UNDERSTANDING THE ROLE OF PREDATORS FOR THE MANAGEMENT OF FALL ARMYWORM (LEPIDOPTERA: NOCTUIDAE) IN TURFGRASS

by

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(Under the Direction of SHIMAT V. JOSEPH)

ABSTRACT

The aim of the study was to understand the potential role of predators against the fall armyworm, *Spodoptera frugiperda* (JE Smith) (Lepidoptera: Noctuidae), in turfgrass. The first project focused on characterizing the impressions generated by the common arthropods on clay models. Nine impression types were characterized after exposing 17 arthropod taxa to caterpillar-shaped clay models. When non-expert volunteers assessed the impression types, their responses were > 85% accurate. The arthropods initially interacted with the terminal regions of the models according to video recordings. In the second project, the influence of the color, shape, and size of clay models on arthropod interactions during daytime and nighttime were studied in a turfgrass field. The results showed greater numbers of impressions on the blue and green models than on the yellow models during the daytime, and no differences were observed during nighttime. The caterpillar-shaped and large-sized models captured greater impression densities than the beetle-shaped or small-sized models. The third project explored the vertical distribution of predator-prey interactions after placing clay models at lower, intermediate, and upper canopy of turfgrass in choice and no-choice assays. The results showed that significantly more densities of predator-mediated impressions were observed on clay models placed at a lower level than on those placed at the intermediate and upper levels of the turfgrass canopy. The fourth project assessed the incidence and severity of predation in residential lawns and sod farms. The percentage of predation on live *S. frugiperda* sentinel larvae and the percentage incidence and severity of interaction on clay models were significantly greater in the residential lawns than in the sod farms. Eleven impression types were recorded on clay models. Significantly greater densities of formicids interacted with live sentinel larvae than other predatory groups, such as carabids. In the fifth project, the effects of water deprivation on *S. frugiperda* and *Orius insidiosus* (Say) (Hemiptera: Anthocoridae) were studied on bermudagrass. There was a significantly greater *S. frugiperda* larval mortality with *O. insidiosus* across water-deprived treatments than without *O. insidiosus*. The survival and development of *S. frugiperda* larvae were affected by increased levels of water deprivation.

INDEX WORDS: predator-prey interaction, clay model, impressions, turfgrass, artificial caterpillar, sentinel prey, attack marks, predatory activity, video monitoring, residential lawn, sod farm, fall armyworm, *Spodoptera frugiperda*, insidious flower bug, *Orius insidiosus*, biological control, predation, bermudagrass, canopy, water deprivation, conservation biological control

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Turfgrass landscapes are irreplaceable urban vegetation land cover and are expanding in the U.S. and globally (Thompson and Kao-Kniffin 2016). Turfgrass is managed perennial grass that uniformly covers the landscape and provides many economic, aesthetic, and ecological benefits (Beard and Green 1994, Monteiro 2017). Among economic benefits, the turfgrass industry contributes $35.1 billion USD to the U.S. economy (Haydu et al. 2008). Turfgrass landscapes, including residential lawns, public parks, golf courses, and sports fields, constitute around 20 million hectares, making it the largest managed vegetation in the United States (Milesi et al. 2005, Steinke and Ervin 2015). The turfgrass offers a range of ecological benefits to the ecosystem, such as its role to sequester atmospheric carbon and increase soil organic matter (Qian and Follett 2002), contribute to net primary productivity, i.e., carbon accumulated by plant, excluding carbon consumed during respiration, which is directly proportional to oxygen production (Wu and Bauer 2012), aid urban cooling caused by evapotranspiration, which also helps with energy-saving (Wang et al. 2016) and minimizes water runoff and improves water infiltration, which reduces erosion and optimizes groundwater recharge (Monteiro 2017).

Fall armyworm

The fall armyworm, *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae), is a highly fecund (Johnson 1987), sporadic (Potter and Braman 1991), polyphagous (Luginbill 1928), and long-distance migratory pest (Harrison et al. 2019), causing post-migratory outbreaks in various cropping systems and managed landscapes, including the turfgrasses (Sparks 1979, Nagoshi and Meagher 2004, Blubaugh et al. 2015). It is native to the western hemisphere, affecting the southeastern United States, Mexico, Central and South America, and Caribbean regions (Andrews 1988). It has a broad host range of more than 80 plant species (Luginbill 1928), attributed to the two genetically distinct strains with specialized host plant distribution (Pashley and Martin 1987, Pashley 1988). Two host strains of *S. frugiperda* include C-strain (corn-strain), usually found on corn, *Zea mays* L., cotton, *Gossypium hirsutum* L., and sorghum, *Sorghum bicolor* (L.) Moench, while the R-strain (rice-strain) infest rice, *Oryza sativa* L., sugarcane, *Saccharum officinarum* L., millet, *Pennisetum glaucum* (L.) R. Br., and grasses, including bermudagrass, *Cynodon dactylon* (L). Pers (Pashley et al. 1985, Pashley 1988, Juárez et al. 2012, Murúa et al. 2015). Host strains show differences in host preference (Juárez et al. 2012), development and physiology (Whitford et al. 1988), sex pheromone composition (Groot et al. 2008, Lima and McNeil 2009), temporal mating separation (Schofl et al. 2009, Groot et al. 2010), and oviposition (Whitford et al. 1988).

The *Spodoptera frugiperda* adults are nocturnal and copulate after sunset. Moths prefer to oviposit near suitable hosts that favor larval development. The females emit sex pheromones as mating calls, attracting males following the pheromone plume (Sparks 1979, Batista-Pereira et al. 2006). The older females spend more time on mating calls (~250 min) and start the calling earlier (~50 min) than the younger moths, which spend less time on mating calls (~50 min) and higher onset calling time (~200 min) (Cruz-Esteban et al. 2017). The calling rhythms of females may differ within the population types, as Ramaswamy et al. (1988) found female *S. frugiperda* Mississippi populations showed two peaks of calling, while Honduras populations showed one peak of calling.

Mating occurs during the night, and it lasts approximately 130 mins (Simmons and Marti 1992). The male moths mate 6.7 times, whereas the females mate 3.7 times on an average during their lifetime (Simmons and Marti 1992). Eggs are laid in clusters or masses on the hosts or non-host surfaces (Meagher et al. 2011). At 70-80 °F, their eggs hatch in 2-4 days (Sparks 1979). Larvae consume the turfgrass blades and stem, causing extensive defoliation. Extensive feeding damage causes the turfgrass to turn brown from green. Larval duration ranges from 14-30 d and relies on prevalent temperatures (Pitre et al. 1983).

Biological control

Natural enemies, predators, and parasitoids reduce the *S. frugiperda* by naturally managing its populations. The major predator reported against fall armyworm included *Orius insidiosus* (Say) (Hemiptera: Anthocoridae) (n = 3 (number of studies), *Doru* spp. (Dermaptera: Forficulidae) (n = 3) and *Solenopsis* spp. (Hymenoptera: Formicidae) (n = 3). Most predators were reported from corn *Zea mays* L. (n =14), while a few have been reported from turfgrass (n = 2). The majority of predators have been reported from the U.S. (n = 9), followed by Brazil (n = 5) and Honduras (n = 2) (Table 1.1).

Among parasitoids, most studies indicate the prevalence of larval (n = 169) and egg (n = 57) parasitoids. Major species documented included egg parasitoid *Telenomus remus* (Nixon) (Hymenoptera: Platygastridae) (n = 25), egg and larval parasitoid *Chelonus insularis* Cresson (Hymenoptera: Braconidae) (n = 20) and larval parasitoid *Campoletis sonorensis* (Cameron) (Hymenoptera: Ichneumonidae) (n = 12). Most of the parasitoids were reported from Mexico (n = 97), Brazil (n = 46), and U.S. (n = 20). Most parasitoids were reported from *S. frugiperda* infestation in corn during June-October (Table 1.2).

Predators in turfgrass

Predation is an important biological interaction essential for the function and stability of an ecosystem (Lövei and Ferrante 2017). Insects are diverse and adaptable arthropods (Cranston and Gullan 2009), and they offer predation services in various ecosystems. Many beneficial arthropods, including predators and parasitoids, have been documented on *S. frugiperda*.

Insect predators play an important role in suppressing *S. frugiperda* (Table 1.1). However, fewer studies have been conducted in turfgrass to understand the predatory potential of insects. The proposed study will investigate the incidence of predation in sod farms and residential turfgrass using photography and sentinel live larvae and clay models techniques. Predators and parasitoids suppress pest outbreaks and help with the management of ecosystems. Surrounding natural habitats play a critical role in the incidence of natural enemies (Chaplin-Kramer et al. 2013), and their abundance is associated with increased plant biodiversity (Gerard et al. 2018). The surrounding vegetation around the crops supports diverse groups of beneficial arthropod assemblages, which reduce insect pest outbreaks compared to a simplified landscape without surrounding vegetation (Karp et al. 2016).

Several arthropod species, including the herbivores and beneficial insects, are present in the turfgrass system (Potter and Braman 1991). Predatory arthropods, including ants (Formicidae: Hymenoptera), ground beetles (Coleoptera: Carabidae), spiders (Araneae), rove beetles (Coleoptera: Staphylinidae), and big-eyed bugs (Hemiptera: Geocoridae), have been widely reported from turfgrass systems. A two-year study using pitfall traps found 13 genera of carabids and 14 genera of staphylinids occurring in centipedegrass [*Eremochola ophiuroides* (Munro.) Hack.] residential lawn (Braman and Pendley 1993). Braman et al. (2002) reported several arthropod predators in the turfgrass and their association with the surrounding vegetation. Joseph and Braman (2009) evaluated the predatory potential and activity of predatory heteropterans, including *O. insidiosus* and *Geocoris uliginosus* (Say), *G. punctipes* (Say)against *S. frugiperda* using different turfgrass cultivars of varying levels of resistance, where predator-mediated mortality was observed in moderately resistant turfgrass.

In a study, Frank and Shrewsbury (2004) showed that the susceptibility of various life stages of the black cutworm *Agrotis ipsilon* (Hufnagel) (Lepidoptera: Noctuidae) to predation varies by predatory taxa, such as carabid, staphylinid, and arachnid predators. The predators, *Amara impuncticollis* (Say) (Coleoptera: Carabidae) and *Philonthus* sp. (Coleoptera: Staphylinidae), consumed all instars of *A. ipsilon*, and the authors concluded that they were more effective than other generalist predators examined. All predators consumed at least one larval stage of *A. ipsilon* and concluded that generalist predators effectively reduce cutworm populations in turfgrass.

Quantifying predation

Studying predation can be challenging because predator activity is a rapid event, and the predator leaves minimal evidence of the event. Many techniques have been used to estimate predation in laboratory and field experiments, where video recording (Merfield et al. 2004) and time-lapse photography (Khan and Joseph 2021a) provide real-time images of predator-prey interactions. The gut DNA detection analysis of the predator estimates the presence and proportion of prey DNA (Li et al. 2017). The quantitative fatty acid signature analysis (QFASA) utilizes the fatty acid accumulation to estimate the type and proportion of prey species consumed by the predator

(Iverson et al. 2004). Finally, the sentinel live prey or clay model method involves exposing live and artificial prey. This technique quantifies predatory activity (Lövei and Ferrante 2017).

Clay model to estimate predation

Clay models resembling the prey species have been widely used to assess predation (Bateman et al. 2017, Lövei and Ferrante 2017). The caterpillar-shaped models made from flour, lard, and food-grade color were first used to study avian predators (Edmunds and Dewhirst 1994). The prey models of specific size, shape, color, usually made up of pre-formulated clay, are being exposed, with or without a substrate, in an ecosystem to estimate predatory activity. When a predator interacts with the prey model, it leaves behind unique marks or impressions on the surface of the model. The impressions were evaluated to understand the type of predators and the intensity of the predatory interaction.

Most of the prey models used in previous studies were prepared from materials in raw forms, such as flour; or pre-formulated, non-toxic, commercially available clay material. Prey models were prepared using raw materials, such as flour and lard at 3:1 ratio, and food-grade colors were added to obtain a specific color (Church et al. 1997, Hossie and Sherratt 2012, 2013, Suzuki and Sakurai 2015). The models in some other studies were pre-formulated, odorless plasticine (Howe et al. 2009, Bereczki et al. 2014, Gray and Lewis 2014, Nurdiansyah et al. 2016, Tiede et al. 2017, Magagnoli et al. 2018, Valdés-Correcher et al. 2019, Meyer et al. 2019, Muchula et al. 2019, González et al. 2020, Hernández-Agüero et al. 2020, Sinu et al. 2021).

The green-colored caterpillar model served as an unprotected prey to assess predatory interactions in different ecosystems (Nurdiansyah et al. 2016, Lövei and Ferrante 2017, Gunnarsson et al. 2018, Eötvös et al. 2020, Long and Frank 2020, Kuli-Révész et al. 2021, Leuenberger et al. 2021, Valdés-Correcher et al. 2021). Other colored models were also utilized to study predation. Zvereva et al. (2019) studied avian predation using clay models with eight colors, white, yellow, violet, red, green, blue, brown, and black. Zvereva and Kozlov (2021) used four different colored caterpillar-shaped models, black, green, red, and yellow, to study the seasonal response of birds to prey with different colors. In some studies, a combination of colors was used, such as blue-red (Aslam et al. 2020) and brown-green (Seifert et al. 2015, Witwicka et al. 2019).

Clay models have been used to estimate predation in different ecosystems, including forest, agricultural, and urban landscapes. The predation rates on artificial caterpillars in a tropical forest were determined using two types of clay models clay and dough-based models (Molleman et al. 2016). The results showed that ants were the dominant predators in the tropical forest, and ant predation was greater on the dough models than the clay models (Molleman et al. 2016). Similarly, Remmel et al. (2009) quantified the predatory activity of leaf-feeding insects in boreal forests by exposing the clay models to avian predators by restricting access to arthropods, and their results showed that impressions created by birds on the clay models were greater during June than those during other months. When the predatory services were compared among mixed fruit orchards, oil palm, and rubber tree plantations, predation offered by arthropods was greater than mammals and birds (Denan et al. 2020). Also, there were no differences in predation on larval stages of lepidopterans in these agroecosystems (Denan et al. 2020). In another study, the predatory effects of arthropod and bird densities on herbivorous insects were compared in forest and residential landscapes. When the green-colored clay models were placed on vegetation, bird and arthropod-mediated predation were evident in these landscapes (Roels et al. 2018). Thus, these studies suggest that the clay models can be used to estimate predation in various ecosystems.

After exposing the clay models, they are evaluated for the presence of attack marks, and in some cases, the causal predators were determined. Low et al. (2014) provided guidelines to identify attack marks on the clay models created by arthropod, bird, and mammalian predators. Khan and Joseph (2021) characterized the impressions created by arthropods collected from turfgrass.

Abiotic factors and predator-prey interactions

Abiotic factors, including temperature, water, atmospheric gases, light, and wind, can affect predator-prey interactions. The insect communities are adaptable but are still vulnerable to the sudden fluctuations of biotic and abiotic in the environment. The climate-driven changes to abiotic factors, such as limited water availability (Castagneyrol et al. 2018) and extreme temperatures (Jamieson et al. 2012), affect the plant-herbivore (Bale et al. 2002) and natural enemy-herbivore interactions (Rall et al. 2010) in various ecosystems. These climate-mediated effects can further alter the beneficial services of the insects against insect pest outbreaks (Hughes 2000).

The changing climate is causing global warming, extreme temperatures, and changes in precipitation rates (Field et al. 2014). Global temperatures are predicted to increase by 2 – 6 °C by 2100, which indicates the urgent need to study the effects of climate change in various ecosystems (Pureswaran et al. 2018). The sudden fluctuations of abiotic factors could affect the abundance and distribution of many insect species (Stange and Ayres 2010) and could influence insect predator-prey interactions (Laws 2017).

Predation is an important intra- and inter-species interaction that shapes the dynamics of communities (Guiden et al. 2019) and transforms the ecosystem (Estes et al. 2011). Predator-prey interactions alter community composition (Kneitel and Chase 2004), dampen trophic cascades (Finke and Denno 2004), influence species invasions (Snyder et al. 2004), and regulate biodiversity (Letnic et al. 2012). Predators also function as indirect defense working in favor of plants by responding to herbivore-induced plant volatiles and reducing the herbivore densities (Aljbory and Chen 2018).

Water stress

Changes in water availability can affect the physiology of plants and herbivores (Hale et al. 2003, Mody et al. 2009). The stressed herbivore could enhance the activity of insect predators (Banfield-Zanin and Leather 2016). Water deprivation can cause bottom-up effects and alter the behavior of the natural enemies (Han et al. 2015) and dynamics of the food web (Huberty et al. 2008). Water stress can decrease predatory activity, possibly due to the inadequate availability and uptake of water and nutrients required for optimum prey digestion and growth. Han et al. (2015) examined the predatory strength of green mirid bug *Macrolophus pygmaeus* (Rambur)(Hemiptera: Miridae) on the eggs of Mediterranean flour moth *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae) feeding on water and fertilizer stressed tomato (*Solanum lycopersicum* L.) and found a 30% reduction in predator’s survival along with decreased predatory potential of *M. pygmaeus* (Han et al. 2015).

The prey-mediated effects on the insect predators can increase the prey consumption rate. A recent study on green spruce aphid, *Elatobium abietinum* (Walker) (Hemiptera: Aphididae), and its coccinellid predators, *Aphidecta obliterata* (L.) and *Adalia bipunctata* L., exposed to various water-deprived states demonstrated that the predation increased with increase in severity of water-deprivation in plants (Banfield-Zanin and Leather 2016). The water stress induces contrasting responses in the feeding patterns and development of the insect herbivores. Gutbrodt et al. (2011) showed that cabbage butterfly *Pieris brassicae* (L.) (Lepidoptera: Pieridae) and cotton leafworm, *Spodoptera littoralis* (Boisduval) (Lepidoptera: Noctuidae) elicited a varying degree of feeding responses on drought-stressed garlic mustard, *Alliaria petiolata* (M. Bieb.) Cavara & Grande (Brassicaceae) plants. The larvae of *P. brassicae* consumed more food in well-watered plant treatment than in stressed plant treatments. In contrast, larvae of *S. littoralis* consumed more amount from stressed plant treatment than well-watered plant treatment. Moreover, both the species showed varied developmental responses on the well-watered and stressed plants, i.e., *P. brassicae* showed faster larval development and higher pupal weight, while *S. littoralis* larvae showed retarded development. In turfgrass, the effects of water deprivation on herbivory and insect predation are not studied.

Water availability can affect insect predation (Han et al. 2015). Wade et al. (2017) showed that increased weight of harlequin ladybird beetle, *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) adults consuming aphids developing on water-stressed plants possibly because of decreasing in the host plant quality, such as amino acid concentrations. Water is essential for the development of insect predators. The generalist mirid predator *Dicyphus errans* (Wolff) was studied for its nymphal development in the presence or absence of water and animal/plant food, and the study indicated that, for the optimum nymphal development, water is essential in addition to the offered prey, i.e., *E. kuehniella* eggs (Arvaniti et al. 2018).

Uneven precipitation patterns can also lead to changes in species richness. Zhu et al. (2014) showed that above-ground biomass increased with an increase in precipitation. However, the decreased precipitation levels caused a decline in insect species richness. The water stress can reduce the primary production (plants), leading to the lower abundance and diversity of the insects (Wagner 2020). As per the ‘resource productivity’ hypothesis, a robust plant community supports consumer communities owing to adequate food supplies (Perner et al. 2005). However, the abundance of water availability suppresses plant groups, such as forbs and legumes, and supports other plant groups, such as grasses (Zhu et al. 2014). The grass-dominated system supports fewer herbivore species and their densities than mixed-plant groups (Haddad et al. 2001), probably due to weak structural complexity, reducing refugia options for the prey species (Brose 2003). In addition, the decrease in water availability can alter the optimal microclimate of soil surface (Frampton et al. 2000) and nutrient content in the plants (Masters et al. 1998), and these changes can cascade on to the health of insect communities. These studies showed that water regulates the metabolic processes in plants and insects, which affects the survival and development of herbivores and their predators.

Research Objectives

Objective 1: Characterization of impressions created by turfgrass arthropods on clay models

Diverse groups of arthropods, including predators, inhabit the turfgrass system. When the predators interact with the clay models, they create diverse and unique impressions on the surface of clay models. Low et al. (2014) developed general guidelines to determine the impressions created by various arthropods, birds, reptiles, and mammals on the clay model. However, these guidelines were not specific to either arthropods or turfgrass ecosystems. The turfgrass system has unique groups of predators, and little has been explored on how the common predator community in turfgrass interact with the clay models. The first objective was to identify and characterize the different impressions created on the clay model by common predaceous arthropods in turfgrass.

Objective 2: Influence of the color, shape, and size of clay model on arthropod interactions in turfgrass

Khan and Joseph (2021) characterized nine distinct impressions on clay models when the arthropods collected from the turfgrass were exposed to clay models. However, there is limited information on the attributes of the clay models, such as color, shape, and size, that would generate interaction in the field conditions. Therefore, the objective of this project was to determine the effects of color, shape, and size when placed in the turfgrass field.

Objective 3: Vertical distribution of predator-prey interactions within turfgrass

The cutworms and fall armyworms occupy independent feeding niches, and the effects of predation on these pests could depend on the behavior of the predator community. When placed near thatch, Khan and Joseph (2021b) found that the larval-shaped models had significantly greater densities of impressions than beetle-shaped models. However, little is known about the behavior of the predator community within the turfgrass canopy at varying levels. Thus, the objective of this project was to determine the vertical distribution of prey-predator interaction within turfgrass canopy using clay models.

Objective 4: Assessment of predatory activity in residential lawns and sod farms

Turfgrass, produced and harvested from sod farms and planted in the residential and plots, serves as an essential urban and suburban vegetative cover. Turfgrass is managed at varying intensity levels for pest and disease control and horticultural attributes, such as mowing frequency and nutrient management across various turfgrass systems. The abundance of beneficial arthropods, predators and parasitoids, has been previously reported from the residential turfgrass and commercial sod farms (Joseph and Braman 2009b, Singh 2020); however, the role of predatory activity in the less intensive turfgrass systems, such as and residential lawns and sod production farms, respectively is still lacking. Thus, the objective of this project was to assess and compare predatory activity in residential lawns and sod farms.

Objective 5: Effects of water-deprived turfgrass on fall armyworm and its predator, insidious flower bug

Prolonged dry spells can be caused by the changing climate or local weather cycles. They can induce physiological changes within plants, including turfgrass, which could produce cascading effects on dependent insect communities. The fall armyworm is an important pest of turfgrass, and predators play a pivotal role in reducing the intensity of outbreak populations. It is unclear how the predator community responds to the changing physiological effects in turfgrass caused by prolonged, water-deprived conditions. Thus, the objective of this project was to determine the effects of water deprived, drought-resistant, and -susceptible turfgrass on fall armyworm and its predator, insidious flower bug.

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Table 1.1. Predators attacking fall armyworm reported during 1991-2020.

Scientific name (Order: Family)	Country	Crop	Month	Year	Reference
Chlaenius tomentosus (Say) (Coleoptera: Carabidae)	U.S.	-	-	-	(Young 2005)
Cicindela punctulata Oliver (Coleoptera: Carabidae)	U.S.	-	-	-	(Young 2005)
Coccinella transversalis Fabricius (Coleoptera: Coccinellidae)	India	Corn	June-August	2018	(Sharanabasappa et al. 2019)
Coleomegilla maculata (DeGeer) (Coleoptera: Coccinellidae)	Colombia	Corn/Cotton	-	-	(Murillo 2014)
Doru luteipes (Scudder) (Dermaptera: Forficulidae)	Brazil	Corn	-	2009-11	(Varella et al. 2015)
	Brazil	Corn	-	2008	(Toscano et al. 2012)
Doru taeniatum (Dorhn) (Dermaptera: Forficulidae)	Honduras	Corn	May-October	2002-03	(Wyckhuys and O’Neil 2006)
Eriopis connexa (Germar) (Coleoptera: Coccinelidae)	Brazil	Corn	-	2009-12	(Varella et al. 2015)
Forficula sp. (Dermaptera: Forficulidae)	India	Corn	June-August	2018	(Sharanabasappa et al. 2019)
Geocoris spp. (Hemiptera: Geocoridae)	U.S.	Turfgrass	August	-	(Joseph and Braman 2009a)
Haematochares obscuripennis Stål (Hemiptera: Reduviidae)	Ghana	Corn	May-November	2017	(Koffi et al. 2020)
Harmonia axyridis (Pallas) (Coleoptera: Coccinellidae)	Brazil	Corn	-	2009-11	(Varella et al. 2015)
Harmonia octomaculata (Fabricius) (Coleoptera: Coccinellidae)	India	Corn	June-August	2018	(Sharanabasappa et al. 2019)
Megacephala carolina carolina L. (Coleoptera: Carabidae)	U.S.	-	-	-	(Nachappa et al. 2006)
Orius insidiosus (Say) (Hemiptera: Anthocoridae)	Brazil	Corn	-	2009-11	(Varella et al. 2015)

	U.S.	Turfgrass	August	-	(Joseph and Braman 2009a)
	U.S.	-	-	-	(Isenhour et al. 1990)
Peprius nodulipes (Signoret) (Hemiptera: Reduviidae)	Ghana	Corn	May-November	2017	(Koffi et al. 2020)
Pheidole megacephala (Fabricius) (Hymenoptera: Formicidae)	Ghana	Corn	May-November	2017	(Koffi et al. 2020)
Scarites subterraneus Fabricius (Coleoptera: Carabidae)	U.S.	-	-	-	(Young 2005)
Solenopsis geminata (Fabricius) (Hymenoptera: Formicidae)	Honduras	Corn	May-October	2002-03	(Wyckhuys and O'Neil 2006)
	U.S.	-	-	-	(Perfecto 1991)
Solenopsis invicta Buren (Hymenoptera: Formicidae)	U.S.	Sorghum	-	-	(Fuller et al. 1997)
Toxomerus politus Say (Diptera: Syrphidae)	Mexico	Corn	July-October	2013	(Jirón-Pablo et al. 2018)

The literature review was performed from 1990-2020 using the keywords "*Spodoptera frugiperda*" AND pred* from Web of Science Core Collection.

Table 1.2. Parasitoids reported from different stages of fall armyworm during 2003-2020.

