficient supply of P is necessary for development of plant reproductive structures and increases root growth. In cereal crops it speeds grain ripening and increases stem strength. It also improves the quality of certain fruits, forages, vegetables and cereal-grains, and it has been linked to increase in disease resistance. The amount of P naturally present in soils is very low (Brady and Weil 1996). Fortunately, P does not form gasses that can escape and it does not readily leach out of the soils.

Potassium in soil was significantly increased in the Sudangrass pots with dung beetle activity relative to the control pots (Table 5). There were no significant differences between the dung only and the dung + beetles treatments, which could be a result of the lack of affinity of *O. taurus* for sand and sandy-loam. In a previous study *O. taurus* produced significantly less brood in washed sand and sandy-loam than in clay soil (Bertone 2006). Similar results were observed in the pots with the ryegrass crop. Dung beetle activity significantly ($P < 0.05$) increased the amount of potassium regardless of soil type and for combined applications (Table 6). An increase in K occurred after each of the three dung + *O. taurus* treatment applications regardless of soil type.

Potassium is crucial for enzyme activation and regulation of stomatal openings (Havlin et al. 1999). Potassium aids in ATP formation and therefore it helps in translocation of sugars and N uptake. Optimum K presence improves winter hardiness and drought tolerance in plants (Brady and Weil 1996). Potassium is easily leached from soils by rainfall and erosion. Potassium is taken up in excess by plants so as the crop is removed from soil surface excess K is lost to future agricultural crops.

Plants absorb nitrogen in two forms ammonium (NH_4^+) and nitrate (NO_3^-). As a result of dung beetle activity, NO_3 and NH_4 were increased in pots with the Sudangrass over the dung only treatment and the control regardless of soil type except after the first application (Table 7). Similarly, dung beetle activity increased NO_3 in the pots with ryegrass in all cases regardless of soil type and the difference was significant ($P < 0.05$) after the 1st application and when three applications were combined (Table 8). NH_4 was increased by the dung beetle activity in the ryegrass pots regardless of the soil type except after the first application and for all three applications combined.

NO_3 and NH_4 were combined for a total plant available N. Total available N was increased in the Sudangrass pots with dung + *O. taurus* over the pots with dung only and untreated control regardless of the soil type (Table 10). This difference was significant ($P < 0.05$) over the control treatments post both applications regardless of the soil type. Similar results were found for ryegrass where beetle dung incorporation increased total available N over the dung only treatment (Table 11). Total N was increased significantly ($P < 0.05$) over the control treatment except post 2nd application (Table 11).

Nitrogen is an important part of chlorophyll, the primary absorber of light for photosynthesis. To be used by plants NO_3^- must be reduced to NH_4^+ or NO_3 before it can be constructed into amino acids for assimilation of proteins and nucleic acids. N is the most commonly deficient nutrient in crop production (Havlin et al. 1999). I expected an increase in nitrogen in the soils where dung was manipulated by beetles (Yokoyama et al. 1991b). Although not in this study, the number of dung beetles per dung pad often exceeds its capacity resulting in a quicker removal of feces (Ridsdill – Smith 1982). Based on the findings of the current study where only 5 pairs of beetles were sufficient to incorporate N into the soil, beetle field populations have a great potential to increase the primary nutrients in soil.

Grass Yield.

This laboratory study was designed to examine the effects of dung beetle activity on the yield of Sudangrass and ryegrass under a simulated rotational grazing schedule (Figure 1). Dung beetle activity increased ryegrass and Sudangrass yield over the dung only treatment and the control in all three types of soil and for both cuttings (Table 9). Dung + *O. taurus* treatment increased the yield of ryegrass over fertilizer treatment except in sandy-loam soil (Table 12). Ryegrass fertilizer treatment was not significantly different ($P > 0.05$) from the dung + *O.taurus* and dung only treatment. Fertilizer yielded more grass than the dung only treatment regardless of soil type (Table 9). Fertilizer treatment for Sudangrass was not included in the analysis because the crop was lost due to unknown reasons. Kabir et al. (1985) observed that two beetles in the genera *Onthophagus spp.* and *Aphodius spp.*

increased plant height, number of leaves and number of grains and grain weight per plant for wheat plants containing only dung + beetles compared to dung only, dung removed after 9 days, dung mixed with soil manually, soil alone and fertilizer. In a similar study, dung beetles significantly increased the yield of pasture grass *Brachiaria decumbens* Staph. over the fertilizer treatment (Behling Miranda et al. 2000).

When results were combined, dung beetles significantly ($P < 0.05$) increased the yield of Sudangrass after both cuttings over the dung only treatment and untreated soils (Table 9). When ryegrass weights for different soil types were combined dung beetle activity significantly increased yield ($P < 0.0001$) over the dung only treatment and the control for both cuttings combined (Table 9). A significant increase in yield ($P < 0.05$) after each cutting was seen for the pots where dung + *O. taurus* were added (Table 9). Yield of Sudangrass and ryegrass in dung-only treatment was numerically higher than the control in all cases regardless of soil type. For Sudangrass these differences were not significant ($P > 0.05$), while for ryegrass this difference was not significant only after the first cutting.

In a comparative study on the effects of dung beetle activity, unburied dung and fertilizer, wheat grass yields and crude protein were significantly greater as a result of beetle activity but less than the fertilizer treatments with two different rates of nitrogen (MacQueen and Beirne 1975). A possible negative impact of nitrogen fertilizer on the overwintering young beardless grass was discussed, explaining that activity of dung beetles lowered acid detergent fiber of grass and prevented N surplus (Bang 2005).

Dung beetles in sandy-loam soil produced the lowest yield of ryegrass and Sudangrass as compared to dung + *O. taurus* in clay and sand (Table 9). Dung beetles prefer certain soil types for their reproduction. For instance *Onthophagus* species prefer sandy soils, *O. taurus* lives mostly in the sandy areas with sparse vegetation (Halffter and Matthews 1966). In South Texas 11 of 16 species of Scarabaeinae and Coprinae preferred sandy to clay soils (Nealis 1977). Interestingly, Piedmont clay soil was most favorable for *O. taurus* and *O. gazella* brood production in a previous study (Bertone et al. 2006). In sandy-loam soil and play sand *O. taurus* produced significantly less brood.

The current study and others clearly demonstrate that dung beetles are actively engaged in nutrient cycling, improved soil tilth, increased soil aeration and moisture percolation (Kabir et al. 2005, Bornemissza and Williams 1970, Bornemissza 1970, Yokoyama et al. 1991a, Yokoyama et al. 1991b). Primary soil nutrients, nitrogen (N), phosphorus (P), and potassium (K), are commonly deficient in soils (Follett and Wilkinson 1995). Pasture grasses in North Carolina are subject to a range of abiotic stresses from nutrient deprivation. Endocoprid dung beetles particularly *O. taurus* have the potential to improve pastures through the incorporation of feces into pasture soils, increasing percolation and providing nutrients (Bornemissza 1960). This study demonstrates that the activity of *O. taurus* even in low densities increased the amount of primary nutrients, P, K, and N, in Piedmont Cecil clay, sandy-loam and a nutrient deficient play sand enough to significantly increase the yield of common pasture grasses in North Carolina.

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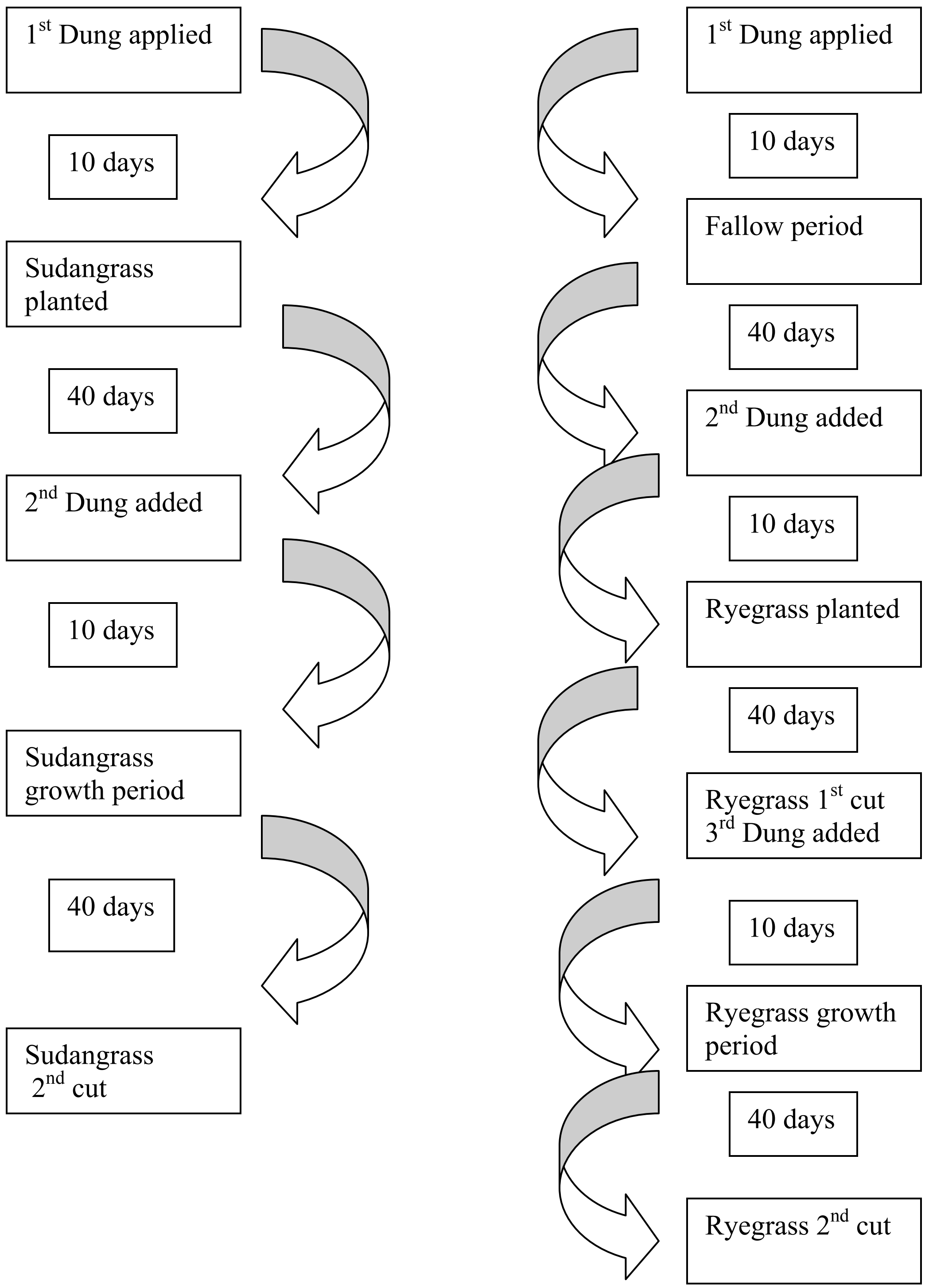

Figure 1. Diagram illustrating the experimental timeline mimicking rotational grazing.

Table 1. P and K levels (mean ± SD) of each soil type before (pre-treatment) and after exposure to *O. taurus* or dung only for Sudangrass and ryegrass combined.

	P (µg/ml)			K (µg/ml)		
	1st application	2nd application	1st & 2nd application	1st application	2nd application	1st & 2nd application
Cecil red clay						
Dung + *O. taurus*	38.8 ± 34.1 a	40.4 ± 37.2 a	39.6 ± 34.5 a	145.3 ± 23.6 a	137.7 ± 65.0 a	141.5 ± 47.4 a
Dung only	33.7 ± 33.8 b	27.4 ± 33.3 b	30.5 ± 32.6 b	123.1 ± 34.9 b	118.1 ± 55.5 a	120.6 ± 44.9 b
Pre-treatment	30.5 ± 31.4 b	22.2 ± 28.3 b	26.3 ± 29.2 b	91.7 ± 35.1 c	75.5 ± 47.7 b	83.6 ± 41.3 c
Sandy-loam						
Dung + *O. taurus*	32.2 ± 28.6 a	28.3 ± 28.7 a	30.2 ±27.8 a	114.5 ± 30.7 a	125.5 ± 66.9 a	120.0 ± 50.6 a
Dung only	27.2 ± 25.6 ab	22.4± 25.9 b	24.8 ± 25.0 b	97.6 ± 25.0 a	84.2 ± 60.7 ab	90.9 ± 45.4 b
Pre-treatment	23.5 ± 24.1 b	19.3 ± 24.6 c	21.4 ± 23.7 c	69.4 ± 24.5 b	52.4 ± 40.2 b	60.9 ± 33.4 c
Sand						
Dung + *O. taurus*	30.3 ± 21.7 a	15.9 ± 22.4 a	23.1 ± 22.6 a	91.9 ± 29.5 a	76.2 ± 58.6 a	84.1 ± 45.6 a
Dung only	25.0 ± 24.9 b	14.9 ± 21.4 b	19.9 ± 23.0 b	84.0 ± 29.3 a	52.7 ± 35.3 ab	68.3 ± 35.2 b
Pre-treatment	21.6 ± 22.3 c	10.2 ± 16.0 b	15.9 ± 19.7 c	61.5 ± 33.1 b	40.4 ± 24.3 b	51.0 ± 30.1 c
Soils combined						
Dung + *O. taurus*	33.7 ± 27.6 a	28.2 ± 30.5 a	31.0 ± 28.9 a	117.2 ± 34.9 a	113.1 ± 66.6 a	115.2 ± 52.6 a
Dung only	28.6 ± 27.4 b	21.5 ± 26.6 b	25.1 ± 27.0 b	101.5 ± 33.1 b	85.0 ± 56.4 b	93.3 ± 46.5 b
Pre-treatment	25.2 ± 25.4 c	17.2 ± 23.1 b	21.2 ± 24.3 c	74.2 ± 32.6 c	56.1 ± 39.8 c	65.2 ± 37.1 c

Different letters within columns and within soils indicate significant differences using Tukey's Studentized Range Test (α = 0.05).

Table 2. NO_3 and NH_4 levels (mean ± SD) of each soil type before (pre-treatment) and after exposure to *O. taurus* or dung only for Sudangrass and ryegrass combined.