Scientific name (Order: Family)	Type	Distribution	Crop	Month	Year	Reference
Aleiodes laphygmae (Viereck) (Hymenoptera:Braconidae)	larval	Florida, U.S.	Corn	August-October, June-October, May	2008-2010	(Hay-Roe et al. 2016)
	larval	Florida, U.S.	Tifton-85 Bermudagrass	August-October, June-October, May	2008-2010	(Hay-Roe et al. 2016)
	larval	Florida, U.S.	Corn	November-December, February-April	2010-2015	(Meagher et al. 2016)
	larval	Mexico	Corn	June-September	2005	(Jourdie et al. 2008)
	larval	Mexico	Corn	June-August	2001	(Ruíz-Nájera et al. 2007)
	larval	Honduras	Corn	May-October	2002-2003	(Wyckhuys and O'Neil 2006)
Aleiodes vaughani (Muesebeck) (Hymenoptera: Braconidae)	larval	Mexico	Corn	June-August	2001	(Ruíz-Nájera et al. 2007)
Anatrichus erinaceus Loew (Diptera: Chloropidae)	larval	Ghana	Corn	May-November	2017	(Koffi et al. 2020)
Apanteles sp. (Hymenoptera: Braconidae)	larval	Peru	Corn	-	2017	(Quispe et al. 2017)
Aprostocetus sp. Westwood (Hymenoptera: Eulophidae)	larval	Mexico	Corn	June-September	2005	(Jourdie et al. 2008)
Archytas incertus (Macquart) (Diptera, Tachinidae)	larval	Brazil	Corn	March-October	2012-2014	(Toma et al. 2018)
	larval	Argentina	Corn	-	1999-2003	(Murúa et al. 2009)
Archytas marmoratus (Townsend) (Diptera: Tachinidae)	pupal	Mexico	Corn	June-August	2016	(Gurrola-Pérez et al. 2018)
	pupal	Mexico	Corn	June-August	2016	(González-Maldonado et al. 2018)
	larval	Mexico	Corn	August-November	2011-2012	(Vírgen et al. 2013)
	pupal	Mexico	Corn	July-September		(Rios-Velasco et al. 2011)

	larval	Argentina	Corn	-	1999-2003	(Murúa et al. 2009)
	larval	Mexico	Corn	June-September	1999	(Delfín-González et al. 2007)
	larval	Mexico	Corn	June-August	2001	(Ruíz-Nájera et al. 2007)
	pupal	Honduras	Corn	May-October	2002-2003	(Wyckhuys and O'Neil 2006)
Archytas spp. (Diptera: Tachinidae)	larval	Paraguay	Corn	-	2014-2016	(Cabral Antúnez et al. 2018)
	larval	Argentina	Corn	-		(Murúa et al. 2006)
Campoletis chlorideae Uchida (Hymenoptera: Ichneumonidae)	larval	India	Corn	June-August	2018	(Sharanabasappa et al. 2019)
Campoletis flavicincta (Ashmead) (Hymenoptera: Ichneumonidae)	egg	Brazil	Corn	-	2009-2010-2011	(Varella et al. 2015)
	egg	Brazil		-		(Zanuncio et al. 2013)
	egg	Brazil	Corn	-		(Signoretti et al. 2012)
	egg	Brazil		-		(Dequech et al. 2005)
Campoletis grioti (Blanchard) (Hymenoptera: Ichneumonidae)	larval	Argentina	Corn	-	1999-2003	(Murúa et al. 2009)
	larval	Argentina	Corn	-		(Murúa et al. 2006)
Campoletis sonorensis (Cameron) (Hymenoptera: Ichneumonidae)	larval	Mexico	Corn	-	2017	(Araiza 2018)
	larval	Mexico	Corn	-		(Contreras-Cornejo et al. 2018)
	larval	Mexico	Corn	August-October	2010	(de Lange et al. 2018)
	larval	Mexico		-		(Barreto-Barriga et al. 2017)
	larval	Brazil	Corn	-		(Camargo et al. 2015)
	larval	Mexico	Corn	Spring-Summer	2012-2013	(Gutiérrez-Ramírez et al. 2015)
	larval	Mexico	Corn	June-August	2012	(García-Gutiérrez et al. 2013)

	larval	Mexico	Corn - Sorghum	February-December	2010	(Cortez-Mondaca et al. 2012)
	larval	Mexico	Corn	July-September		(Rios-Velasco et al. 2011)
	larval					(Jourdie et al. 2010)
	larval	Mexico	Corn	June-September	2005	(Jourdie et al. 2008)
	larval	Honduras	Corn	May-October	2002-2003	(Wyckhuys and O'Neil 2006)
Campoletis sp. (Hymenoptera: Ichneumonidae)	larval	Mexico	Corn	August-November	2011-2012	(Vírgen et al. 2013)
	larval	Brazil	Corn	-	2008	(Toscano et al. 2012)
Charops ater Szépligeti (Hymenoptera: Ichneumonidae)	larval	Kenya	Corn	April-August	2017	(Sisay et al. 2019)
	larval	Tanzania	Corn	July-November	2017	(Sisay et al. 2019)
	larval	Kenya	Corn	June-August	2018	(Sisay et al. 2019)
	larval	Tanzania	Corn	June-August	2018	(Sisay et al. 2019)
	larval	Kenya	Corn	July-October	2017	(Sisay et al. 2018)
	larval	Tanzania	Corn	July-November	2017	(Sisay et al. 2018)
Charops sp. (Hymenoptera: Ichneumonidae)	larval	Ghana and Benin	Corn	July-November	2018	(Agboyi et al. 2020)
Chelonus bifoveolatus Szépligeti (Hymenoptera:Braconidae)	egg, larval	Tanzania	Corn, Cowpea, Silverleaf desmodium	September-February	2018-2019	(Ngangambe and Mwatawala 2020)
	egg, larval	Ghana and Benin	Corn	July-November	2018	(Agboyi et al. 2020)
	larval	Ghana	Corn	May-November	2017	(Koffi et al. 2020)
Chelonus cautus Cresson (Hymenoptera: Braconidae)	larval	Mexico	Corn	Spring-Summer	2012-2013	(Gutiérrez-Ramírez et al. 2015)
	egg,larval	Mexico	Corn	June-August	2012	(García-Gutiérrez et al. 2013)
	egg, larval	Mexico	Corn	July-September		(Rios-Velasco et al. 2011)
	egg, larval	Mexico	Corn	June-September	2005	(Jourdie et al. 2008)

	egg, larval	Mexico	Corn	June-August	2001	(Ruíz-Nájera et al. 2007)
Chelonus curvimaculatus Cameron (Hymenoptera: Braconidae)	egg	Kenya	Corn	April-August	2017-18	(Sisay et al. 2019)
	egg	Kenya	Corn	July-October	2017	(Sisay et al. 2018)
Chelonus insularis Cresson (Hymenoptera: Braconidae)	egg	Mexico	Corn	January, May, September	2018	(Roque-Romero et al. 2020)
	egg, larval	Mexico	Corn	-	-	(Ortiz-Carreon et al. 2019)
	larval	Mexico	Corn	January-December	2016-2017	(López et al. 2018)
	larval	Mexico	Corn	-	2016-2017	(Hernández-García et al. 2017)
	egg, larval	Mexico	Corn	-	2017	(Araiza 2018)
	egg, larval	Peru	Corn	-		(Quispe et al. 2017)
	larval	Florida, U.S.	Corn	November-December, February-April	2010-2015	(Meagher et al. 2016)
	larval	Mexico	Corn	Spring-Summer	2012-2013	(Gutiérrez-Ramírez et al. 2015)
	egg, larval	Mexico	Corn	June-August	2012	(García-Gutiérrez et al. 2013)
	egg, larval	Mexico	Corn	August-November	2011-2012	(Vírgen et al. 2013)
	egg,larval	Mexico	Corn - Sorghum	February-December	2010	(Cortez-Mondaca et al. 2012)
	egg, larval	Mexico	Corn	July-September		(Rios-Velasco et al. 2011)
	egg, larval	-	-	-		(Jourdie et al. 2010)
	egg, larval	Argentina	Corn	-	1999-2003	(Murúa et al. 2009)
	egg, larval	Mexico	Corn	June-September	2005	(Jourdie et al. 2008)

	egg, larval	Mexico	Corn	June-August	2001	(Ruíz-Nájera et al. 2007)
	egg	Columbia	Corn			(Zenner et al. 2006)
	egg	Honduras	Corn	May-October	2002-2003	(Wyckhuys and O’Neil 2006)
	egg	Argentina	Corn	-		(Murúa et al. 2006)
	egg	Mexico	Corn - Sorghum - Sudan Grass	-		(Molina-Ochoa et al. 2004)
Chelonus sp. (Hymenoptera: Braconidae)	larval	Paraguay	Corn	-	2014-2016	(Cabral Antúnez et al. 2018)
	egg	Brazil	Corn	-	2009-2010-2011	(Varella et al. 2015)
	egg, larval	Brazil	Corn	-	2008	(Toscano et al. 2012)
Chetogena scutellaris (Wulp) (Diptera: Tachinidae)	larval	Honduras	Corn	May-October	2002-2003	(Wyckhuys and O’Neil 2006)
Coccygidium luteum (Brullé) (Hymenoptera: Braconidae)	larval	Ethiopia	Corn	March-October	2017	(Sisay et al. 2019)
	larval	Kenya	Corn	April-August	2017	(Sisay et al. 2019)
	larval	Tanzania	Corn	July-November	2017	(Sisay et al. 2019)
	larval	Tanzania	Corn, cowpea, silverleaf desmodium	September-February	2018-2019	(Ngangambe and Mwatawala 2020)
	larval	Ghana and Benin	Corn	July-November	2018	(Agboyi et al. 2020)
	larval	Ghana	Corn	May-November	2017	(Koffi et al. 2020)
	larval	Ethiopia	Corn	March-October	2017	(Sisay et al. 2018)
	larval	Kenya	Corn	July-October	2017	(Sisay et al. 2018)
	larval	Tanzania	Corn	July-November	2017	(Sisay et al. 2018)
Coccygidium melleum (Roman) (Hymenoptera: Braconidae)	larval	India	Corn	June-August	2018	(Sharanabasappa et al. 2019)
Coccygidium transcaspicum (Kokujev) (Hymenoptera: Braconidae)	larval	India	Corn	-	2019	(Gupta et al. 2020)
	larval	Ghana	Corn	May-November	2017	(Koffi et al. 2020)

Cotesia icipe Fernandez-Triana & Fiaboe (Hymenoptera: Braconidae)	larval	Ethiopia	Corn	March-October	2017	(Sisay et al. 2018)
	larval	Kenya	Corn	July-October	2017	(Sisay et al. 2018)
	larval	Ethiopia	Corn	March-October	2017	(Sisay et al. 2019)
	larval	Ethiopia	Corn	June-August	2018	(Sisay et al. 2019)
	larval	Kenya	Corn	June-August	2018	(Sisay et al. 2019)
	larval	Tanzania	Corn	June-August	2018	(Sisay et al. 2019)
Cotesia marginiventris (Cresson) (Hymenoptera: Braconidae)	larval	Mexico	Corn	January-December	2016-2017	(López et al. 2018)
	larval	U.S.	Corn	-	-	(Block et al. 2018)
	larval	Florida, U.S.	Corn	November-December, February-April	2010-2015	(Meagher et al. 2016)
	larval	Mexico	Corn	Spring-Summer	2012-2013	(Gutiérrez-Ramírez et al. 2015)
	larval	Mexico	Corn - Sorghum	February-December	2010	(Cortez-Mondaca et al. 2012)
	larval					(Desneux et al. 2010)
	larval	Mexico	Corn	June-September	2005	(Jourdie et al. 2008)
	larval	Honduras	Corn	May-October	2002-2003	(Wyckhuys and O’Neil 2006)
Cotesia spp. (Hymenoptera, Braconidae)	larval	Florida, U.S.	Corn	August-October 2008, June-October 2009 and May 2010.	2008-2010	(Hay-Roe et al. 2016)
	larval	Mexico	Corn	August-November	2011-2012	(Vírgen et al. 2013)
	larval	Mexico	Corn	Spring-Summer	2012-2013	(Gutiérrez-Ramírez et al. 2015)
	larval	Tanzania	Corn, cowpea, silverleaf desmodium	September-February	2018-2019	(Ngangambe and Mwatawala 2020)
	larval	Ghana and Benin	Corn	July-November	2018	(Agboyi et al. 2020)

Dissomphalus spp. (Hymenoptera: Bethylidae)	larval	Paraguay	Corn	-	2014-2016	(Cabral Antúnez et al. 2018)
Distichona auriceps Coquillett (Diptera: Tachinidae)	larval	Mexico	Corn	June-July	2014	(Salas-Araiza 2017)
Dolichozele koebelei Viereck (Hymenoptera: Braconidae)	larval	Brazil	Corn - Common bean	May	2010-2011	(Silva et al. 2014)
Eiphosoma sp (Hymenoptera: Ichnuemonidae)	larval	Mexico	Corn	-	2016-2017	(Hernández-García et al. 2017)
Eiphosoma vitticolle Cresson (Hymenoptera: Ichneumonidae)	larval	Mexico	Corn	Spring-Summer	2012-2013	(Gutiérrez-Ramírez et al. 2015)
	larval	Mexico	Corn	June-September	2005	(Jourdie et al. 2008)
Eriborus sp. (Hymenoptera: Ichneumonidae)	larval	India	Corn	June-August	2018	(Sharanabasappa et al. 2019)
Eucelatoria bryani Sabrosky (Diptera: Tachinidae)	larval	Mexico	Corn	-	2017	(Araiza 2018)
Eucelatoria rubentis (Coquillett) (Diptera: Tachinidae)	larval	Florida, U.S.	Tifton-85 bermudagrass	August-October 2008, June-October 2009 and May 2010.	2008-2010	(Hay-Roe et al. 2016)
Eucelatoria sp. (Diptera: Tachinidae)	larval	Peru	Corn	-		(Quispe et al. 2017)
	larval	Honduras	Corn	May-October	2002-2003	(Wyckhuys and O’Neil 2006)
Euplectrus furnius Walker (Hymenoptera: Eulophidae)	larval	Brazil	Corn	January-February	2011	(Sturza et al. 2013)
Euplectrus plathypenae Howard (Hymenoptera: Eulophidae)	larval	Mexico	Corn	July-September	-	(Rios-Velasco et al. 2011)
	larval	Mexico	Corn	June-September	2005	(Jourdie et al. 2008)
	larval	Mexico	Corn	June-September	1999	(Delfín-González et al. 2007)
	larval	Mexico	Corn	June-August	2001	(Ruíz-Nájera et al. 2007)
	larval	Florida, U.S.	Corn	August-October 2008, June-October 2009 and May 2010.	2008-2010	(Hay-Roe et al. 2016)

	larval	Florida, U.S.	Corn	November-December, February-April	2010-2015	(Meagher et al. 2016)
	larval	Argentina	Corn	-	1999-2003	(Murúa et al. 2009)
Euplectrus sp. (Hymenoptera: Eulophidae)	larval	Brazil	Corn	-	2008	(Toscano et al. 2012)
Exasticolus fuscicornis (Cameron) (Hymenoptera: Braconidae)	larval	Paraguay	Corn	-	2014-2016	(Cabral Antúnez et al. 2018)
	larval	Brazil	Corn	-	2002-2004	(Figueiredo et al. 2006)
Exorista sorbillans (Diptera: Tachinidae)	larval	India	Corn	June-August	2018	Sharanabasappa et al. 2019
Glyptapanteles militaris (Walsh) (Hymenoptera: Braconidae)	larval	Mexico	Corn	June-September	2005	Jourdie, 2008
	larval	Mexico	Corn	June-August	2001	Ruíz-Nájera, 2007
Homolobus truncator (Say) (Hymenoptera: Braconidae)	larval	Mexico	Corn	Spring-Summer	2014-2017	(González-Maldonado and Coronado-Blanco 2020)
	larval	Mexico	Corn	June-September	2005	(Jourdie et al. 2008)
Horismenus sp. nr. *ignotus* Burks (Hymenoptera: Eulophidae)	larval	Florida, U.S.	Corn	August-October 2008, June-October 2009 and May 2010.	2008-2010	(Meagher et al. 2016)
Hyposoter didymator (Hymenoptera: Ichneumonidae)	larval	France	-	-		(Visconti et al. 2019)
Hyposoter sp. (Hymenoptera: Ichneumonidae)	larval	Mexico	Corn	August-November	2011-2012	(Vírgen et al. 2013)
Hypovoria discalis (Brooks) (Diptera: Tachinidae)	larval	Mexico	Corn	June-July	2014	(Salas-Araiza 2017)
Incamyia chilensis (Aldrich) (Diptera Tachinidae)	larval	Argentina	Corn	-	1999-2003	(Murúa et al. 2009)
Lespesia aletiae (Riley) (Diptera: Tachinidae)	larval	Mexico	Corn	June-August	2016	(González-Maldonado et al. 2018)
	larval	Florida, U.S.	Tifton-85 Bermudagrass	August-October 2008, June-	2008-2010	(Meagher et al. 2016)

				October 2009 and May 2010.		
Lespesia archippivora (Riley) (Diptera: Tachinidae)	larval, pupal	Mexico	Corn	June-August	2016	(Gurrola-Pérez et al. 2018)
	larval, pupal	Mexico	Corn	June-August	2016	(González-Maldonado et al. 2018)
	larval, pupal	Florida, U.S.	Corn	August-October, June-October, and May	2008-2010	(Hay-Roe et al. 2016)
	larval	Florida, U.S.	Tifton-85 Bermudagrass	August-October 2008, June-October 2009 and May 2010.	2008-2010	(Hay-Roe et al. 2016)
	larval,pupal	Mexico	Corn	June-September	1999	(Delfín-González et al. 2007)
	larval,pupal	Mexico	Corn	June-August	2001	(Ruíz-Nájera et al. 2007)
	larval	Honduras	Corn	May-October	2002-2003	(Wyckhuys and O’Neil 2006)
	larval	Mexico	Corn	April-May	2016	(Hernández-García et al. 2017)
	larval	Mexico	Corn	June-August	2016	(Gurrola-Pérez et al. 2018)
Lespesia sp. (Diptera: Tachinidae)	larval,pupal	Mexico	Corn - Sorghum	February-December	2010	(Cortez-Mondaca et al. 2012)
Megaselia scalaris Loew (Diptera: Phoridae)	pupal	Mexico	Corn	June-August	2001	(Ruíz-Nájera et al. 2007)
Meteoridea testacea (Granger) (Hymenoptera: Braconidae)	larval, pupal	Ghana and Benin	Corn	July-November	2018	(Agboyi et al. 2020)
	larval	Ghana	Corn	May-November	2017	(Koffi et al. 2020)
	larval	Mexico	Corn	August-September	2012	(Gutiérrez-Ramírez et al. 2015)

Meteorus autographae Muesebeck (Hymenoptera: Braconidae)	larval	Florida, U.S.	Corn	August-October 2008, June-October 2009 and May 2010.	2008-2010	(Hay-Roe et al. 2016)
Meteorus laphygmae Viereck (Hymenoptera: Braconidae)	larval	Mexico	Corn	January-December	2016-2017	(López et al. 2018)
	larval	Mexico	Corn	Spring-Summer	2012-2013	(Gutiérrez-Ramírez et al. 2015)
	larval	Mexico	Corn	-	-	(Villegas-Mendoza et al. 2015)
	larval	Mexico	Corn	June-September	2005	(Jourdie et al. 2008)
	larval	Mexico	Corn - Sorghum - Sudan Grass	-		(Molina-Ochoa et al. 2004)
Meteorus sp. (Hymenoptera: Braconidae)	larval	Florida, U.S.	Corn	November-December, February-April	2010-2015	(Meagher et al. 2016)
	larval	Mexico	Corn	June-August	2012	(García-Gutiérrez et al. 2013)
	larval	Mexico	Corn - Sorghum	February-December	2010	(Cortez-Mondaca et al. 2012)
Metopius discolor Tosquinet (Hymenoptera: Ichneumonidae)	larval, pupal	Ghana and Benin	Corn	July-November	2018	(Agboyi et al. 2020)
Neotheronia sp. (Hymenoptera: Ichneumonidae)	larval	Mexico	Corn	June-August	2001	(Ruíz-Nájera et al. 2007)
Odontepyris sp. (Hymenoptera: Bethylidae)	larval	India	Corn	June-August	2018	(Sharanabasappa et al. 2019)
Ophion flavidus Brulle (Hymenoptera: Ichneumonidae)	larval	Florida, U.S.	Corn	August-October 2008, June-October 2009 and May 2010.	2008-2010	(Hay-Roe et al. 2016)
Ophion flavidus Brullé (Hymenoptera: Ichneumonidae)	larval	Mexico	Corn - Sorghum	February-December	2010	(Cortez-Mondaca et al. 2012)
	larval	Mexico	Corn	June-September	2005	(Jourdie et al. 2008)
	larval	Mexico	Corn	June-August	2001	(Ruíz-Nájera et al. 2007)

	larval	Florida, U.S.	Tifton-85 Bermudagrass	August-October 2008, June-October 2009 and May 2010.	2008-2010	(Hay-Roe et al. 2016)
	larval	Florida, U.S.	Corn	November-December, February-April	2010-2015	(Meagher et al. 2016)
	larval	Honduras	Corn	May-October	2002-2003	(Wyckhuys and O’Neil 2006)
Ophion spp. (Hymenoptera: Ichneumonidae)	egg	Brazil	Corn	-	2009-2010-2011	(Varella et al. 2015)
	larval	Argentina	Corn	-	1999-2003	(Murúa et al. 2009)
	larval	Paraguay	Corn	-	2014-2016	(Cabral Antúnez et al. 2018)
	larval	Argentina	Corn	-		(Murúa et al. 2006)
Palexorista quadrizonula (Thomson) (Diptera: Tachinidae)	larval	Ghana and Benin	Corn	July-November	2018	(Agboyi et al. 2020)
Palexorista zonata (Curran) (Diptera: Tachinidae)	larval	Ethiopia	Corn	March-October	2017	(Sisay et al. 2019)
	larval	Kenya	Corn	April-August	2017	(Sisay et al. 2019)
	larval	Ethiopia	Corn	June-August	2018	(Sisay et al. 2019)
	larval	Ethiopia	Corn	March-October	2017	(Sisay et al. 2018)
	larval	Kenya	Corn	July-October	2017	(Sisay et al. 2018)
Palmistichus elaeisis Delvare & Lasalle (Hymenoptera: Eulophidae)	pupal	Brazil	-	-	-	(Rolim et al. 2020)
	pupal	Brazil	-	-		(Martins et al. 2019)
Peckia (*Sarcodexia*) *lambens* (Wiedemann) (Diptera: Sarcophagidae)	larval	Brazil	Corn	March-October	2012-2014	(Toma et al. 2018)
Pristomerus pallidus (Kriechbaumer) (Hymenoptera: Ichneumonidae)	larval	Ghana and Benin	Corn	July-November	2018	(Agboyi et al. 2020)
Pristomerus sp. (Hymenoptera: Ichneumonidae)	larval	Mexico	Corn	July-September		(Rios-Velasco et al. 2011)
	larval	Mexico	Corn	June-August	2001	(Ruíz-Nájera et al. 2007)

Pristomerus spinator (Fabricius) (Hymenoptera: Ichneumonidae)	larval	Mexico	Corn		2017	(Araiza 2018)
	larval	Mexico	Corn	June-August	2012	(García-Gutiérrez et al. 2013)
	larval	Mexico	Corn	August-November	2011-2012	(Vírgen et al. 2013)
	larval	Mexico	Corn - Sorghum	February-December	2010	(Cortez-Mondaca et al. 2012)
	larval	Mexico	Corn	June-September	2005	(Jourdie et al. 2008)
	larval	Honduras	Corn	May-October	2002-2003	(Wyckhuys and O’Neil 2006)
	larval	Mexico	Corn - Sorghum - Sudan Grass	-		(Molina-Ochoa et al. 2004)
	larval	Mexico	Corn	Spring-Summer	2012-2013	(Gutiérrez-Ramírez et al. 2015)
Pristomerus vulnerator (Panzer) (Hymenoptera: Ichneumonidae)	larval	Mexico	Corn	-	2016-2017	(Hernández-García et al. 2017)
Sarcodexia sternodontis Townsend (Diptera: Sarcophagidae)	larval	Honduras	Corn	May-October	2002-2003	(Wyckhuys and O’Neil 2006)
Telenomus remus Nixon (Hymenoptera: Platygastridae)	egg	Brazil	-	-		(Pomari-Fernandes et al. 2015)
	egg	Ghana and Benin	Corn	July-November	2018	(Agboyi et al. 2020)
	egg	Venezuela	-	-	-	(Naranjo-Guevara et al. 2020)
	egg	Brazil	Corn and Soybean	-	2012-2013	(Pomari-Fernandes et al. 2018)
	egg	Brazil	-	-	-	(Queiroz et al. 2017)
	egg	Brazil	-	-	-	(Vieira et al. 2017)
	egg	Brazil	Corn	-		(Queiroz et al. 2017)
	egg	Brazil	Corn	May	2010	(Dasilva et al. 2015)
	egg	Brazil	Corn	-	2009-2010-2011	(Varella et al. 2015)

	egg	Brazil	Corn - Cotton - Soybean	-	2009-2010	(Pomari et al. 2013)
	egg	Brazil	-	-	-	(Carneiro and Fernandes 2012)
	egg	Brazil	Corn	-	-	(Pomari et al. 2012)
	egg	Brazil	-	-	-	(Carneiro et al. 2010)
	egg	Brazil	-	-	-	(Bueno, Carneiro, et al. 2010)
	egg	China	Corn	May and June	2019	(Liao et al. 2019)
	egg	Kenya	Corn	June-August	2018	(Sisay et al. 2019)
	egg	Tanzania	Corn	June-August	2018	(Sisay et al. 2019)
	egg	Benin	-	-	2017-2018	(Kenis et al. 2019)
	egg	Côte d’Ivoire	-	-	2017-2019	(Kenis et al. 2019)
	egg	Kenya	-	-	2017-2020	(Kenis et al. 2019)
	egg	Niger	-	-	2017-2021	(Kenis et al. 2019)
	egg	South Africa	-	-	2017-2022	(Kenis et al. 2019)
	egg	Brazil	Corn	-		(Michereff et al. 2019)
Trichogramma atopovirilia Oatman & Platner (Hymenoptera: Trichogrammatidae)	egg	Brazil	Corn	May	2010	(Dasilva et al. 2015)
	egg	Brazil	Corn	-	2006-2007-2008	(Dequech et al. 2013)
	egg	Brazil	Corn	January-April	2007	(Camera et al. 2010)
	egg	Mexico	Corn	June-September	2005	(Jourdie et al. 2008)
	egg	Brazil	Corn	-		(Beserra and Parra 2005)
	egg	Kenya	Corn	June-August	2018	(Sisay et al. 2019)
Trichogramma pretiosum Riley (Hymenoptera: Trichogrammatidae)	egg	Brazil	Rice	-	2018	(Lopes and Sant’Ana 2019)
	egg	Brazil	-	-		(Vargas et al. 2017)
	egg	Brazil	Corn	May	2010	(Dasilva et al. 2015)
	egg	Brazil	Corn	-	2006-2007-2008	(Dequech et al. 2013)

	egg	Brazil	-	-		(Carneiro and Fernandes 2012)
	egg	Brazil	-	-		(Bueno, Bueno, et al. 2010)
	egg	Brazil	Corn	January-April	2007	(Camera et al. 2010)
	egg	Brazil	Corn	January		(Figueiredo et al. 2015)
Trichogramma rojasi Nagaraja & Nagarkatti (Hymenoptera: Trichogrammatidae)	egg	Brazil	Corn	January-April	2007	(Camera et al. 2010)
Trichogramma spp. (Hymenoptera: Trichogrammatidae)	egg	Brazil	Corn	-	2009-2010-2011	(Varella et al. 2015)
	egg	Ghana and Benin	Corn	July-November	2018	(Agboyi et al. 2020)
Winthemia deilephilae (Osten Sacken) (Diptera: Tachinidae)	larval	Mexico	Corn	June-August	2016	(González-Maldonado et al. 2018)
Winthemia spp. (Diptera: Tachinidae)	larval	Mexico	Corn	June-September	1999	(Delfín-González et al. 2007)
	larval	Mexico	Corn	June-August	2001	(Ruíz-Nájera et al. 2007)
	larval	Paraguay	Corn	-	2014-2016	(Cabral Antúnez et al. 2018)
Winthemia trinitatis Thompson (Diptera: Tachinidae)	larval	Brazil	Corn	March-October	2012-2014	(Toma et al. 2018)

A literature review was done using the keywords “*Spodoptera frugiperda*” AND parasitoid* from the Web of Science Core Collection. Studies from 2003-2020 focusing on the recovery of parasitoids from *S. frugiperda* were selected. The review was started from 2003 because Molina-Ochoa et al. (2003) had already published a comprehensive inventory on parasitoids of fall armyworm from the Americas and Caribbean region.

CHAPTER 2

CHARACTERIZATION OF IMPRESSIONS CREATED BY TURFGRASS ARTHROPODS ON CLAY MODELS

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ABSTRACT Lepidopteran pests such as fall armyworm, *Spodoptera frugiperda* (JE Smith), and black cutworm, *Agrotis ipsilon* Hufnagel (both Noctuidae), are serious problems of turfgrass (Poaceae) in the U.S. Several predators in turfgrass systems attack lepidopteran larvae; however, their predaceous activity is rarely recorded, as they leave hardly any evidence. Predaceous activity can be studied using clay models, an approach still rarely employed in turfgrass. Thus, assays were conducted to determine the types of impressions that common turfgrass arthropods leave on clay models simulating lepidopteran larvae. Nine impression types were characterized after exposing 16 arthropod taxa in enclosed arenas in the laboratory and one taxon in the field to two sizes of clay models, including scratches, paired marks, pricks, deep distortions, disturbed surfaces, detached segments, granulated surfaces, dents, and elongated scratches. Most arthropods produced scratches and paired marks, whereas granulated surfaces and elongated scratches were produced by only a few of the selected arthropods. To ensure that the impressions were correctly identified, non-expert volunteers reviewed the impressions, and they were accurately identified in >85% of the responses. Video recordings of arthropod interactions were captured to determine the behavior of the arthropods during their first interaction with the clay models. Most arthropods first interacted with the terminal rather than the middle regions of the models. There were no differences between their interactions with the large or small models, and they used their mouthparts as often as their legs. Knowledge of the impression types caused by common arthropods will improve the utilization of the clay model technique for field studies in turfgrass. This could contribute to improved management of natural enemies as part of an integrated pest management approach.

KEYWORDS: plasticine larvae, predator–prey interactions, turfgrass system, biological control, predation, artificial caterpillar, sentinel prey, attack marks, video monitoring, visual cues

Turfgrass (Poaceae), produced on sod farms, is an integral component of several types of landscapes, including residential and public lawns, athletic fields, and golf courses. In 2002, the estimated value of the turfgrass industry in the U.S. was around $35.1 billion (Haydu et al. 2008). In Georgia, U.S., annual sod production is valued at $118.3 million; it is grown over 10,785 ha in 64 counties (Wolfe and Stubbs 2020). Turfgrass hosts diverse arthropod communities, including predators (Cockfield and Potter 1985, Joseph and Braman 2009), parasitoids (Joseph and Braman 2011), and herbivores and detritivores (Joseph and Braman 2009). Common predators include formicids, carabids, staphylinids, and Araneae (Joseph and Braman 2009, Bixby-Brosi et al. 2012, Dupuy and Ramirez 2019). Predatory arthropods have been used to manage turfgrass insect pests such as fall armyworm, *Spodoptera frugiperda* (JE Smith) (Lepidoptera: Noctuidae) (Terry et al. 1993), black cutworm, *Agrotis ipsilon* Hufnagel (Lepidoptera: Noctuidae) (López and Potter 2000, Frank and Shrewsbury 2004, Hong et al. 2011), billbugs of the genus *Sphenophorus* spp. (Coleoptera: Curculionidae) (Dupuy and Ramirez 2019), and Japanese beetle, *Popillia japonica* Newman (Coleoptera: Scarabaeidae) (Terry et al. 1993, López and Potter 2000). These reports suggest that beneficial arthropods play a critical role in pest suppression and outbreak prevention in turfgrass.

Invertebrate predators are active and quick to consume prey (Sorribas et al. 2016, Krey et al. 2017, Rewicz and Jaskuła 2018), potentially leaving no trace behind (Sam et al. 2015), which makes it challenging to document predaceous activity (Tvardikova and Novotny 2012). Various techniques and strategies have been used to study predation, such as video analysis (Merfield et al. 2004), gut-content analysis (Yang et al. 2017, Jacobsen et al. 2019), stable isotope analysis (Boecklen et al. 2011), quantitative fatty acid signature analysis (Iverson et al. 2004), and the application of sentinel prey baits (Bateman et al. 2017, Lövei and Ferrante 2017, Greenop et al.

2019). The use of clay models mimicking prey is an emerging tactic to record predation (Low et al. 2014). In such experiments, clay models with various sizes, shapes, and colors, resembling certain types of prey, are deployed in the field; when a predator interacts with the model, distinct patterns or impressions are left behind (Howe et al. 2009, Rößler et al. 2019, Witwicka et al. 2019). Recent studies reported clay models resembling various prey organisms, including arthropods (Mason et al. 2018, Zvereva et al. 2019, Aslam et al. 2020), birds (Valentine et al. 2018), amphibians (Lawrence et al. 2018), and reptiles (Taylor and Cox 2019). Clay models have been used to study predator-prey interactions in various ecosystems, including tropical forests and cultivated systems (Molleman et al. 2016, Castagneyrol et al. 2017, Mansion-Vaquié et al. 2017, Roels et al. 2018, Zvereva et al. 2019). However, this strategy has rarely been applied in turfgrass systems.

A wide variety of impressions in size, shape, and depth can be observed on the surface of clay models, which can be backtraced to organisms interacting with them (Low et al. 2014, Krenn 2019). The interaction marks and signature impressions produced by predators, such as arthropods, birds, mammals, and reptiles, improve our understanding of the key predators under certain environmental conditions, as well as their level of predaceous activity (Low et al. 2014). Because models lack chemical cues and defense responses, the observed impressions may not fully reflect predaceous activity (Libra et al. 2019, Rößler et al. 2019). Nevertheless, several studies have demonstrated the utility of clay models as a replacement for sentinel prey to estimate predaceous activity, for instance, in forests (González-Gómez et al. 2006, Ferrante et al. 2017) and maize ecosystems (Ferrante et al. 2019). Clay models are underutilized for the determination of the key active predators and their level of activity associated with important arthropod pests in turfgrass, such as *S. frugiperda* and *A. ipsilon*. Thus, the objective of the current study is to document the types of impressions created by common arthropods in turfgrass, most of which predators, on clay models simulating lepidopteran larvae. The results of this study can be used to back trace the identity of prevalent predators and their activity to refine integrated pest management tools for various turfgrass systems, such as residential and public lawns, sod farms, and golf courses.

Materials and Methods

Clay models. Clay models simulating 3rd– and 5th– instar fall armyworm larvae were constructed using nontoxic, green oven-bake modeling clay (Sculpey III, Polyform Products Co., Elk Grove Village, Illinois, USA). Because this clay product remains soft at ambient temperatures, any impressions created by interacting entities, including living organisms, are preserved (Roels et al. 2018). Green-colored clay was used because the green-colored larva models represent undefended and more palatable prey items compared to models produced from the clay of other colors (Howe et al. 2009). Two clay models of 10 × 2 mm and 30 × 4 mm (length × diameter) were produced to mimic two different stages of lepidopteran larvae (early and late larval instars). For the assay, one clay model of each size was placed inside a disposable polystyrene Petri dish of 100 × 15 mm (VWR Scientific, Inc., San Francisco, California, USA), which served as the experimental unit. The clay models were not glued to the Petri dishes to avoid additional synthetic odors that were present. The clay models and the introduced test arthropods were enclosed in dishes with a lid, and the top edges were sealed with Parafilm to prevent desiccation.

Arthropod collection. The arthropods were collected during June-October 2019 from turfgrass lawns at the University of Georgia campus in Griffin, Georgia, USA. The collected arthropods, the method employed, and the time of collection are listed in Table 2.1. Pitfall traps (Solo cup, 250 mL), vacuum (Vortis vacuum sampler, Burkhard Manufacturing Co., Ltd., Herefordshire, England), and handpicking (at night between 2200-0200 h) methods were used to collect 17 taxa of arthropods, including spiders and insects. Larger arthropods (~3 cm long) were handpicked and temporarily stored in vented plastic containers for transport to the laboratory. After collection, the arthropods were transported to the entomology laboratory and immediately released in the experimental arena. The collected arthropods represented the major groups reported in turfgrass by Joseph and Braman (2009).

Arthropod exposure experiment. In this assay, an arthropod was introduced to a Petri dish containing one clay model of each size. The experiment was arranged in a completely randomized design with uneven replications (Table. 2.2) due to the varying availability of arthropods. Each Petri dish served as an experimental unit. The experiment was conducted in an environmental control chamber (Percival Scientific Inc., Model I-36LL, Perry, Iowa, USA) at 21±1°C, under ~40% relative humidity and a 16:8 h (Light: dark) photoperiod. The arthropods were not starved before introduction into their respective assay to simulate the natural variation in predator interactions found in the field. The 48 h interval was sufficient to gather responses of arthropods to the clay models. After 48 h of exposure, the arthropods were preserved in 70% ethanol for taxonomic identification.

Interaction video. We monitored the Petri dishes containing the clay models (two sizes) and arthropods using a Wingscapes BirdCam (Wingscape, model#Pro WCB-00116, Calera, Alabama, USA) camera mounted on a 30 cm-tall wooden dowel. The cameras were placed at a focal length of 30.5 cm, and 2 h video recordings were obtained. Two video recordings were obtained at a given time. Arthropods including *Agonum* sp., *Euborellia annulipes* (Lucas), *Harpalus pensylvanicus* (DeGeer), *Labidura riparia* (Pallas), *Scarites subterraneus* Fabricius, *Tetracha carolina* (L.), *Pterostichus* sp. and *Sphenophorus* spp. were released at a rate of one arthropod per Petri dish containing the two sizes of clay models. The videos were saved and evaluated to determine which body part of the arthropod made the first contact (mouthparts or legs) with a model, the region of the clay model that was contacted (terminal or middle), and the clay model size. The videos were evaluated to the point when the first interaction occurred and not beyond this observation. The first interaction was studied in detail to show how the arthropod is likely to interact in the field setting. Moreover, the arena's restricted space presented challenges considering that the arthropod could interact multiple times with the model, leading to overestimating the interaction and difficulty in interpreting these data.

Ant assay. To record the impressions caused by formicids, clay models were placed on weatherproof paper cards (JL Darling LLC., Tacoma, Washington, USA) and randomly positioned in the field near a mound of the red imported fire ant, *Solenopsis invicta* Buren (Hymenoptera: Formicidae). The ant mound was disturbed using metal wire to increase ant activity and ultimately increase the chances of obtaining impressions. The ants were also collected for identification using disposable polystyrene 100 × 15 mm Petri dishes and were later stored in glass vials with 70% ethanol. The clay models (large and small) were observed in person for 30 min to ensure that *S. invicta* had enough time to create impressions on the clay models.

Evaluation. The clay models were maintained in the environmental control chamber at 21±1°C under ~40% relative humidity and a 16:8 h (light: dark) photoperiod until evaluation. After exposure to the arthropods, the models were carefully evaluated under a dissecting stereomicroscope (40×), and the types of patterns or impressions that were produced were quantified. The distinct impressions were given unique names and definitions based on their characteristic signatures on the clay surface.

A multiple-choice questionnaire was developed to determine the accuracy of the types of impressions recorded on the clay models. Thirty-two volunteers, including graduate students, lab technicians, post-docs, and faculty members, were recruited to identify the impression types. This non-expert audience (having no previous experience evaluating such clay models) was asked to identify the damage types. Non- experts included both entomological and non-entomological majors. The intention was to verify if varying majors and education levels could identify the impression types. Examples of why a specific impression was identified as belonging to a certain category were provided with illustrations at the beginning of the questionnaire. The volunteers were asked to read the necessary information before completing the survey questionnaire. In the questionnaire, a photo of the actual impression type was included. The multiple-choice answers included one correct answer and other possible answers. The responses were evaluated as correct (1) or wrong (0) and later converted to percentages.

Statistical analyses. The numbers of the impressions (paired marks, scratches, pricks, detached segments, and dents) generated by the different arthropods were analyzed using a general linear mixed model with a binomial error distribution and a log link function using the PROC GLIMMIX procedure in SAS (SAS Institute, 2012). The tested arthropods were the treatment and served as a fixed effect, whereas the replications served as the random effect. The estimation method was maximum likelihood with the Laplace approximation. The percentages of the different types of impressions generated by different arthropods, such as granulated surfaces, deep distortions, disturbed surfaces, and elongated scratches, were analyzed using arcsine square root transformation, followed by the general linear model GLM procedure in SAS (SAS Institute, 2012). For the analysis, different impression types were assessed according to the associated arthropod taxa. The significance of the fixed effect (treatment) was calculated using the F value, significance was evaluated (α = 0.05), and the mean values from the different treatments were compared (α = 0.05). Means were back-transformed using the PLM procedure in SAS with the ILINK option and were separated using the lsmeans paired t-test method (α = 0.05). When the same impression type was observed upon exposure to one or two arthropod species or the number of impressions was very low, the PROC GLIMMIX procedure in SAS did not converge. Those impressions were not analyzed to determine arthropod interaction effects. The body parts of the arthropods that first contacted the clay models and the regions of contact extracted from the videos were subjected to a chi-square test contingency table analysis to examine the relationship between the arthropods, which of their body parts were used for interaction, and the region of contact (SAS Institute, 2015). The responses from non-experts were converted into percentages, and graphs were generated using Microsoft Excel.

Results

Impression types. Nine types of impressions were recorded during the study. The impression types included paired marks, scratches, pricks, deep distortion, disturbed surfaces, detached segments, granulated surfaces, dents, and elongated scratches. Paired marks were defined as attack marks occurring in pairs, resulting mostly from mandibular interaction (Figure 2.1A). Scratches were uneven light surface scraping (Figure 2.1B). A prick was a fine hole-like attack mark (Figure 2.1C). Deep distortions were intensive attack marks that destroyed the standard structure of the clay model (Figure 2.1D). Disturbed surfaces were slight surface abrasions that were less severe compared to deep distortions (Figure 2.1E). Detached segments were recorded when a clay model was broken into two or more segments (Figure 2.1F). A granulated surface was identified as small granular structures on the surface of the clay model (Figure 2.1G). A dent was a surface mark due to the exertion of pressure of a body part (Figure 2.1H). Elongated scratches were deep, elongated scrape marks (Figure 2.1I).

A significantly higher number of paired marks were found on the clay models when *S. invicta* (omnivore), *T. carolina* (predator), and *E. annulipes* (omnivore) interacted with the clay models than when the experiments involved *H. pensylvanicus* (omnivore), *Amara* sp. (omnivore), *Anisodactylus* sp. (omnivore), *Calosoma sayi* Dejean (predator), *Agonum* sp. (predator), *Neocurtilla hexadactyla* (Perty) (herbivore) and Lycosidae (predator) (Table 2); however, the number of paired marks created by *S. invicta*, *T. carolina*, and *E. annulipes* were not significantly different from each other. A granulated surface was only observed when *E. annulipes* (omnivore) and *L. riparia* (predator) interacted with the clay models. The number of scratches was significantly higher when *N. hexadactyla* (herbivore), *Sphenophorus* spp. (herbivore), and the carabids *S. subterraneus* (predator), *C. sayi*, and *T. carolina* were exposed to the clay models than when *S. invicta*, *Amara* sp. (omnivore), *Agonum* sp. (predator), *L. riparia*, *Pseudopachybrachius vinctus* (Say) (granivore), and Lycosidae were tested (Table 2). However, there were no significant differences in the number of scratch impressions on the clay models when *N. hexadactyla* (herbivore), *Sphenophorus* sp. (herbivore), and carabids, *S. subterraneus.*, *C. sayi*, and *T. carolina*, were tested. The number of deep distortion impressions was significantly greater on clay models exposed to *Sphenophorus* sp., *S. subterraneus*, and *T. carolina* than those exposed to *H. pensylvanicus* (Table 2). Detached segments were observed in the experiments with *S. subterraneus*, *C. sayi*, and *T. carolina*, but there was no significant difference among them. The number of pricks on the clay models was significantly higher when *N. hexadactyla* was tested than when *Anisodactylus* sp., *L. riparia*, and Lycosidae were tested. Dents were only created when the clay models were exposed to *H. pensylvanicus* and Elateridae (herbivore), and there was no significant difference between their numbers. Similarly, disturbed surface impressions on the clay models were generated by *Sphenophorus* sp, *Anisodactylus* sp., and *E. annulipes*, and there was no significant difference among them. Elongated scratch impressions were only created by *N. hexadactyla*.

Overall, 85.4% of the responses from volunteers were accurate and consistent with our classification (Figure 2.2). The highest accuracy was found for the scratch impressions (100%), followed by granulated surfaces (93.8%), paired marks (90.6%), deep distortions (84.4%), dents (84.4), pricks (81.3%), disturbed surfaces (81.3%), elongated scratches (78.1%), and detached segments (75%).

Interaction video. Using the video recordings, the first interaction between the arthropods and their body parts, the area of the clay model contacted, and the size of the clay model contacted were determined (Figure 2.3). Overall, there was no significant difference in whether it was the mouthparts or the legs of the arthropods that contacted the models first (X^2 = 0.4; df = 4; p = 0.180; N = 29). There were significant differences (X^2 = 0.3; df = 4; p = 0.03; N = 29) between the different arthropods in the region of the clay model (terminal versus middle) contacted first. The arthropods *E. annulipes* and *Agonum* sp. first contacted the terminal ends of the clay models (Figure 2.4B), whereas the other arthropods contacted the terminal ends as well as the middle region of the clay model. Overall, the arthropods evenly chose both the small and large models, and there was no significant difference in the size selected (X^2 = 0.2; df = 4; p = 0.20; N= 29). The arthropods *S. subterraneus* and *Agonum* sp. only chose the large-sized clay models (Figure 2.4C), whereas the other arthropods chose both small and large-sized clay models.

Discussion

We sought to understand the impressions created by common turfgrass arthropods in central Georgia to allow key predators and their levels of activity to be assessed in various turfgrass systems, such as sod production farms, golf courses, and residential and public lawns. The results showed nine unique impressions or patterns on the clay models when exposed to various arthropods. The impression types observed in the current study were paired marks, scratches, pricks, deep distortions, disturbed surfaces, detached segments, granulated surfaces, dents, and elongated scratches. Some types of impressions found on the clay models, such as paired marks, scratches, or distorted surfaces, were more common than others, such as pricks, granulated surfaces, or elongated scratches. The results also showed that certain arthropods (*E.* annulipes, *L. riparia*, and *N. hexadactyla*) left unique impressions (Table 2). Under field conditions, several different types of predators, including arthropods, birds, small-to-medium-sized mammals, and reptiles, have been shown to interact with clay models, producing damage ranging from subtle surface damage to substantial destruction of the clay model (Low et al. 2014). The current laboratory study attempted to characterize specific arthropod-related damage to clay models, and this work may improve the utility of clay models in turfgrass field studies.

Arthropods create diverse types of impressions that could be related to variations in the size and shape of their mouthparts, the body parts contacting the models, such as their mouthparts or legs, and their feeding behavior. Scratches were the most common type of impression identified on the clay models in the current study (Table 2). Low et al. (2014) observed scratches on clay models under field conditions but were unsure about the specific organisms producing the marks. Scratches were observed on the clay models used in the current study when exposed to most of the tested arthropods except elaterids, geocorids, and

Coproporus sp. This suggests that scratches may be created on the clay models by arthropods during probing activity without actual feeding attempts. The second most common type of impression was paired marks, which were observed when the clay models were exposed to carabids, formicids, anisolabids, and labidurids in the restricted arena. This result is consistent with previous studies in which paired marks were associated with chewing marks produced by predaceous arthropods (Howe et al. 2009, Greenop et al. 2019, Vieira et al. 2019). Impressions such as pricks and dents were associated with some predators; however, it is unclear whether these marks can be reliably used to identify specific arthropod groups in field conditions. Some of the impression types were found for only one specific arthropod taxon exposed to the clay models. For example, a granulated clay model surface was only observed when anisolabidids and labidurids (earwigs) were caged in the arena. Similarly, elongated scratches were only found when gryllotalpids (mole cricket) were allowed to interact with the clay model. It is highly likely that elongated scratches are created when the fossorial legs are in contact with the model. Detached segments of the clay models were observed in some arenas when the 3 cm-long carabid *C. sayi* was placed in the arena. These data suggest that some arthropods leave behind impressions or patterns (Table 2) on clay models, which can be utilized as a tool for studying arthropod groups and their activities in turfgrass fields.

The current study also presents several limitations. First, although most arthropods leave behind impressions on clay models that can be easily detected, a few arthropods such as *Geocoris* sp. and *Coproporus* sp. never interacted with the clay model, or their impressions were so subtle that they were challenging to decipher. In the current study, when the clay models were exposed to geocorids and staphylinids, the impressions on the models were hardly detectable (Table 2). When the two common predators *Pterostichus madidus* (Fabricius) (Coleoptera:

Carabidae), foraging on the soil surface, and *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae), foraging on foliage, were compared, the soil-foraging beetle was found to interact with the clay model, leaving behind impressions, whereas the foliage-foraging beetle did not leave any detectable impressions (Greenop et al. 2019). Second, some of the impressions attributed to arthropods may be caused by other organisms, such as mammals, birds, and reptiles. The detachment of segments of the clay models by large-sized carabids, as observed in the current study, may be misinterpreted as damage caused by a bird, mammal, or reptile (Low et al. 2014). Third, arthropods were not starved before exposure to preserve the natural predaceous behavior, and hence, arthropods were tested in the arena almost immediately upon collection. There was no record of when they had their previous meal and knowledge on their feeding habits such as satiation point, and the optimal interval between meals was poorly understood. Perhaps, a standardized starvation protocol before the experiment could have enhanced the arthropod interaction with the clay model, and thus, the quality of impressions could have been improved. We suppose that a standardized starvation protocol would also reduce variation between different individuals of the same species tested. Finally, all the arthropod interaction assays were conducted in enclosed arenas in the current study. The purpose of choosing the enclosed arena was to ensure the incidence of arthropod-clay model interaction and thus, characterize the impressions caused by specific turfgrass arthropods, including predaceous and non-predaceous arthropods. In the field conditions, non-predaceous arthropods would rarely encounter prey and cause an impression.

Because the impressions were characterized and labeled by workers who were very familiar with the arthropods, we were unsure how non-experts would interpret the same impressions. To address this question, a survey in which the impression that was identified by us was offered for identification by the non-expert group. More than 80% of the time, the non-experts agreed with our characterization of the impression types. The non-experts were presented with representative photographs of impressions and corresponding descriptions. In a previous study in which respondents were asked to choose between coarse and fine damage on clay models, the accuracy of identification was lower for fine damage than for course damage (Low et al. 2014). In the current study, non-experts were not initially involved in identifying and classifying the impression types. Most of the respondents accurately identified most of the impression types (Figure 2.2).

The video recordings of arthropods in arenas with clay models showed that the arthropods first interacted with the models most often with their mouthparts (Figures 2.3 and 2.4A), but impressions were also created by other body parts when in contact. These video recordings also revealed that the legs of some arthropods were the first body part to contact the model first rather than the mouthparts. Because the experimental arena was restricted space, the arthropods could repeatedly crawl over the clay models, creating various types of impressions. Thus, we only noted the first contact of the arthropods with the clay models when it occurred in these arenas from 2 h video recordings. Some arthropods only approached the terminal sections of the clay model, whereas others approached both terminal ends and middle section of the clay model. These observations suggest that arthropods might exhibit distinct probing or feeding behavior. The size of the clay models also influenced when the arthropod first interacted with the models, as the arthropods interacted with the large-sized clay models first more often than with the small-sized clay models. Field video recording studies have been previously conducted to complement clay model experiments for understanding the predatory interaction with clay models in other studies. In one previous study, the camera recording revealed the predation activity of mammalian and avian predators on clay models of snakes (Akcali et al. 2019). Another study involved the use of camera recordings to obtain accurate measures of the size of the clay model preferred by an avian predator (Sinkovics et al. 2018). Because all of these video recordings were captured under lighted conditions, it is plausible that arthropod interactions were mostly driven by visual cues. More studies are warranted to determine the predator behavior mediated by host volatiles in dark conditions.

In summary, the results revealed nine impression types made on clay models when arthropods that are common in turfgrass were caged with clay models. Among these impressions, scratches and paired marks were the most common types of impressions recorded on the clay models when most of the arthropods were exposed to the clay models in arenas. Unique impressions such as granulated surfaces and elongated scratches were observed on the clay models in association with certain arthropods. Additionally, non-expert volunteers accurately validated most of the characterized impression types. The data showed that arthropods exhibited distinctive probing or feeding behavior when they first approached the large-sized clay models, mostly involving their mouthparts and terminal regions. These clay models were constructed to simulate the size and shape of fall armyworm larvae because fall armyworm is a major insect pest of turfgrass. The observed impression types will serve as a baseline for applied field studies in turfgrass so that the clay model technique can be effectively utilized to understand ecological functions involving predators and prey organisms. The arthropods belonging to various functional groups were included in the assay because they occur in the turfgrass system; however, herbivore organisms would rarely interact with the prey organism. The arthropods collected for assay were collected from turfgrass fields so that their behavior and interaction specifically reflect the turfgrass system and can be utilized for future studies. If active groups of predators in the turfgrass systems such as golf courses, residential lawns, or sod farms are known, or arthropods are collected using collection devices such as pitfall traps, this clay model technique can be utilized to document the key players as well as the severity of attacks. Because of the potential overlap of impression types caused by both predaceous and non-predaceous arthropods and their body parts observed in enclosed assays, follow-up field studies are warranted to understand the degree of overestimation of impressions and refine the utility of clay model technique for accurate assessment of predatory activity in the field. In addition, failure of adoption of a standardized starvation protocol before the assay could have compromised the quality of impressions recorded in the current study. This suggests that impression types reported in the current study should be further evaluated under varied hunger levels in future research and cautiously utilized when interpreting field data.

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Table. 2.1. Details of various taxa collected from turfgrass in the laboratory interaction assay.

Scientific or common name	Family	Order	Functional Group	Method of collection	Time of collection
Calosoma sayi Dejean	Carabidae	Coleoptera	Predator	Handpicking	Night
Tetracha carolina (L.)	Carabidae	Coleoptera	Predator	Handpicking	Night
Scarites subterraneus F.	Carabidae	Coleoptera	Predator	Handpicking	Night
Harpalus pensylvanicus (DeGeer)	Carabidae	Coleoptera	Omnivore	Handpicking	Night
Anisodactylus sp.	Carabidae	Coleoptera	Omnivore	Handpicking	Night
Amara sp.	Carabidae	Coleoptera	Omnivore	Handpicking	Night
Agonum sp.	Carabidae	Coleoptera	Predator	Handpicking	Night
Coproporus sp.	Staphylinidae	Coleoptera	Predator	Vacuum	Day
Click beetle	Elateridae	Coleoptera	Herbivore	Handpicking	Night
Sphenophorus sp.	Curculionidae	Coleoptera	Herbivore	Handpicking	Night
Neocurtilla hexadactyla (Perty)	Gryllotalpidae	Orthoptera	Herbivore	Handpicking	Night
Labidura riparia (Pallas)	Labiduridae	Dermaptera	Predator	Handpicking	Night
Euborellia annulipes (Lucas)	Anisolabididae	Dermaptera	Omnivore	Handpicking	Night
Solenopsis invicta Buren*	Formicidae	Hymenoptera	Omnivore	-	-
Geocoris sp.	Geocoridae	Hemiptera	Predator	Vacuum	Day
Pseudopachybrachius vinctus (Say)	Rhyparochromidae	Hemiptera	Granivore	Vacuum	Day
Wolf spider	Lycosidae	Araneae	Predator	Pitfall trap	Day/Night

*Not collected from the field.

Table 2.2. Mean numbers (±SE) of impression types observed when various arthropods were exposed to clay models for 48 h in a laboratory assay.

Arthropod type	No. replications	No. paired marks[a]	Granulated surface[b] (%)	No. scratches[a]	Deep distortion[b] (%)	No. detached segments[a]	No. pricks[a]	No. dents[a]	Disturbed surface[b] (%)	Elongated scratches[b, λ] (%)
S. invicta (Formicidae)	10	14.30 ± 1.71a	0.00 ± 0.00	0.90 ± 0.46cd	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Sphenophorus spp. (Curculionidae)	12	0.00 ± 0.00	0.00 ± 0.00	18.16 ± 4.06a	3.33 ± 1.88a	0.00 ± 0.00	9.92 ± 2.48ab	0.00 ± 0.00	1.67 ± 1.12a	0.00 ± 0.00
Geocoris sp. (Geocoridae)	10	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
H. pensylvanicus (Carabidae)	13	3.54 ± 0.66cd	0.00 ± 0.00	7.46 ± 2.92ab	0.07 ±0.07b	0.00 ± 0.00	0.00 ± 0.00	0.08 ± 0.8a	4.61 ± 2.68a	0.00 ± 0.00
Amara sp. (Carabidae)	9	4.88 ± 1.14bcd	0.00 ± 0.00	0.22 ± 0.14d	2.22 ± 1.46ab	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
S. subterraneus (Carabidae)	6	7.66 ± 2.86abc	0.00 ± 0.00	28.66 ± 10.69a	15.33 ± 9.47a	0.17 ± 0.17a	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Anisodactylus sp. (Carabidae)	4	1.50 ± 0.86de	0.00 ± 0.00	13.25 ± 2.56ab	0.00 ± 0.00	0.00 ± 0.00	1.00 ± 1.00bc	0.00 ± 0.00	2.50 ± 2.50a	0.00 ± 0.00
C. sayi (Carabidae)	4	4.50 ± 2.53bcd	0.00 ± 0.00	33.25 ± 10.96a	0.00 ± 0.00	0.25 ± 0.25a	10.00 ± 10.00ab	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Agonum sp. (Carabidae)	12	0.25 ± 0.18f	0.00 ± 0.00	0.50 ± 0.41cd	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
T. carolina (L.) (Carabidae)	10	12.50 ± 1.97a	0.00 ± 0.00	14.60 ± 4.88a	5.00 ± 5.00a	0.3 ± 0.15a	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00

Elateridae	8	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.50 ± 0.37a	0.00 ± 0.00	0.00 ± 0.00
E. annulipes (Anisolabididae)	13	12.31 ± 2.35a	38.46 ± 11.59a	11.15 ± 8.18ab	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	3.84 ± 2.41a	0.00 ± 0.00
L. riparia (Labiduridae)	8	10.50 ± 3.56ab	6.25 ± 6.25a	2.00 ± 0.96bc	0.00 ± 0.00	0.00 ± 0.00	0.75 ± 0.49c	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
P. vinctus (Rhyparochromidae)	5	0.00 ± 0.00	0.00 ± 0.00	0.60 ± 0.40cd	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
N. hexadactyla (Gryllotalpidae)	5	0.40 ± 0.40ef	0.00 ± 0.00	25.20 ± 9.71a	0.00 ± 0.00	0.00 ± 0.00	29.60 ± 10.58a	0.00 ± 0.00	0.00 ± 0.00	22.00 ± 22.00
Lycosidae	10	0.20 ± 0.13f	0.00 ± 0.00	0.70 ± 0.39cd	0.00 ± 0.00	0.00 ± 0.00	2.6 ± 1.79bc	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Coproporus sp. (Staphylinidae)	10	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
F		10.0	2.8	7.0	2.0	0.1	3.6	1.9	0.6	–
df		11, 80	1, 7	13, 95	4, 33	2, 8	5, 26	1, 7	3, 26	–
P		< 0.001	0.140	< 0.001	0.118	0.879	0.012	0.206	0.623	–

[a] Analyses of variance (PROC GLIMMIX procedure in SAS) were performed on paired marks, scratches, pricks, detached segments, and dents. Means in a column for the impression types followed by different letters are significantly different (pairwise t-test; $P < 0.05$).

[b] Analyses of variance (PROC GLM procedure in SAS) were performed on proportional data for granulated surfaces, deep distortions, disturbed surfaces, and elongated scratches after arcsine square root transformation. Means in a column for these impression types followed by different letters are significantly different (Tukey HSD test; $P < 0.05$). [λ] statistical analysis was not performed. Means in a column without letters were not included in the analysis.

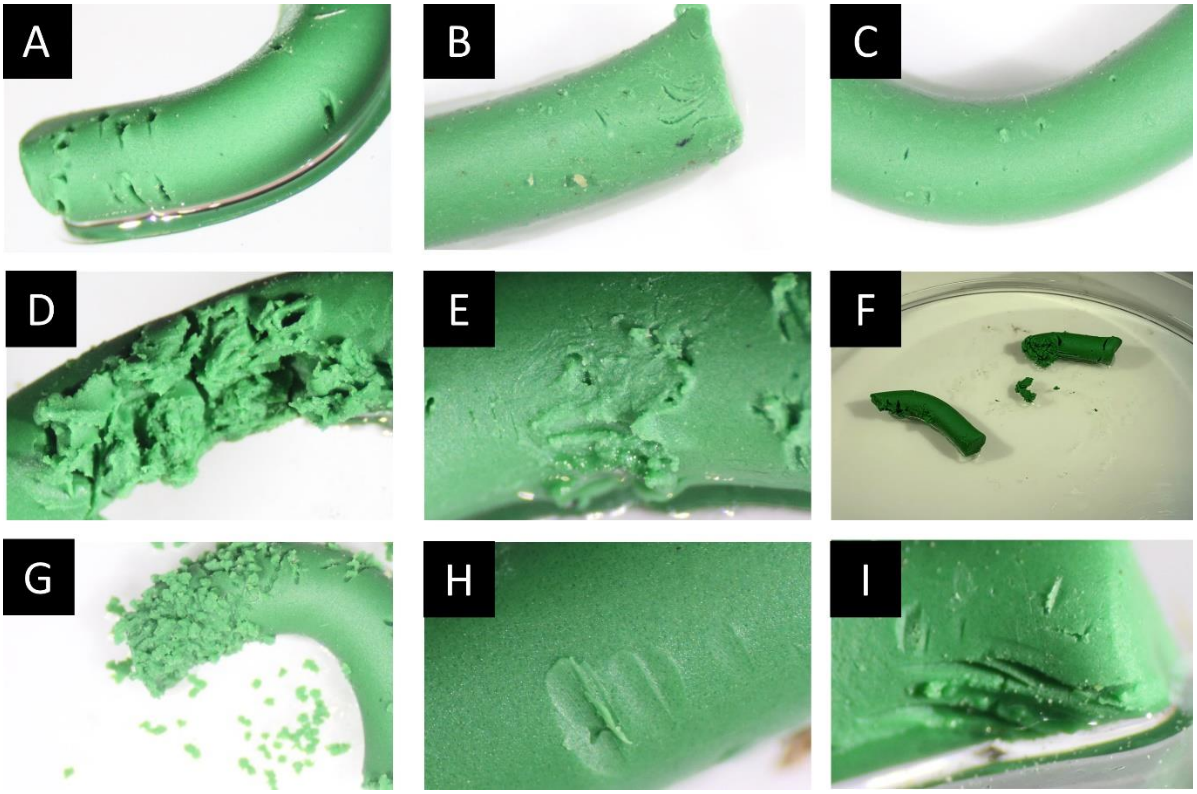

Figure 2.1. Impressions created by arthropods on clay models (A) paired marks, (B) scratches, (C) pricks, (D) deep distortion, (E) disturbed surface, (F) detached segments, (G) granulated surface, (H) dents, and (I) elongated scratches.