	NO_3 (µg/ml)			NH_4 (µg/ml)		
	1st application	2nd application	1st & 2nd application	1st application	2nd application	1st & 2nd application
Cecil red clay						
Dung + *O. taurus*	3.0 ± 3.1 a	3.0 ± 2.1 a	3.0 ± 2.6 a	6.5 ± 2.8 a	6.1 ± 4.2 a	6.3 ± 3.5 a
Dung only	1.5 ± 1.0 a	1.6 ± 1.4 ab	1.6 ± 1.2 ab	6.0 ± 1.5 a	4.6 ± 3.4 a	5.3 ± 2.6 ab
Pre-treatment	1.9 ± 2.2 a	0.9 ± 0.9 b	1.4 ± 1.7 b	4.8 ± 1.8 a	3.5 ± 2.2 a	4.1 ± 2.1 b
Fertilizer	115.5 ± 70.0	94.8 ± 59.8	105.1 ± 63.8	114.1 ± 57.8		103.1 ± 56.2
Sandy-loam						
Dung + *O. taurus*	2.5 ± 2.6 a	1.2 ± 1.1 a	1.8 ± 2.1 a	6.8 ± 3.7 ab	3.8 ± 3.2 a	5.3 ± 3.7 a
Dung only	2.3 ± 1.6 a	1.1 ± 0.8 a	1.7 ± 1.4 a	8.1 ± 4.5 a	4.4 ± 3.8 ab	6.3 ± 4.5 a
Pre-treatment	1.9 ± 2.6 a	0.9 ± 0.8 a	1.4 ± 1.9 b	4.4 ± 1.0 b	2.8 ± 2.0 b	3.6 ± 1.8 b
Fertilizer	152.4 ± 67.5	76.2 ± 51.0	114.3 ± 69.9	139.0 ± 49.1	82.4 ± 58.4	110.7 ± 59.7
Sand						
Dung + *O. taurus*	3.9 ± 4.5 a	2.0 ± 1.7 a	3.0 ± 3.4 a	6.71 ± 2.23a	4.8 ± 3.7 a	5.7 ± 3.1 a
Dung only	1.4 ± 1.1 a	1.3 ± 1.2 b	1.4 ± 1.1 b	5.88 ± 0.91a	5.5 ± 4.9 a	5.7 ± 3.4 a
Pre-treatment	2.1 ± 3.0 b	0.9 ± 1.1 c	1.5 ± 2.2 b	4.66 ± 1.46b	3.5 ± 2.8 b	4.1 ± 2.2 b
Fertilizer	122.3 ± 57.3	84.5 ± 46.5	103.4 ± 54.0	124.21 ± 54.31	93.6 ± 61.8	108.9 ± 58.4
Soils combined						
Dung + *O. taurus*	3.1 ± 3.4 a	2.1 ± 1.8 a	2.6 ± 2.7 a	6.67 ± 2.83a	4.5 ± 3.8 a	5.8 ± 3.4 a
Dung only	1.8 ± 1.3 b	1.3 ± 0.9 ab	1.5 ± 1.2 b	6.67 ± 2.87a	3.7 ± 3.1 ab	5.8 ± 3.5 a
Pre-treatment	2.0 ± 2.5 b	0.9 ± 0.9 b	1.4 ± 1.9 b	4.61 ± 1.41b	4.7 ± 3.4 b	3.9 ± 2.0 b
Fertilizer	130.1 ± 64.4	85.2 ± 51.0	107.6 ± 61.8	125.76 ± 52.52	92.2 ± 56.1	107.6 ± 57.0

Different letters within columns and within soils indicate significant differences using Tukey's Studentized Range Test ($\alpha = 0.05$).

Table 3. Total N levels (mean ± SD) of each soil type before (pre-treatment) and after exposure to *O. taurus* or dung only for Sudangrass and ryegrass.

	total N (µg/ml)		
	1st application	2nd application	1st & 2nd application
Cecil red clay			
Dung + *O. taurus*	9.5 ± 3.8 a	9.1 ± 5.8 a	9.3 ± 4.7 a
Dung only	7.5 ± 1.9 a	6.2 ± 3.6 ab	6.9 ± 2.8 ab
Pre-treatment	6.5 ± 3.5 a	4.5 ± 2.7 b	5.5 ± 3.2 b
Fertilizer	229.6 ± 125.4	186.9 ± 114.2	208.3 ± 117.9
Sandy-loam			
Dung + *O. taurus*	9.3 ± 3.6 a	4.9 ± 3.9 a	7.1 ± 4.3 a
Dung only	10.5 ± 5.2 a	5.5 ± 4.3 a	8.0 ± 5.3 a
Pre-treatment	6.2 ± 2.6 b	3.6 ± 2.7 b	4.9 ± 2.9 b
Fertilizer	291.4 ± 106.0	158.6 ± 109.0	225.0 ± 124.4
Sand			
Dung + *O. taurus*	10.6 ± 5.0 a	6.8 ± 4.8 a	8.7 ± 5.1 a
Dung only	7.3 ± 1.3 b	6.8 ± 5.6 a	7.1 ± 4.0 b
Pre-treatment	6.8 ± 3.9 b	4.4 ± 3.5 b	5.6 ± 3.8 c
Fertilizer	246.5 ± 109.1	178.1 ± 107.5	212.3 ± 110.4
Soils combined			
Dung + *O. taurus*	9.8 ± 4.0 a	6.9 ± 5.0 a	8.4 ± 4.7 a
Dung only	8.4 ± 3.5 a	6.2 ± 4.4 a	7.3 ± 4.1 a
Pre-treatment	6.5 ± 3.2 b	4.2 ± 2.9 b	5.3 ± 3.3 b
Fertilizer	255.8 ± 111.9	174.6 ± 106.1	215.2 ± 115.4

Different letters within columns and within soils indicate significant differences using Tukey's Studentized Range Test ($\alpha = 0.05$).

Table 4. P levels (mean ± SD) of each soil type before (pre-treatment) and after exposure to *O. taurus* or dung only for ryegrass.

	P (µg/ml)			
	1st application	2nd application	3rd application	1st, 2nd & 3rd application
Cecil red clay				
Dung + *O. taurus*	7.3 ± 5.0 a	16.5 ± 4.5 a	11.1 ± 4.9 a	11.6 ± 5.9 a
Dung only	2.3 ± 0.5 b	3.3 ± 1.8 b	5.3 ± 1.5 b	3.6 ± 1.8 b
Pre-treatment	1.3 ± 0.1 b	2.0 ± 0.8 b	2.6 ± 0.5 c	1.9 ± 0.8 c
Sandy-loam				
Dung + *O. taurus*	6.0 ± 4.1 a	9.4 ± 7.7 a	9.4 ± 3.4 a	8.3 ± 5.2 a
Dung only	3.5 ± 2.7 ab	4.2 ± 1.9 ab	4.0 ± 1.0 b	3.9 ± 1.8 b
Pre-treatment	1.0 ± 0.1 b	1.9 ± 0.6 b	2.2 ± 0.3 b	1.7 ± 0.7 c
Sand				
Dung + *O. taurus*	12.0 ± 13.3 a	4.7 ± 1.4 a	7.8 ± 3.3 a	8.2 ± 7.9 a
Dung only	1.9 ±0.4 ab	3.9 ± 2.5 a	3.7 ± 1.8 b	3.1 ± 1.9 b
Pre-treatment	0.8 ± 0.1 ab	2.0 ± 1.3 a	1.8 ± 0.1 b	1.5 ± 0.9 b
Soil combined				
Dung + *O. taurus*	8.5 ± 8.2 a	10.2 ± 6.9 a	9.5 ± 3.8 a	9.4 ± 6.4 a
Dung only	2.5 ± 1.6 b	3.8 ± 1.9 b	4. 3 ± 1.5 b	3.5 ± 1.8 b
Pre-treatment	1.0 ± 0.2 b	1.9 ± 0.9 c	2.2 ± 0.4 c	1.7 ± 0.8 c

Different letters within columns and within soils indicate significant differences using Tukey's Studentized Range Test ($\alpha = 0.05$).
Fertilizer excluded from the analysis since it did not contain P or K.

Table 5. P and K levels (mean ± SD) of each soil type before (pre-treatment) and after exposure to *O. taurus* or dung only for Sudangrass.

	P (µg/ml)			K (µg/ml)		
	1st application	2nd application	1st & 2nd application	1st application	2nd application	1st & 2nd application
Cecil red clay						
Dung + *O. taurus*	70.3 ± 6.5 a	64.3 ± 41.1 a	67.3 ± 27.4 a	157.9 ± 26.50a	165.5 ± 54.1 a	161.7 ± 39.7 a
Dung only	65.1 ± 5.0 ab	51.5 ± 32.1 b	58.3 ± 22.5 b	149.0 ± 29.09ab	155.5 ± 38.8 a	152.3 ± 32.0 a
Pre-treatment	59.8 ± 2.9 b	42.3 ± 28.0 c	51.1 ± 20.1 c	122.5 ± 8.03b	111.3 ± 40.3 b	116.9 ± 27.6 b
Sandy-loam						
Dung + *O. taurus*	58.3 ± 8.2 a	47.2 ± 30.2 a	52.8 ± 21.3 a	130.3 ± 24.25a	127.2 ± 31.5 a	128.8 ± 26.1 a
Dung only	50.9 ± 4.4 ab	40.5 ±26.2 ab	45.7 ± 18.2 b	112.0 ± 20.22a	124.3 ± 47.7 a	118.2 ± 34.6 a
Pre-treatment	46.0 ± 1.5 b	36.7 ± 24.7 b	41.4 ± 16.9 c	90.9 ± 7.80b	83.2 ± 33.8 b	87.0 ± 23.1 b
Sand						
Dung + *O. taurus*	48.5 ± 6.3 a	27.2 ± 28.8 a	37.8 ± 22.4 a	105.9 ± 34.10a	109.3 ± 59.0 a	107.6 ± 44.7 a
Dung only	48.1 ± 4.5 a	25.9 ± 27.2 a	37.00 ± 21.6 a	108.9 ± 15.62a	75.4 ± 31.3 ab	92.2 ± 29.0 ab
Pre-treatment	42.5 ± 1.9 a	18.4 ± 20.4 b	30.5 ± 18.6 b	91.6 ± 11.80a	55.8 ± 22.7 b	73.7 ± 25.4 b
Soils combined						
Dung + *O. taurus*	59.0 ± 11.3 a	46.2 ± 34.4 a	52.6 ± 25.9 a	131.4 ± 34.07a	134.0 ± 51.2 a	132.7 ± 42.5 a
Dung only	54.7 ± 8.8 a	39.3 ± 28.1 a	47.0 ± 21.8 ab	123.3 ± 27.78a	118.4 ± 49.8 a	120.9 ± 39.5 a
Pre-treatment	49.4 ± 8.0 b	32.5 ± 24.6 a	41.0 ± 19.9 b	46.2 ± 34.44b	83.4 ± 38.1 b	92.5 ± 30.5 b

Different letters within columns and within soils indicate significant differences using Tukey's Studentized Range Test (α = 0.05). Fertilizer excluded from the analysis since it did not contain P or K.

Table 6. K levels (mean ± SD) of each soil type before (pre-treatment) and after exposure to *O. taurus* or dung only for ryegrass.

	K (µg/ml)			
	1st application	2nd application	3rd application	1st, 2nd & 3rd application
Cecil red clay				
Dung + *O. taurus*	132.7 ± 13.0 a	110.0 ± 69.7 a	96.7 ± 91.8 a	113.1 ± 62.5 a
Dung only	97.1 ± 14.2 b	80.8 ± 44.4 ab	154.6 ± 136.8 a	110.8 ± 82.4 ab
Pre-treatment	60.8 ± 16.7 c	39.7 ± 15.9 b	93.7 ± 88.8 a	64.7 ± 53.2 b
Sandy-loam				
Dung + *O. taurus*	98.6 ± 30.6 a	123.8 ± 97.1 a	64.2 ± 75.1 ab	95.5 ± 70.8 ab
Dung only	83.2 ± 22.3 a	44.1 ± 45.0 b	23.3 ± 18.9 b	50.2 ± 38.2 b
Pre-treatment	48.0 ± 10.7 b	21.7 ± 11.0 b	246.5 ± 288.0 a	105.4 ± 183.5 a
Sand				
Dung + *O. taurus*	77.9 ± 18.6 a	43.1 ± 40.3 a	108.4 ± 73.4 a	76.5 ± 52.7 a
Dung only	59.1 ± 10.1 b	30.0 ± 23.4 a	72.5 ± 108.8 ab	53.8 ± 61.3 ab
Pre-treatment	31.5 ± 3.7 c	74.9 ± 101.2 a	10.3 ± 2.5 b	38.9 ± 59.9 b
Soils combined				
Dung + *O. taurus*	103.1 ± 30.9 a	92.3 ± 75.5 a	89.8 ± 75.4 a	95.0 ± 62.5 a
Dung only	79.8 ± 22.1 b	51.6 ± 41.7 ab	83.5 ± 107.9 a	71.6 ± 67.6 b
Pre-treatment	46.8 ± 16.4 c	45.4 ± 58.6 b	116.8 ± 187.7 a	69.7 ± 115.7 b

Different letters within columns and within soils indicate significant differences using Tukey's Studentized Range Test ($\alpha = 0.05$).
Fertilizer excluded from the analysis since it did not contain P or K.

Table 7. NO_3 and NH_4 levels (mean ± SD) of each soil type before (pre-treatment) and after exposure to *O. taurus* or dung only for Sudangrass.

	NO_3 (µg/ml)			NH_4 (µg/ml)		
	1st application	2nd application	1st & 2nd application	1st application	2nd application	1st & 2nd application
Cecil red clay						
Dung + *O. taurus*	1.1 ± 1.3 a	3.5 ± 1.9 a	2.3 ± 2.0 a	6.9 ± 3.2 a	7.2 ± 3.2 a	7.1 ± 3.0 a
Dung only	0.6 ± 0.5 a	2.3 ± 1.6 a	1.4 ± 1.4 a	6.3 ± 2.2 a	5.5 ± 3.0 a	5.9 ± 2.5 a
Pre-treatment	2.0 ± 3.1 a	1.2 ± 1.2 a	1.6 ± 2.2 a	6.1 ± 1.6 a	5.0 ± 2.0 a	5.5 ± 1.8 a
Fertilizer	72.6 ± 11.6	129.1 ± 43.1	100.9 ± 42.0	80.7 ± 29.6	131.7 ± 26.7	106.2 ± 37.7
Sandy-loam						
Dung + *O. taurus*	0.6 ± 0.5 ab	1.6 ± 1.4 a	1.1 ± 1.0 ab	7.5 ± 3.3 a	6.5 ± 1.6 a	7.0 ± 2.4 a
Dung only	1.1 ± 0.6 a	1.4 ± 1.0 a	1.2 ± 0.7 a	5.8 ± 2.5 a	7.6 ± 2.3 a	6.7 ± 2.4 a
Pre-treatment	0.3 ± 0.3 b	1.3 ± 0.9 a	0.8 ± 0.8 b	4.3 ± 0.5 a	4.2 ± 1.7 b	4.3 ± 1.1 b
Fertilizer	128.0 ± 53.0	106.4 ± 20.7	117.2 ± 39.0	136.1 ± 60.5	120.0 ± 28.0	128.1 ± 44.5
Sand						
Dung + *O. taurus*	0.9 ± 0.7 a	3.3 ± 1.6 a	2.1 ± 1.7 a	6.8 ± 2.4 a	7.3 ± 1.7 a	7.0 ± 2.0 a
Dung only	0.4 ± 0.3 a	2.0 ± 1.5 ab	1.2 ± 1.3 b	5.9 ± 0.8 ab	9.2 ± 3.6 a	7.5 ± 3.0 a
Pre-treatment	0.3 ± 0.1 a	1.3 ± 1.4 b	0.8 ± 1.0 b	4.4 ± 1.5 b	4.6 ± 1.6 b	4.5 ± 1.4 b
Fertilizer	88.7 ± 50.0	109.1 ± 15.3	98.9 ± 35.9	85.8 ± 34.4	121.2 ± 35.8	103.5 ± 37.6
Soils combined						
Dung + *O. taurus*	0.8 ± 1.8 a	2.8 ± 1.7 a	1.8 ± 1.7 a	7.1 ± 2.7 a	7.0 ± 2.1 a	7.0 ± 2.4 a
Dung only	0.7 ± 0.5 a	1.9 ± 1.3 ab	1.3 ± 1.1 ab	6.0 ± 1.8 ab	7.4 ± 3.1 a	6.7 ± 2.6 a
Pre-treatment	0.8 ± 0.8 a	1.3 ± 1.0 b	1.1 ± 1.5 b	4.9 ± 1.5 b	4.6 ± 1.6 b	4.8 ± 1.5 b
Fertilizer	96.4 ± 45.5	114.9 ± 28.3	105.7 ± 38.2	100.9 ± 47.3	124.3 ± 28.1	112.6 ± 39.9

Different letters within columns and within soils indicate significant differences using Tukey's Studentized Range Test (α = 0.05). Fertilizer treatment excluded from the analysis to allow for data normalization.