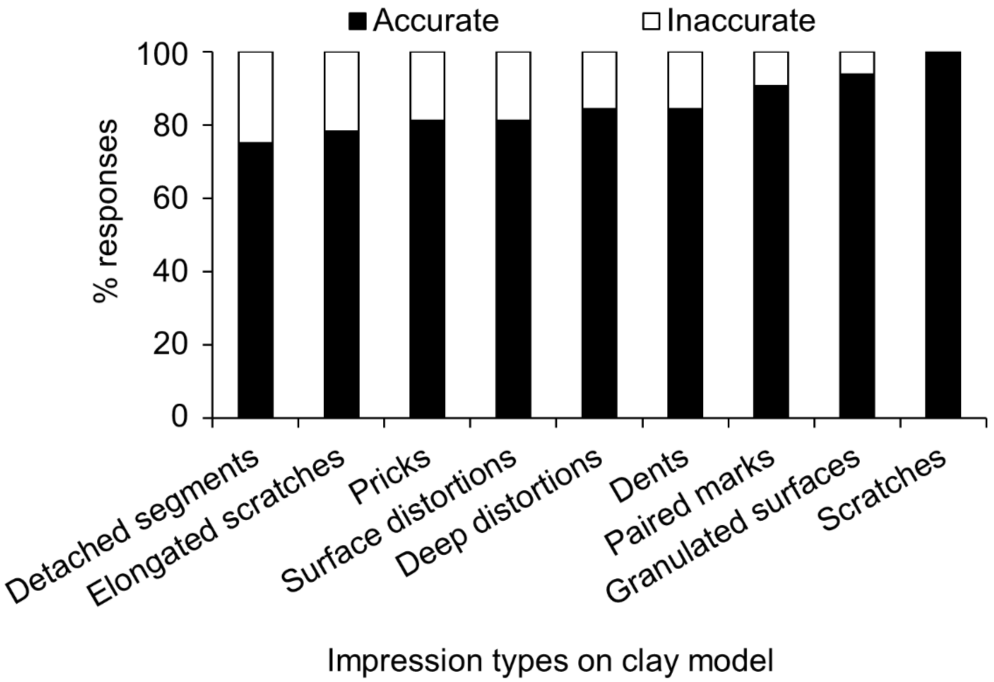

Figure 2.2. Volunteer responses to the questionnaire indicating the accurate identification of impression type after observing a photo of a specific impression type.

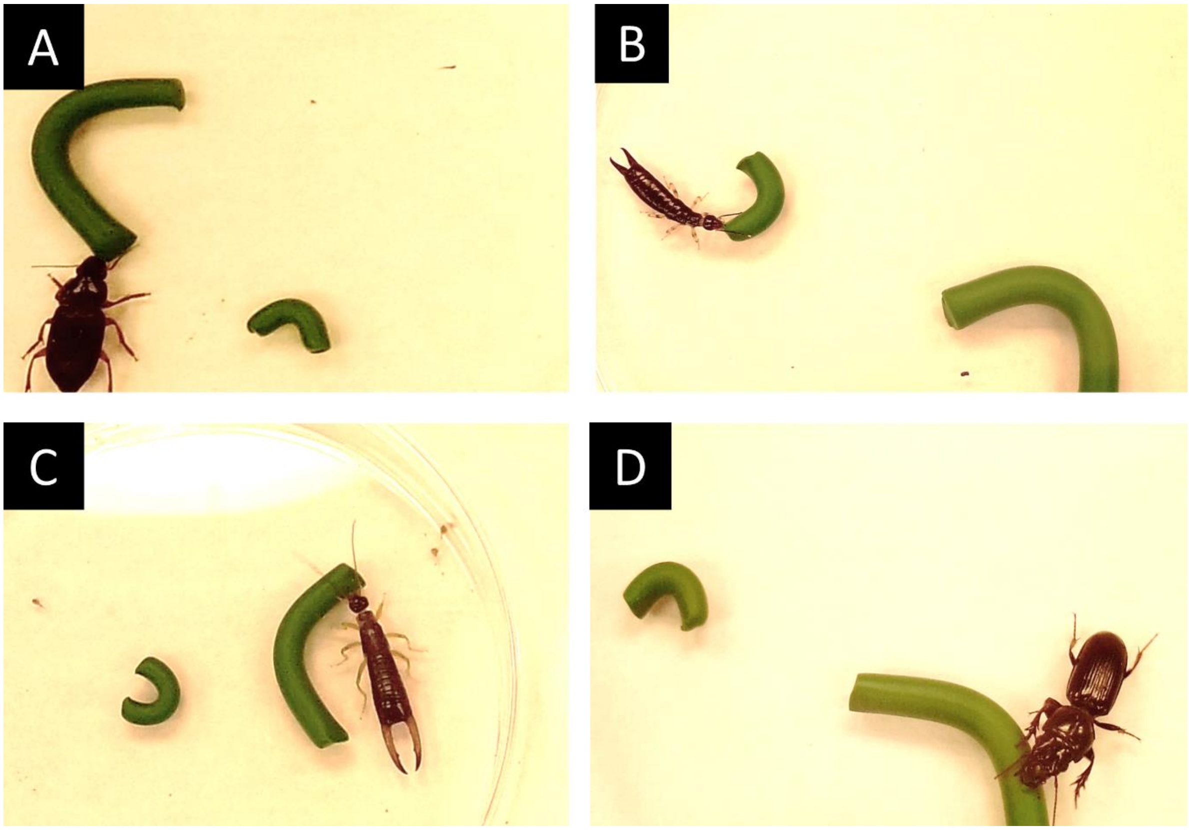

Figure 2.3. Interactions of arthropods captured on video, including (A) mouthpart interaction of *H. pensylvanicus* with the terminal region of a large clay model, (B) mouthpart interaction of *E. annulipes* with the terminal region of a small clay model, (C) mouthpart interaction of *L. riparia* with the terminal region of a large clay model, and (D) mouthpart interaction of *S. subterraneus* with the terminal region of a small clay model.

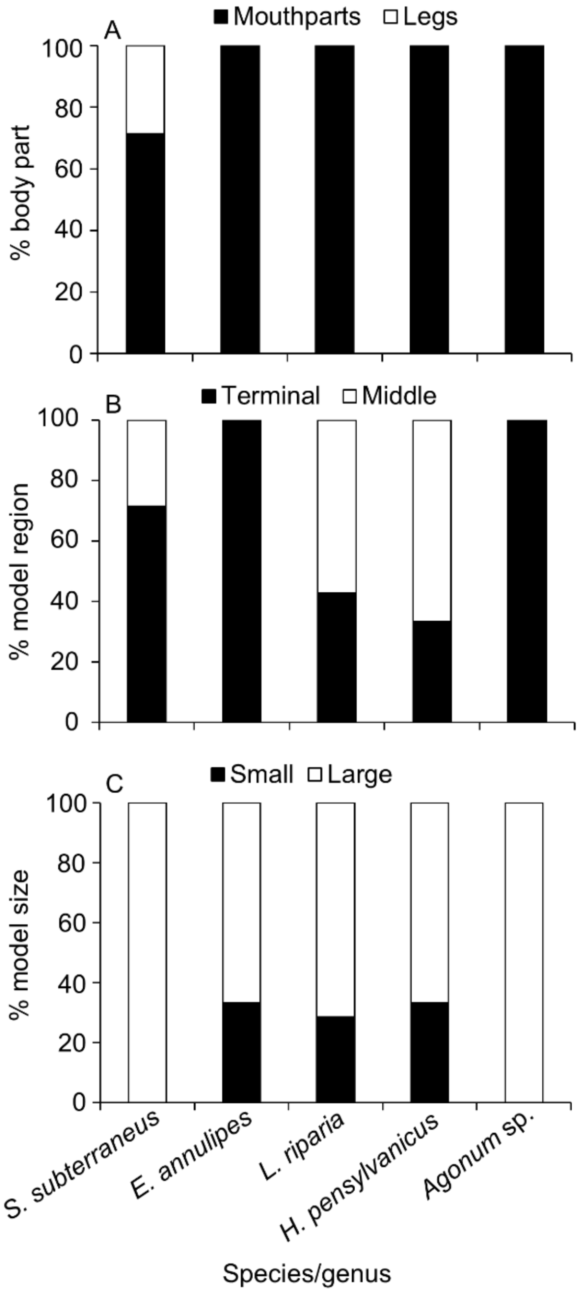

Figure 2.4. Relationship between (A) the insect and the body part that first contacted the model, (B) the insect and the region of the clay model contacted, and (C) the insect and the size of the clay model contacted.

CHAPTER 3

INFLUENCE OF THE COLOR, SHAPE, AND SIZE OF THE CLAY MODEL ON ARTHROPOD INTERACTIONS IN TURFGRASS

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ABSTRACT Many predatory arthropods occur naturally in turfgrass, and they provide adequate control of lepidopteran pests, such as fall armyworm, *Spodoptera frugiperda* (JE Smith), and black cutworm, *Agrotis ipsilon* (Hufnagel) (Lepidoptera: Noctuidae). Recording predation is challenging under field conditions because predators rarely leave any evidence. Clay models were successfully employed for studying predation, and this technique is underutilized in turfgrass. Little is known about whether the characteristics of clay models, such as color, shape, and size, influence arthropod interactions in turfgrass. To improve the utility of clay models in turfgrass, the influence of the color, shape, and size of clay models on arthropod interactions was studied by exposing clay models during daytime and nighttime in a turfgrass field. The results showed that arthropods interacted with clay models, and various types of impressions were recorded, including paired marks, scratches, cuts, and pricks. Although the color of the clay model had no significant effects on arthropod interactions during the night, significantly greater numbers of impressions were noticed on the blue and green models than on the yellow models during the daytime. The caterpillar-shaped models captured significantly greater densities of impressions than the beetle-shaped models. Additionally, the number of impressions significantly increased with an increase in the size of the model regardless of shape.

KEYWORDS: biological control, predator-prey interactions, impressions

Turfgrass is a perennial grass regularly managed at low height as a uniform green ground cover (Robbins and Birkenholtz 2003, Held and Potter 2012), which adds aesthetic, recreational, and environmental benefits to the landscape (Stier et al. 2015). Turfgrass is the largest cultivated crop in the U.S., covering approximately 20.2 million ha (Milesi et al. 2009) and contributing $58 billion annually to the U.S. economy (Haydu et al. 2008). Turfgrass supports a diverse group of arthropod fauna, such as herbivores (Potter and Braman 1991, Eickhoff et al. 2006, Nair et al. 2021), pollinators (Del-Toro and Ribbons 2020, Joseph et al. 2020), predators (Braman et al. 2002, 2003, Joseph and Braman 2016), parasitoids (Braman et al. 2004, Joseph and Braman 2011), and detritivores (Joseph and Braman 2009a). Predatory arthropods, such as anthocorids, Araneae, carabids, formicids, geocorids, mirids, lasiochilids, and staphylinids are abundant and common on turfgrass (Joseph and Braman 2009a, Singh 2020). These predators can control key turfgrass pests, such as fall armyworm, *Spodoptera frugiperda* (JE Smith) (Lepidoptera: Noctuidae) (Joseph and Braman 2009b), black cutworm, *Agrotis ipsilon* (Hufnagel) (Lepidoptera: Noctuidae) (López and Potter 2000), Japanese beetle, *Popillia japonica* Newman (Coleoptera: Scarabaeidae), billbugs, *Sphenophorus* spp. (Coleoptera: Curculionidae) (Dupuy and Ramirez 2019), and southern chinch bug, *Blissus insularis* Barber (Hemiptera: Blissidae) (Nachappa et al. 2006). Thus, to obtain sustained benefits from natural pest control in turfgrass systems, these predators should be conserved.

Predator-prey interactions can be studied through various techniques, such as direct observations (Pfannenstiel and Yeargan 2002, Cabrera et al. 2019), video recordings (Zou et al. 2017, Manubay and Powell 2020), caged experiments (Li et al. 2017), live sentinel prey baits (Tillman et al. 2020), quantitative fatty acids (Iverson et al. 2004), stable isotopes (Boecklen et al. 2011, Kamenova et al. 2018), DNA in gut content (Eitzinger et al. 2019, Oliveira-Hofman et al. 2020) and impressions on clay models (Bateman et al. 2017, Rößler et al. 2019, Khan and Joseph 2021). Among these techniques, the use of a clay model resembling insect prey is a cost-effective and emerging tool that could be utilized to estimate predation in various ecosystems (Howe et al. 2009, Lövei and Ferrante 2017, Rößler et al. 2018), including forest (Sam et al. 2015, Molleman et al. 2016, Gunnarsson et al. 2018, Hariraveendra et al. 2020), agricultural (Mansion-Vaquié et al. 2017, Denan et al. 2020), and urban ecosystems (Long and Frank 2020, Nason et al. 2021, Pena et al. 2021). To record predaceous activity, clay models simulating prey organisms are prepared and exposed to predators in the ecosystem. After the exposure, the clay models are recovered, and impressions created on the clay models are evaluated to estimate possible predatory interactions. Distinct impressions found on the clay model provide insights into understanding predator species and their activity and behavior (Low et al. 2014, Khan and Joseph 2021).

Invertebrate and vertebrate predators interact with clay models and create distinct impressions (Bateman et al. 2017, Lövei and Ferrante 2017, Khan and Joseph 2021). Arthropod predators are active in the ground, especially on the temperate forest floor (Ferrante et al. 2017). They use chemical, tactile, visual, and gustatory cues to search and locate prey (Yasuda 1997, Halpin and Rowe 2016, Duong et al. 2017, Xue et al. 2018, Yamazaki et al. 2020). Along with the color and color patterns, the ambient light availability, shape, and size of the insect also play a role in determining the visual perception of the predator (Troscianko et al. 2009). Previous studies showed that body size (Remmel and Tammaru 2009, Moura et al. 2018, Sahayaraj and Fernandez 2021), coloration (Théry and Gomez 2010, Zvereva et al. 2019, Aslam et al. 2020), and shape (Paluh et al. 2015) could influence the behavior of arthropod predators and how they interact with clay models. Additionally, predation rates can vary and could be subject to the difference in the appearance of prey or the reflectance of light from the model (Rojas et al. 2014, Cheng et al. 2018). However, the effects of the characteristics of the clay model, such as color, size, and shape, on arthropod predator interactions are not documented in turfgrass field settings. Moreover, the activity of arthropod predators and prey insects can vary during the daytime and nighttime hours. Thus, the objectives of the current study were to determine the effects of 1) color, 2) size, 3) shape of the clay model, and 4) time of exposure on predatory interactions in the turfgrass system.

Materials and Methods

Study site and clay model. In 2020, experiments were conducted on 'Tifway' bermudagrass (*Cynodon* spp.) plot (2896.4 m^2) located at the University of Georgia, Griffin Campus, Griffin, GA (33.2622, -84.2829). The plot is part of a 71,890.5 m^2 open turfgrass research field with no trees within 50 m from all directions. The bermudagrass was mowed weekly at 8 cm height and irrigated daily for 30 min. However, regular fertilizer and pesticide applications were not administered. Although the bermudagrass field was partially infested with weeds, treatments were deployed where bermudagrass was continuously present. All the experiments were conducted on the same turfgrass plot.

The clay models were prepared using nontoxic clay (Sculpey III®, Polyform Products, Elk Grove Village, IL). This clay product was selected because it stays soft under field summer temperatures (Roels et al. 2018).

Color and time of exposure. Clay models were prepared using yellow- (Sculpey III® yellow), blue- (Sculpey III® blue), green- (Sculpey III® string bean), black- (Sculpey III® black), red- (Sculpey III® red), white- (Sculpey III® white), and brown- (Sculpey III® hazelnut) colored clay (Fig. 1). The treatments included light and dark shades of colors. For each color, 10 × 2 mm (small) and 30 × 4 mm (large) (length × diameter) models were prepared to simulate early (third) and late (fifth) instars of *S. frugiperda* larvae, respectively. The treatments were seven colored clay models and time of exposure, daytime and nighttime hours. The colored models were deployed from 6:30 AM to 8:30 PM for daytime and from 8:30 PM to 6:30 AM for the nighttime. The clay models, a small and a large model, were glued on a 7.5 × 2 cm (length × width) weatherproof paper card (JL Darling, Tacoma, WA) using nontoxic glue (Newell Rubbermaid Inc. Westerville, OH), and it served as the experimental unit. The colored clay model treatments were arranged in a randomized complete block design (RCBD) with six or ten replications, whereas the time of exposure treatment was replicated three times. The colored clay model treatments were deployed at 3-m spacing within a block and between blocks. The colored clay model treatments were deployed 6 m from the edge of the turfgrass field. The individually colored treatment was placed on the surface of the thatch after clearing the turfgrass canopy (Fig. 2). The experiment was repeated where colored clay model treatments were replicated six times in the first trial and replicated ten times in the second trial. Trial 1 was conducted from 19 to 21 May, and trial 2 was conducted from 29 to 31 July 2020, representing the early and mid-summer months in Georgia.

Shape and size. For clay model preparation, the same procedure as described previously was adopted, but only green-colored clay was used. Previous studies showed that predators interacted with green-colored clay models (Low et al. 2014, Sam et al. 2015, Roels et al. 2018, Long and Frank 2020, Khan and Joseph 2021). For the experiment, elongated cylindrical and rectangular-octagonal-shaped models were prepared. The elongated cylindrical shape represented *S. frugiperda* larvae, whereas large, medium, and small shapes represented various stages of larvae. The three rectangular-octagonal shapes represented adults of predaceous carabids, *Calosoma* *sayi* Dejean, *Tetracha carolina* (L.), and *Agonum* spp., respectively (Fig. 4). The three sizes for *S. frugiperda* larvae were 30 mm × 5 mm, 17 mm × 3.5 mm, and 10 mm × 2.5 mm (length × diameter), whereas the predatory beetles were 26 mm × 12 mm × 8 mm (*C. sayi*), 14 mm × 8 mm × 6 mm (*T. carolina*), and 7 mm × 4 mm × 3.5 mm (*Agonum* spp.) (length × width × height). The models were individually glued on a 7.5 cm × 2 cm (length × width) weatherproof paper card using nontoxic glue.

Clay model treatments were deployed at 3-m spacing within a block and between blocks. To reduce the edge effect, the first block was 6 m away from the edge of the turfgrass field. The treatments were placed on the soil surface after mowing the turfgrass canopy and were exposed for 24 h, from one morning (10:00 AM to 12:00 PM) to the following day (Fig. 2). The treatments in the experiment were clay model shape and size, and they were arranged in RCBD with ten replications. The experiment was conducted twice, from 01 to 03 July and from 04 to 06 August 2020. The assays were replicated ten times for each trial.

Evaluation. Clay models were recovered from the field, transported to the laboratory, and stored at room temperature (21 °C) until evaluation. The clay models were evaluated, referring to the impression types characterized by Khan and Joseph (2020) using a dissecting stereomicroscope (40 ×). The impression types were categorized as paired marks, scratches, detached segments, pricks, dents, and U-shaped marks. Some impressions, such as deep distortions, merged surfaces, and scooped marks, were quantified as a percentage of the affected clay model surface area. Additionally, the clay models were evaluated for damage scales from 0-10. The damage scale could be interpreted as 0 (0%), 1 (1-10%), 2 (11-20%), 3 (21-30%), 4 (31-40%), 5 (41-50%), 6 (51-60%), 7 (61-70%), 8 (71-80%), 9 (81-90%), and 10 (91-100% of the clay model surface covered with the impressions).

Statistical analyses. All the data analyses were performed in SAS (SAS Institute 2012). For the color experiment, the numbers of impressions on the clay model treatments were subjected to analysis of variance (ANOVA) using the PROC GLIMMIX procedure in SAS. The procedure used a generalized linear mixed model with a negative binomial distribution and log link function. The colored clay model, time of exposure, and their interaction were the treatments. The treatments served as a fixed effect, whereas replications (six or ten) served as a random effect. The estimation method was maximum likelihood with the Laplace approximation. To understand the effects of clay model color, the impressions were further subjected to one-way ANOVA by time exposure using the PROC GLIMMIX procedure in SAS. The clay model color and replication were included in the generalized linear model. Because data were analyzed using a generalized linear model, the data were neither assessed for normality nor transformed. Pearson's correlation analysis was performed between impression types and total impressions using the PROC CORR procedure in SAS. If correlations existed between impression types and total impression, multicollinearity was removed by adding a PARTIAL statement to the PROC CORR procedure.

For the shape experiments, the number of impressions on the clay models was subjected to ANOVA by a generalized linear mixed model with a negative binomial distribution and log link function using the PROC GLIMMIX procedure in SAS. The treatments, shape, and size of the clay model were the fixed effects, and replications served as a random effect. The estimation method was maximum likelihood with the Laplace approximation. To understand the effects of size, the impressions were further subjected to one-way ANOVA by shape using the PROC GLIMMIX procedure in SAS. The clay model size and replication were included in the generalized linear model. Pearson's correlation analysis between impression types and total impressions at a 95% significance level was performed using the PROC CORR procedure in SAS. If a correlation existed between impression types and total impressions, the multicollinearity was removed by adding a PARTIAL statement to the PROC CORR procedure in SAS. The means and standard errors of the variables were calculated using the PROC MEANS procedure in SAS.

Results

Impression types. Ten impression types were observed during four trials in the field, and they were paired marks, scratches, cuts, detached segments, deep distortion, pricks, dents, merged surface impressions, scooped marks, and U-shaped impressions (Fig. 3). Of these impressions, paired marks, scratches, and cuts were most frequent. The less frequent impression types were summed up under the “other impressions” category.

Color and time of exposure. In trial 1 (May 2020), the clay model color and time of exposure had a significant effect on the total number of impressions, but the color × time of exposure interaction was not significantly different (Table 3.1). For the paired marks, the effects of model color and model color × time of exposure interaction were significantly different but not significantly different for the time of exposure. There was no significant effect of model color × time of exposure for cut, scratch, and other impressions (Table 3.1). When one-way ANOVA was performed by the time of exposure, none of the colors showed significant differences between each other for numbers of impression types and total impressions (Table 3.2).

In trial 2 (July 2020), the time of exposure and model color were significantly different for the number of total impressions, but the model color × time of exposure interaction was not significantly affected (Table 3.1). The paired marks were only significantly different for the time of exposure. The model color significantly affected the number of scratches and other impressions (detached segments, deep distortion, pricks, dents, merged surface feeding impressions, scooped marks, and U-shaped marks). The interaction between color × time of exposure was not significant for all impression types (Table 3.1). To understand the effects of model colors, one ANOVA was performed by the time of exposure. The number of scratches and total impressions was significantly greater on the blue model than on the yellow model during the daytime (Table 3.3). There were no significant differences between the black, brown, green, red, and white models for scratches and the total number of impressions. For paired marks, cuts, and other impressions, model colors were not significantly different during the daytime. During the night, a significantly greater number of scratches were found on the red models than on the white and yellow models (Table 3.3). Other impression types showed significant differences between model colors, but the mean number of impressions failed to separate using the Tukey-Kramer test. Paired marks, cuts, and total impressions were not significantly affected by the model colors during the night (Table 3.3).

When the effects of model color were evaluated for impressions during the daytime and night, a significantly greater number of total impressions was observed at night than during the daytime (F = 12.7; df = 1, 244; P < 0.001; Fig. 3.5A) during trial 1. In trial 2 (July 2020), the total number of impressions did not significantly differ (F = 2.6; df = 1, 409; P = 0.105; Fig. 3.5B). A similar trend was observed at the damage scale (0-10), which differed significantly between daytime and night during May (F = 102.8; df = 1, 244; P < 0.001; Fig. 3.5C) and July 2020 (F = 7.1; df = 1, 409; P = 0.008; Fig. 3.5D), with night having a significantly higher damage scale than daytime.

During the daytime in trial 1 (May 2020), paired marks were significantly correlated with scratches for the brown, green, and red models (Table 3.4). In the red model, cut impressions were significantly associated with scratches. The cut impression was significantly correlated with total impressions for black, brown, yellow, and white models. On blue, green, and red, a significant correlation was found between paired marks and total impression. The other impressions were significantly associated with total impressions on white models (Table 3.4). In July 2020, during the daytime, scratches were significantly correlated with total impressions in all the color models. The cut and paired mark impressions were significantly associated with the total number of impressions on the red and white models. Other impressions were significantly correlated with the total number of impressions on yellow models (Table 3.4).

During the night in trial 2, the paired marks were significantly correlated with the total number of impressions in all the color treatments (Table 3.5). Additionally, paired marks were significantly associated with the other impressions in black models. In July 2020, a significant association between scratches and other impressions was observed in the brown, green, and yellow models. Cut impression and paired marks were significantly correlated with the red model, whereas the cut impression was significantly correlated with scratches on the yellow model. Paired marks were significantly correlated with the total number of impressions in the brown and white models. The scratches were significantly associated with the total number of impressions in all the color treatments.

Shape and size. In trial 1 (July 2020), the effect of shape and the size of the clay model was significant on the total number of impressions observed on clay models; however, their interaction was not significant (Table 3.6). The shape was significantly different on the number of paired marks, but there were no significant differences in size and shape and size interaction. The shape and size were significantly different in the number of scratches. A significant effect was found on shape and size interaction on prick impressions on clay models. When the effect of size was analyzed by shape, significantly greater numbers of scratches and total impressions were found on large models than on medium models, followed by small models (Table 3.7). The prick impressions were significantly greater on large-sized models than on medium- and small-sized models. For the beetle-shaped models, the large and medium-sized models captured significantly greater impressions than the small models. The size of the beetle shape was not significantly different for any distinct impression type (Table 3.7).

In trial 2 (August 2020), the size was significantly different on the total number of impressions, whereas shape and shape, and size interaction was not significantly different (Table 3.6). Paired marks were not significantly different for shape, size, or their interaction. The effect of size and shape was significantly different for the number of scratches on clay models. There were no significant effects of prick impression on shape, size, or their interaction. For other impressions, shape, size, and shape and size interactions were significantly different (Table 3.6). When the analysis was performed by shape to understand the effect of size, for larvae shape, there were no differences between sizes for any distinct impression type and the total number of impressions (Table 8). For beetle shape, the total number of impressions was significantly greater on the large models than on the small models. The impression types were not significantly different between sizes.

When the effects of shape were evaluated for total impressions, a significantly greater numbers of total impressions were observed on the larva-shaped models than on the beetle-shaped models (F = 21.9; df = 1, 177; P < 0.001; Fig. 6A) in trial 1 (July 2020). In trial 2 (August 2020), the total numbers of impressions did not significantly differ (F = 1.5; df = 1, 177; P = 0.216; Fig. 3.6B) between the larva-shaped and the beetle-shaped models. The damage scale values were significantly greater for larva-shaped models than for beetle-shaped models in July

2020 (*F* = 30.2; df = 1, 177; *P* < 0.001; Fig. 3.6C). In trial 2 (August 2020), the damage scale values did not significantly differ between the larva-shaped and the beetle-shaped models (*F* = 3.8; df = 1, 177; *P* = 0.053; Fig. 3.6D).

In the Pearson's correlation analysis for trial 1 (July 2020), paired marks were significantly correlated with prick impression, and scratches were significantly correlated with prick impression for beetle shape (Table 3.9). For larvae and beetle shapes, paired marks, scratches, and prick impressions were significantly correlated with the total number of impressions. In trial 2 (August 2020), paired marks were significantly different from prick impressions for larval shape. There were significant correlations between paired marks, scratches, and prick impressions, and the total number of impressions on both the caterpillar and beetle-shaped models (Table 3.9).

Discussion

The results showed that the clay model is an effective tool in capturing a range of arthropod-mediated impressions in turfgrass. The blue and green models had greater densities of impressions than the yellow or white models during daytime. During the nighttime, however, all colored models captured similar numbers of impressions, although a greater number of impressions were recorded during the night than during the day, implying that either densities of predators or their activity were greater during the night than during the day, and predaceous behavior was not influenced by prey color. Previously, studies showed that successful host searching and acceptance involved chemical cues from prey (Yasuda 1997, Xue et al. 2018), herbivore-induced plant volatiles (Drukker et al. 2000, Schuman and Baldwin 2016), or a combination of tactile, visual, olfactory (smell) and gustatory (taste) cues (Halpin and Rowe 2016, Duong et al. 2017, Manubay and Powell 2020, Yamazaki et al. 2020). Data also suggest that diurnal predators, especially birds, use visual cues to spot suitable prey (Zvereva et al. 2019, Yamazaki et al. 2020). Green models were used the most in past research due to their resemblance to foliage-feeding larvae and lack of warning coloration (Low et al. 2014, Sam et al. 2015, Roels et al. 2018, Long and Frank 2020, Khan and Joseph 2021).

The larval-shaped models captured more impressions than the beetle-shaped clay models, and the density of impressions increased with the increase in the size of the model. Troscianko et al. (2009) suggested that the shape of the prey subject is one of the important factors that can influence predatory interactions. Although it is unclear why predators preferred one shape over the other, it is possible that arthropod predators evolved on preying on larval stages of insects, and they are selected for traits that can recognize less mobile immature stages of arthropods. Additionally, the number of impressions increased with an increase in the size of the model in the current study. A previous study showed that the size of the body of the prey influenced the preference of ground beetle, *Pterostichus melanarius* (Illiger) (Coleoptera: Carabidae) (McKemey et al. 2001). Similarly, the size of the mandibles of different species of tiger beetles in the genus *Cicindela* was correlated with the average size of prey (Pearson and Mury 1979). Smaller prey subjects are preferred by carabids, *Nebria brevicollis* (Fabricius) and *Pterostichus madidus* (Fabricius) when compared to larger slugs (Mair and Port 2001). A previous study also showed that predator size and morphology could influence how they interact with prey. The macrocephalic morph of the ground beetle *Damaster blaptoides* Kollar, with a large head and strong jaws, prefers to crush the prey, the snail species in the genera *Acusta*, *Aegista*, *Bradybaena*, *Cochlicopa*, *Discus*, *Euhadra*, *Succinea*, *Satsuma*, *Stereophaedusa*, and *Zaptychopsis*; whereas, the stenocephalic morph of the same predator species with a narrow head and weak jaws prefers to consume the soft body by inserting the head into the snail shell aperture

(Konuma and Chiba 2007), suggesting that predator interactions could vary by species, and more research is warranted to understand species-specific effects on clay models. Clearly, the current study indicated that the increased size of the prey model would benefit the capture of more predatory interactions if the goal is to monitor predatory activity.

Predators leave behind unique impressions on the clay model, and some of those impressions can be used to identify the specific type of predators active in the system (Low et al. 2014, Khan and Joseph 2021). Most of the impressions found in the current study were characterized by Khan and Joseph (2020) by exposing common turfgrass arthropods to clay models in laboratory assays. Paired marks, scratches, cuts and pricks, and other impressions were the impression types observed in the current study (Fig. 3). Some of the common arthropods reported from the central Georgia turfgrass fields are *Calosoma sayi* DeJean, *Tetracha carolina* (L.), *Scarites subterraneus* Fabricius, *Harpalus pensylvanicus* De Geer, *Anisodactylus* sp., *Amara* sp., *Agonum* sp. (All Coleoptera: Carabidae), Elateridae (Coleoptera), *Sphenophorus* spp. (Coleoptera: Curculionidae), *Neocurtilla hexadactyla* (Perty) (Orthoptera: Gryllotalpidae), *Labidura riparia* (Pallas) (Dermaptera: Labiduridae), *Euborellia annulipes* (Lucas) (Dermaptera: Anisolabididae), *Solenopsis invicta* Buren (Hymenoptera: Formicidae), *Pseudopachybrachius vinctus* (Say) (Hemiptera: Rhyparochromidae) and Lycosidae (Araneae) and these arthropods interacted with clay models (Khan and Joseph 2021). Besides arthropods, the avian community can cause impressions on the clay models (Low et al. 2014). Specifically, cut impressions can be caused by birds (Low et al. 2014) as well as carabids (Khan and Joseph 2021). In the current study, the clay models were placed within the grass canopy, which reduced light reflected from the surface of the model. This suggests that the incidence of avian predation is minimal in the current study. However, the hunting birds, such as European starling, *Sturnus vulgaris* L.

(Passeriformes: Sturnidae), often search for prey while walking on the turfgrass (Vittum 2020) and they may locate the clay model and potentially interact with them.

More impressions were found during nighttime than during the daytime, suggesting that most of the predators present in turfgrass could be active at night. Our result is consistent with a previous study conducted in a temperate forest, where a greater level of predation was observed during the night than during the daytime (Ferrante et al. 2017). In contrast, in another study, higher predatory activity was observed on the clay models during the daytime than during the nighttime in a rainforest habitat (Seifert et al. 2016). Cheng et al. (2018) showed that lower levels of predation on dark-shaded lepidopteran models than on those models placed in open habitats, suggesting that the timing of model deployment can vary by ecosystem-specific characteristics and activity behavior of prevalent prey and predator species (Ferrante et al. 2017, Hernández-Agüero et al. 2020). Noctuid pests, such as *S. frugiperda* larvae, have a nocturnal habit, and it is possible that predators in turfgrass systems have also evolved with the nocturnal habits of prey. When surveys were conducted at night on creeping bentgrass (*Agrostis stolonifera* L.), active populations of carabids and ants were documented attacking nocturnal turfgrass pest, *A. ipsilon* (Hong et al. 2011). In addition to light, other abiotic factors, such as variations in temperature, relative humidity, and precipitation, can influence predator-prey interactions (Laws 2017). The effects of abiotic factors on predator activity and interactions in clay models warrant more research to enhance the utility of clay models in turfgrass environments.

The incidence of types of impressions was not similar across various colored models. The scratch impressions were relatively lower on light-colored shades such as white- and yellow-colored models than on dark-shaded models, perhaps an issue of reduced detectability because of poor light contrast under the lighted stereomicroscope. These results are consistent with a recent study conducted in Mediterranean woodlands, where lower levels of predatory interactions were observed with lighter-shaded clay models (yellow models) than with the darker-shaded (brown and black colored models) (Hernández-Agüero et al. 2020). Similarly, Ferrante et al. (2017) also showed greater interaction events from predators on red clay models than green clay models. Scratch impressions were associated with paired marks, and in some instances, paired marks were associated with prick impressions (Fig. 3f; Tables 4, 5, and 9). These results indicate that some of the predators make multiple impressions when they interact with models. It is also possible that impressions on clay models are generated from non-predatory origins. For example, scratch impressions can be caused by accidental crawling of adult billbugs (*Sphenophorus* spp.) on the models (Khan and Joseph 2021) or through unintentional contact with grass blades. Impressions can be generated through anthropogenic origins, such as while handling and transporting clay models. Thus, the implications of certain impressions, such as scratches, should be carefully interpreted, as knowledge of the arthropod community prevalent in a given system is essential and will complement the utility of the clay model.

To summarize, the results showed that impressions created on the clay model were not influenced by the color of the model during the night, whereas more impressions were found on the blue and green models than on the white or yellow models during the day. When the shape of the models represented lepidopteran larvae and carabid adults, more impressions were found in lepidopteran larvae-shaped models than in adult beetle-shaped models. More impressions were found on the models as the size of the models increased, regardless of shape. These results lay out characteristics of clay models to maximize the detection of predator activity in a turfgrass system. The use of the clay model tool can be enhanced to understand the relative activity of predators, which emphasizes the need for the conservation of predators for pest management and improves integrated pest management approaches in turfgrass.

Acknowledegments

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Table 3.1. Summary of analysis of variance results for the model used to find the effect of the color, exposure time, and their interaction on different impression types and their total number in May and July 2020.

Impression	Exposure time			Color			Exposure time × Color		
	F	df	*P*	*F*	df	*P*	*F*	df	*P*
May 2020									
Cut	0.0	1, 232	0.993	0.0	6, 232	1.000	0.0	6, 232	1.000
Paired	0.0	1, 232	0.950	2.1	6, 232	0.049	2.5	6, 232	0.022
Scratch	0.0	1, 232	0.992	1.5	6, 232	0.165	0.9	6, 232	0.473
Other	3.4	1, 232	0.065	0.9	6, 232	0.600	0.5	6, 232	0.832
Total	24.0	1, 232	<0.001	2.2	6, 232	0.047	2.1	6, 232	0.060
July 2020									
Cut	0.0	1, 397	0.986	0.4	6, 397	0.875	0.2	6, 397	0.990
Paired	21.7	1, 397	<0.001	1.3	6, 397	0.246	1.2	6, 397	0.323
Scratch	0.0	1, 397	0.999	6.1	6, 397	<0.001	1.4	6, 397	0.204
Other	0.6	1, 397	0.441	2.8	6, 397	0.010	1.1	6, 397	0.374
Total	5.0	1, 397	0.025	6.0	6, 397	<0.001	2.0	6, 397	0.069

Table 3.2. Analysis of variance and mean (± SE) number of impressions on various colors of clay models evaluated in May 2020.

Exposure time		Impression type				
Daytime	Color	Paired mark	Scratch	Cut	Others*	Total
	Black	0.00 ± 0.00	0.11 ± 0.11	2.94 ± 1.81	0.33 ± 0.24	3.28 ± 1.91
	Blue	0.35 ± 0.35	0.18 ± 0.18	0.00 ± 0.00	0.41 ± 0.26	0.53 ± 0.38
	Brown	0.06 ± 0.06	0.33 ± 0.23	0.89 ± 0.68	0.33 ± 0.20	1.33 ± 0.76
	Green	1.28 ± 0.76	2.28 ± 1.43	0.11 ± 0.11	0.44 ± 0.22	3.83 ± 1.30
	Red	0.72 ± 0.43	2.28 ± 1.43	3.61 ± 2.45	0.72 ± 0.36	7.28 ± 4.12
	White	0.22 ± 0.13	1.06 ± 0.95	1.17 ± 1.05	0.33 ± 0.28	2.72 ± 2.33
	Yellow	0.17 ± 0.12	0.22 ± 0.22	1.33 ± 0.98	0.39 ± 0.16	1.83 ± 1.13
	F	1.3	1.9	1.6	0.2	1.2
	df	6, 113	6, 113	6, 113	6, 113	6, 113
	P	0.269	0.080	0.140	0.982	0.320
Nighttime						
	Black	6.44 ± 1.65	0.11 ± 0.08	0.00 ± 0.00	0.28 ± 0.19	6.72 ± 1.66
	Blue	7.22 ± 1.85	0.39 ± 0.27	0.00 ± 0.00	0.06 ± 0.06	7.67 ± 1.84
	Brown	5.56 ± 1.44	0.00 ± 0.00	0.00 ± 0.00	0.28 ± 0.06	5.56 ± 1.44
	Green	5.00 ± 1.05	0.44 ± 0.20	0.00 ± 0.00	0.11 ± 0.08	5.50 ± 1.03
	Red	7.89 ± 1.84	0.11 ± 0.11	0.00 ± 0.00	0.56 ± 0.26	8.00 ± 1.81
	White	5.89 ± 0.80	0.00 ± 0.00	0.00 ± 0.00	0.11 ± 0.08	5.94 ± 0.80
	Yellow	6.56 ± 1.21	0.06 ± 0.06	0.00 ± 0.00	0.39 ± 0.20	6.67 ± 1.19
	F	0.4	0.8	-	1.1	0.4
	df	6, 114	6, 114	-	6, 114	6, 114
	P	0.897	0.588	-	0.394	0.886

Means within a column followed by letter were not provided as they were not significantly different (Tukey-Kramer test at $P < 0.05$).
*Includes detached segments, deep distortion, pricks, dents, merged surface impressions, scooped marks, and U-shaped impressions.

Table 3.3. Analysis of variance and mean (± SE) number of impressions on various colors of clay models evaluated in July 2020.

Exposure		Impression type				
Daytime	Color	Paired mark	Scratch	Cut	Others*	Total
	Black	0.23 ± 0.11	4.70 ± 0.77ab	0.13 ± 0.06	0.60 ± 0.29	5.43 ± 0.82ab
	Blue	0.07 ± 0.05	5.73 ± 1.21a	0.13 ± 0.08	0.70 ± 0.25	6.53 ± 1.25a
	Brown	0.13 ± 0.08	2.30 ± 0.57bc	0.17 ± 0.10	0.10 ± 0.07	2.70 ± 0.63bc
	Green	0.37 ± 0.14	5.57 ± 0.92ab	0.20 ± 0.12	0.37 ± 0.13	6.43 ± 0.89a
	Red	0.10 ± 0.10	4.60 ± 0.71ab	0.30 ± 0.17	0.37 ± 0.13	5.37 ± 0.81ab
	White	0.60 ± 0.37	2.93 ± 0.61abc	0.10 ± 0.07	0.53 ± 0.18	4.03 ± 0.88abc
	Yellow	0.13 ± 0.10	1.53 ± 0.35c	0.00 ± 0.00	0.20 ± 0.07	1.83 ± 0.38c
	F	1.3	4.9	0.3	1.7	5.5
	df	6, 194	6, 194	6, 194	6, 194	6, 194
	P	0.279	< 0.001	0.948	0.129	< 0.001
Nighttime	Black	0.83 ± 0.27	4.27 ± 0.71ab	0.73 ± 0.36	0.23 ± 0.11	5.97 ± 0.81
	Blue	0.57 ± 0.22	3.97 ± 0.73ab	0.33 ± 0.24	0.60 ± 0.17	5.40 ± 0.79
	Brown	0.53 ± 0.18	3.70 ± 0.89ab	0.60 ± 0.43	0.17 ± 0.07	5.00 ± 1.00
	Green	0.80 ± 0.29	3.79 ± 0.84ab	0.87 ± 0.44	0.70 ± 0.25	5.83 ± 1.04
	Red	0.50 ± 0.20	6.07 ± 0.90a	0.53 ± 0.27	0.97 ± 0.33	8.07 ± 0.99
	White	0.60 ± 0.23	2.33 ± 0.46b	0.30 ± 0.15	0.60 ± 0.33	3.83 ± 0.72
	Yellow	1.20 ± 0.54	2.17 ± 0.58b	0.33 ± 0.30	0.23 ± 0.12	3.93 ± 1.00
	F	0.6	2.7	0.6	2.3	2.1
	df	6, 194	6, 194	6, 194	6, 194	6, 194
	P	0.725	0.017	0.764	0.038	0.055

Means within a column followed by different letters were significantly different (Tukey-Kramer test at $P < 0.05$). Where no differences were observed, no letters are included.

*Includes detached segments, deep distortion, pricks, dents, merged surface impressions, scooped marks, and U-shaped impressions.

Table 3.4. Pearson's correlation between impression types by the color of the clay model during the daytime

Color		May 2020					July 2020				
		Cut	Paired	Scratch	Others	Total	Cut	Paired	Scratch	Others	Total
Black	Cut					0.99^{***}					
	Paired										
	Scratch										0.96^{***}
	Others										
	Total										
Blue	Cut										
	Paired					0.89^{***}					
	Scratch										0.98^{***}
	Others										
	Total										
Brown	Cut					0.92^{***}					
	Paired			0.71^{**}							
	Scratch										0.98^{***}
	Others										
	Total										
Green	Cut										
	Paired			0.56^{*}		0.86^{***}					
	Scratch					0.87^{***}					0.97^{***}
	Others										
	Total										
Red	Cut			0.87^{***}		0.96^{***}					0.38^{*}
	Paired			0.59^{**}		0.59^{**}					0.50^{*}
	Scratch				0.60^{*}	0.96^{***}					0.96^{***}
	Others										
	Total										
White	Cut					0.99^{***}					0.57^{**}
	Paired										0.74^{***}
	Scratch										0.88^{***}
	Others					0.99^{***}					

	Total		
Yellow	Cut	0.97***	
	Paired		
	Scratch		0.95***
	Others		0.37*
	Total		

The notations indicate the correlation (*P*: *, <0.05; **, <0.01; and ***, <0.001) between different impression types.

Table 3.5. Pearson's correlation between impression types by the color of clay model during nighttime

Color		May 2020					July 2020				
		Cut	Paired	Scratch	Others	Total	Cut	Paired	Scratch	Others	Total
Black	Cut										
	Paired					0.99^{***}					
	Scratch				0.56^{*}						0.84^{***}
	Others										
	Total										
Blue	Cut										
	Paired					0.99^{***}					
	Scratch										0.91^{***}
	Others										
	Total										
Brown	Cut										
	Paired					1.00^{***}					0.41^{*}
	Scratch									0.42^{*}	0.90^{***}
	Others										
	Total										
Green	Cut										
	Paired					0.98^{***}					
	Scratch									0.57^{**}	0.85^{***}
	Others										0.62^{**}
	Total										
Red	Cut							0.41^{*}			
	Paired					1.00^{***}					
	Scratch										0.85^{***}
	Others										
	Total										
White	Cut										
	Paired					1.00^{***}				0.40^{*}	0.45^{*}
	Scratch										0.78^{***}
	Others										0.70^{***}

	Total				
Yellow	Cut		0.50^{**}		0.68^{***}
	Paired	1.00^{***}			
	Scratch			0.37^{*}	0.76^{***}
	Others				
	Total				

The notations indicate the correlation (*P*: *, <0.05; **, <0.01; and ***, <0.001) between different impression types.

Table 3.6. Summary of analysis of variance results for the model used to find the effect of the shape, size and their interaction on different impression types in July and August 2020.

Impression	Shape			Size			Shape × Size		
	F	df	*P*	*F*	df	*P*	*F*	df	*P*
July 2020									
Paired	13.9	1, 173	<0.001	2.7	2, 173	0.069	0.1	2, 173	0.913
Scratch	16.2	1, 173	<0.001	10.6	2, 173	<0.001	1.7	2, 173	0.178
Prick	0.0	1, 173	0.872	2.9	2, 173	0.058	3.8	2, 173	0.024
Other	0.0	1, 173	0.997	0.0	2, 173	0.992	1.0	2, 173	0.367
Total	22.1	1, 173	<0.001	12.8	2, 173	<0.001	1.3	2, 173	0.270
August 2020									
Paired	0.0	1, 173	0.960	2.9	2, 173	0.056	0.0	2, 173	0.959
Scratch	3.9	1, 173	0.049	6.0	2, 173	0.003	0.1	2, 173	0.892
Prick	0.1	1, 173	0.799	1.3	2, 173	0.288	0.9	2, 173	0.391
Other	193.8	1, 173	<0.001	128.2	2, 173	<0.001	486.0	1, 173	<0.001
Total	2.3	1, 173	0.130	7.2	2, 173	0.001	0.3	2, 173	0.769

Table 3.7. Analysis of variance and mean (± SE) number of impressions on various shapes of clay models evaluated in July 2020.

Shape		Impression type				
	Size	Paired mark	Scratch	Prick	Others*	Total
Larvae	Large	1.60 ± 0.35	3.47 ± 0.50a	0.83 ± 0.19a	0.07 ± 0.05	5.97 ± 0.70a
	Medium	1.13 ± 0.36	1.67 ± 0.41b	0.20 ± 0.09b	0.17 ± 0.10	3.17 ± 0.55b
	Small	0.77 ± 0.22	0.60 ± 0.18c	0.20 ± 0.11b	0.10 ± 0.06	1.67 ± 0.43c
	F	2.1	13.5	6.7	0.5	13.7
	df	2, 78	2, 78	2, 78	2, 78	2, 78
	P	0.134	<0.001	0.002	0.609	<0.001
Beetle	Large	0.57 ± 0.19	0.83 ± 0.26	0.30 ± 0.13	0.20 ± 0.11	1.90 ± 0.42a
	Medium	0.47 ± 0.31	0.80 ± 0.18	0.57 ± 0.21	0.07 ± 0.07	1.90 ± 0.52a
	Small	0.23 ± 0.14	0.37 ± 0.14	0.17 ± 0.07	0.00 ± 0.00	0.76 ± 0.29b
	F	1.3	1.9	2.0	0.5	4.0
	df	2, 78	2, 78	2, 78	2, 78	2, 78
	P	0.284	0.161	0.138	0.597	0.023

Means within a column followed by different letters were significantly different (Tukey-Kramer test at $P < 0.05$). Where no differences were observed, no letters were included.

* Includes dents, merged surface impressions, elongated scratches, scooped marks.

Table 3.8. Mean ± SE number of impressions on various shapes of clay models evaluated in August 2020.

Shape		Impression type				
	Size	Paired	Scratch	Prick	Others*	Total
Larvae	Large	1.23 ± 0.45	2.10 ± 0.69	0.30 ± 0.17	0.37 ± 0.17	4.00 ± 0.89
	Medium	0.53 ± 0.13	1.63 ± 0.32	0.23 ± 0.09	0.13 ± 0.09	2.53 ± 0.46
	Small	0.87 ± 0.26	0.77 ± 0.27	0.36 ± 0.21	0.10 ± 0.06	2.10 ± 0.50
	F	1.6	3.0	0.2	1.5	2.7
	df	2, 78	2, 78	2, 78	2, 78	2, 78
	P	0.215	0.056	0.822	0.240	0.072
Beetle	Large	1.33 ± 0.71	1.47 ± 0.33a	0.63 ± 0.19	0.20 ± 0.10	3.63 ± 0.80a
	Medium	0.53 ± 0.18	0.87 ± 0.28ab	0.20 ± 0.09	0.13 ± 0.10	1.73 ± 0.38ab
	Small	0.77 ± 0.20	0.47 ± 0.22b	0.27 ± 0.10	0.00 ± 0.00	1.50 ± 0.34b
	F	0.6	2.9	2.8	0.1	4.4
	df	2, 78	2, 78	2, 78	2, 78	2, 78
	P	0.547	0.058	0.068	0.868	0.015

Means within a column followed by different letters were significantly different (Tukey-Kramer test at $P < 0.05$). Where no differences were observed, no letters were included.

* Includes dents, merged surface impressions, elongated scratches, scooped marks.

Table 3.9. Pearson's correlation between impression types by the shape of clay model

Shape		July 2020					August 2020				
		Paired	Scratch	Prick	Others	Total	Paired	Scratch	Prick	Others	Total
Larvae											
	Paired					0.66^{***}					0.67^{***}
	Scratch					0.84^{***}					0.81^{***}
	Prick					0.40^{***}	0.22^{*}				0.38^{***}
	Others										
	Total										
Beetle											
	Paired					0.78^{***}					0.81^{***}
	Scratch			0.24^{**}		0.69^{***}					0.56^{***}
	Prick	0.42^{***}				0.70^{***}					0.32^{**}
	Others										
	Total										

The notations indicate the correlation (*P*: *, <0.05; **, <0.01; and ***, <0.001) between different impression types.

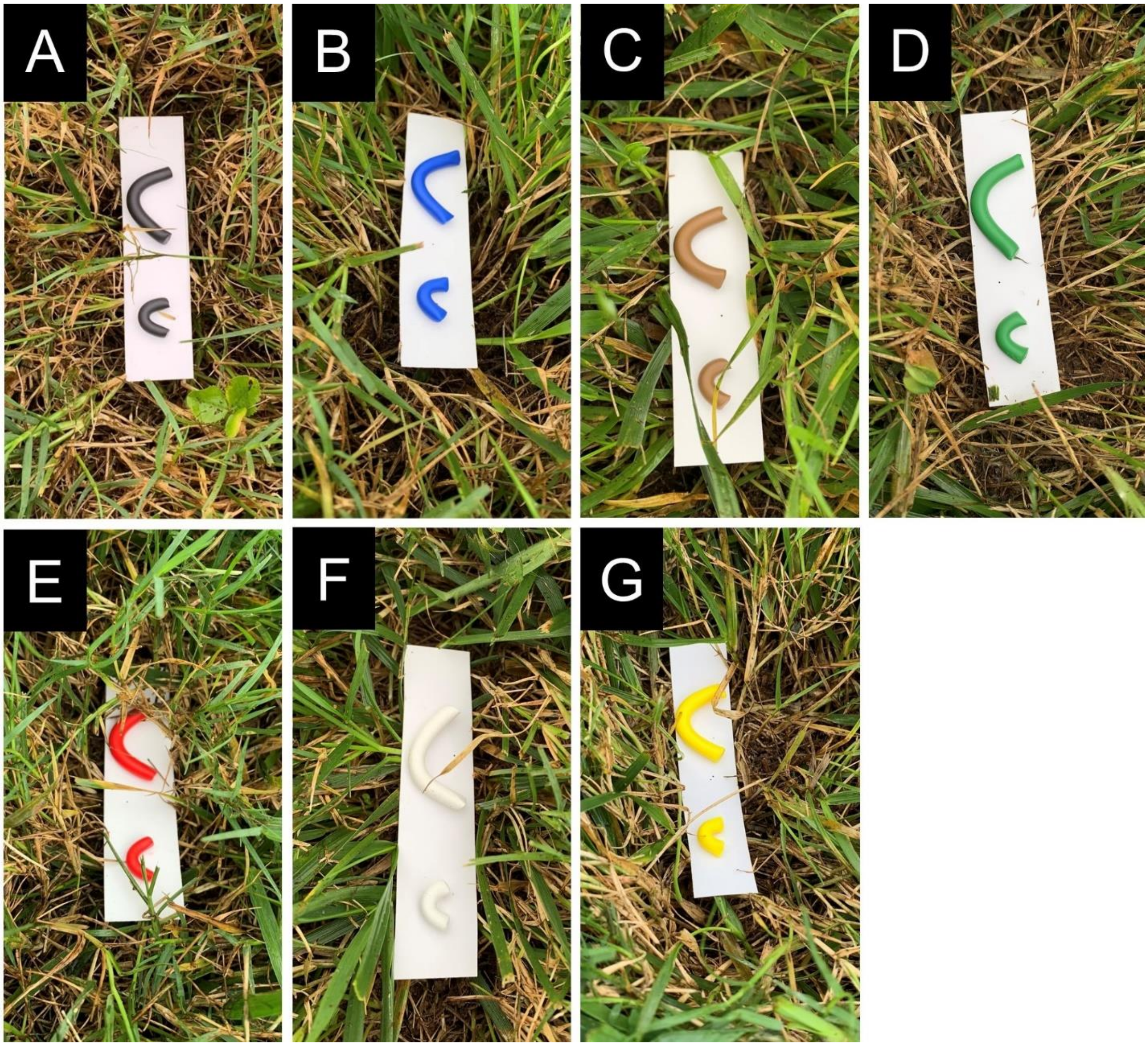

Fig. 3.1. Clay models of different colors – A) black-, B) blue-, C) brown-, D) green-, E) red-, F) white-, and G) yellow-colored models.

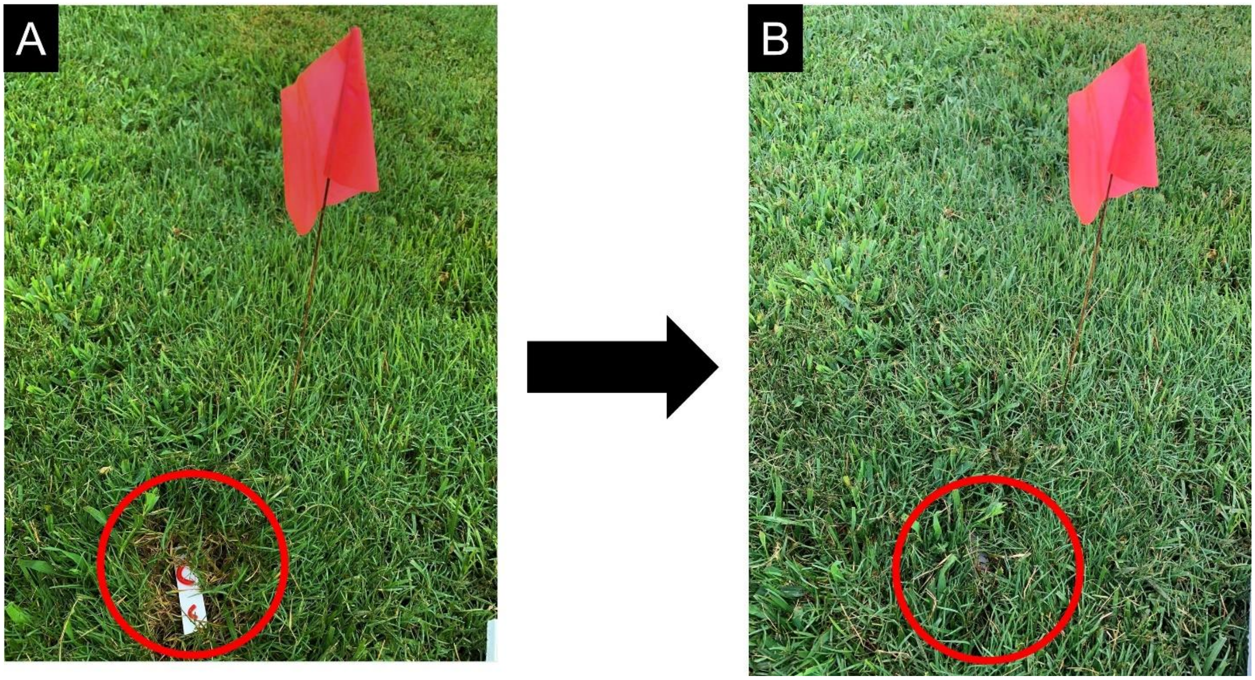

Fig. 3.2. Method of placing the clay model experimental unit in turfgrass (A) pre-deployment and B) post-deployment.

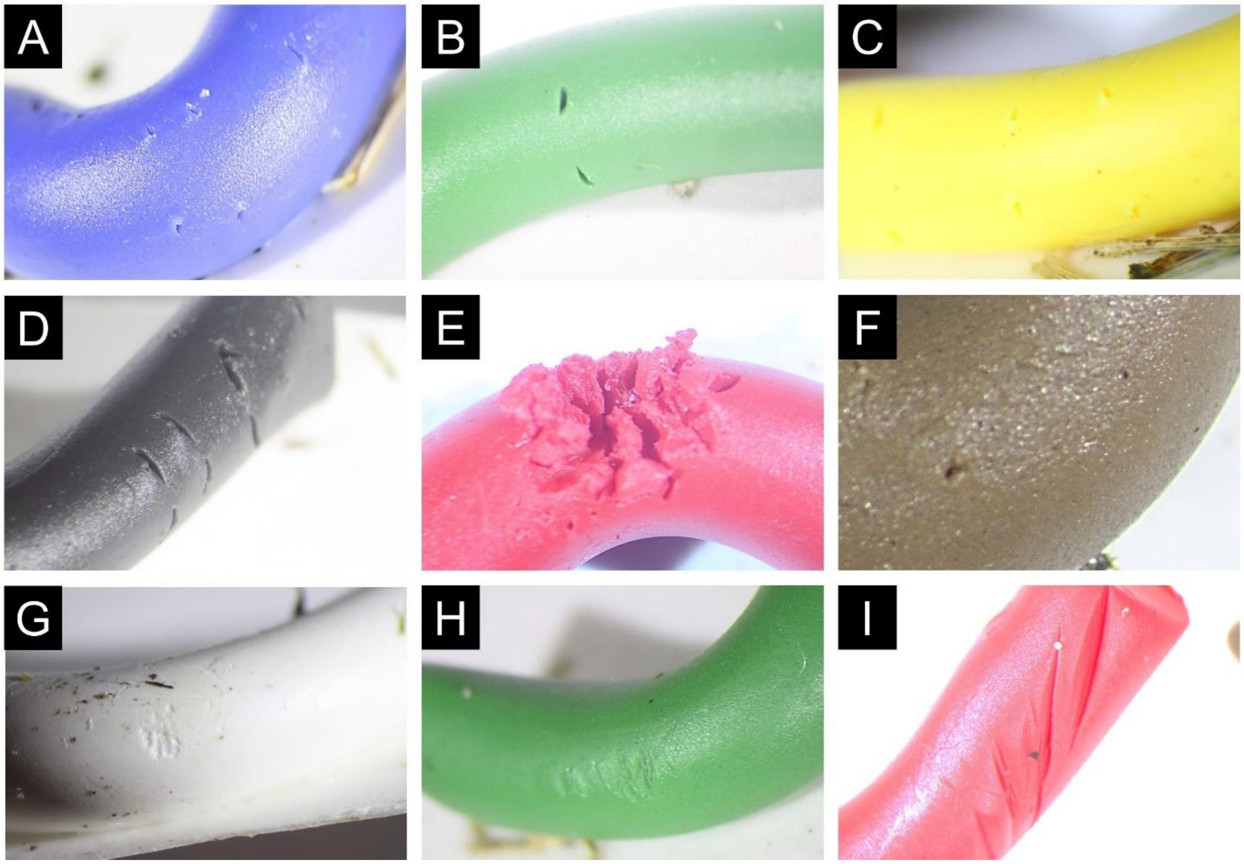

Fig. 3.3. Impression types – A-D) paired marks, E) deep distortion, F) pricks, G) scooped marks, H) scratches, and I) cuts.