Table 8. NO_3 levels (mean ± SD) of each soil type before (pre-treatment) and after exposure to *O. taurus* or dung only for ryegrass.

	NO_3 (µg/ml)			
	1st application	2nd application	3rd application	1st, 2nd & 3rd application
Cecil red clay				
Dung + *O. taurus*	4.9 ± 3.3a	2.5 ± 2.5a	0.4 ± 0.3a	2.6 ± 2.9a
Dung only	2.4 ± 0.4a	1.0 ± 0.8ab	0.5 ± 0.5a	1.3 ± 1.0ab
Pre-treatment	1.8 ± 1.3a	0.6 ± 0.5b	0.2 ± 0.0a	0.9 ± 1.0b
Fertilizer	158.4 ± 79.9	60.4 ± 57.8	6.5 ± 6.0	75.8 ± 83.5
Sandy-loam				
Dung + *O. taurus*	4.4 ± 2.5	0.8 ± 0.6ab	0.8 ± 0.5a	2.0 ± 2.2a
Dung only	3.5 ± 1.4a	0.8 ± 0.6a	0.4 ± 0.2ab	1.6 ± 1.7ab
Pre-treatment	3.6 ± 2.8a	0.5 ± 0.4b	0.2 ± 0.3b	1.4 ± 2.2b
Fertilizer	176.9 ± 79.0	46.0 ± 56.7	23.5 ± 14.4	82.1 ± 87.3
Sand				
Dung + *O. taurus*	7.0 ± 4.7a	0.8 ± 0.6a	1.3 ± 1.2a	3.0 ± 3.9a
Dung only	2.4 ± 0.5b	0.6 ± 0.4a	0.5 ± 0.5ab	1.2 ± 0.9b
Pre-treatment	4.0 ± 3.4ab	0.5 ± 0.6a	0.1 ± 0.1b	1.5 ± 2.5b
Fertilizer	155.9 ± 46.5	59.9 ± 56.5	9.7 ± 6.5	75.2 ± 74.0
Soils combined				
Dung + *O. taurus*	5.4 ± 3.5a	1.3 ± 1.6a	0.8 ± 0.8a	2.5 ± 3.0a
Dung only	2.8 ± 1.0b	0.8 ± 0.6ab	0.5 ± 0.4a	1.4 ± 1.2b
Pre-treatment	3.1 ± 2.6b	0.5 ± 0.5b	0.2 ± 0.2b	1.3 ± 1.9b
Fertilizer	163.7 ± 64.3	55.4 ± 52.0	13.3 ± 11.7	77.5 ± 79.5

Different letters within columns and within soils indicate significant differences using Tukey's Studentized Range Test ($\alpha = 0.05$).
Fertilizer treatment excluded from the analysis to allow for data normalization.

Table 9. NH_4 levels (mean ± SD) of each soil type before (pre-treatment) and after exposure to *O. taurus* or dung only for ryegrass.

	NH_4 (μg/ml)			
	1st application	2nd application	3rd application	1st, 2nd & 3rd application
Cecil red clay				
Dung + *O. taurus*	6.1 ± 2.8 a	5.0 ± 5.2 a	0.3 ± 0.0 a	3.8 ± 4.0 a
Dung only	5.7 ± 0.6 a	3.7 ± 3.9 a	0.2 ± 0.3 a	3.2 ± 3.1 ab
Pre-treatment	3.4 ± 0.5 a	2.1 ± 1.5 a	0.5 ± 0.4 a	2.0 ± 1.5 b
Fertilizer	147.5 ± 62.9	52.7 ± 49.6	6.0 ± 5.7	68.7 ± 74.4
Sandy-loam				
Dung + *O. taurus*	6.0 ± 4.4 ab	1.1 ± 1.3 a	0.2 ± 0.1 a	2.4 ± 3.6 ab
Dung only	10.5 ± 5.2 a	1.3 ± 1.5 a	0.2 ± 0.0 a	4.0 ± 5.6 a
Pre-treatment	4.5 ± 1.5 b	1.4 ± 1.1 a	0.4 ± 0.3 a	2.1 ± 2.1 b
Fertilizer	141.8 ± 44.1	44.8 ± 58.3	21.2 ± 12.9	69.2 ± 66.9
Sand				
Dung + *O. taurus*	6.7 ± 2.4 a	2.3 ± 3.6 a	0.3 ± 0.3 a	3.1 ± 3.6 a
Dung only	5.9 ± 1.1 a	1.9 ± 2.8 a	0.2 ± 0.2 a	2.6 ± 2.9 a
Pre-treatment	4.9 ± 1.6 a	2.4 ± 3.5 a	0.4 ± 0.3 a	2.6 ± 2.8 a
Fertilizer	162.6 ± 42.2	65.9 ± 74.7	9.2 ± 7.4	79.2 ± 79.9
Soils combined				
Dung + *O. taurus*	6.3 ± 3.0 ab	2.8 ± 3.8 a	0.3 ± 0.2 a	3.1 ± 3.7 a
Dung only	7.3 ± 3.6 a	2.3 ± 2.8 a	0.2 ± 0.2 a	3.3 ± 4.0 a
Pre-treatment	4.3 ± 1.4 b	1.9 ± 2.1 a	0.4 ± 0.2 a	2.2 ± 2.14 a
Fertilizer	150.6 ± 46.7	54.5 ± 56.6	12.1 ± 10.8	72.4 ± 72.0

Different letters within columns and within soils indicate significant differences using Tukey's Studentized Range Test (α = 0.05).
Fertilizer treatment excluded from the analysis to allow for data normalization.

Table 10. Total N levels (mean ± SD) of each soil type before (pre-treatment) and after exposure to *O. taurus* or dung only for Sudangrass.

	total N (µg/ml)		
	1st application	2nd application	1st & 2nd application
Cecil red clay			
Dung + *O. taurus*	8.0 ± 3.5 a	10.7 ± 3.4 a	9.3 ± 3.5 a
Dung only	6.9 ± 2.5 a	7.8 ± 1.6 ab	7.4 ± 2.0 a
Pre-treatment	7.8 ± 4.7 a	6.2 ± 2.4 b	7.0 ± 3.5 a
Fertilizer	153.3 ± 41.2	260.8 ± 69.6	207.0 ± 78.1
Sandy-loam			
Dung + *O. taurus*	8.1 ± 3.7 a	8.1 ± 2.6 a	8.1 ± 3.0 a
Dung only	6.9 ± 3.0 a	9.0 ± 2.7 a	7.9 ± 2.8 a
Pre-treatment	4.3 ± 0.8 a	5.5 ± 2.5 b	4.9 ± 1.8 b
Fertilizer	264.1 ± 112.5	226.5 ± 47.4	245.3 ± 82.4
Sand			
Dung + *O. taurus*	7.7 ± 2.9 a	10.5 ± 1.5 a	9.1 ± 2.6 a
Dung only	6.3 ± 0.9 ab	11.2 ± 3.9 a	8.7 ± 3.7 a
Pre-treatment	4.7 ± 1.5 b	5.9 ± 2.6 b	5.3 ± 2.1 b
Fertilizer	174.6 ± 84.2	230.3 ± 51.0	202.4 ± 71.0
Soils combined			
Dung + *O. taurus*	2.8 ± 1.7 a	9.8 ± 2.7 a	8.8 ± 3.0 a
Dung only	1.9 ± 1.3 ab	9.3 ± 3.0 a	8.0 ± 2.8 a
Pre-treatment	1.3 ± 1.0 b	5.8 ± 2.3 b	5.7 ± 2.6 b
Fertilizer	114.9 ± 28.3	239.2 ± 53.9	218.3 ± 76.5

Different letters within columns and within soils indicate significant differences using Tukey's Studentized Range Test (α = 0.05).
Fertilizer treatment excluded from the analysis to allow for data normalization.

Table 11. Total N levels (mean ± SD) of each soil type before (pre-treatment) and after exposure to *O. taurus* or dung only for ryegrass.

total N (μg/ml)				
	1st application	2nd application	3rd application	1st, 2nd & 3rd application
Cecil red clay				
Dung + *O. taurus*	6.4 ± 6.3 a	7.4 ± 7.7 a	0.7 ± 0.3 a	6.4 ± 6.3 a
Dung only	4.5 ± 4.0 ab	4.6 ± 4.6 a	0.7 ± 0.4 a	4.5 ± 4.0 ab
Pre-treatment	2.9 ± 2.4 b	2.7 ± 1.9 a	0.7 ± 0.4 a	2.9 ± 2.4 b
Fertilizer	143.8 ± 156.6	113.1 ± 105.0	12.4 ± 11.6	143.8 ± 156.6
Sandy-loam				
Dung + *O. taurus*	4.4 ± 4.9 a	1.8 ± 1.9 a	1.00 ± 0.5 a	4.4 ± 4.9 a
Dung only	5.6 ± 6.8 a	2.1 ± 2.1 a	0.6 ± 0.2 a	5.6 ± 6.8 a
Pre-treatment	3.5 ± 3.8 b	1.8 ± 1.6 a	0.6 ± 0.3 a	3.5 ± 3.8 b
Fertilizer	151.4 ± 150.3	90.8 ± 114.9	44.7 ± 27.3	151.4 ± 150.3
Sand				
Dung + *O. taurus*	6.1 ± 6.5 a	3.1 ± 3.8 a	1.6 ± 1.4 a	6.1 ± 6.5 a
Dung only	3.8 ± 3.8 a	2.5 ± 3.1 a	0.7 ± 0.5 a	3.8 ± 3.8 a
Pre-treatment	4.1 ± 4.9 a	2.9 ± 4.1 a	0.6 ± 0.4 a	4.1 ± 4.9 a
Fertilizer	154.4 ± 152.8	125.9 ± 130.8	19.0 ± 13.9	154.4 ± 152.8
Soils combined				
Dung + *O. taurus*	5.6 ± 5.9 a	4.1 ± 5.2 a	1.1 ± 0.9 a	5.6 ± 5.9 a
Dung only	4.6 ± 4.9 ab	3.1 ± 3.3 a	0.7 ± 0.3 ab	4.6 ± 4.9 ab
Pre-treatment	3.5 ± 3.7 b	2.5 ± 2.5 a	0.6 ± 0.3 b	3.5 ± 3.7 b
Fertilizer	149.9 ± 148.9	109.9 ± 107.2	25.4 ± 22.5	149.9 ± 148.9

Different letters within columns and within soils indicate significant differences using Tukey's Studentized Range Test (α = 0.05).
Fertilizer treatment excluded from the analysis to allow for data normalization.

Table 12. Dry weights of ryegrass and Sudangrass shoots (mean ± SD) for each soil type in pre-treatment, after exposure to *O. taurus* or dung only.

	Dry weight (g)					
	Ryegrass			Sudangrass		
	1st cutting	2nd cutting	1st & 2nd cutting	1st cutting	2nd cutting	1st & 2nd cutting
Cecil red clay						
Dung + *O. taurus*	1.3 ± 0.6 a	1.4 ± 0.7 a	1.3 ± 0.6 a	2.1 ± 0.5 a	0.5 ± 0.2 a	1.3 ± 0.9 a
Dung only	0.5 ± 0.3 b	0.7 ± 0.3 b	0.6 ± 0.3 b	2.1 ± 1.1 a	0.5 ± 0.4 a	1.3 ± 1.2 a
Pre-treatment	0.5 ± 0.2 b	0.2 ± 0.1 bc	0.3 ± 0.2 b	0.9 ± 0.7 a	0.3 ± 0.2 a	0.6 ± 0.6 b
Fertilizer	0.6± 0.4 b	0.4 ± 0.2 c	0.5 ± 0.3 b			
Sandy-loam						
Dung + *O. taurus*	1.1 ± 0.4 ab	1.0 ± 0.5 ab	1.0 ± 0.4 ab	1.7 ± 0.6 a	1.1 ± 0.4 a	1.4 ± 0.6 a
Dung only	0.8 ± 0.3 b	0.7 ± 0.2 bc	0.7 ± 0.3 b	1.3 ± 1.0 a	0.4 ± 0.5 b	0.9 ± 0.8 b
Pre-treatment	0.4 ± 0.2 c	0.3 ± 0.1 c	0.3 ± 0.2 c	1.1 ± 0.6 a	0.2 ± 0.2 b	0.7 ± 0.6 b
Fertilizer	1.4 ± 0.8 a	2.1 ± 1.8 a	1.7 ± 1.3 a			
Sand						
Dung + *O. taurus*	1.4 ± 0.8 a	1.3 ± 0.5 a	1.3 ± 0.7 a	2.4 ± 1.3 a	1.2 ± 0.6 a	1.8 ± 1.1 a
Dung only	0.7 ± 0.5 ab	0.9 ± 0.4 ab	0.8 ± 0.4 ab	1.1 ± 1.0 ab	0.4 ± 0.2 b	0.7 ± 0.8 b
Pre-treatment	0.4 ± 0.3 b	0.2 ± 0.1 c	0.3 ± 0.2 b	1.0 ± 0.5 b	0.5 ± 0.3 b	0.7 ± 0.5 b
Fertilizer	0.9 ± 0.4 ab	0.7 ± 0.1 b	0.8 ± 0.3 ab			
Soils combined						
Dung + *O. taurus*	1.2 ± 0.6 a	1.2 ± 0.5 a	1.2 ± 0.5 a	2.0 ± 0.9 a	0.9 ± 0.5 a	1.5 ± 0.9 a
Dung only	0.7 ± 0.4 bc	0.7 ± 0.3 b	0.8 ± 0.3 b	1.5 ± 1.0 b	0.4 ± 0.3 b	1.0 ± 0.9 b
Pre-treatment	0.4 ± 0.2 c	0.2 ± 0.1 c	0.3 ± 0.2 c	1.0 ± 0.6 b	0.3 ± 0.2 b	0.7 ± 0.5 b
Fertilizer	0.9 ± 0.6 ab	1.1 ± 1.2 ab	1.0 ± 1.0 ab			

Different letters within columns and within soils indicate significant differences using Tukey's Studentized Range Test (α = 0.05). Fertilizer treatment for Sudangrass excluded from the analysis.