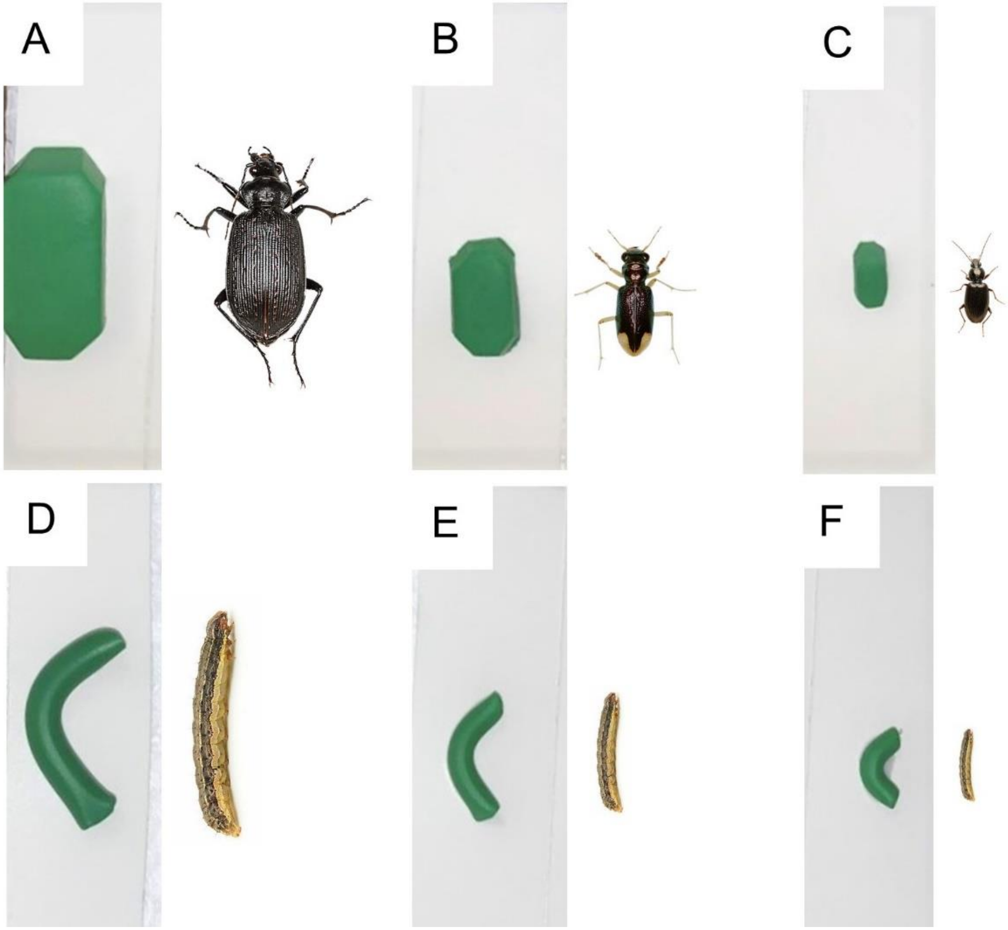

Fig. 3.4. Clay models of different shapes and the corresponding insects – A) large beetle model and *Calosoma sayi* Dejean (Coleoptera: Carabidae), B) medium beetle model and *Tetracha carolina* (L.) (Coleoptera: Carabidae), C) small beetle model, and *Agonum* sp. (Coleoptera: Carabidae), D) large larval model and fall armyworm, E) medium larval model and fall armyworm, and F) small larval model and fall armyworm.

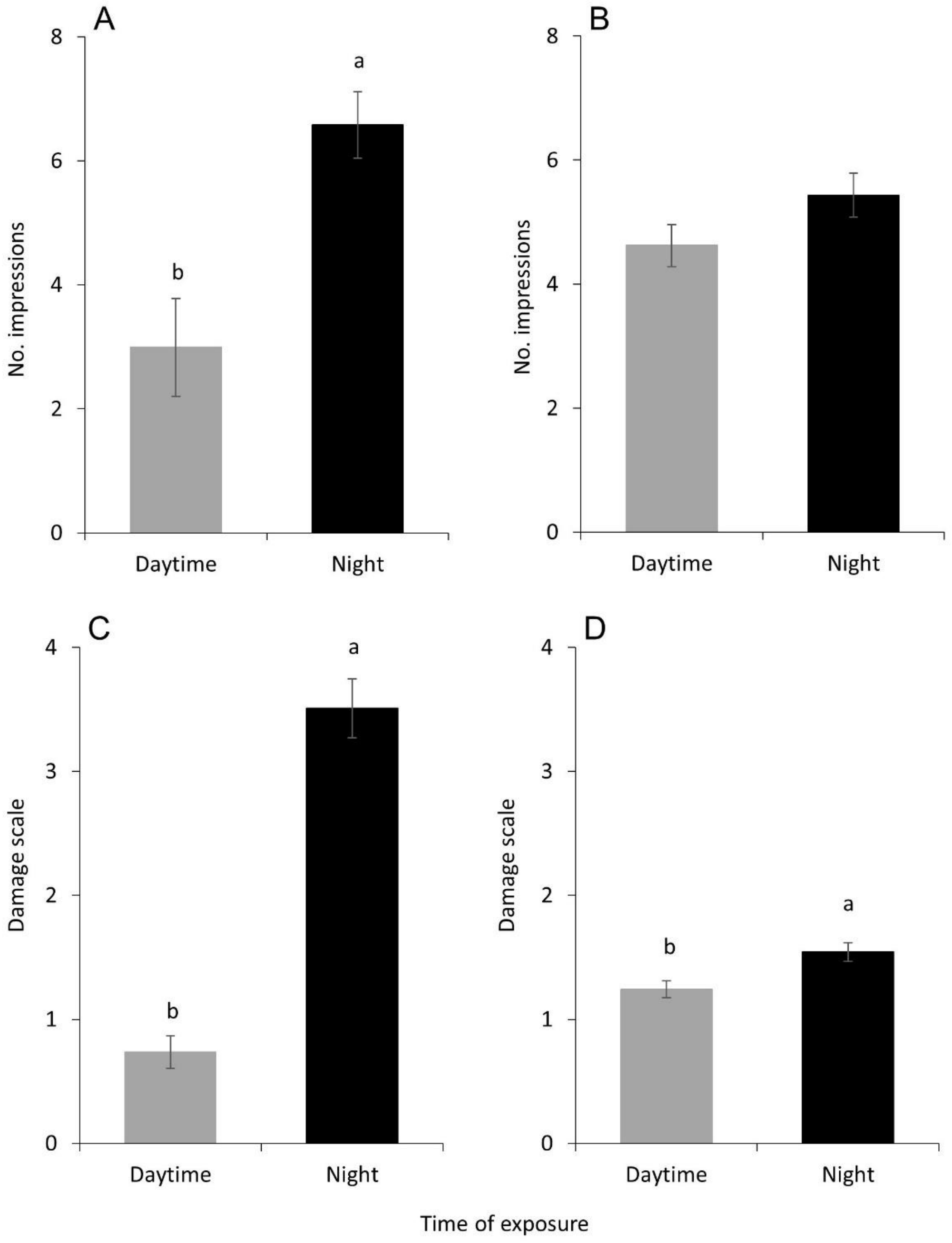

Fig. 3.5. Means (± SE) total impressions recorded in daytime and night during (A) trial 1 (May 2020) and (B) trial 2 (July 2020). Means (± SE) damage scale (0-10) for daytime and night during (C) trial 1 (May 2020) and (D) trial 2 (July 2020). Bars with similar-case letters (upper or lower) are not significantly different (α = 0.05; Tukey-Kramer test).

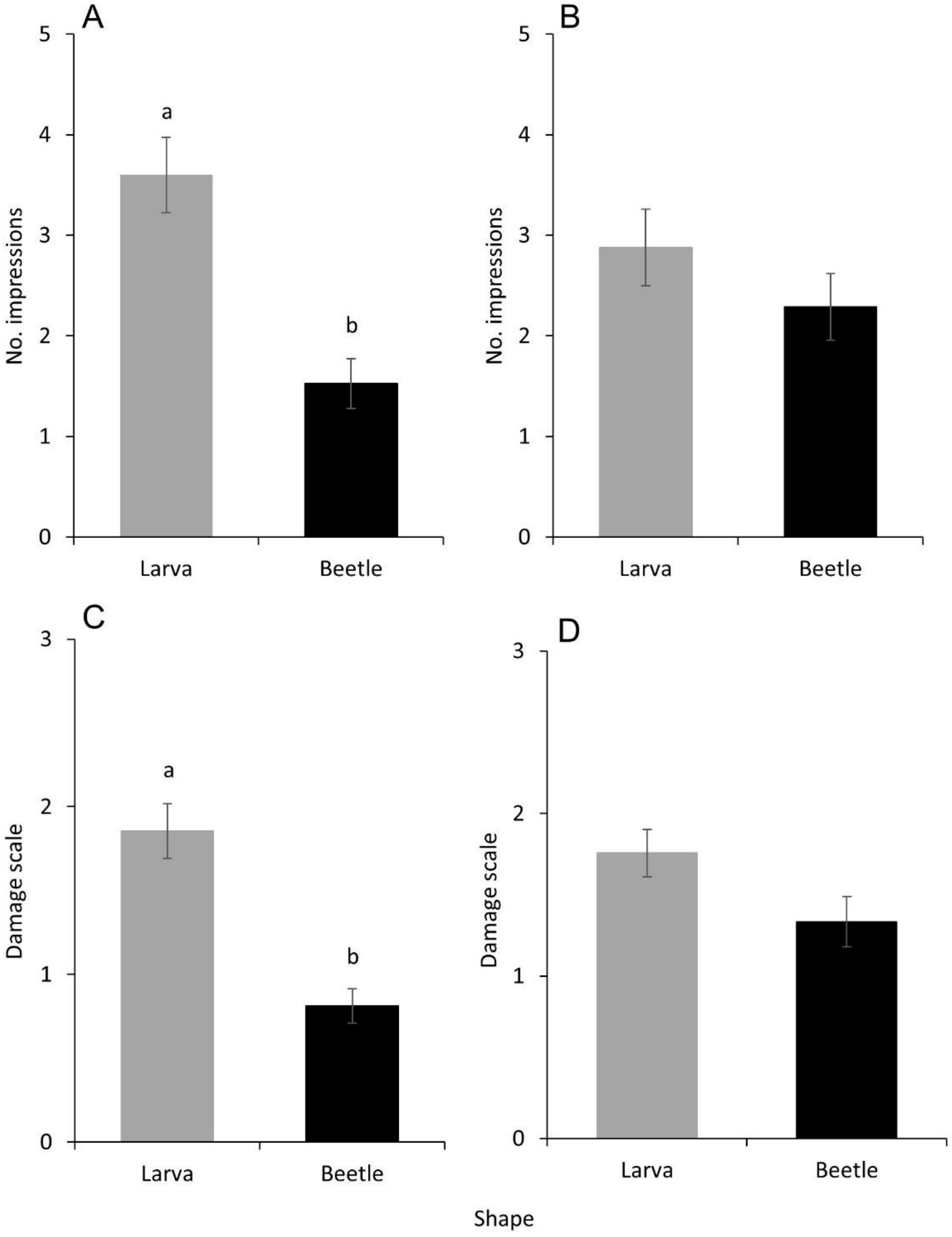

Fig. 3.6. Means (± SE) total impressions recorded on larval- and beetle-shaped models (A) trial 1 (July 2020) and (B) trial 2 (August 2020). Means (± SE) damage scale (0-10) on larval and beetle-shaped models C) trial 1 (July 2020) and (D) trial 2 (August 2020). Bars with similar-case letters (upper or lower) are not significantly different ($\alpha = 0.05$; Tukey-Kramer test).

CHAPTER 4

VERTICAL DISTRIBUTION OF PREDATOR-PREY INTERACTIONS WITHIN TURFGRASS

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ABSTRACT Arthropod predators are abundant in turfgrass systems, and they play an important role in managing pests. Understanding the vertical distribution of predator-prey interactions is critical to developing cultural strategies that enhance and conserve predatory services. However, little is known on how the predator-prey interactions are vertically distributed within the turfgrass canopy. Thus, the objective of this study was to determine the vertical distribution of predator-prey interactions within the turfgrass canopy. Clay models were used to mimic the prey species, fall armyworm, *Spodoptera frugiperda* (JE Smith) (Lepidoptera: Noctuidae), to estimate the predatory activity. The choice and no-choice experiments were conducted by placing clay models at 2.54, 5.08, and 7.62 cm from the thatch surface and denoted as lower, intermediate, and upper levels, respectively, within turfgrass canopy. The predator-mediated impressions, paired mark, scratch, deep cut mark, deep distortion, prick, dent, stacked surface impression, scooped mark, granulation, and U-shaped mark, were identified on clay models. The incidence and severity of impressions were significantly greater on clay models placed at the lower canopy level than on those placed at the intermediate and upper canopy levels in the choice and no-choice experiments ($P < 0.05$). The implication of the results on the utility of the clay model tool for monitoring and developing the integrated pest management strategies for key pests, such as *S. frugiperda* in turfgrass, are discussed.

KEYWORDS: clay model, canopy, conservation biological control, predation, impressions

Turfgrass is an important component of residential lawns, golf courses, athletic fields, and public parks. In the U.S., the turfgrass industry contributes an annual revenue of $35.1 billion USD (Haydu et al. 2008). In Georgia, the annual turfgrass production in sod farms has been valued at $118.3 million USD, produced across 10,785 ha in 64 counties (Wolfe and Stubbs 2020). Turfgrass provides a green cover and adds aesthetic value to the landscape. Turfgrass helps to improve dust stabilization, groundwater recharge, soil improvement, temperature moderation, and carbon sequestration (Beard and Green 1994). In addition, it functions as a venue for recreational sport and a meeting place for social events. Thus, managing arthropod pests in turfgrass is critical in retaining aesthetic and commercial value to serve the industry adequately.

Turfgrass pests reduce the aesthetic and commercial value of turfgrass (Potter and Braman 1991). Based on the activity of various stages of arthropod pests, turfgrass is categorized into three zones, 1) stem and leaves, 2) thatch, and 3) soil and root region (Williamson et al. 2015). Most of the pests fall into these zones. For example, the fall armyworm, *Spodoptera frugiperda* (JE Smith) and black cutworm, *Agrotis ipsilon* (Hufnagel) (both Noctuidae: Lepidoptera) are the major turfgrass pests, and larval stages of these pests are most active in the stem and foliar or thatch zones of turfgrass (Watschke et al. 2013). The behavior of arthropod predators, particularly foraging and feeding behavior within the zones of turfgrass, determines the fate of natural pest management. For example, many formicids are active within the turfgrass canopy, and they effectively encounter and prey on larval stages of *A. ipsilon* (López and Potter 2000) and *S. frugiperda* (Braman et al. 2002). However, the vertical distribution of predator-prey interactions within the turfgrass canopy is poorly understood. This information can improve or refine the integrated pest management programs against the major arthropod pests in turfgrass.

Clay models simulating prey species have been used to estimate and document predator-prey interactions in urban, forest, and cropping ecosystems (Molleman et al. 2016, Seifert et al. 2016, Ferrante et al. 2017, Roels et al. 2018, Zvereva et al. 2019, Nason et al. 2021). In these studies, the prey models were deployed in the specific environment and recovered after specified intervals, and the impressions created on the models were evaluated (Stuart et al. 2012, Rößler et al. 2018, Witwicka et al. 2019, Khan and Joseph 2021a). The types of impressions on the clay model surface provide information about the types of organisms, such as arthropods, mammals, birds, and reptiles, that interacted with the models (Low et al. 2014, Khan and Joseph 2021a). The clay model tool has not been utilized fully to determine predator-prey interactions in turfgrass.

Turfgrass management involves maintaining turfgrass at a specific mowing height, which varies with factors, such as the aesthetic needs, growing climatic zone, the utility of turfgrass, and the grass genotype installed. In Georgia (U.S.), for example, the recommended mowing height for the bermudagrass (*Cynodon dactylon* (L.) Pers.) is 2.5 – 5 cm, while it is 5 – 7.5 cm for the St. Augustinegrass (*Stenotaphrum secundatum* (Walt.) Kuntze) (Waltz et al. 2020). Taller turfgrasses provide refugia sites for predatory arthropods, improving conservation biological control (Dobbs and Potter 2014). For example, greater predation of *Ataenius spretulus* (Haldeman) (Coleoptera: Scarabaeidae) grubs has been reported on rough of annual bluegrass (*Poa annua* L.) maintained at 5 cm height than on fairways maintained at 1.5 cm height in a golf course (Jo and Smitley 2003). Similarly, the abundance of rove beetles (Coleoptera: Staphylinidae) and spiders (Araneae) increased with an increase in mowing height of cool-season turfgrass (Dobbs and Potter 2013). However, the vertical distribution of predator-prey interactions patterns within the canopy of warm-season turfgrass is still unclear. Thus, the objective of this study was to determine predator-prey interactions within the turfgrass canopy after placing the clay models at lower, intermediate, and upper canopy levels of turfgrass.

Materials and Methods

Study site and general methods. In 2020, experiments were conducted on the 'Tifway' bermudagrass field in the University of Georgia, Griffin Campus at Griffin, Georgia, U.S. To determine the vertical distribution of the predator-prey interactions within the turfgrass canopy, the turfgrass was maintained at 8 cm high based on the University of Georgia recommendations and was mowed at 7 d intervals for eight weeks. The turfgrass was irrigated 30 minutes daily from 5:30 to 6:00 AM for eight weeks. The fertilizers and pesticides were not applied. The turfgrass site was infested with weeds, such as southern crabgrass, *Digitaria ciliaris* (Retz.), white clover, *Trifolium repens* L., which covered < 10% of the experimental area. The 2,604.73 m^2 experimental site was part of the 80,042.21 m^2 open turfgrass field with no trees within a 70 m radius.

Clay model. The clay models were prepared using green, nontoxic clay (Sculpey III, Polyform Products, Elk Grove Village, Illinois, USA). The green-colored clay was selected to mimic an undefended prey. The stability of this clay product was proven under summer temperatures (Roels et al. 2018). The green-colored clay models effectively captured predatory interactions, and as a result, the impressions were clearly visible on the clay surface (Low et al. 2014, Sam et al. 2015, Roels et al. 2018, Long and Frank 2020, Khan and Joseph 2021a). A 30 × 4 mm (length × diameter) model, simulating the fifth instar of *S. frugiperda* larva, was prepared by rolling the clay on a smooth wooden surface using a piece of a 10 cm × 5 cm clear acrylic sheet (Khan and Joseph 2021a). The consistency of the cylindrical shape of the model was ensured by regularly measuring the diameter of the rolled clay using a Vernier caliper (model #1468417; General

UltraTech, Friendswood, Texas, USA). The rolled clay was then cut into 4 × 30 mm (diameter × length) cylinders. The clay models were molded to a C-shape to resemble stationary posture of a fifth-instar S. frugiperda. This C-shaped clay model was then glued on 7.62 × 1.79 cm (length × width) weatherproof paper card (JL Darling, Tacoma, Washington, USA) using ~300 mg of silicone glue (Arrow Fastener Co., LLC., Saddle Brook, New Jersey, USA) by using an electric hot melt glue gun.

Experimental design. As described in the previous section, the clay models were prepared and glued to paper cards, and the cards with the clay models were then glued to a 15.24 × 1.79 cm × 0.17 cm (length × width × height) wooden stake. Both choice and non-choice studies were conducted. For the choice study, three clay models were glued individually to a wooden stake at three heights 2.54, 5.08, and 7.62 cm from the thatch surface, and the three height or level treatments were denoted as lower, intermediate, and upper canopy levels, respectively (Fig. 4.1A). The height was determined by measuring the length from the thatch surface to the center of each clay model attached to the stake. The tip of the lower clay model treatment was at ~0 cm from the thatch surface upon deployment. For the no-choice study, only one clay model was attached to a wooden stake at one of the three heights (2.54, 5.08, or 7.62 cm) (Fig. 4.1B-D). The clay model was placed at a specific height on the wooden stake, and it served as the experimental unit. The treatments of the choice experiment were arranged in a randomized complete block design with 30 replications. For the no-choice experiment, the treatments were replicated 10 times. The treatments in the choice and no-choice experiments were deployed 6 m away from the edge of the field and were 3 m apart within and between the blocks (Fig. 4.2). The clay models were exposed to turfgrass arthropods for 24 h. The choice and no-choice experiments were simultaneously conducted from 8 to 11 July 2020 on the same experimental site and were repeated from 2 to 5 September 2020.

Clay model evaluation. Clay models were recovered from the field, transported to the laboratory, and stored at room temperature (21 °C) until evaluation. Khan and Joseph (2021b) characterized nine impression types on the clay models. The impressions found on the clay models were evaluated using the impressions characterized by Khan and Joseph (2021b) using a dissecting stereomicroscope (40 ×) (M3, Wild Heerbrugg AG, St. Gallen, Switzerland). The impression types: paired mark, scratch, deep cut mark, prick, dent, and U-shaped mark, were quantified. The impression types: deep distortion, stacked surface impression, scooped mark, and granulation, were evaluated as a percentage of damaged clay model surface area. To understand the severity of damage, percentages of model surface area affected were estimated using a scale system (0 = 0% impressions, 1 = 1–10%, 2 = 11–20%, 3 = 21–30%, 4 = 31–40%, 5 = 41–50%, 6 = 51–60%, 7= 61–70%, 8 = 71–80%, 9 = 81–90% and 10 = 91–100% of surface exhibiting at least one impression type).

Statistical analyses. All the data analyses were performed in SAS (SAS Institute 2012). For the prey placement choice and no-choice experiments, the numbers of impressions on the clay model treatments were subjected to analysis of variance (ANOVA) using the PROC GLIMMIX procedure in SAS. The procedure used a generalized linear mixed model with negative binomial distribution and log link function. The treatments were the placement heights of the models in the turfgrass canopy and served as the fixed effect, and replications served as the random effect. The estimation method was maximum likelihood with the Laplace approximation. Because data were analyzed using a generalized linear model with a log-link function, the data were not assessed for normality. The means were separated using Tukey–Kramer multiple comparison test

($P < 0.05$). The interaction intensity data recorded as scale values and those impression data recorded as percentages were arcsine square-root transformed before running the PROC GLM procedure. The means were separated using Tukey's studentized range HSD test. Pearson's correlation analyses between individual impression types at a 95% significance level were performed using the PROC CORR procedure in SAS. If significant correlations existed between impression types, the multicollinearity was removed by adding a PARTIAL statement to the PROC CORR procedure in SAS. The means and standard errors of the variables were calculated using the PROC MEANS procedure in SAS.

Results

Of 720 clay models exposed at three levels, 661 had predatory impressions, which suggested 91.8% overall predation in choice and no-choice experiments (conducted in July and September 2020. All the clay models were recovered after exposure.

Choice experiment. Ten distinct impression types, paired mark, scratch, deep cut mark, deep distortion, prick, dent, stacked surface impression, scooped mark, granulation, and U-shaped mark, were observed on the clay models. In July 2020, the numbers of paired marks were significantly greater on the clay models at the lower canopy level than those at the intermediate canopy level (Table 4.1). Similarly, the numbers of scratches were significantly greater on the clay models placed at the lower canopy level than those placed at intermediate and upper canopy levels. Significantly greater percentages of deep distortions and granulations were observed at the lower canopy level than those at intermediate and upper canopy levels. The scooped marks were significantly greater on clay models placed at the lower canopy level than those on the other two upper levels. In contrast, pricks were significantly greater on the models at the upper canopy level than on the lower and intermediate canopy levels. The numbers of deep cuts and dents and the percentages of stacked surface marks were not significantly different on clay models placed among various heights (Table 4.1). In July 2020, impressions were significantly more severe on the clay models at the lower canopy level than at intermediate and upper canopy levels ($F = 35.4$, df = 2, 238, $P < 0.001$, Fig. 4.4A).

In September 2020, the numbers of paired marks were significantly greater on clay models at the lower canopy level than at intermediate and upper canopy levels (Table 4.1). The numbers of scratch marks on the clay models at the lower and upper canopy levels were significantly greater than those on the intermediate canopy level. The numbers of deep cut marks, pricks, dents, and U-shaped marks, as well as the percentages of deep distortion, stacked surface marks, scooped marks, and granulations on the clay models, were not significantly different among placement heights (Table 4.1). The scale values of impressions were more severe on the clay models at the lower canopy level than those at intermediate and upper canopy levels ($F = 20.3$, df = 2, 238, $P < 0.001$, Fig. 4.4B).

Pearson's correlation analysis revealed a significant positive association between the paired mark and stacked surface mark, whereas a significant negative association between the paired mark and U-shaped mark (Table 4.3). The scratch mark was significantly correlated with paired marks, pricks, or scooped marks. Moreover, the granulation impression was positively associated with the deep distortion impression. There was a significant positive correlation between the stacked surface mark and the U-shaped mark (Table 4.3).

No-choice experiment. Nine distinct impression types were identified in the no-choice experiments, and they were paired mark, scratch, deep cut mark, deep distortion, prick, dent, stacked surface impression, scooped mark, and granulation. In July 2020, the numbers of paired marks were significantly greater on clay models at the lower canopy level than those at the intermediate and upper canopy levels (Table 4.2). Significantly greater numbers of scratches were observed on clay models at the lower canopy level than at the intermediate canopy level. In contrast, the numbers of pricks were significantly greater on the clay models at the upper canopy level than those at the intermediate canopy level. The numbers of other impressions, deep cut marks, and dents, as well as the percentages of deep distortion, stacked surface impressions, scooped marks, and granulation, on the clay models were similar across the canopy levels (Table 4.2). The scale values related to the severity of impressions on the clay models were significantly greater at the lower canopy level than those placed at the intermediate and upper canopy levels ($F = 14.0$, df = 2, 238, $P < 0.001$, Fig. 4.3A).

In September 2020, the clay models placed at the lower canopy level captured significantly greater numbers of paired marks than those placed at the upper canopy level (Table 4.2). The numbers of other impression types, including scratches, deep cut marks, pricks, and the percentages of deep distortion, were not significantly different among canopy levels. The severity of impressions was significantly greater on the clay models at the lower canopy level than those placed at the intermediate and upper canopy levels ($F = 8.7$, df = 2, 238, $P < 0.001$, Fig. 4.3B). There was a significant positive correlation between scratch and prick impressions (Table 4.4). The granulation impression was positively associated with scratch or deep distortion impressions (Table 4.4).

Discussion

The results showed that the clay models placed near the thatch surface captured most impressions, which suggests arthropod predators are more active on the soil or thatch surface in turfgrass. The chances of the larval stages of *A. ipsilon* and *S. frugiperda* being eaten by the predators are less during the night, as they are mostly feeding on turfgrass leaf blades away from the thatch surface when the predators are active on the thatch surface within the turfgrass canopy. Both predators and these lepidopteran larvae share nocturnal feeding habits in turfgrass (Sparks 1979, Khan and Joseph 2021b). In addition to these consumptive effects, active foraging activity of predators on the thatch surface can induce non-consumptive effects, such as disrupting mating, oviposition, or dispersal behavior of insect pests, in addition to direct predation (Dupuy and Ramirez 2019). Previously, many studies in urban, forest, and agricultural systems showed that arthropod predation-prey interactions are more active at the ground level than at the above-ground levels (Ferrante et al. 2014, 2017, 2019, Lövei and Ferrante 2017, Eötvös et al. 2020).

The predatory interactions were more severe at the thatch surface than at the upper strata of the turfgrass canopy. This finding suggests that either the densities of a predator species were greater on the thatch surface, or a diverse group of predator species was active on the thatch surface of the turfgrass canopy. In addition, some of the impression types were more severe than others on the thatch surface. The paired marks were the most abundant impression type on the thatch surface than other types of impression. Previously, the paired marks were documented on the clay models when they were exposed to carabids, formicids, anisolabidids, labidurids, and lycosids (Khan and Joseph 2021a). Also, Braman et al. (2002) showed that formicids were the most abundant predators in turfgrass and were observed to consume the egg and larval stages of *S. frugiperda*. In addition to the prevalence and effects of individual impression types, the associations among various impressions suggest that the same arthropod taxa could generate more than one type of impression. For example, paired marks were positively correlated with deep distortions, pricks, scratches, and stacked surface marks. This result was consistent with the previous study where the same turfgrass predators created paired marks and other impression types on caterpillar-shaped clay models (Khan and Joseph 2021a).

Although predator-prey interactions were most abundant at the thatch surface of the turfgrass, the methodology of the current study brings a few limitations. First, all the clay models have been vertically positioned, assuming the larval climbing posture at the various levels of the turfgrass canopy. It is unclear if the vertical placement method of the clay model reduced or overestimated the interaction events from the approaching predators. Previous turfgrass field studies estimated predation by placing the clay models horizontally on the thatch or the top of the grass canopy (Khan and Joseph 2021b). However, it is unclear which placement positions (vertical or horizontal) would yield more predator-prey interactions in turfgrass. Second, because the clay models were attached to one side of the wooden stake, it is unclear if it reduced the predator-prey interactions events as exposure of clay models to predators was restricted from one side. Third, the experiments were conducted on bermudagrass, and thus it is unclear if predator behavior varies by turfgrass genotype and their growth pattern, leaf texture, and management practices, as Joseph and Braman (2009) showed that the occurrence and abundance of the beneficial arthropods could vary by turfgrass types. Finally, the experiment was performed on the turfgrass maintained at a constant height. A taller or shorter grass height may influence the abundance of arthropod predators in the turfgrass (Dobbs and Potter 2013).

The data show that the predator-prey interactions were more prevalent at the thatch surface within the turfgrass canopy than in upper regions of the turfgrass. The results also indicate that the placement of clay models at the thatch surface within the turfgrass canopy leads to more interactions. Dobbs and Potter (2014) showed that staphylinids and Araneae were less abundant in the shorter than the taller turfgrass. In contrast, the abundance of other predatory groups, such as formicids, remained unaffected by turfgrass height. Thus, more research is warranted to determine how the turfgrass height and other disruptive cultural management practices influence the predator-prey interactions in various turfgrass genotypes.

Acknowledegments

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Table 4.1. Mean (± SE) number or percentage of impressions recorded on clay models deployed at different heights in choice experiments.

Model placement	Impressions									
	[a] Paired marks	[a] Scratches	Deep cut marks	[b] Deep distortion	[a] Pricks	[a] Dents	[b] Stacked surface marks	[b] Scooped marks	[b] Granulation	[a] U-shaped marks
July 2020										
Upper	0.69 ± 0.17ab	3.96 ± 0.41b	0.02 ± 0.02	0.00 ± 0.00b	0.99 ± 0.27a	0.01 ± 0.01	0.00 ± 0.00	7.44 ± 1.42b	0.00 ± 0.00b	0.00 ± 0.00
Intermediate	0.46 ± 0.12b	3.07 ± 0.33b	0.02 ± 0.02	0.00 ± 0.00b	0.34 ± 0.10b	0.07 ± 0.03	0.00 ± 0.00	9.67 ± 1.76ab	0.00 ± 0.00b	0.00 ± 0.00
Lower	1.14 ± 0.21a	6.30 ± 0.47a	0.09 ± 0.03	3.00 ± 1.03a	0.68 ± 0.15ab	0.02 ± 0.02	0.22 ± 0.22	15.9 ± 2.34a	0.78 ± 0.32a	0.00 ± 0.00
F; df	5.6; 2, 238	14.8; 2, 238	2.4, 2, 238	9.1; 2, 238	3.6; 2, 238	1.9; 2, 238	1.0; 2, 238	5.4; 2, 238	6.1; 2, 238	-
P	0.004	<0.001	0.095	<0.001	0.029	0.148	0.369	0.005	0.003	-
September 2020										
Upper	0.52 ± 0.19b	4.07 ± 0.43a	0.08 ± 0.03	0.00 ± 0.00	0.42 ± 0.13	0.09 ± 0.03	0.00 ± 0.00	0.11 ± 0.11	0.00 ± 0.00	0.00 ± 0.00
Intermediate	1.23 ± 0.55b	2.60 ± 0.29b	0.10 ± 0.04	0.22 ± 0.22	0.43 ± 0.13	0.10 ± 0.04	1.00 ± 0.89	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Lower	2.58 ± 0.55a	4.39 ± 0.44a	0.12 ± 0.04	0.33 ± 0.33	0.89 ± 0.21	0.18 ± 0.06	0.33 ± 0.33	0.33 ± 0.19	0.11 ± 0.11	0.01 ± 0.01
F; df	11.0; 2, 238	6.9; 2, 238	0.5; 2, 238	0.5; 2, 238	2.9; 2, 238	1.0; 2, 238	0.9; 2, 238	1.9; 2, 238	1.0; 2, 238	0.1; 2, 238
P	<0.001	0.001	0.625	0.601	0.057	0.372	0.396	0.155	0.369	0.954

[a] Means within a column followed by the same letters are not significantly different (Tukey-Kramer multiple comparisons test at $P < 0.05$).