V. Impact of a feed-through methoprene application on dung beetle (Coleoptera: Scarabaeidae and Geotrupidae) populations in North Carolina pastures

Abstract

Area-wide treatment for control of horn flies, *Haematobia irritans* L. and its non-target effects on dung beetle populations were evaluated in this study. The treatment area consisted of ten adjoining farms in Nash Co., North Carolina, where the insect growth regulator, methoprene, formulated as a mineral supplement was administered to 1,340 mixed breed beef cows and their nursing calves during 17 weeks in the summer of 2004. Horn fly densities were monitored weekly on 10 animals from each of the methoprene treated farms and two untreated control farms, one located near the treatment group and another in Wayne Co., NC. Dung beetles were captured using dung-baited pitfall traps. Dung beetle traps were placed on two methoprene treated farms every two weeks for a 24-hour period. The results were compared to those of the untreated control farm in Wayne Co., NC.

Methoprene effectively reduced horn fly population. Mean horn fly densities were significantly lower for the treated animals, 19.6 ± 10.0 per animal, compared to 100.9 ± 50.3 (Nash Co.) and 467.5 ± 140.3 (Wayne Co.) for two control groups. Dung beetles were most abundant on the untreated control farm in Wayne Co. During the study 15,039 dung beetles representing 17 species were trapped from Wayne Co. and 4,463 dung beetles representing 12 species were trapped from Nash Co. The most abundant species at both sites were *Ontophagus taurus* Schreber, *Aphodius pseudolividus* Olivier, *Onthophagus pennsylvanicus* Harold and *Onthophagus hecate hecate* Panzer. Methoprene treatments did not appear to have a negative effect on common *Onthophagus* species. Densities of *Aphodius* *pseudolividus* were low during the study, although it could not be ascertained if this was caused by the methoprene application.

Keywords: Dung beetles, horn fly, *Haematobia irritans*, methoprene, insect growth regulator, pasture fly control

Introduction

Horn Fly, *Haematobia irritans* (L.) is one of the primary cattle pests in North Carolina pastures and it causes great economic loses to cattle producers (Watson et al. 2002, Drummond 1981). A blood-feeding insect, the horn fly is an annoyance to cattle and decreases milk production and weight gain (Campbell 1976). More importantly, the horn fly is a carrier of mastitis causative agent *Staphylococcus aureus* and is capable of transmitting intramammary infection in dairy heifers (Owens et al. 1998, Gillespie et al. 1999).

Predilection sites for horn flies are usually the back, neck, belly and occasionally around the horns of an animal. They tend to remain with the host, taking up to 20 blood meals every 24 hours (Bruce 1964). Females leave the host to lay eggs in the freshly deposited feces, where the larvae will develop through three instars, then move into the soil to pupade. Teneral adults emerge 10 – 20 days after the eggs were deposited. Development and diapause is temperature dependent (Lysyk 1992). Each spring, post-diapausing horn flies emerge as a new generation of adult flies following more than 60 days of temperatures above 25ºC.

Insecticides applied as dusts, sprays, pour-ons, boluses, feed additives, and insecticide impregnated ear tags have been traditionally used to control horn flies (Butler and Okine 1999). Insecticide resistance has made horn fly control more difficult (Miller et al. 1983, Sheppard 1984, Quisenberry et al. 1984, Hogsette et al. 1991, Sheppard and Joyce 1992). Of concern in the use of these insecticides and certain anthelmintics is their impact on non-target arthropods found in feces, particularly dung beetles (Wardhaugh 2005). Fundamental to the concepts of Integrated Pest Management is the use of multiple strategies for the management of pests and reduced reliance on pesticides. These strategies include sanitation programs to remove pest resources, and the employment of mechanical or biological control methods (Watson et al. 2002). If pesticides are needed to help reduce the number of horn flies resistant to pyrethroids or organophosphates, it is important to rotate insecticide classes. In the last 25 years, the use of endectocides such as ivermectin, abamectin, moxidectin, and eprinomectin have been used effectively against pyrethroid-resistant horn flies. However, concernes have been raised that these active ingredients may negatively impact beneficial dung dwelling arthropods.

In Australia two endectocides, moxidectin and abamectin, in the macrocyclic lactone insecticide class, were examined for their impact on the survival of *Haematobia irritans exigua* De Meijere (buffalo fly) and the dung beetle, *Onthophagus gazella* (F.) (Doherty et al. 1994). The following concentrations were tested in dung: 4, 8, 16, 32, 64, 128, 256, and 512 µg/kg dung. While moxidectin reduced the mean percent pupadion of buffalo fly in concentrations up to 256µg/kg dung and completely prevented pupadion at 512 µg/kg dung, there was no significant reduction in percent survival for *O. gazella* in all but the highest concentration. In the lowest concentration abamectin produced mean pupadion of 1% for the buffalo fly, and completely prevented pupadion at all of the other concentrations. However, *O. gazella* survival was reduced by 15% when raised on feces with abamectin concentration of 4 µg/kg dung and by 52% at 8 µg/kg dung. At concentrations above 8µg/kg dung, no *O. gazella* survived to the adult stage.

Moxidectin (0.5 mg per kg of animal) had no impact on development and survival of *Onthophagus taurus* Schreber when fed feces of cattle treated with a pour-on application (Wardhaugh et al. 2001). In contrast, brood developing on feces collected from cattle 3 and

7 days after pour-on application of eprinomectin had 0.0 ± 0.0 and 6.4 ± 1.6 percent survival, respectively.

Both avermectin and ivermectin when used for horn fly control have a toxic effect on adult dung beetles and their progeny (Wardhaugh and Rodriguez-Menendez 1988, Floate and Gill 1998, Floate et al. 2002). Floate and Gill (1998) topically applied ivermectin to cattle at the recommended dose of 500µg/kg to determine the effect of endectocide residues on the emergence of dung feeding arthropods. Dung was collected at 0, 1, 2, 3, 4, 6, 8, and 12 weeks post treatment. *Aphodius fimetarius* (L.) emergence was significantly reduced in dung collected one-week post treatment. Emergence of *Aphodius vittatus* Say was significantly lower for dung at weeks 1, 2, 3, and 12.

Wardhaugh and Mahon (1991) found that adults of *Onthophagus australis* (Guerin), *O. pexatus* Harold 1869, *O. penthacantus* Harold, *Euoniticellus fulvus* (Goeze) and *O. taurus* all preferred cattle dung collected 3 and 25 days after the individuals were treated with subcutaneous injections of avermectin at a dose of 200 µg/kg. Similarly, *O. australis* preferred dung collected 1 day after sheep were drenched with avermectin (200 µg/kg), but not dung collected 2 and 6 days post treatment (Wardhaugh and Mahon 1991). Importance of these findings suggests that dung beetles can detect feces with avermectin or its metabolites contained within and will not avoid it. Although horn fly larvae in the feces are the obvious target for ivermectin treatments in cattle, such research was important for recognizing the non-target effects on other dung breeding arthropods including dung beetles.

Like ivermectin, methoprene is excreted in the feces (Harris et al. 1974, Chamberlain et al. 1975). Methoprene (isopropyl (*E,E*)-(*RS*)-11-methoxy-3,7,11- trymethyldodeca-2,4-dienoate) is an insect growth regulator (juvenile hormone analogue) used for the control of horn flies. Methoprene can be administered orally, as a bolus, mineral supplement, feed additive, or directly in the drinking water of cattle (Fincher 1991, Blume et al. 1974, Harris et al. 1974, Beadles et al. 1975). Because it is excreted in cattle feces, effects of methoprene on dung beetles and other beneficial insects have been a topic of discussion. In the past there has been conflicting evidence on its impact on beneficial insects.

Fincher (1991) fed methoprene boluses to steers and presented their feces to two dung beetle species, *O. gazella* and *Sisyphus rubrus* Pashalidis. He found no significant difference in number of brood balls constructed and number of emerged adults between the beetles fed methoprene-treated feces and those fed untreated feces. He did find that the number of horn flies feeding on the treated dung declined by 95.3%.

Blume et al. (1974) found that methoprene mixed directly into the dung at 100, 10, 5 and 1 ppm inhibited egg hatch of *O. gazella* by 100, 56, 33.3 and 8.7% respectively. Dung from the steer treated with methoprene at the rate of 1mg/kg body weight also inhibited egg hatch by up to 32.6%. There was no apparent effect on the surviving larvae and adults. However in a field study, dung pads collected twelve days after administering 3% methoprene boluses to the cattle had a significantly lower number of Scarabaeidae (primarily *Aphodius* genera) than the control dung pads (Watson et al. 1986).

Bertone (2004) conducted a single season study in Nash Co., NC where methoprene was used for horn fly control. Dung beetles were collected during the 17 weeks of study and numbers compared to control collections in Wayne Co. North Carolina. Methoprene successfully reduced horn fly numbers below 200 flies per animal during the study. There was no apparent negative impact on dung beetle populations in the treated area. Statistical analysis of mean numbers of the most common species, *O. taurus*, *Onthophagus hecate*

hecate Panzer and *Onthophagus pennsylvanicus* Harold, showed no impact of methoprene on these species. *Aphodius pseudolividus* Olivier numbers were lower in Nash Co. than on the control site, but he could not determine if methoprene was responsible for these lower numbers.

The objective of the current study was to determine if methoprene when incorporated into an area wide horn fly control program, would negatively impact dung beetle populations, especially *O. taurus,* the most abundant dung beetle in NC pastures.

Materials and Methods

As a part of a 2-year study (Bertone 2004), a second-season field study determining the impact of methoprene on dung beetle population in North Carolina was conducted during the summer of 2004. The control site was located at the Center for Environmental Farming Systems (CEFS) in Goldsboro Wayne Co., North Carolina. Dung beetles were trapped from both the dairy and beef units at CEFS. An area-wide study for control of horn flies with feed-through application of methoprene was conducted in Nash County, North Carolina. Included were 10 adjacent farms covering 30.5 km^2 where methoprene was administered to mixed breed beef cattle *ad libitum* in the form of 0.12% active ingredient (0.08 ppm in dung) formulated in a proprietary mineral (Sam Galphin Services, 6509 Saddle Padh Circle, Raleigh, NC 27600) beginning 24 June, 2004. Although methoprene was provided to the farmers gratis, each farmer purchased the granular mineral. Two farms, Rose Hill and Bass, were chosen as the dung beetle trapping sites, consistent with the 2003 season (Bertone 2004).

Trapping was done by placing ten pitfall traps at 50-meter intervals in close proximity to cattle at each of the sites (Bertone 2004). Custom made pitfall traps were baited with fresh cattle feces collected from CEFS and Nash County farms. Dung was homogenized and dung baits made by scooping dung with a 55ml ice-cream scoop, dropping it on to a 16 by16 cm square of white paper towel, which was tied with a twist-tie and the package then frozen (-10^{o}C) until use. Traps were placed in the field every two weeks and picked up after 24 hours. Trapping was performed from 11 June to 1 October, 2004. Collected dung beetles were placed into plastic bags labeled according to farm and trap location and taken to the laboratory where they were counted and identified to species.

Densities of horn flies were monitored by estimating the number of flies on the entire body of 10 animals on each of the ten participading farms and the untreated controls (Watson et al. 2002). Locally, one control farm was located 5 miles from the treated area, and the second was located at CEFS. Horn flies were monitored weekly at approximately the same time during the day.

Weekly means for the four most common dung beetles were compared between the two sites (PROC GLM; SAS 9.1.3, SAS Institute, Cary 2005). Weekly means were separated using Tukey's Studentized Range Test ($\alpha = 0.05$). Weekly horn fly density means between Nash and Wayne Co. controls and the treated farms were analyzed by one-way ANOVA (SAS 8.2, SAS Institute, Cary, NC 2005). Climatological data were obtained from Cherry Research Station in Wayne Co., NC and at the Rocky Mount-Wilson Airport Nash Co., NC to establish environmental differences between sites.

Results and Discussion

Emergence of a new generation of dung beetles is often stimulated by rainfall (Tyndale-Biscoe 1990). Sum of the accumulated daily precipitation during the study period for Wayne Co. site was 53.5 cm and the average daily temperature for the same period was 23.8º C. Sum of the accumulated daily precipitation during the 17-week study period for Nash Co. site was 36.0 cm and the average daily temperature for the same period was 23.6º C. Increases in dung beetle trap collections in Wayne Co. during weeks 11 and 13 coincide with rain events beginning week 9 (Figure 1). Although less clear in Nash Co., an increase in beetle collections during week 15 followed rain events beginning week 9 (Figure 2).

Granular mineral containing 0.12% methoprene when fed *ad libitum*, effectively controlled horn fly populations over the 14 weeks of the study (data not available for the last three weeks of the study) (Figure 3). Mean densities of horn flies on treated farms were significantly lower (20 ± 10 per animal, $P < 0.05$) compared to Wayne Co. control (477 ± 140) and Nash Co. control (101 ± 50). Harris et al. (1974) showed that proprietary mineral formulations containing 0.94, 0.12, or 0.01% methoprene inhibited horn fly development by 87% in the field. Subsequent laboratory bioassay results indicated 99% and 100% control of horn fly at concentrations of 0.01% and 0.12% methoprene (Harris et al. 1974). Similarly, a 98% reduction in the number of horn flies was achieved when 0.03 ppm of methoprene was applied to drinking water of cattle (Beadles et al. 1975). Cattle mineral supplements containing 0.02 or 0.0049 % methoprene (Altosid® IGR) formulated as a granular mineral or molasses mineral block, respectively, reduced numbers of horn flies in pastures when compared to control herds (Paysinger and Adkins 1977). Although the concentration of methoprene in the block was less, cattle preferred the molasses-flavored mineral and thus consumed equal amounts of active ingredient.

Nine collection dates produced a total of 15,039 dung beetles at the CEFS site in Wayne Co. The Beef Unit produced 5,480 dung beetles and 9,559 beetles were trapped at the Dairy Unit. During the 17-week trapping period 4,463 beetles were collected from Nash County, where 2,581 beetles were trapped from Rose Hill farm and 1,882 beetles were trapped from Bass farm. Seventeen species were identified from Wayne Co. traps and twelve species were collected from Nash Co. traps (Table 1, Figure 4).

During the summer of 2003, Bertone (2004) collected a total of 26,546 dung beetles from the Nash Co. sites. Dung beetle collections from these sites in 2004 totaled 4,463 beetles, a significant decrease from the 2003 collections ($P < 0.0001$). A similar reduction was observed in the control pastures and its cause could not be attributed to the use of methoprene. Only during week 3 were there significantly ($P < 0.05$) more beetles collected in 2004 (Figure 5). In Wayne Co. two collection dates, weeks 1 and 17, had significantly higher number of beetles in 2004 (Figure 5). Dung beetle populations were clearly bimodal during the summer of 2004. The first peak in the Wayne Co. beetle population was during the first trapping date when total of 2,253 beetles were collected. The second peak in the beetle population started in week 13 when 2,333 beetles were collected. Week 15 did not yield a great number of beetles, but in week seventeen 6,541 individuals total were collected from Wayne Co. In Nash Co. the first peak in beetle numbers was during the second trapping date when a total of 1,446 beetles were collected. The second population peak was during week 15 when a total of 1,740 dung beetles were collected.