[b] Means within a column followed by the same letters are not significantly different (Tukey's Studentized Range HSD test at $P < 0.05$).

Table 4.2. Mean (± SE) number or percentage of impressions recorded on clay models deployed at different heights in no-choice experiments.

Model placement	Impressions								
	[a] Paired mark	[a] Scratch	[a] Deep cut mark	[b] Deep distortion	[a] Prick	[a] Dent	[b] Stacked surface mark	[b] Scooped mark	[b] Granulation
July 2020									
Upper	0.80 ± 0.39b	3.73 ± 0.62ab	0.43 ± 0.20	0.00 ± 00.00	2.17 ± 0.93a	0.00 ± 00.00	0.00 ± 0.00	2.00 ± 1.21	0.00 ± 00.00
Intermediate	0.27 ± 0.17b	2.10 ± 0.44b	0.03 ± 0.03	0.00 ± 00.00	0.30 ± 0.10b	0.00 ± 00.00	0.00 ± 0.00	4.67 ± 2.70	0.00 ± 0.00
Lower	3.30 ± 1.20a	5.30 ± 1.17a	0.37 ± 0.14	3.06 ± 1.67	0.70 ± 0.30ab	0.07 ± 0.07	0.33 ± 0.33	7.00 ± 3.33	1.73 ± 0.97
F; df	11.0; 2, 78	5.0; 2, 78	2.6; 2, 78	3.8; 2, 78	5.8; 2, 78	0.1; 2, 78	1.0; 2, 78	0.9; 2, 78	2.4; 2, 78
P	<0.001	0.009	0.083	0.028	0.004	0.897	0.3727	0.426	0.094
September 2020									
Upper	0.50 ± 0.18b	4.27 ± 0.70	0.06 ± 0.05	0.00 ± 0.00	0.40 ± 0.16	0.07 ± 0.05	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Intermediate	0.93 ± 0.33ab	2.77 ± 0.67	0.10 ± 0.06	0.33 ± 0.33	0.57 ± 0.25	0.07 ± 0.05	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Lower	3.07 ± 0.94a	3.63 ± 0.75	0.13 ± 0.06	1.33 ± 0.79	0.80 ± 0.37	0.17 ± 0.08	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
F; df	6.0; 2, 78	1.1; 2, 78	0.3; 2, 78	2.2; 2, 78	0.6; 2, 78	0.8; 2, 78	-	-	-
P	0.004	0.322	0.725	0.113	0.555	0.435	-	-	-

[a] Means within a column followed by the same letters are not significantly different (Tukey-Kramer multiple comparisons test at $P < 0.05$).

[b] Means within a column followed by the same letters are not significantly different (Tukey's Studentized Range HSD test at $P < 0.05$).

Table 4.3. Pearson's correlation between impression types on clay models deployed at three heights in choice experiments

Impression types	Paired mark	Scratch	Deep cut mark	Deep distortion	Prick	Dent	Stacked surface mark	Scooped mark	Granulation	U-shaped mark
Paired mark		0.09^{*}								
Scratch										
Deep cut mark										
Deep distortion										
Prick		0.09^{*}								
Dent										
Stacked surface mark	0.57^{***}									
Scooped mark		0.09^{*}								
Granulation				0.80^{***}						
U-shaped mark	-0.18^{***}						0.37^{***}			

The notations show the correlation (*P*: *, <0.05; **, <0.01; and ***, <0.001) between impression types

Table 4.4. Pearson's correlation between impression types on clay models deployed at three heights in no-choice experiments

Impression types	Paired mark	Scratch	Deep cut mark	Deep distortion	Prick	Dent	Stacked surface mark	Scooped mark	Granulation
Paired mark									
Scratch									
Deep cut mark									
Deep distortion									
Prick		0.18^{*}							
Dent									
Stacked surface mark									
Scooped mark									
Granulation		0.21^{**}		0.62^{***}					

The notations show the correlation (P: *, <0.05; **, <0.01; and ***, <0.001) between impression types.

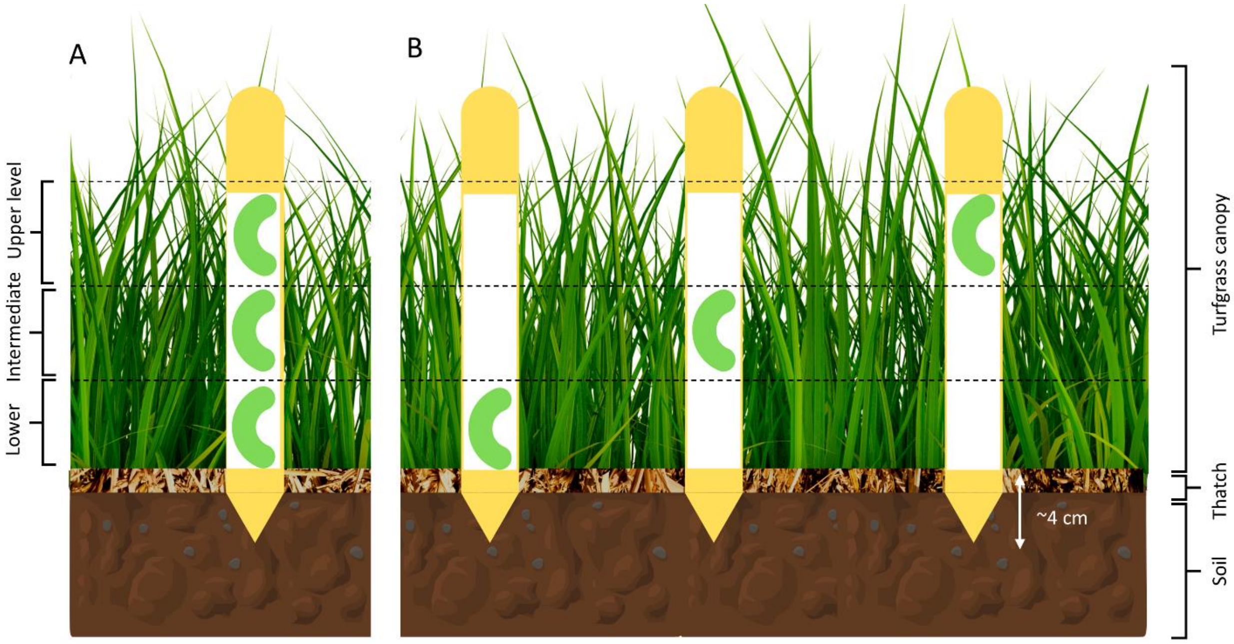

Fig. 4.1. Schematic diagram of (A) choice, (B) no-choice study. The figure shows the placement of various treatments within the turfgrass canopy.

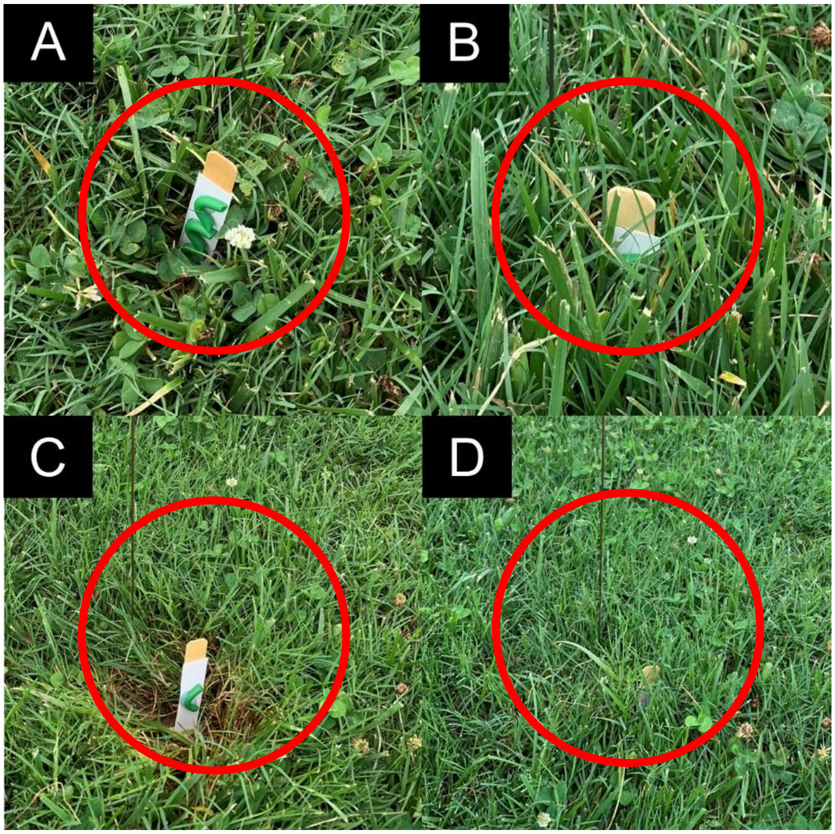

Fig. 4.2. Placement of the clay model within turfgrass canopy (A) at and (B) after deployment in the choice experiment and (C) at and (D) after deployment in the no-choice experiment.

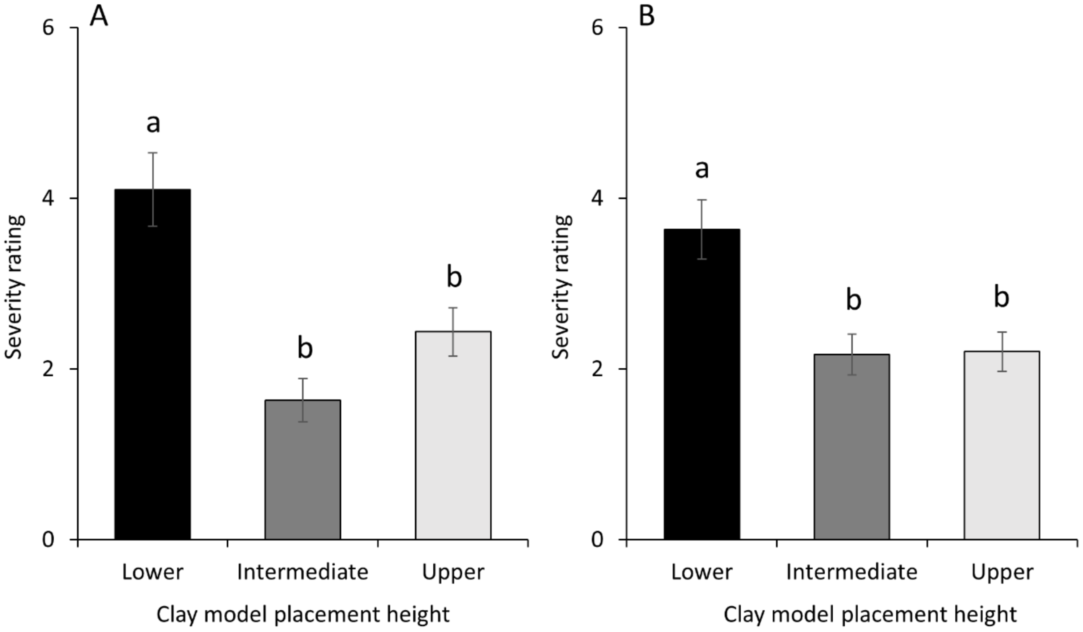

Fig. 4.3. Mean (±SE) severity rating observed on clay models in choice experiments during (A) July 2020 and (B) September 2020. The same letters above the bars denote no significant difference (Tukey's Studentized Range HSD test; *P* < 0.05).

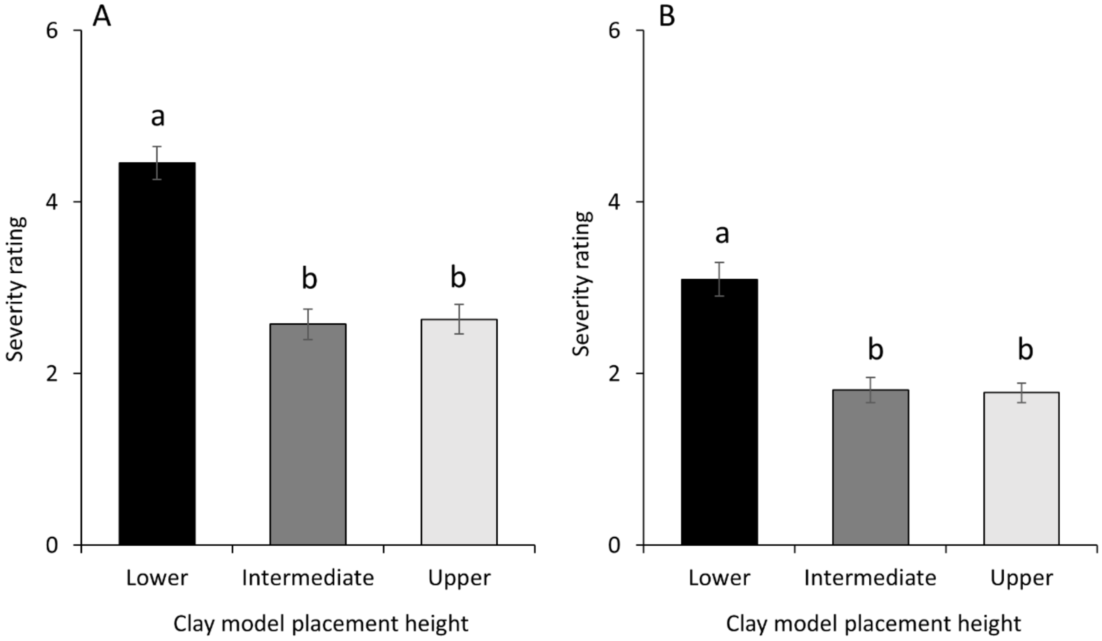

Fig. 4.4. Mean (±SE) severity rating observed on clay models in no-choice experiments during (A) July 2020 and (B) September 2020. The same letters above the bars denote no significant difference (Tukey's Studentized Range HSD test; $P < 0.05$).

CHAPTER 5

ASSESSMENT OF PREDATORY ACTIVITY IN RESIDENTIAL LAWNS AND SOD FARMS

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ABSTRACT The occurrence and abundance of predatory fauna in turfgrass systems have been reported; however, the activity of predators has rarely been described. The fall armyworm *Spodoptera frugiperda* (JE Smith) (Lepidoptera: Noctuidae) is a major pest of turfgrass in the United States for which arthropod predation is not considered a key pest management option, but the role of predation on *S. frugiperda* has not been assessed in turfgrass systems, which are managed at varying intensities. Thus, the objective of this study was to determine (1) the incidence and (2) the severity of predation in less intensively managed residential lawns and intensively managed sod farms. The percentage of predation on live *S. frugiperda* sentinel larvae and the percentage of interaction and its severity on clay models were significantly greater in residential lawns than in sod farms. Among the seven impression types recorded on clay models, paired marks were the most abundant. Four new impression types, deep cut marks, stacked surface marks, scooped marks, and U-shaped marks, were observed on clay models in both turfgrass systems. Formicids were documented at significantly greater densities than were other predatory groups, such as carabids. Thus, the results show the need for enhanced predatory activity in sod farms by developing integrated pest management strategies and adopting measures to conserve natural enemies.

KEYWORDS: fall armyworm, *Spodoptera frugiperda*, turfgrass, clay model, impressions, conservation biological control

Turfgrass is an essential component of urban and suburban landscapes, providing economic, aesthetic, and ecological benefits (Beard and Green 1994, Monteiro 2017). In the United States, turfgrass covers 163,812 km^2, approximately 1.9% of residential and commercial land (Milesi et al. 2005). Furthermore, these turfgrass lawns are expected to expand in coverage with increased urbanization (Robbins and Birkenholtz 2003). The turfgrass industry in Georgia (U.S.) contributes $7.8 billion USD to the state economy (Kane and Wolfe 2012). Turfgrass enhances the value of the general landscape through its aesthetic appearance and improves living standards and the working environment (Potter and Braman 1991, van den Bosch and Ode Sang 2017). Turfgrass provides a range of environmental services, such as regulating soil and air temperature, reducing surface water runoff, improving water infiltration, sequestering carbon, and reducing air and noise pollution (Beard and Green 1994, Monteiro 2017). Through these services, turfgrass serves as an integral component of residential, recreational, and institutional landscapes.

Turfgrass supports a diverse group of arthropod communities (Potter and Braman 1991), including herbivores (Joseph and Braman 2009), predators (Braman et al. 2003), parasitoids (Joseph and Braman 2011), and pollinators (Joseph et al. 2020). Among herbivores, pest species attacking leaf blades, stems, and roots decrease the aesthetic and commercial value of turfgrass (Williamson et al. 2015). Predatory arthropods inhabiting turfgrass have demonstrated natural management of insect pests, including fall armyworm, *Spodoptera frugiperda* (JE Smith) (Terry et al., 1993; Held et al., 2008), and black cutworm, *Agrotis ipsilon* Hufnagel (both Lepidoptera: Noctuidae) (López and Potter, 2000; Frank and Shrewsbury, 2004; Hong et al., 2011). Multiple predatory taxa have been reported in various turfgrass systems. For example, anthocorids, lasiochilids, geocorids, and mirids were found to be abundant in residential zoysiagrass and St. Augustinegrass lawns (Joseph and Braman 2009), and anthocorids, Araneae, carabids, formicids, geocorids, and staphylinids were abundant in sod farms in central Georgia, U.S. (Singh 2020). These studies showed that predaceous arthropods commonly occur and are abundant in turfgrass. However, little is known about real-time predatory activity in various turfgrass systems.

Pest management in turfgrass is driven mainly by insecticides, and conservation of beneficial fauna is rarely considered during management decisions (Braman and Latimer 1997). This insecticide-driven approach could affect the incidence, abundance, and activity of arthropod predators in turfgrass (Potter 1994). For example, López and Potter (2000) demonstrated that spot applications of fipronil targeted for ant management reduced predation on eggs of black cutworm, *A. ipsilon*, and Japanese beetle, *Popillia japonica* Newman (Coleoptera: Scarabaeidae) in turfgrass. Similarly, insecticide applications targeting *A. ipsilon* and *P. japonica* reduced the abundance of predatory ants, mostly *Solenopsis molesta* (Say) (Hymenoptera: Formicidae) (Zenger and Gibb 2001). Most previous research has mainly focused on the prevalence of predators and how densities of predators were influenced by management tactics adopted.

Turfgrass is commercially produced in sod farms, with sod propagating from sprigs (shredded pieces of turfgrass), grass ribbons (postharvest residual narrow turfgrass strips), and rhizomes within two years. Turfgrass in sod farms is grown under intensive management, which includes fertilizer and pesticide applications and intense mowing regimes to reduce production time. When completely grown, the sod is machine-harvested and planted at residences or businesses or installed at recreational sites to develop new golf courses and athletic fields or regularly maintain these sports grounds. When planted at these sites, turfgrass remains permanently and is routinely managed to maintain the aesthetic, real estate, and recreational value. In residential lawns, turfgrass is generally maintained under reduced levels of management inputs such as fertilizers, pesticides, and mowing. To assess and compare the prevalence of predatory activity in turfgrass systems, sod farms and residential lawns were chosen because they are typically managed with contrasting degrees of rigor and different maintenance goals. Thus, the objectives of the current study were to determine (1) the incidence and (2) the severity of predation in sod farms and residential lawns.

Materials and Methods

Study sites and experimental design. In 2019 and 2020, surveys were conducted at sod farms and residential lawns in central Georgia, U.S. The sod farms were located in Macon and Peach Counties in Georgia, U.S. They were selected based on frequent reports of *S. frugiperda* infestations from July to October in recent years. The sod farms were open fields approximately 1.2 km^2 in area and surrounded by either woodlots or tree nut orchards. Management practices at the sod farms included insecticide and fertilizer applications and triweekly mowing operations during the growing season. Insecticides used at the sod farms included diamides, such as chlorantraniliprole, or pyrethroids, such as lambda-cyhalothrin or cyfluthrin, for *S. frugiperda*; phenylpyrazoles, such as fipronil, for ants (Hymenoptera: Formicidae) and mole crickets (Orthoptera: Gryllotalpidae); and neonicotinoids, such as imidacloprid, dinotefuran, and chlorantraniliprole, for billbugs, *Sphenophorus* spp. (Coleoptera: Curculionidae) management. Other pesticides, such as fungicides and herbicides, were applied on a calendar-based schedule. Each sod field was irrigated every day using sprinklers mounted on a center pivot irrigation system.

The residential lawns were located in Spalding and Fayette counties in Georgia, U.S. Residential lawns, approximately 782.9 m^2 in area, were selected after homeowner consent and confirmation of appropriate grass type. Most residential lawns were mowed weekly or biweekly, although insecticides, fungicides, or herbicides were rarely used. None of the selected residential lawns were under any irrigation system.

The turfgrass genotypes in the selected sod farms were bermudagrass (*Cynodon dactylon* (L.) Pers.) and zoysiagrass (*Zoysia* spp.), whereas residential lawns included in the study contained bermudagrass (*C. dactylon*), zoysiagrass (*Zoysia* spp.), centipedegrass (*Eremochloa ophiuroides* (Munro) Hack.), and St. Augustinegrass (*Stenotaphrum secundatum* (Walt.) Kuntze) (Table 1). For each survey, a square area of 15.2 × 15.2 m was randomly selected in a sod field, ~10 m from the wood edge. Similarly, a square area (15.2 × 15.2 m) was selected in each residential lawn ~5 m away from any street, driveway, or vegetation. Each selected square area in a sod field or residential lawn was then subdivided into quadrants, where live sentinel *S. frugiperda* larvae and clay models were deployed. Details on the preparation of the sentinel larvae and clay models are provided in the following sections. A bird-view camera (Pro WCT-00126; Wingscapes TimelapseCam, Calera, Alabama, USA) was installed in the center of the square area in each site. The sod field or residential lawn sites served as replicates and were arranged in a completely randomized design. The live sentinel *S. frugiperda* larvae and clay models were deployed twice a year, and these deployments were referred to as trials 1 and 2 every year. The cameras were installed only once in 2019 (referred to as trial 1) but twice in 2020 (referred to as trials 1 and 2). The specific details of the deployment dates and recovery of sentinel larvae cards and models and camera methods are outlined in Table 1.

Live sentinel larvae. The *S. frugiperda* larvae were used for live sentinel cards. The *S. frugiperda* larvae were purchased from a commercial laboratory (Benzon Research Inc., Carlisle, Pennsylvania, USA). Once the 2nd instar *S. frugiperda* larvae arrived at the University of Georgia entomology laboratory, Griffin, Georgia, they were maintained in an environmentally controlled chamber (Model I-36LL, Percival Scientific, Perry, Iowa, USA) at 28 °C, 40% r.h., and L16:D8 photoperiod for 24 h. The 2nd instars of *S. frugiperda* molted into 3rd instars in the controlled chamber and were field-deployed. Five 3rd instars were glued onto a white, 10.2 × 10.2 cm weatherproof paper card (JL Darling, Tacoma, Washington, USA) by adding ~300 mg of silicone glue (Arrow Fastener Co., LLC., Saddle Brook, New Jersey, USA) per larva to the distal end using a hot glue gun. One larva was placed approximately 2 cm inward from each corner, and one was placed in the center of the card. The larval mortality was low as the applied hot glue cooled off or hardened within 10 s, and they were alive or moribund when deployed in the field. In the field, one live sentinel larvae card was randomly placed within each quadrant (experimental area) of each sod field and residential lawn. The cards were secured to the turfgrass surface using two landscape pins. After 24 h of exposure, the sentinel larvae cards were recovered and transported to the entomology laboratory at the University of Georgia, Griffin, Georgia. The deployment and recovery dates are listed in Table 1. The number of *S. frugiperda* larvae partially or entirely removed from each paper card was quantified as evidence of predatory activity. However, any dead larvae with no damage were not counted. The proportion of larvae predation was calculated for each site after dividing the number of *S. frugiperda* larvae partially or entirely removed by the total number of larvae deployed.

Clay models. Models simulating *S. frugiperda* larvae were used to determine the percentage of larval predation and severity of predation in the turfgrass systems. The clay models were prepared using green, nontoxic, oven-baked modeling clay (Sculpey III, Polyform Products, Elk Grove Village, Illinois, USA). Green-colored clay material was used to represent unprotected and palatable prey (Howe et al. 2009). The clay material was molded into a cylindrical or worm-like shape by rolling the clay on a smooth wooden surface using a smooth 10 cm × 5 cm × 2 mm (length × width × height) acrylic sheet. The elongated cylindrical clay rolls were then cut into 2 × 10 mm and 4 × 30 mm (diameter × length) models and are denoted small- and large-sized models, respectively. The consistency of the cylindrical models was ensured by repeatedly measuring the diameters and lengths of the models using a Vernier caliper (model #1468417, General UltraTech, Friendswood, Texas, USA). These models simulated the 3rd (small) and 5th (large) instars of *S. frugiperda*. Five small and five large clay models were separately placed on 5.1 × 5.1 and 10.2 × 10.2 cm white, weatherproof paper cards, respectively, without using any glue. One model was placed approximately 2 cm interior from each of the four corners, and one was placed in the center of the card. A C-shaped larval posture was adopted for the models when they were individually placed on the paper cards. The paper cards with the worm-shaped models were carefully transferred to Petri dishes for transport to the field. Each paper card with models was horizontally secured to the turfgrass surface using two landscape pins at opposite corners. One small and one large clay model card were randomly deployed in each quadrant at every site. During the exposure period in the field, the clay models remained soft and preserved the impressions created by interacting organisms (Roels et al., 2018, Khan & Joseph, unpublished data). After 3 d of exposure, the clay models were recovered from the sites and transported to the entomology laboratory at the University of Georgia, Griffin, Georgia. The deployment and recovery dates are listed in Table 1. At the entomology laboratory, the clay models were maintained at room temperature (21 °C), and types of impressions in the clay model surfaces were evaluated and quantified under a dissecting microscope (M3, Wild Heerbrugg AG, St. Gallen, Switzerland). The seven impression types previously characterized by Khan and Joseph (2020), paired marks, scratches, pricks, deep distortions, dents, granulation, and detached segments, were used for the identification of impression types in the samples. The current study characterized new impression types not previously characterized by Khan and Joseph (2020). The proportion of predation was calculated for each sample by dividing the total number of clay models with impressions by the total number of clay models. For those impression types (deep distortion and granulation) that were challenging to quantify, percentages of model surface area affected were estimated using a scale system (0 = 0% impressions, 1 = 1–10%, 2 = 11–20%, 3 = 21–30%, 4 = 31–40%, 5 = 41–50%, 6 = 51–60%, 7= 61–70%, 8 = 71–80%, 9 = 81–90% and 10 = 91–100% of surface exhibiting at least one impression type) (Khan and Joseph, 2021). The data on percentages of clay surface affected were not included in the calculation of the proportions of predation. Regardless of impression type, the overall severity of impressions was evaluated using the same scale system for each clay model and recorded.

Time-lapse photography. For this experiment, one live *S. frugiperda* sentinel larvae card was used per site. The sentinel larvae cards were prepared as described in the previous section. Five 3rd instar *S. frugiperda* were glued to each paper card and deployed in the field as described in the previous section. One time-lapse camera (Pro WCT-00126, Wingscapes TimelapseCam, Calera, Alabama, USA) was deployed at each site (sod farm or residential lawn). The time-lapse cameras were mounted on 60-cm steel rebars staked into the ground. The flashlight on each camera was covered with three layers of paper towels to reduce the light intensity. The focal length between each camera and sentinel larvae card was set at 30.5 cm by adjusting the camera on the rebar. All the time-lapse cameras were programmed to capture 6080 × 3420 pixel images every 30 s for 24 h. The camera deployment and recovery dates are listed in Table 1. The image files were transferred from the cameras and saved. The predators observed in the images were identified to order and family. The numbers of predators per event, the numbers of events, and the duration of events were quantified. The duration of the first appearance of each predator was recorded.

Diversity indices. Diversity indices are mathematical measures of species diversity and are based on species richness (number of recorded species) and abundance (number of individuals of a given species) in a given community (Purvis and Hector 2000, Schleuter et al. 2010). In the current study, diversity indices were calculated for the impression types recorded on the clay models instead of species of arthropods. Diversity indices were separately calculated for sod farms and residential lawns. Diversity indices and evenness measures calculated for the diversity of impressions included the Shannon diversity index (H), Shannon evenness measure (E_H), Simpson's diversity index (D), and Simpson's measure of evenness (E_D). The Shannon index (H) incorporates statistical information based on the diversity principle (initially developed for similarity in information or messages) and is a widely accepted measure of ecological diversity (Shannon 1948). The Simpson index (D) is a dominance measure that is heavily influenced by the most abundant species in the sample, and it is less sensitive to species richness (Magurran 2013). The formulas for the diversity indices and evenness measures used in the experiments are as follows:

$H = -\sum_{i=1}^{S} pi \ln pi$

$E_H = H/\ln S$

$D = 1/\sum_{i=1}^{s} pi^2$

$E_D = D \times 1/S$

where H = impression-based Shannon diversity index, E_H = impression-based Shannon evenness measure, S = richness of impression types, *pi* = proportion of individual impressions that are of the i^{th} impression type, ln = natural logarithm, D = impression-based Simpson diversity index, and E_D = impression-based Simpson evenness measure.