The most abundant specie at four sites in Wayne and Nash counties was *O. taurus*. At the Wayne Co. collection sites *O. taurus* comprised 82.5 % of the total, and in Nash Co. it represented 89.5 % of all the collected beetles. The second most abundant species in both counties was *A. pseudolividus.* From all the beetles collected in Wayne Co., 8.2 % were *A. pseudolividus* and in Nash Co. 5.3 % were *A. pseudolividus.* The remaining 16 species collected (Table 1) were relatively minor groups. According to Howden and Scholtz (1986) species comprising less than 5 % of the total are said to be minor groups.

The most numerous species in Wayne Co. following *O. taurus* and *A. pseudolividus,* were *O. gazella* (4.6 %), *O. pennsylvanicus* (1.2 %) and *O. hecate hecate* (1.0 %). Similarly in Nash Co. the following species were most numerous (after *O. taurus* and *A. pseudolividus*): *O. hecate hecate* (2.0 %) and *O. pennsylvanicus* (1.0 %). Although in 2003, Bertone (2004) found few *O. gazella* in Nash Co., this species was not collected from the same county in the current study. Statistical comparison of the mean number of beetles between Wayne Co. and Nash Co. collections was performed on the 4 most numerous species, *O. taurus*, *O. pennsylvanicus*, *O. hecate* and *A. pseudolividus*.

Similar to most insects, dung beetle development is temperature dependant. To evaluate the possible effects of methoprene on dung beetle populations, I compared published developmental times to predict field emergence. For example, developmental time of *O. taurus* under laboratory conditions at 26˚ C is 4 to 6 weeks (Wardaugh et al. 2001). A lower temperature of 24.1˚ C (range 21.9˚C – 26.3˚C) in Nash Co. could have lengthened the developmental time (Figure 2). Average temperature at Wayne Co. was slightly higher at 24.5˚ C. Predicted and actual developmental time for immature dung beetles ranges from 3 to 6 weeks (Table 2).

Characteristically, insect growth regulators (IGR's) are most active against the immature stages of insects but also impact reproduction in adults (Daglish and Wallbank 2005). In principle, if methoprene adversely effected the dung beetle populations, one could predict the absence of adult beetles emerging at specific time intervals following treatment with an IGR.

Weekly mean numbers of *O. taurus* were significantly ($P < 0.05$) greater during the weeks 1, 11, 13 and 17 in Wayne Co. (Figure 6). Nash Co. collections during weeks 3 and 15 produced a significantly higher number of *O. taurus* individuals. There was no significant ($P > 0.05$) difference among the collections on weeks 5, 7, and 9. Although two weeks after treatment began there was a reduction in the number of *O. taurus* collected from Nash Co., these emerging beetles were not exposed to methoprene in the larval stage. There was no significant ($P > 0.05$) difference between the trap catches between treatment and control sites during weeks 5, 7, and 9.

In the current study, *A. pseudolividus* numbers were significantly higher ($P < 0.05$) in Wayne Co. during weeks 3, 5, and 13 (Figure 7). During other weeks there was no significant ($P > 0.05$) difference in number of *A. pseudolividus* between the two counties. There was a 43% reduction in the number of individuals collected from Nash Co. from 2003 to 2004. Reduction of numbers on the control site in Wayne Co. suggests that other factors may have contributed to the decrease in *A. pseudolividus* population. However, delay in the appearance of the second generation during 2004 collections suggests that methoprene might have a negative impact on this endocoprid species. Similar results were observed during 2003 (Bertone 2004). When utilizing feces produced by a cow fed methoprene at a rate of 2.5mg/kg of body weight, *Aphodius fimetarius* (L.) did not experience reduction in numbers compared to the untreated control under field conditions (Pickens and Miller 1975). Methoprene rates in my study (0.10 to 0.067 mg/kg weight for animals 450 to 675 kg) were well below those of Pickens and Miller. This discrepancy suggests that the susceptibility of Aphodiine species may be highly variable.

Mean number of trapped *O. h. hecate* individuals was constant in Nash Co. during the study (Figure 8). Although the difference was not significant ($P > 0.05$) numerically more beetles were collected from Nash Co. during all but three weeks of study. During trapping week 7 significantly more *O. h. hecate* were collected from Nash Co., and during weeks 11, 13, and 17 there were significantly more *O. h. hecate* collected from Wayne Co. Because developmental time for *O. h. hecate* is undefined, a developmental time of 4 to 6 weeks was assumed, based on development of *O. taurus* and *O. pennsylvanicus*. There was an increase in the number of collected individuals during week 7. This peak and consistency in number of beetles trapped suggests that 0.12% methoprene had no negative impact on this species.

During weeks 11, 13, and 17 significantly ($P < 0.05$) more *O. pennsylvanicus* were collected from the control sites at Wayne Co. (Figure 9). During other weeks there was no significant ($P > 0.05$) difference between the numbers of beetles collected at both sites, but during weeks 7 and 15 numerically more beetles were collected from Nash Co. Developmental time for *O. pennsylvanicus* is 3 to 4 weeks (Howden and Cartwright 1963) and the increase in the number of *O. pennsylvanicus* during week 7 suggests that methoprene, at the rate tested, did not impact beetle populations.

It should be noted that collections from CEFS during week 17 produced high number of beetles as compared to Nash Co. collections. However, during the study, peaks in Nash Co. beetle collections usually followed two weeks after the peaks in CEFS beetle collections.

Because the trapping did not go beyond week 17 we do not know if there was another peak in Nash Co., therefore we can not say that during week 17 difference in numbers was due to methoprene treatment.

In 2003 only eight individuals of *Onthophagus gazella* were collected from methoprene treated sites in Nash Co., NC, but none were collected in 2004 (Bertone 2004). Bertone (2004) speculated that the distribution of *O. gazella* populations had not yet moved beyond north-central North Carolina.

The insect growth regulator methoprene effectively controls horn flies at 0.08 ppm in dung when administered to cattle as a feed additive or a mineral supplement. Control failures are most often the result of poor utilization by the cattle. Uniform consumption of mineral additives can not be assumed (Cockwill et al. 2000). Another contributing factor to control failure is limited area wide use. It is often difficult to have all farms in the area use the same treatment strategy, and migrating horn flies from untreated farms readily colonize the cattle on the treated farms resulting in no apparent decrease in pest pressure. In this study, 10 adjoining farms agreed to participade in the study. During the study horn fly populations were controlled with methoprene and the potential impact of IGR treatment on the major species, *O. taurus, O. pennsylvanicus, O. hecate* and *A. pseudolividus* was negligible, suggesting that label rates of methoprene were not lethal to immature dung beetles, particularly *Onthophagus*. Further studies are needed to determine with certainty if methoprene rates used for horn fly control also have a negative impact on *Aphodius pseudolividus* populations.

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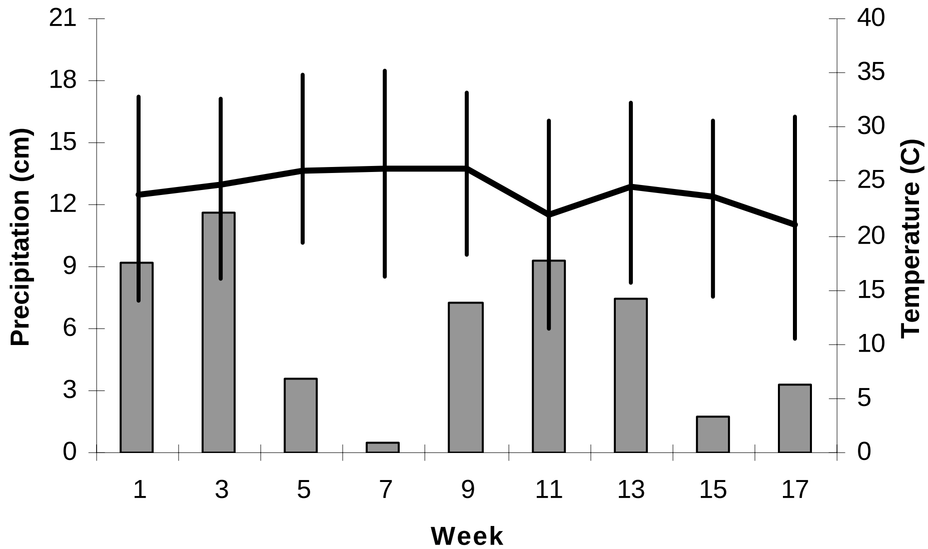
Table 1. Total number and percentage of dung beetles by species collected in 2004 every other week for a total of 9 collections on the Dairy and Beef units in Goldsboro, North Carolina and on the Rose Hill and Bass farms in Nash Co., NC.

Species	Beef Unit # of beetles (% beetles)	Dairy Unit # of beetles (% beetles)	Rose Hill # of beetles (% beetles)	Bass # of beetles (% beetles)
Aphodius *erraticus*	1 (0.02)	8 (0.08)	40 (1.55)	2 (0.11)
A. fimetarius	0 (0.00)	2 (0.02)	16 (0.62)	4 (0.21)
A. haemorrhoidalis	72 (1.31)	0 (0.00)	10 (0.39)	0 (0.00)
A. pseudolividus	763 (13.92.)	471 (4.93)	215 (8.33)	20 (1.06)
A. rubeolus	1 (0.02)	1 (0.01)	0 (0.00)	0 (0.00)
Ataenius *imbricatus*	1 (0.02)	0 (0.00)	0 (0.00)	0 (0.00)
At. erratus	4 (0.07)	11 (0.11)	0 (0.00)	0 (0.00)
At. platensis	0 (0.00)	0 (0.00)	1 (0.04)	0 (0.00)
Canthon *depressipennis*	0 (0.00)	2 (0.02)	0 (0.00)	0 (0.00)
C. pilularius	0 (0.00)	1 (0.01)	0 (0.00)	0 (0.00)
Geotrupes *blacburnii*	1 (0.02)	5 (0.05)	1 (0.04)	0 (0.00)
Onthophagus *gazella*	555 (10.13)	133 (1.39)	0 (0.00)	0 (0.00)
O. hecate hecate	19 (0.35)	137 (1.43)	31 (1.20)	58 (3.08)
O. oklahomensis	30 (0.52)	166 (1.74)	5 (0.19)	2 (0.11)
O. pennsylvanicus	64 (1.17)	112 (1.17)	26 (1.01)	18 (0.96)
O. taurus	3940 (71.90)	8462 (88.52)	2221 (86.05)	1773 (94.21)
Phaneus *vindex*	27 (0.49)	48 (0.50)	11 (0.43)	5 (0.27)
Dichotomius *carolinus*	2 (0.04)	0 (0.00)	4 (0.15)	0 (0.00)
Total # of beetles	**5480**	**9559**	**2581**	**1882**

Table 2. Predicted and true developmental timelines of *O. taurus*, *O. pennsylvanicus*, *O. h. hecate* and *A. pseudolividus* post methoprene application. Methoprene was applied two days prior to week three collections.

Species	Developmental Time	Emergence Timeline	1	3	5	7	9	11	13	15	17
O. taurus	4-6 weeks	Predicted									
		Nash Co.									
		Wayne Co.									
O. hecate	4-6 weeks	Predicted									
		Nash Co.									
		Wayne Co.									
O. pennsylvanicus	3-4 weeks	Predicted									
		Nash Co.									
		Wayne Co.									
A. pseudolividus	4 weeks	Predicted									
		Nash Co.									
		Wayne Co.									

Note: Shaded areas mark the range of predicted beetle emergence and true emergence range for Nash Co. and Wayne Co.



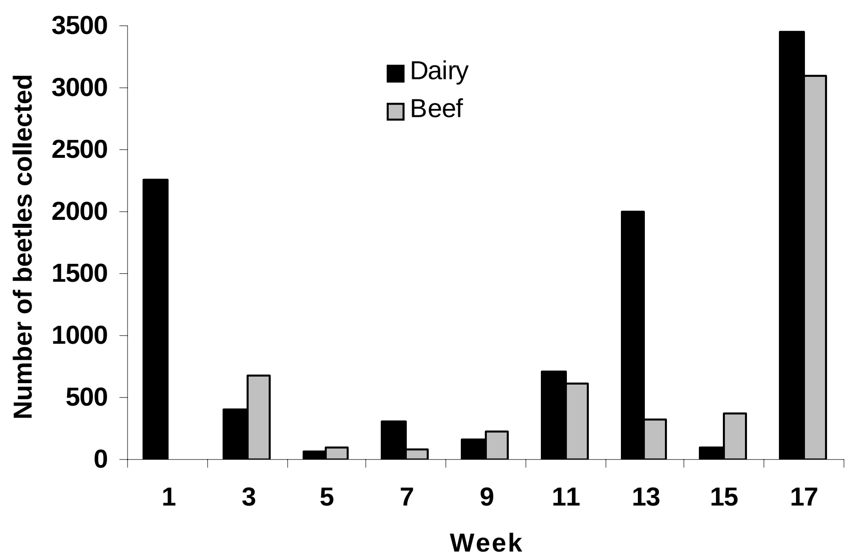


Figure 1. Top: Average biweekly temperature and accumulated precipitation at CEFS (Wayne Co., North Carolina) during the study period. Bottom: Total number of beetles collected from the traps at CEFS (Wayne Co., North Carolina) during nine trapping dates in 2004.

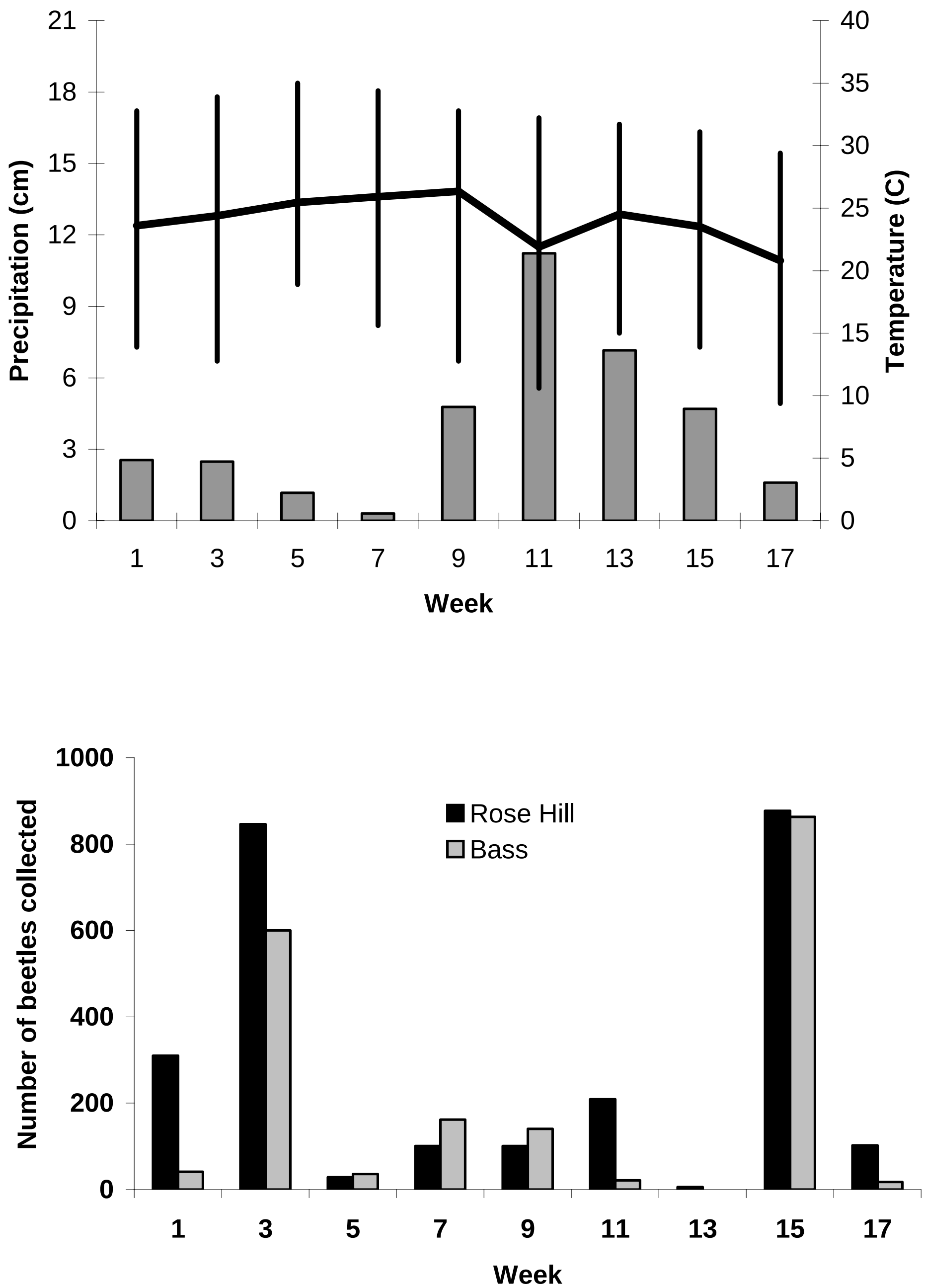


Figure 2. Top: Average biweekly temperature and accumulated precipitation in Nash Co., North Carolina during the study period. Bottom: Total number of beetles collected from the traps in Nash Co., North Carolina during nine trapping dates in 2004.

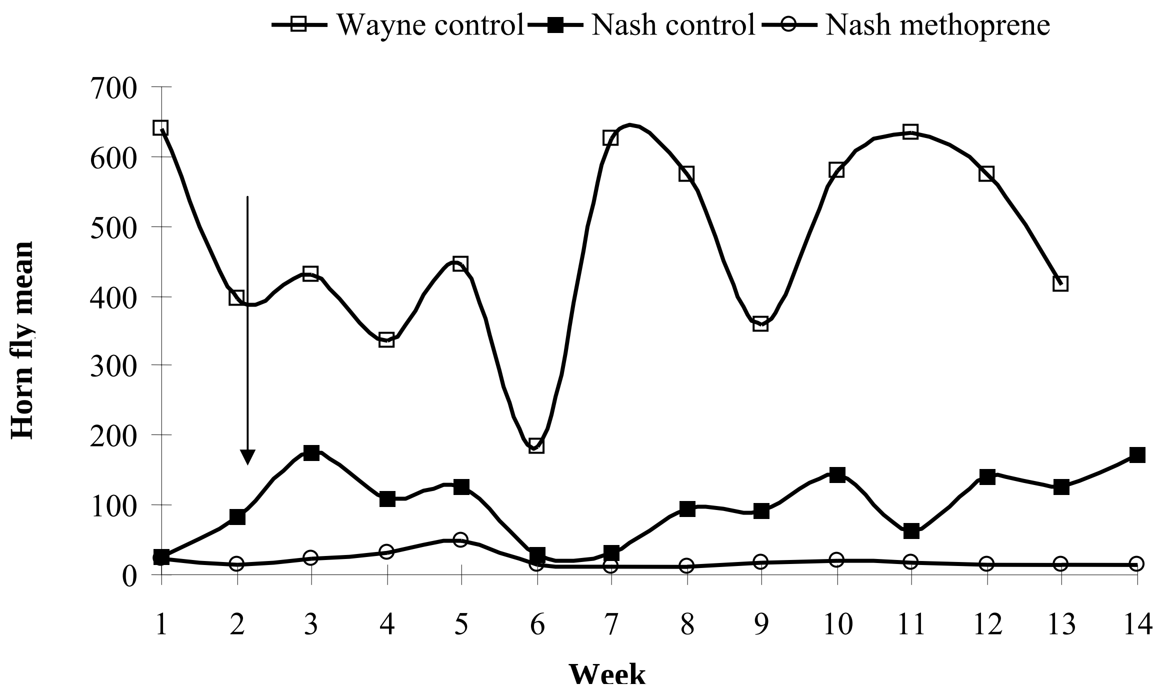


Figure 3. Mean horn fly densities on 10 methoprene treated herds, one untreated control in Nash Co., and one untreated control in Wayne Co. Arrow indicates the initial administration of methoprene on June 24, 2004.

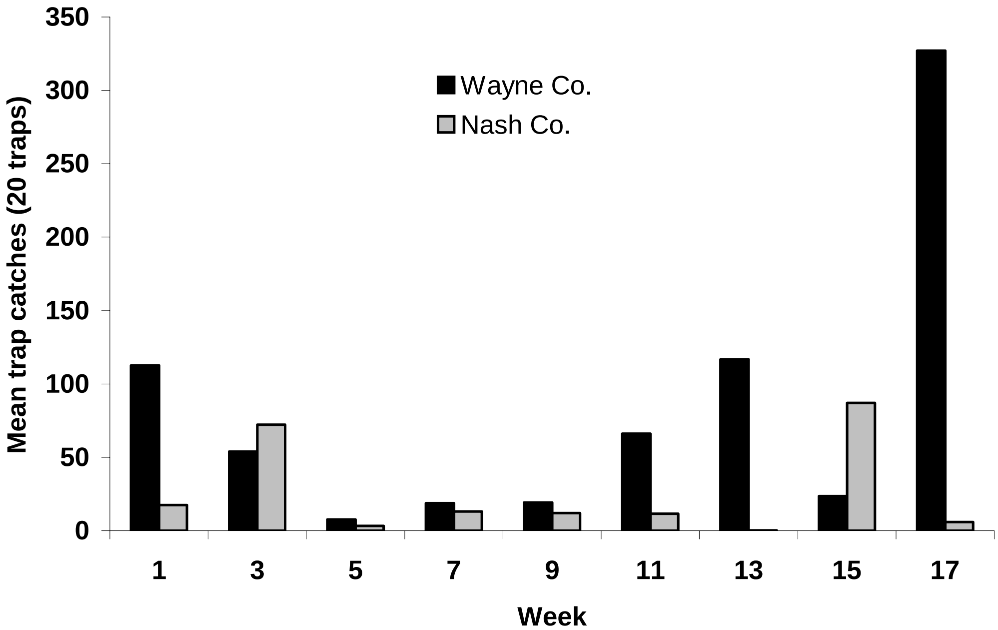
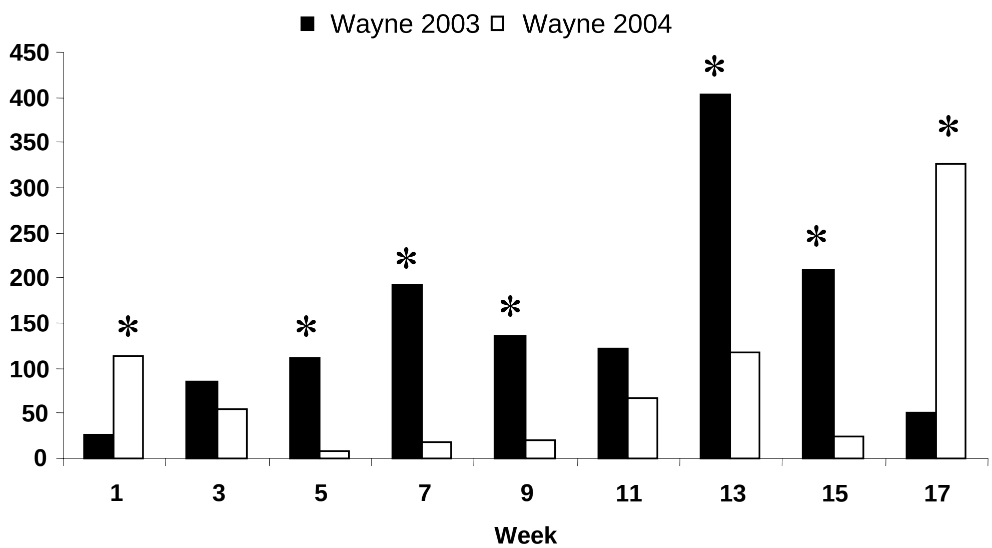


Figure 4. Mean number of beetles trapped from methoprene treated area (Nash Co., NC) and control (Wayne Co., NC) during the nine trapping dates.



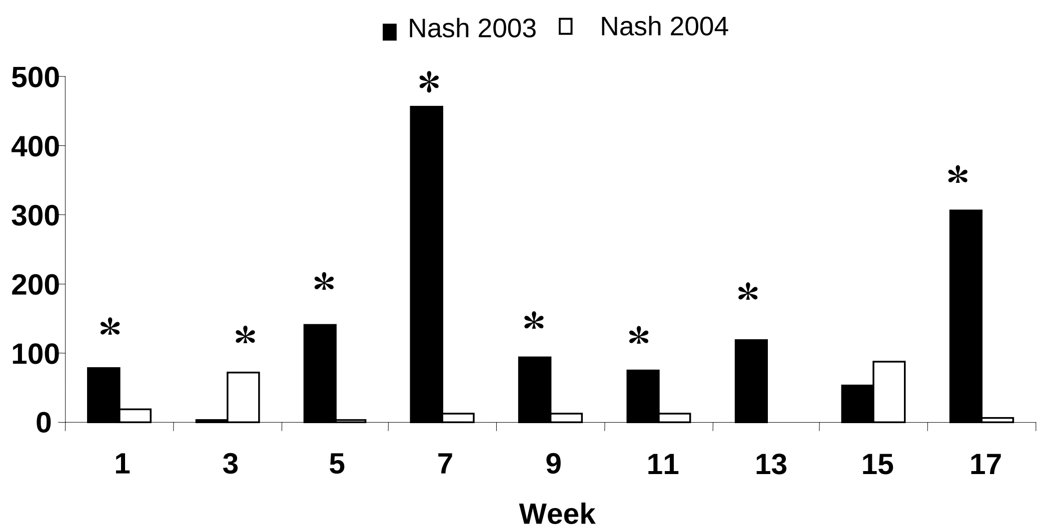


Figure 5. Comparison of mean catches between 2003 and 2004 from Wayne Co. (top) and Nash Co. (bottom). Columns with stars are significantly different between years (2003 data taken from Bertone 2004).

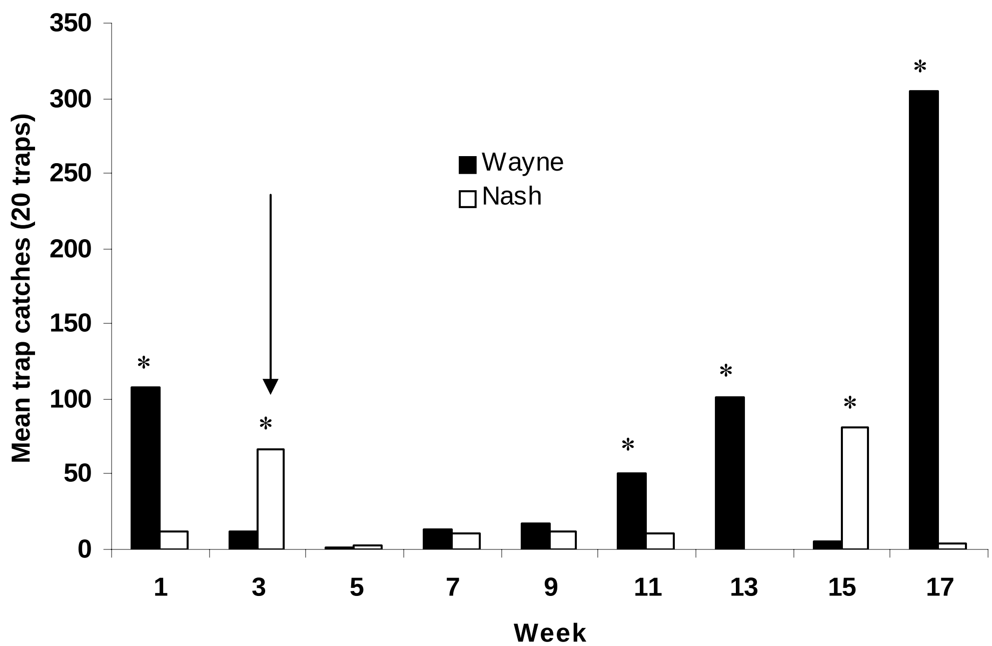


Figure 6. Mean number of *Onthophagus taurus* collected from Nash and Wayne counties during the nine weeks of study. Arrow indicates when methoprene was first distributed. Stars mark the dates where there is a significant difference in numbers of beetles collected from the two counties ($\alpha = 0.05$).

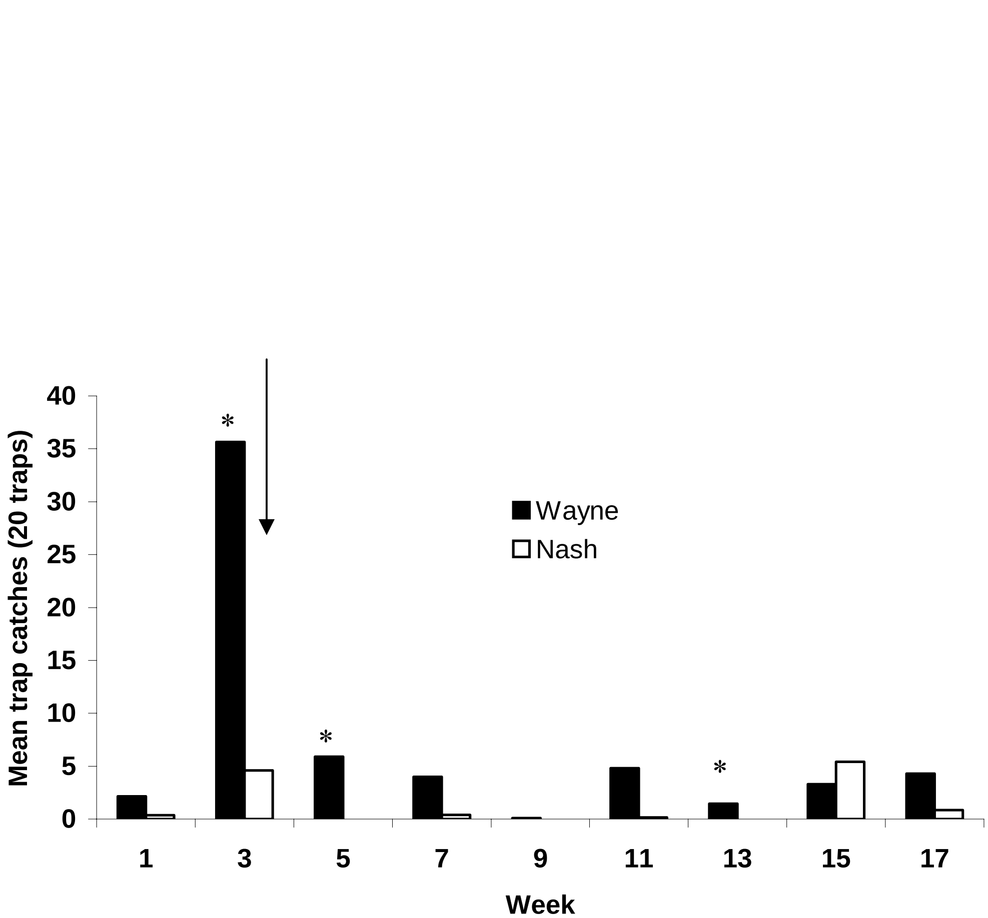


Figure 7. Mean number of *Aphodius pseudolividus* collected from Nash and Wayne counties during the nine weeks of study. Arrow indicates when methoprene was first distributed. Stars mark the dates where there is a significant difference in numbers of beetles collected from the two counties (α = 0.05).

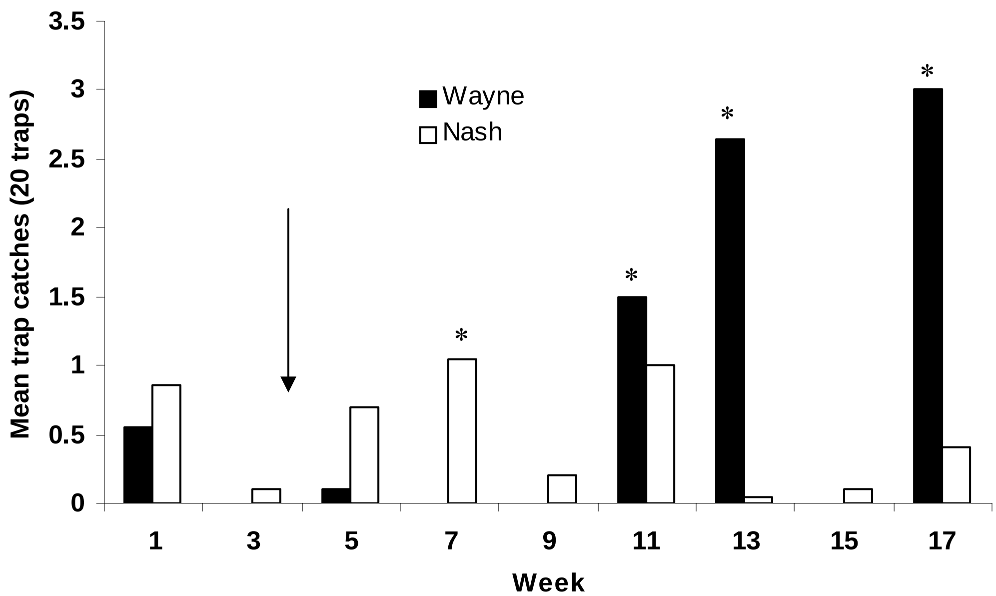


Figure 8. Mean number of *Onthophagus hecate hecate* collected from Nash and Wayne counties during the nine weeks of study. Arrow indicates when methoprene was first distributed. Stars mark the dates where there is a significant difference in numbers of beetles collected from the two counties ($\alpha = 0.05$).

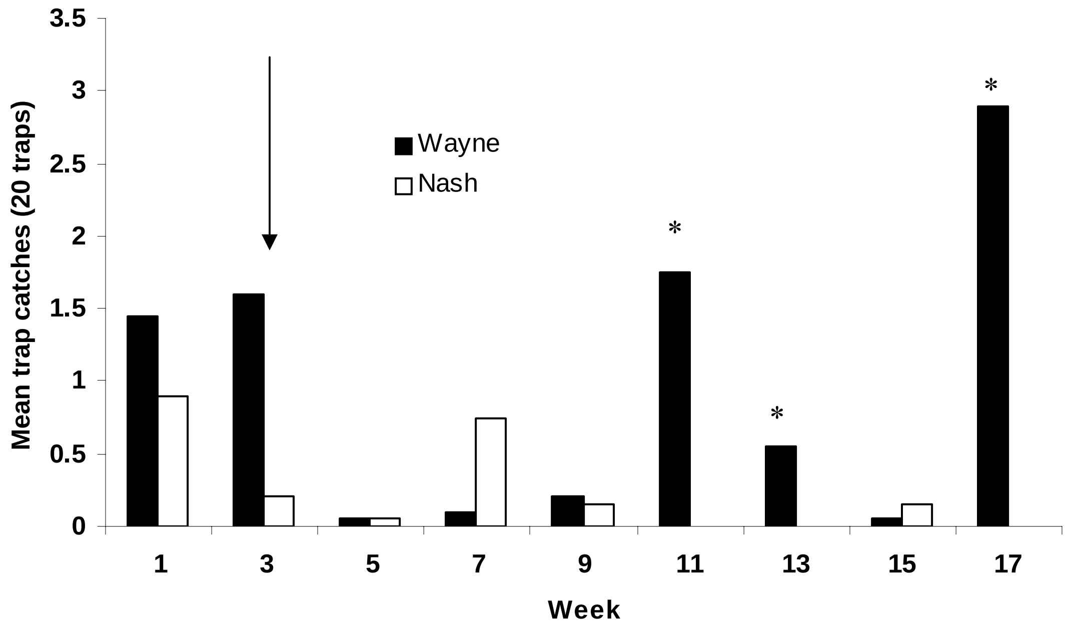


Figure 9. Mean number of *Onthophagus pennsylvanicus* collected from Nash and Wayne counties during the nine weeks of study. Arrow indicates when methoprene was first distributed. Stars mark the dates where there is a significant difference in numbers of beetles collected from the two counties ($\alpha = 0.05$).

V. Laboratory study on the impact of methoprene, an insect growth regulator, on the fecundity and survival of *Onthophagus taurus* (Coleoptera: Scarabaeidae)

Abstract

A bioassay was conducted to determine the impact of methoprene, an insect growth regulator, on the fecundity of adult *Onthophagus taurus* Schreber and the survival and size of their progeny. Adult beetles were offered dung from cattle fed methoprene in a feed mix or placed in pots containing methoprene-treated dung at the following rates 0.08, 0.45, and 4.5 ppm. Lastly, adult beetles were immersed in a solution of methoprene in water after which they were placed in containers with untreated dung and left to reproduce. Data from all treatments were compared to the untreated control dung.

Methoprene in all treatments did not negatively impact brood production. Interestingly, number of brood balls produced was higher when *O. taurus* was offered dung from methoprene-treated cattle.

O. taurus survival was not impacted by feeding on the feces from methoprene-fed cattle, methoprene-treated dung (0.08 ppm) or when parent beetles were immersed in a solution of methoprene in water. Survival was significantly ($P < 0.05$) reduced when dung beetles fed on methoprene treated feces at 4.5 ppm rate. Mean pronotal width of *O.taurus* progeny was significantly smaller in beetles fed methoprene treated feces (4.5 ppm).

Keywords: *Onthophagus taurus*, dung beetles, methoprene, insect growth regulator

Introduction

The horn fly, *Haematobia irritans* (L.), a blood feeding dipteran is one of the primary cattle pests in North Carolina pastures, and it causes great economic loses to cattle producers (Watson et al. 2002, Drummond 1981). Traditionally, control of horn flies included the use of insecticides applied as dusts, sprays, pour-ons, boluses, feed additives, and insecticide-impregnated ear tags (Butler and Okine 1999). Insecticide resistance has made horn fly control more difficult (Miller et al. 1983, Sheppard 1984, Quisenberry et al. 1984, Hogsette et al. 1991, Sheppard and Joyce 1992). Of concern is the impact of these insecticides and certain anthelmintics on non-target arthropods found in dung, particularly dung beetles (Wardhaugh 2005). In the last 25 years, the use of endectocides such as ivermectin, abamectin, moxidectin, and eprinomectin have been used effectively against pyrethroid-resistant horn flies, while simultaneously raising concern that these active ingredients may negatively impact beneficial dung dwelling arthropods, especially dung beetles. To avoid resistance in horn flies and reduce negative impact on beneficial insects an effort should be made to rotate between insecticide classes and use dung beetle compadible insecticides such as insect growth regulators (e.g. methoprene).

Methoprene (isopropyl (*E,E*)-(*RS*)-11-methoxy-3,7,11-trymethyldodeca-2,4-dienoate) is an insect growth regulator that disrupts the normal development of the insect. A juvenile hormone analogue, methoprene has been successfully used for the control of immature stages of the horn fly developing in dung at rates of < 0.08ppm (Fincher 1991, Blume et al. 1974). It can be administered orally, as a bolus, mineral supplement, feed additive, or directly in the drinking water of cattle (Fincher 1991, Blume et al. 1974, Harris et al. 1974, Beadles et al.

1975). Because methoprene is excreted in cattle dung, the susceptibility of beneficial insects (especially dung beetles) has been a topic of discussion.

Published accounts suggest that certain species may be less susceptible to the effects of methoprene than others. Feces from steers treated with methoprene boluses was presented to two dung beetle species, *Onthophagus gazella* and *Sisyphus rubrus* Pashalidis (Fincher 1991). There was no significant difference in number of brood balls constructed and number of emerged adults between the beetles fed methoprene-containing dung and those fed untreated control. The number of horn flies feeding on the treated dung declined by 95.3%.

In contrast, a field study where fresh dung pads were collected twelve days after administering 3% methoprene boluses to the cattle the number of Scarabaeidae members in the *Aphodius* genera were significantly lowered compared to the dung pads from untreated cattle (Watson et al. 1986).

The effects of methoprene appear to be dose and life stage dependent. When methoprene was mixed directly into the feces at different rates it inhibited egg hatch in *O. gazella* according to the rates applied (Blume et al. 1974). Feces from the steer treated with methoprene at the rate of 1mg/kg body weight also inhibited egg hatch up to 32.6%. There was no apparent effect on the surviving larvae and adults (Blume et al. 1974).

Topical application of methoprene (400µg/g larval weight) to the larvae of *O. taurus* delayed the onset of metamorphosis during the first critical period (6 to 10 days before pupadion) (Emlen and Nijhout 1999, 2001). As a result of the treatment, the number of male *O. taurus* developing horns was reduced, and males were smaller relative to untreated larvae. When methoprene was administered during the second sensitive period towards the end of the third instar larvae, normally minor males produced large horns in 80% of the cases (Emlen and Nijhout 1999, 2001).

O. taurus is a very common and successful paracoprid dung beetle from the Middle East, Europe, and North Africa. By 1974 this beetle was established in Florida where it had been accidentally introduced in 1971. Fincher and Woodruff (1975) collected *O. taurus* in areas of Georgia and southeast Alabama. Subsequent collections revealed presence of *O. taurus* in Mississippi, Louisiana, South Carolina, and North Carolina (Fincher et al. 1983) as well as California and Missouri (Macrae and Penn 2001). *O. taurus* is the most common dung beetle in the Piedmont and Coastal regions of North Carolina, making up over 60% of the total dung beetle fauna in these two regions (Bertone 2005). Cattle producers, recognizing the importance of this beetle in the NC pasture ecosystem, need horn fly control strategies that are compadible with dung beetles. An area wide study on methoprene control of horn fly was conducted in Nash Co., North Carolina during the fly season in 2003 (Bertone 2004) and in 2004 (Chapter IV this thesis). Impact of methoprene on the four most common dung beetles present in the area (including *O. taurus*) seemed to be negligible in the field.

The objective of this laboratory study was to determine the fecundity of adult *O. taurus* when fed dung containing different methoprene rates or when methoprene was applied topically. Survival rate and size of *O.taurus* progeny was determined when brood balls were made from methoprene-treated dung or by adults treated topically with methoprene.

Materials and Methods

This study was conducted during the spring and summer of 2005 and 2006. *Onthophagus taurus* adults were collected with dung-baited pitfall traps (Bertone 2005) from an untreated wild population at the Center for Environmental Farming Systems (CEFS) in Goldsboro (Wayne Co.), North Carolina. Sexes were separated and held in 2-liter ice cream containers filled with sifted and moistened Black Kow soil (Black Gold Compost Co., Oxford, Florida). Containers were covered with mesh tops (Fisherbrand Buoffants, Latex-Free, white, Fisher Scientific) and held at room temperature with a 16:8 hours light-dark regimen.

The following treatments were applied:

I) Dung from methoprene-fed cattle – 9 replicates

II) Methoprene-treated dung (0.08ppm) – 3 replicates

III) Methoprene-treated dung (0.45ppm) – 4 replicates

IV) Methoprene-treated dung (4.5ppm) – 5 replicates

V) Topically applied methoprene – 5 replicates

Data from all methoprene treatments were compared to the untreated control. Control dung was collected from the CEFS Dairy Unit. Dung containing methoprene was collected from the Lewis dairy farm in Alamance County, North Carolina during the summer 2005 and 2006. Dairy cows were fed a methoprene feed mix where 0.68 kg of 0.4% active methoprene feed (SSC – 31 – 770620 cattle premix w/ Altosid®) was added to 0.907 metric tons of regular feed. Collected fresh dung was frozen to prevent any insect activity. Dung was thawed overnight at room temperature and homogenized. Experimental units were 3.8-liter pots filled with sifted Black Kow soil up to 4 cm of the rim.

Technical grade methoprene was added to achieve following dilution rates 0.08, 0.45 and 4.5 ppm in dung in the three treated dung treatments. Adult beetles immersed in a solution of 5.96µl methoprene in 2ml of water were placed on the untreated dung. Each treatment consisted of 300 g of cow dung and five beetle pairs (male-female). Five pots were used in each replicate.

To prevent beetle, escape pots were covered with hair nets held in place with rubber bands. Pots were held at room temperature (27º C) with a 16:8 h photoperiod. Adult beetles were given two weeks to produce brood balls after which they were removed from the pots. Pots were opened and brood balls removed after 14 days. Brood balls were counted and placed in 2-liter ice cream containers according to treatment and with 2 cm of Black Kow soil on the bottom. A maximum of 10 brood balls were placed on the soil and covered with an additional 2 cm of soil. This was repeated until there were no more brood balls. After all the brood balls were placed in the container they were sheltered with 5 cm of soil, covered with a paper towel and a screened top. Containers were moistened periodically with 25 ml of water to prevent desiccation. After four weeks, adults were counted and all brood balls checked for the presence of teneral adults. The number of brood balls and the percent survival were compared between the treatments. Size comparison among progeny in different treatments was done by measuring the pronotum width with electronic calipers (Fowler 54-100-330, Euro-Cal 6"/150mm).

Statistical analyses were done using SAS 9.1.3 (SAS Statistical institute Cary, North Carolina 2005). PROC GLM was used to compare the number of brood balls among different treatments. Treatment comparisons were separated with a t-test ($\alpha = 0.05$). PROC MIXED including a contrast statement was used to compare the mean percent emergence among different treatments taking into account number of brood balls produced in different treatments. PROC MIXED ($\alpha = 0.05$) was also used to compare mean pronotum widths for beetles emerging from different treatments.

Results and Discussion

Brood produced from dung beetles offered dung from methoprene-fed cattle in 2005 was not significantly different ($P > 0.05$, 4 replicates) from the control beetles (Table 1). Control beetles produced 0 to 36 brood balls, while the number of brood produced by beetles offered dung with methoprene ranged from 0 to 45. There was no significant difference in the percent survival between progeny fed dung from methoprene-treated cattle and untreated dung ($P > 0.05$) (Table 1).

Results for the 5 replicates conducted in 2006 were similar, but regardless of the treatment, beetles on average produced less brood as compared to 2005. Adult beetles offered dung from methoprene-fed cattle produced significantly ($P < 0.05$) more brood balls than the adults on the untreated dung (Table 2). Although not significantly different ($P > 0.05$), percent survival was numerically higher for progeny fed on dung containing methoprene (Table 2). Number of brood balls for the control beetles ranged from 0 to 36, and for the methoprene-exposed adults, number of brood ranged from 3 to 21.

Data from 2005 and 2006 were combined to increase the number of replicates. Adult beetles that used methoprene-treated dung for reproduction produced numerically more brood balls than the control beetles (Table 3). Likewise, percent survival was numerically higher for the progeny reared in dung from methoprene-fed cattle (Table 3), but these differences were not significant ($P > 0.05$).

Pronotal size was measured on 714 male and female *O.taurus* progeny fed on dung from methoprene-fed cattle and untreated control. There was no significant size difference for beetles from the two treatments ($P > 0.05$) (Table 4).

When beetles were exposed to laboratory-treated dung (0.08 ppm) they produced between 0 and 18 brood balls which was similar to the untreated beetles that produced between 0 and 25 brood balls per container. Mean number of brood balls for treated parent beetles was not significantly different ($P = 0.05$, 3 replicates) from the control (Table 5). Similarly, percent survival between the two treatments was not significantly different ($P > 0.05$) even though it was numerically lower for methoprene-treated group (Table 5)

Pronotal widths of 115 adult progeny were measured. Mean pronotal width was significantly higher ($P < 0.05$) in *O. taurus* progeny fed on methoprene-treated dung (0.08 ppm) suggesting that methoprene at this rate did not have a negative impact on the size of surviving *O.taurus* (Table 4).

At 0.45 ppm, the number of brood balls produced between treatments was not significant ($P > 0.05$) (Table 6). Control beetles made between 0 and 21 brood balls, whereas the number of brood produced by methoprene-exposed beetles ranged between 0 and 18 per container. This supports findings of Fincher (1991) in which he did not find significant difference in *O. gazella* brood production when fed methoprene-treated or untreated dung. Due to mite infestation, brood from the 0.45 ppm methoprene trial did not finish development so the percent survival of the progeny could not be calculated.

There was no significant difference ($P > 0.05$) in brood ball production among the untreated control, methoprene treated dung (4.5 ppm) and methoprene topically applied to the adults (Table 7). However, the number of beetles in both methoprene treatments was lower than in the untreated control. Number of brood produced by control beetles ranged from 5 to 51. Adults in methoprene-treated dung (4.5 ppm) produced between 2.0 and 55.0 brood balls and beetles with topical application of methoprene produced between 0.0 and 56.0 brood balls.

Percent survival of larvae feeding on methoprene treated dung (4.5 ppm) was significantly lower ($P < 0.05$, 5 replicates) when compared to larvae exposed to the untreated dung (Table 7). Progeny survival from parents topically treated with methoprene was lower, but this difference was not significant ($P < 0.05$) (Table 6). Although larval survival was lower when progeny were fed methoprene-treated dung, there was no significant difference in percent survival between the larvae from the two methoprene treatments ($P > 0.05$) (Table 6).

A total of 697 adult progeny were measured. Mean pronotal widths were significantly lower for the progeny fed on methoprene-treated dung ($P < 0.05$) (4.5 ppm) compared to the untreated control and progeny from methoprene-exposed parents (Table 7) There were no significant differences ($P > 0.05$) in pronotal widths between the progeny from the two methoprene treatments.

In this experiment, the application of methoprene at the labeled rate in feed that is recommended to kill horn flies (0.08 ppm) did not have a negative effect on fecundity and brood survival of *O. taurus.* Under laboratory conditions brood ball numbers vary greatly (Blume and Aga 1975, Fincher 1991) as was true for the current study. Adults produced between 0 and 56 brood balls with an average of 12 per pot and 3 per adult pair. These results were similar to a previous study where *O. taurus* produced an average of 12 ± 2 brood balls in Coastal Plain sandy-loam and 14 ± 5 in washed sand (Bertone 2006). In the current study, numbers were lower than the average number of brood produced by isolated *O. taurus* pairs over a 14-day period (Hunt and Simmons (2002). They held beetle pairs separately, preventing competition for food resources, which may explain the higher number of brood.

Susceptibility of dung beetles to doses of methoprene appears to be variable. In a previous field study 3% methoprene bolus application significantly reduced the number of Scarabaeidae, mostly belonging to the genus *Aphodius* (Watson et al. 1986). However, Pickens and Miller (1975) found no significant negative impact of methoprene on *Aphodius fimetarius* (L.) when they inhabited dung pads from methoprene-fed cattle at the dose of 2.5 mg/kg cattle weight.

When applied to ventral abdominal segments of *Oryctes rhinoceros* (L.) male pupae, methoprene (20, 50, and 100 μg or circa 2.5, 6.25, and 12.5 ppm) inhibited normal development of the male reproductive system (Jacob 1989). In the current study the topical application of methoprene to *O. taurus* adults did not seem to inhibit reproductive ability. Because adult *O. taurus* were in their post-developmental stage, topical application of methoprene did not seem to have a negative effect. After applying topically or via injection 125, 25, and 5 ppm of methoprene to rhinoceros beetle pupae, Dhondt (1976) found that pupae died with newly formed beetles inside. When adult *O. taurus* were immersed in methoprene in this study there was no notable negative impact.

In the present study, dung treated in the laboratory or from methoprene-fed cattle at a rate sufficient for horn fly control did not negatively affect fecundity of *O.taurus*. Methoprene and its metabolites in the feces of treated cattle did not inhibit development of *O. taurus*. The same was true for methoprene-treated dung at 0.08 ppm.

Similarly, feces from cattle treated with 3% methoprene boluses had no significant negative effect on brood ball construction and adult emergence of *O. gazella* and *Sisyphus rubrus* Paschalidis when compared to the untreated controls (Fincher 1991). However, when methoprene (52.5% EC) was applied to dung at rates of 100, 10, 5, and 1 ppm and offered to *O. gazella*, developmental inhibition of 100, 56, 33.3, and 8.7 % respectively was observed (Blume et al. 1974). All rates were above the rate (0.08 ppm) sufficient to kill the target insect horn fly. Similarly, the rate of 4.5 ppm methoprene used in the present study did negatively affect survival of *O. taurus.*

Size of *O. taurus* depends on the food quality and availability and there is no significant size difference between the sexes (Moczek 1998). In the present study there was no significant difference ($P > 0.05$) between male and female pronotal widths. Although larval survival was reduced after methoprene exposure (50, 10, 5, and 1 ppm) there was no apparent difference in the surviving *O. gazella* progeny (Blume and Aga 1974). However, the present study shows that methoprene in dung will stunt the growth of feeding *O. taurus* progeny. This was only observed for the highest methoprene rate (4.5 ppm). Since the rate normally present in pasture dung (0.08 ppm) did not have a negative impact on the adult size, it seems that methoprene would be a dung beetle compadible insecticide.

Methoprene at a rate (0.08 ppm) sufficient to kill horn flies, did not have a negative effect on fecundity and progeny percent survival of *O. taurus.* The high rate methoprene (4.5 ppm) did inhibit progeny development, but this rate far exceeds the recommendation for horn fly reduction. Higher rates, 7.5 to 10 ppm, were suggested for house fly control in poultry houses (Breeden et al. 1981) where *O. taurus* is not present. The current study suggests that methoprene used as a part of a horn fly control program would not reduce population of the most common North Carolina endocporid dung beetle *O. taurus*.

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Table 1. Number (mean ± SD) of brood balls produced (mean ± SD) by adult *O. taurus* and progeny percent survival (mean ± SD) in the dung from methoprene-fed cattle in 2005.

	Brood Balls		% survival	
Replicate	**Control**	**Methoprene**	**Control**	**Methoprene**
1	6.0 ± 4.1	7.2 ± 4.4	83.1 ± 18.0	84.7 ± 13.4
2	21.2 ± 8.8	22.6 ± 12.9	90.5 ± 8.9	82.5 ± 8.0
3	24.2 ± 7.9	27.4 ± 11.3	92.7 ± 4.7	85.7 ± 9.9
4	7.8 ± 4.8	7.8 ± 4.8	62.7 ± 38.1	75.2 ± 14.8
Total	**14.8 ± 6.4**	**16.25 ± 8.3**	**82.3 ± 17.4**	**82.0 ± 11.5**

Table 2. Number (mean ± SD) of brood balls produced by adult *O. taurus* and progeny percent survival (mean ± SD) in the dung from methoprene-fed cattle in 2006.

	Brood Balls		% survival	
Replicate	**Control**	**Methoprene**	**Control**	**Methoprene**
1	2.0 ± 2.0	14.2 ± 6.2	70.0 ± 47.6	92.8 ± 5.2
2	18.4 ± 10.7	11.6 ± 7.3	61.5 ± 37.2	5.5 ± 8.0
3	5.8 ± 1.3	14.2 ± 3.6	81.8 ± 4.7	84.2 ± 21.3
4	9.3 ± 11.0	11.2 ± 6.5	60.6 ± 24.8	88.9 ± 8.4
5	5.2 ± 3.6	12.2 ± 6.2	87.5 ± 21.6	99.0 ± 2.0
Total	**8.1 ± 5.7**	**12.7 ± 5.9**	**72.3 ± 27.1**	**74.1 ± 9.0**

Disclaimer: The author had no control over methoprene treatment distribution to cattle.

Table 3. Number (mean ± SD) of brood balls produced by adult *O. taurus* and progeny percent survival (mean ± SD) in the dung from methoprene-fed cattle 2005 and 2006 combined.

	Brood Balls		% survival	
Replicate	**Control**	**Methoprene**	**Control**	**Methoprene**
1	6.0 ± 4.1	7.2 ± 4.4	83.1 ± 18.0	84.7 ± 13.4
2	21.2 ± 8.8	22.6 ± 12.9	90.5 ± 8.9	82.5 ± 8.0
3	24.2 ± 7.9	27.4 ± 11.3	92.7 ± 4.7	85.7 ± 9.9
4	7.8 ± 4.8	7.8 ± 4.8	62.7 ± 38.1	75.2 ± 14.8
5	2.0 ± 2.0	14.2 ± 6.2	70.0 ± 47.6	92.8 ± 5.2
6	18.4 ± 10.7	11.6 ± 7.3	61.5 ± 37.2	5.5 ± 8.0
7	5.8 ± 1.3	14.2 ± 3.6	81.8 ± 4.7	84.2 ± 21.3
8	9.3 ± 11.0	11.2 ± 6.5	60.6 ± 24.8	88.9 ± 8.4
9	5.2 ± 3.6	12.2 ± 6.2	87.5 ± 21.6	99.0 ± 2.0
Total	**11.1 ± 6.0**	**14.3 ± 7.0**	**76.7 ± 22.8**	**77.6 ± 10.1**

Disclaimer: The author had no control over methoprene treatment distribution to cattle.

Table 4. Pronotal widths (mean ± SD) of the adult progeny fed on methoprene dung either treated (4.5 ppm and 0.08 ppm) or from methoprene fed-cattle (0.08 ppm) and untreated control

	Lab treated				Farm collected	
	4.5ppm		0.08ppm		0.08ppm	
Treatment	**Female**	**Male**	**Female**	**Male**	**Female**	**Male**
Control	4.64 ± 0.61a	4.67 ± 0.51a	4.64 ± 0.35b	4.60 ± 0.42b	3.61 ± 0.30a	3.66 ± 0.33a
Methoprene	4.32 ± 0.59b	4.33 ± 0.53b	4.78 ± 0.34a	4.85 ± 0.37a	3.66 ± 0.37a	3.88 ± 0.58a
Topical	4.67 ± 0.57a	4.67 ± 0.53a	na	na	na	na

Means followed by the same letter withing columns are not significantly different at α=0.05.

Disclaimer: The author had no control over methoprene treatment distribution to cattle.

Table 5. Number (mean ± SD) of brood balls produced by adult *O. taurus* and progeny percent survival (mean ± SD) in the methoprene-treated dung (0.08 ppm).

	Brood Balls		% survival	
Replicate	**Control**	**Methoprene**	**Control**	**Methoprene**
1	15.6 ± 7.5	11.4 ± 4.4	73.9 ± 9.0	57.4 ± 22.9
2	11.3 ± 5.7	4.2 ± 2.9	25.4 ± 11.4	35.1 ± 14.5
3	4.0 ± 2.0	2.7 ± 1.5	55.6 ± 9.6	47.2 ± 41.1
Total	**10.3 ± 5.1**	**6.1 ± 2.9**	**51.63 ± 10.0**	**46.6 ± 26.2**

Table 6. Number (mean ± SD) of brood balls produced by adult *O. taurus* in the methoprene-treated dung (0.45 ppm).

Replicate	Control	Methoprene
1	5.2 ± 1.3	5.0 ± 3.5
2	12.6 ± 5.8	4.2 ± 2.9
3	7.2 ± 3.5	2.7 ± 1.5
4	0.6 ± 1.3	2.6 ± 2.6
Total	**6.4 ± 2.9**	**3.6 ± 2.6**

Table 7. Number (mean ± SD) of brood balls produced by adult *O. taurus* in the methoprene-treated dung (4.5 ppm) and for methoprene topical application as well as the progeny percent survival (mean ± SD).

	Brood Balls			% survival		
Replicate	**Control**	**Methoprene**	**Topical**	**Control**	**Methoprene**	**Topical**
1	44.2 ± 3.4	28.8 ± 7.7	18.2 ± 10.7	76.8 ± 3.3	45.4 ± 10.9	69.3 ± 10.7
2	39.6 ± 5.1	17.4 ± 3.9	32.2 ± 4.6	71.5 ± 12.6	27.0 ± 7.6	62.0 ± 9.0
3	9.2 ± 1.5	7.4 ± 1.2	15.0 ± 5.2	94.1 ± 2.8	64.2 ± 7.9	32.4 ± 10.2
4	32.4 ± 0.9	28.6 ± 0.5	36.6 ± 0.7	77.0 ± 10.6	2.1 ± 1.5	54.4 ± 7.8
5	31.2 ± 0.3	25.0 ± 0.8	27.2 ± 0.8	51.7 ± 10.4	2.9 ± 3.3	60.8 ± 5.5
Total	**20.8 ± 2.3**	**12.7 ± 2.8**	**15.3 ± 4.4**	**74.2 ± 7.9**	**28.3 ± 6.2**	**55.8 ± 8.6**