Risk index. To determine the intensity of management practices, such as pesticide use and mowing frequency, at sod farms and residential lawns, a risk index (RI) was developed following the procedure described by Joseph and Zarate (2015). The parameters used to develop the index were mowing frequency and use of fertilizers and pesticides. The growing season for turfgrass is from April to October (seven months) in central Georgia. The ranges of values assigned to the parameters reflected the current practices administered in the turfgrass industry and were determined after consultations with homeowners, managers of landscape maintenance and installation companies, and sod farm managers. The scores assigned to the parameters are as follows: mowing frequency: 0–6, where 0 = no mowing operations, 1 = 1–7 times, 2 = 8–14 times, 3 = 15–28 times, 4 = 29–56 times, 5 = 57–84 times, 6 = 85 or more times per growing season; fertilizer use: 0–4, where 0 = no application, 1 = 1–2 times, 2 = 3–4 times, 3 = 4–7 times, and 4 = 8 or more times per growing season; insecticide use: 0–5, where 0 = no application, 1 = 1 time, 2 = 2 times, 3 = 3 times, 4 = 4 times, and 5 = 5 or more times per growing season; fungicide use: 0–4, where 0 = no application, 1 = 1 time, 2 = 2 times, 3 = 3 times, and 4 = 4 or more times per growing season; herbicide use: 0–4, where 0 = no application, 1 = 1 time, 2 = 2 times, 3 = 3 times, and 4 = 4 or more times per growing season. The sum of the individual scores of the five parameters was determined for each experimental site and divided by 23 (sum of the maximum scores of the five parameters) to generate a risk score for a site. This proportion was multiplied by 100 to obtain the percentage risk index. The risk index equation can be expressed as follows:

$$\text{Risk index (RI)} = \frac{(\mathrm{MI})+(\mathrm{FRU})+(\mathrm{PU})+(\mathrm{FNU})+(\mathrm{HU})}{23} \times 100$$

where MI= mowing intensity score, FRU = fertilizer use score, PU = pesticide use score, FNU = fungicide use score, and HU = herbicide use score.

Statistical analyses. The data were analyzed using Statistical Analysis System (SAS) software (SAS Institute 2013). The proportional data on predation of the sentinel larvae and clay models and data on severity of specific clay model impression types and overall severity regardless of impression type were arcsine square root transformed and analyzed using independent sample *t* tests (PROC TTEST) in SAS ($\alpha = 0.05$); the turfgrass system (sod or lawn) was the dependent variable. Missing clay models were not included in the analyses.

The numbers of impressions by impression type on clay models were square-root transformed and subjected to the independent sample *t*-test (PROC TTEST) in SAS ($\alpha = 0.05$). The analysis was performed for each of the trials in 2019 and 2020.

The average numbers of predators observed per event and predatory events recorded from the residential lawns and sod farms during 2019 and 2020 were square-root transformed and analyzed with the independent sample *t*-test (PROC TTEST) in SAS ($\alpha = 0.05$). The numbers of predatory taxa recorded by cameras were subjected to analysis of variance for the turfgrass system using a generalized linear mixed model (PROC GLIMMIX) with a binomial error distribution and a log link function in SAS. The turfgrass system was the fixed effect, whereas replication was the random effect in the model. The estimation method was maximum likelihood with the Laplace approximation. The means were separated using the Tukey–Kramer method ($\alpha = 0.05$).

The Shannon and Simpson diversity indices and evenness data were subjected to independent sample *t*-tests (PROC TTEST) in SAS ($\alpha = 0.05$). The turfgrass system and sites served as the treatment and replication, respectively. The indices were analyzed for all the trials in 2019 and 2020. To understand the association between predatory activity and the risk index, Spearman's rank correlations between the percentages of live sentinel larval predation and the risk indices were analyzed (PROC CORR with SPEARMAN statement) in SAS. Spearman's rank correlations were used for these analyses because the distribution of percentages could not be normalized with data transformations (Sadof and Snyder 2005). The data from residential lawn and sod farm sites were combined for the analysis.

Results

New impressions. Four new impression types were observed from turfgrass sites and are termed stacked surface marks (Fig. 5.1A-C), scooped marks (Fig. 5.1D-F), deep cut marks (Fig. 5.1G-I), and U-shaped marks (Fig. 5.1J-L). Stacked surface marks showed many stacked and interconnected paired-mandibular marks on the clay model. The scooped marks appeared as spots of clay consumed or scooped out and later coalesced into patches on the clay model surface. Deep cut marks appeared as sharp cuts deeper than scratch impressions. The U-shaped marks appeared as horseshoe-shaped impressions on the clay surface. Because stacked surface marks and scooped marks were challenging to quantify, they were estimated as the percentage of surface area with this damage on the clay model using the same scale system described in the clay model section in materials and methods.

Live sentinel larvae. In 2019, the percentage predatory activity on the live *S. frugiperda* sentinel larvae was significantly greater for the residential lawns than for the sod farms for trial 1 ($t = 5.4$, df = 19, $P < 0.001$, Fig. 5.2A) and trial 2 ($t = 8.1$, df = 19, $P < 0.001$, Fig. 5.2B). Similarly, in 2020, a significantly greater percentage of predatory activity on the live sentinel larvae was found for the residential lawns than for the sod farms in trial 1 ($t = 3.7$, df = 18, $P = 0.002$, Fig. 5.2C) and trial 2 ($t = 4.9$, df = 18, $P < 0.001$, Fig. 5.2D).

Clay models. In 2019, the percentage of clay models with impressions was significantly greater for the residential lawns than for the sod farms in trial 1 ($t = 3.8$, df = 19, $P = 0.001$, Fig. 5.3A) and trial 2 ($t = 3.6$, df = 19, $P = 0.002$, Fig. 5.3B). The overall severity of damage from impressions on clay models was significantly greater for residential lawns than for the sod farms in trial 1 ($t = 3.6$, df = 19, $P = 0.002$, Fig. 5.3C) and trial 2 ($t = 2.6$, df = 19, $P = 0.017$, Fig. 5.3D). In 2020, the percentage of clay models with impressions was significantly greater for the residential lawns than for the sod farms in trial 2 ($t = 3.3$, df = 18, $P = 0.004$, Fig. 5.4B) but not significantly greater in trial 1 ($t = 2.0$, df = 18, $P = 0.060$, Fig. 5.4A). The overall damage caused by impressions on clay models was significantly more severe for the residential lawns than for the sod farms in trial 1 ($t = 3.3$, df = 18, $P = 0.004$, Fig. 5.4C) and trial 2 ($t = 4.0$, df = 18, $P < 0.001$, Fig. 5.4D).

In 2019, the numbers of paired marks, scratches, deep distortions, stacked surface marks, and scooped marks were significantly greater for the residential lawns than for the sod farms in trial 1 (Table 5.2). However, the densities of deep cut marks, detached segments, pricks, dents, and U-shaped marks were not significantly different between the two turfgrass systems. In trial 2, the numbers of paired marks and scooped marks were significantly greater for the residential lawns than for the sod farms (Table 5.2). Significantly greater numbers of detached segments were observed for the sod farms than for the residential lawns (Table 5.2). The numbers of deep cut marks, scratches, deep distortions, pricks, dents, stacked surface marks, and U-shaped marks were not significantly different between the two turfgrass systems. In 2020, the numbers of paired marks, deep distortions, and scooped marks were significantly greater for the residential lawns than for the sod farms in trial 1 (Table 5.3). However, the numbers of scratches and pricks were significantly greater for the sod farms than for the residential lawns. There were no significant differences in the numbers of deep cut marks, detached segments, dents, or stacked surface marks between the two turfgrass systems. In trial 2, the numbers of paired marks, stacked surface marks, and scooped marks were significantly greater for the residential lawns than for the sod farms (Table 5.3). However, there were no significant differences in the numbers of scratches, deep cut marks, deep distortions, detached segments, pricks, dents, or granulations between the two turfgrass systems.

Time-lapse photography. In October 2019, the numbers of formicids per predatory event were significantly greater for the residential lawns than for the sod farms (Table 5.4). However, the numbers of carabids, Araneae, and dermapterans were not significantly different between the two turfgrass systems. In both turfgrass systems, formicids were significantly more abundant than carabids, Araneae, and dermapterans. The numbers of predatory events were not significantly different for any predatory taxa between the turfgrass systems (Table 5.4). When various taxa were compared within the residential lawns, the numbers of predatory events recorded were significantly greater for formicids than for carabids, Araneae, and dermapterans (Table 5.4). In the sod farms, there were no significant differences in the numbers of predatory events recorded for formicids, carabids, Araneae, or dermapterans. The first predatory event observed occurred significantly sooner for the residential lawns than for the sod farms (t = -2.6, df = 15, P = 0.019, Fig. 5A). The first predatory events were all by formicids (100%) in the residential lawns, whereas formicids (71.4%), Araneae (14.3%), and dermapterans (14.3%) appeared first in the sod farms.

In June 2020, the numbers of predators per event were not significantly different between the residential lawns and the sod farms for any predator taxa (Table 5.5). When various taxa were compared within turfgrass systems, the numbers of formicids, geocorids, Araneae, dermapterans, and others (including isopods and gastropods) per predatory event were not significantly different for either the residential lawns or the sod farms (Table 5.5). However, formicids were significantly more numerous than geocorids, Araneae, dermapterans, and others in both turfgrass systems. The numbers of predatory events were not significantly different for any predatory taxa between the turfgrass systems (Table 5.5). When various taxa were compared within the residential lawns, the numbers of predatory events by formicids recorded were significantly greater than those by Araneae and dermapterans. Similarly, at the sod farms, significantly greater numbers of predatory events were observed for formicids and geocorids than for dermapterans (Table 5.5). The first predatory event recorded on the sentinel larvae occurred significantly sooner on average for the residential lawns than for the sod farms (t = -2.9, df = 15, P = 0.011, Fig. 5.5B). The predatory taxa that were first observed at the residential lawns were formicids (88.9%) and geocorids (11.1%), whereas geocorids (62.5%), formicids (25%), and Araneae (12.5%) were first noted from the sod farms.

In August 2020, numbers of formicids per event were significantly greater for the residential lawns than for the sod farms (Table 5.5). There were no significant differences in the numbers of predators per event for any other taxa between the turfgrass systems. When various taxa were compared within the residential lawns, the numbers of formicids per predatory event were significantly greater than those of carabids, geocorids, Araneae, dermapterans, and others (Table 5.5). However, at sod farms, there were no significant differences in the numbers of formicids, carabids, geocorids, Araneae, or dermapterans recorded (Table 5.5). The numbers of depredations by formicids were significantly greater for the residential lawns than for the sod farms (Table 5.5), although there were no significant differences in predatory events for other predatory taxa between the turfgrass systems. When various taxa were compared within the residential lawns, the number of predatory events recorded for formicids was significantly greater than those for carabids, geocorids, Araneae, and others (Table 5.5). At the sod farms, the numbers of predatory events recorded did not differ significantly for any predatory taxa observed (Table 5.5). The first predatory event recorded occurred significantly sooner for the residential lawns than for the sod farms (t = -4.7, df = 13, P < 0.001, Fig. 5.5B). The predatory taxa that were first observed at the residential lawns were formicids (90%) and geocorids (10%), whereas formicids (40%), dermapterans (40%), and geocorids (20%) were first observed at the sod farms.

Diversity indices. In June and September 2019, the values of Shannon's and Simpson's diversity indices and evenness (Shannon equitability) between the residential lawns and the sod farms were not significantly different for the impression types recorded on clay models (Table 5.6). Significantly greater values of evenness (Simpson equitability) were recorded among types of impression for the sod farms than for the residential lawns (Table 5.6). In June and August 2020, the values of Shannon's and Simpson's diversity indices and evenness (Shannon equitability) of the impression types recorded on clay models did not differ significantly between the residential lawns and sod farms (Table 5.6).

Risk index. The risk index values were significantly greater for the sod farms than for the residential lawns in 2019 (t = -17.3, df = 19, P < 0.001, Fig. 6A) and 2020 (t = -14.3, df = 18, P < 0.001, Fig. 5.6B). Spearman’s correlations between predatory activity on live sentinel larvae and the risk index were significantly negative for residential lawns and sod farms in 2019 and 2020 (r = -0.8, P <0.001, n = 82).

Discussion

The results based on sentinel live larvae and clay models showed that predatory activity on *S. frugiperda* larvae was lower at the sod farms than in the residential lawns. Although the exact reasons for the low predatory activity at the sod farms remain unclear, it may be attributed to intensive management regimes, such as frequent mowing operations and regular pesticide and fertilizer use. The risk index values from the sod farms exceeded those in the residential lawns, and increasing risk index values were associated with decreasing percentages of *S. frugiperda* larval predation. Previously, Dobbs and Potter (2014) showed that tall fescue (*Festuca arundinacea* Schreb.) (Poaceae) mowed at greater height contained a higher abundance of predators, such as rove beetles and spiders, than did fescue mowed at a shorter height. Additionally, short-term insecticide use leads to reductions in the abundance and activity of beneficial local taxa, including Araneae, carabids, formicids, and staphylinids (Terry et al. 1993, Ricci et al. 2019). The residential lawns were less altered by frequent mowing operations and agricultural inputs, based on the risk index values. Second, the turfgrass at the sod farms was harvested within two years, reducing the time frame required for the establishment of robust ecosystems with predators, herbivores, and detritivores. This relentless disruption of the habitat of arthropod communities at sod farms may influence predator survival and the availability of food resources. In contrast, residential lawns are relatively diverse and complex systems with prevalent weeds, flowering plants, shrubs, and trees within or surrounding the lawns, which can provide refugia and supply diverse food sources to enhance arthropod predator populations. Braman et al. (2002) showed that wildflower plants provided refugia to beneficial arthropods in turfgrass. Similarly, improvements in the abundance of beneficial arthropods and predation on *A. ipsilon* have been documented through the establishment of conservation strips with integrated planting of flowering plants and grass species, including alyssum (*Lobularia maritima* L.), coreopsis (*Coreopsis verticillata* L.), and switchgrass (*Panicum virgatum* L.) in a golf course (Frank and Shrewsbury, 2004). This suggests that additional research is warranted to enhance the abundance of beneficial fauna and predatory activity at sod farms as a sustainable pest management option.

The impressions on clay models were less severe at the sod farms than in the residential lawns, which could reflect predator species and their densities in the turfgrass systems. Seven types of impressions were observed on clay models deployed in residential lawns and sod farms. These impression types had been previously characterized using arthropod predators collected from turfgrass in central Georgia (Khan and Joseph 2021). The arthropods examined by Khan and Joseph (2020) represented the turfgrass predator community in central Georgia, including carabids, such as *Calosoma sayi* DeJean, *Tetracha carolina* (L.), *Scarites subterraneus* Fabricius, *Harpalus pensylvanicus* De Geer, *Anisodactylus* sp., *Amara* sp., and *Agonum* sp.; a gryllotalpid, *Neocurtilla hexadactyla* (Perty); dermapterans, such as *Labidura riparia* (Pallas) (Labiduridae) and *Euborellia annulipes* (Lucas) (Anisolabididae); a formicid, the red imported fire ant, *Solenopsis invicta* Buren; a hemipteran, *Pseudopachybrachius vinctus* (Say) (Rhyparochromidae); and a lycosid spider (Araneae). These predators generated various impression types (Khan and Joseph 2020), which were also detected in the current study. The diversity indices generated for the impression types indicated no difference between the residential lawns and sod farms, suggesting that most of the predator taxa were prevalent in both turfgrass systems. The abundance of impressions was mostly driven by a few dominant impression types in residential lawns, and all impression types represent evenness or equitability at sod farms because the evenness/equitability indices of impressions were greater at the sod farms than in the residential lawns. These results suggest that a few predator species may have driven the high predatory activity recorded in the residential lawns. In contrast, all the predator species equally contributed to predation at the sod farms.

Among impression types, paired marks were more abundant in both turfgrass systems than were the other types. Khan and Joseph (2020) showed that *S. invicta* created more paired marks than did a carabid, *Agonum* sp., found in turfgrass. Similarly, other carabids, earwigs, and spiders also created paired marks (Khan and Joseph 2021). Additionally, the current study observed four new impression types on clay models: deep cut marks, stacked surface marks, scooped marks, and U-shaped marks, although the exact organism(s) that created these impression marks are not clear. The stacked surface marks resembling mandibular signatures are aligned with small mandibular arthropods, such as ants. The deep cut marks could be formed by the bird's beak or the mandibles of a carabid beetle, whereas the U-shaped marks resembled the beak marks of birds (Mason et al. 2018, Zvereva et al. 2019). The scooped marks may have been caused by gastropods, such as snails or slugs, because scooped marks showed internal microscopic lines possibly caused by scraping of radular odontophores (Krings et al. 2019). These results suggest that arthropods with mandibular mouthparts play a critical role in the predation of *S. frugiperda* larvae in turfgrass.

Among the predators recorded with the time-lapse cameras, formicids, particularly *S. invicta*, were the most common predators attacking *S. frugiperda* larvae at the residential lawns and sod farms. A previous study showed that *A. ipsilon* larval densities were reduced by the indigenous formicid species *Lasius neoniger* Emery (López and Potter 2000). Occurrence and abundance have been reported for many formicid species, such as *S. invicta,* the winter ant (*Prenolepis impairs* Say), the Argentine ant (*Iridomyrmex humilis* Mayr), *Formica schaufussi* Mayr, and *Ponera pennsylvanica* Buckley in central Georgia, U.S. (Braman et al. 2002). In addition, eggs and larvae of *S. frugiperda* have been observed to be consumed by formicids in turfgrass (Braman et al. 2002) and corn (*Zea mays* L.) (Dassou et al. 2021). However, formicids are regarded as nuisance pests in residential lawns because certain formicid species attack humans, such as *S. invicta*, causing distress and, on some occasions, anaphylactic shock (Goddard 2004, Vittum 2020). At sod farms, formicids are less likely to become a problem for field crews, as they have minimal close interactions with formicids. Thus, formicids are important predators of *S. frugiperda* larvae in turfgrass. More research is warranted to determine the formicid species that are effective against *S. frugiperda* larvae and less aggressive to humans or to develop strategies to improve their service while minimizing interactions with humans in the various turfgrass systems.

In summary, the results showed that the predatory activity on *S. frugiperda* larvae and clay models was lower at the sod farms than in the residential lawns. Similarly, the severity of impressions on clay models was lower at the sod farms than at the residential lawns. Diverse types of impressions were recorded on the clay models in both turfgrass systems, and the paired mark impression was the most dominant impression type recorded. Four new impression types, stacked surface marks, U-shaped marks, deep distortions, and scooped marks, were observed in both turfgrass systems. Based on predatory events recorded using time-lapse cameras, formicids were the most predominant predatory taxa in the turfgrass systems among the predatory groups. The densities of formicids were greater in the residential lawns than at the sod farms. A greater risk index value was reported from the sod farms than from the residential lawns. Moreover, according to diversity indices, the types of impressions recorded were similar at the sod farms and residential lawns. In contrast, the number of impression types was more equitable at the sod farms rather than being dominated by a few predatory taxa as in the residential lawns. This study indicates that predatory activity at sod farms needs improvement, which can be achieved by developing strategies that enhance the establishment of predators and conserve existing beneficial fauna.

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Table 5.1. Turfgrass system, location, grass type, and deployment time of live sentinel prey, clay models, and time-lapse camera in 2019 and 2020.

Year	Turfgrass system	Location	Grass types	Deployment	
				Live sentinel prey and clay model	Time-lapse camera
2019	Residential lawns	Spalding County, GA, U.S. Fayette County, GA, U.S.	Bermudagrass (n=2), Centipedegrass (n=3), St. Augustinegrass (n=4), Zoysiagrass (n=2)	25 June, 10 September	03 October
	Sod farms	Macon County, GA, U.S. Peach County, GA, U.S.	Bermudagrass (n=5), Zoysiagrass (n=5)	15 June, 26 August	06 October
2020	Residential lawns	Spalding County, GA, U.S. Fayette County, GA, U.S.	Bermudagrass (n=2), Centipedegrass (n=3), St. Augustinegrass (n=3), Zoysiagrass (n=2)	16 June, 10 August	16 June, 10 August
	Sod farms	Macon County, GA, U.S. Peach County, GA, U.S.	Bermudagrass (n=5), Zoysiagrass (n=5)	22 June, 17 August	22 June, 17 August

Table 5.2. Mean (± SE) number or percentage of impressions recorded on clay models at the residential lawns and sod farms in 2019

Trial	Turfgrass system	[†]Impressions									
		Paired marks	Scratches	Deep cut marks	[a] Deep distortion	Detached segments	Pricks	Dents	[a] Stacked surface marks	U-shaped marks	[a] Scooped marks
June 2019	Lawn	41.09 ± 12.47 a	31.82 ± 5.36a	3.73 ± 1.09	0.00 ± 0.00a	0.00 ± 0.00	5.91 ± 1.41	1.27 ± 0.47	1.93 ± 0.66a	0.00 ± 0.00	6.20 ± 2.17a
	Sod	8.2 ± 2.92b	15.30 ± 2.54b	3.00 ± 0.84	0.65 ± 0.42b	0.30 ± 0.21	2.60 ± 0.92	0.70 ± 0.34	0.53 ± 0.35b	0.30 ± 0.30	0.00 ± 0.00b
	t, df	3.1, 19	2.8, 19	0.2, 19	-2.2, 19	-1.5, 19	1.9, 19	1.1, 19	2.2, 19	-1.0, 19	4.0, 19
	P	0.006	0.011	0.850	0.043	0.142	0.077	0.307	0.044	0.314	<0.001
August 2019	Lawn	102.45 ± 29.90 a	28.54 ± 3.67	2.45 ± 0.67	0.21 ± 0.10	0.00 ± 0.00b	5.27 ± 0.94	0.18 ± 0.12	7.02 ± 4.44	0.09 ± 0.09	1.02 ± 0.38a
	Sod	9.30 ± 1.51b	32.70 ± 7.34	7.70 ± 3.76	0.05 ± 0.03	1.50 ± 0.65a	7.90 ± 1.70	0.30 ± 0.15	1.17 ± 0.26	0.50 ± 0.50	0.08 ± 0.08b
	t, df	4.1, 19	-0.2, 19	-1.5, 19	1.2, 19	-2.5, 19	-0.8, 19	-0.6, 19	1.7, 19	-0.6, 19	3.8, 19
	P	<0.001	0.867	0.140	0.244	0.021	0.422	0.549	0.104	0.584	0.001

[†] Means within the columns (lawn and sod) with the same letters are not significantly different as determined by the independent sample *t* test ($P < 0.05$)

[a] Impressions expressed as percentage of the affected clay model surface

Table 5.3. Mean (± SE) number or percentage of impressions recorded on clay models at the residential lawns and sod farms in 2020

Year	Turfgrass system	[†]Impressions									
		Paired marks	Scratches	Deep cut marks	[b] Deep distortion	Detached segments	Pricks	Dents	[b] Stacked surface marks	[b] Scooped marks	[b] Granulation
June 2020	Lawn	128.05 ± 38.90a	29.50 ± 5.16b	0.70 ± 0.33	0.40 ± 0.27a	0.30 ± 0.21	1.70 ± 0.54b	0.00 ± 0.00	4.10 ± 1.86	6.55 ± 3.88a	0.00 ± 0.00
	Sod	10.00 ± 2.44b	57.70 ± 6.72a	3.40 ± 2.40	0.00 ± 0.00b	0.60 ± 0.60	7.50 ± 1.88a	0.30 ± 0.21	1.78 ± 0.67	0.03 ± 0.03b	0.00 ± 0.00
	t, df	4.7, 18	-3.3, 18	-0.7, 18	2.3, 18	-0.0, 18	-3.0, 18	-1.5, 18	0.9, 18	2.3, 18	-
	P	<0.001	0.004	0.482	0.033	0.991	0.009	0.163	0.369	0.033	-
August 2020	Lawn	83.40 ± 23.56a	64.80 ± 16.20	2.20 ± 0.76	0.32 ± 0.27	0.00 ± 0.00	21.40 ± 7.87a	0.10 ± 0.10	2.52 ± 1.13a	4.93 ± 3.14a	0.23 ± 0.23
	Sod	11.40 ± 2.27b	39.50 ± 10.64	1.50 ± 0.98	0.42 ± 0.29	0.60 ± 0.43	6.90 ± 2.00b	0.40 ± 0.31	0.00 ± 0.00b	0.00 ± 0.00b	0.00 ± 0.00
	t, df	4.0, 18	1.2, 18	1.0, 18	-0.2, 18	-1.5, 18	1.9, 18	-0.8, 18	3.5, 18	2.5, 18	1.0, 18
	P	<0.001	0.261	0.310	0.840	0.162	0.078	0.431	0.002	0.023	0.340

[†] Means within the columns (lawn and sod) with the same letters are not significantly different as determined by the independent sample *t* test ($P < 0.05$)

[a] Experiments were conducted during June (trial 1) and August 2020 (trial 2).

[b] Impressions expressed as a percentage of the affected clay model surface

Table 5.4. Mean (± SE) number of arthropods within a predatory activity and predatory events per 30 seconds captured by the time-lapse camera at residential lawns and sod farms in October 2019[*]

Year	Variable	Formicidae	Carabidae	Araneae	Dermaptera	[b]*F*, df	*P*
October 2019	No. Predators						
	Lawn	13.46 ± 3.69aA	0.00 ± 0.00b	0.00 ± 0.00b	0.00 ± 0.00b	19.5, 3, 27	<0.001
	Sod	4.95 ± 2.86aB	0.13 ± 0.13b	0.13 ± 0.13b	0.13 ± 0.13b	5.7, 3, 21	0.005
	[a]*t*, df	2.5, 16	-1.1, 16	-1.10, 16	-1.10, 16		
	P	0.026	0.289	0.289	0.289		
	No. Predatory events						
	Lawn	104.4 ± 40.23a	0.00 ± 0.00b	0.00 ± 0.00b	0.00 ± 0.00b	61.1, 3, 27	<0.001
	Sod	71.13 ± 36.91a	5.88 ± 5.88a	15.75 ± 15.75a	2.38 ± 2.38a	1.0, 3, 21	0.409
	t, df	1.4, 16	-1.1, 16	-1.1, 16	-1.1, 16		
	P	0.190	0.278	0.278	0.279		

[a] Means within the columns (lawn and sod) with the same uppercase letters are not significantly different as determined by the independent sample *t* test ($P < 0.05$)

[b] Means among the rows with the same lowercase letters are not significantly different as determined by the Tukey–Kramer test ($P < 0.05$)

Table 5.5. Mean (± SE) number of arthropods within a predatory activity and predatory events per 30 seconds captured by time-lapse camera at residential lawns and sod farms in June and August 2020

Year	Variable	Formicidae	Carabidae	Geocoridae	Araneae	Dermaptera	Others†	*F*, df	*P*
June 2020	No. Predators								
	Lawn	1.88 ± 0.54a	0.00 ± 0.00	0.10 ± 0.10 b	0.00 ± 0.00b	0.00 ± 0.00b	0.20 ± 0.20b	7.1, 4, 36	<0.001
	Sod	1.46 ± 0.96a	0.00 ± 0.00	0.47 ± 0.20 a	0.10 ± 0.10a	0.10 ± 0.10a	0.00 ± 0.00a	2.7, 4, 36	0.044
	t, df	1.0, 18		-1.6, 18	-1.0, 18	-1.0, 18	1.5, 18		
	P	0.330		0.120	0.346	0.346	0.157		
	No. Predatory events								
	Lawn	90.60 ± 25.04a	0.00 ± 0.00	6.30 ± 6.30 ab	0.00 ± 0.00b	0.00 ± 0.00b	3.90 ± 2.83ab	6.3, 4, 36	<0.001
	Sod	27.80 ± 14.67a	0.00 ± 0.00	53.20 ± 23.90a	1.20 ± 1.20ab	0.10 ± 0.10b	0.00 ± 0.00b	5.9, 4, 36	<0.001
	t, df	2.0, 18		-1.8, 18	-1.0, 18	-1.0, 18	1.5, 18		
	P	0.060		0.085	0.335	0.346	0.162		
August 2020	No. Predators								
	Lawn	6.36 ± 1.52aA	0.00 ± 0.00b	0.10 ± 0.10b	0.10 ± 0.10b	0.00 ± 0.00b	0.10 ± 0.10b	13.3, 5, 45	<0.001
	Sod	0.32 ± 0.22B	0.10 ± 0.10	0.10 ± 0.10	0.10 ± 0.10	0.20 ± 0.13	0.00 ± 0.00	0.5, 5, 45	0.778
	t, df	6.0, 18	-1.0, 18	-0.0, 18	0.0, 18	-1.5, 18	1.0, 18		
	P	<0.001	0.346	0.990	1.000	0.157	0.346		

No. Predatory events								
Lawn	153.30 ± 29.67aA	0.00 ± 0.00b	0.10 ± 0.10b	0.80 ± 0.80b	0.00 ± 0.00b	0.70 ± 0.70b	22.1, 5, 45	<0.001
Sod	90.60 ± 63.25B	4.10 ± 4.10	22.40 ± 22.40	0.80 ± 0.80	2.80 ± 1.89	0.00 ± 0.00	1.6, 5, 45	0.175
t, df	2.5, 18	-1.0, 18	-0.9, 18	0.0, 18	-1.5, 18	1.0, 18		
P	0.024	0.333	0.364	1.000	0.154	0.336		

[†] Other includes Isopoda and Gastropoda

Means within the columns (lawn and sod) with the same uppercase letters are not significantly different as determined by the independent sample t test ($P < 0.05$)

Means among the rows with the same lowercase letters are not significantly different as determined by the Tukey–Kramer test ($P < 0.05$)

Table 5.6. Means (±SE) of Shannon diversity index (H), Shannon's equitability (E_H), Simpson's diversity index (D), and Simpson's equitability (E_D) for impression types recorded on clay models at residential lawns and sod farms during 2019 and 2020.

Year[a]	Turfgrass system	H	E_H	D	E_D
June 2019	Lawn	1.255 ± 0.060	0.720 ± 0.022	2.818 ± 0.159	0.493 ± 0.035b
	Sod farm	1.186 ± 0.144	0.765 ± 0.055	2.970 ± 0.374	0.621 ± 0.044a
	t, df	0.5, 19	-0.8, 19	-0.4, 19	-2.3, 19
	P	0.650	0.448	0.704	0.033
August 2019	Lawn	1.151 ± 0.084	0.624 ± 0.041b	2.544 ± 0.236	0.402 ± 0.035b
	Sod farm	1.336 ± 0.058	0.769 ± 0.031a	3.088 ± 0.226	0.546 ± 0.052a
	t, df	-1.8, 19	-2.8, 19	-1.7, 19	-2.3, 19
	P	0.091	0.012	0.114	0.0323
June 2020	Lawn	0.953 ± 0.066	0.612 ± 0.040	2.240 ± 0.178	0.472 ± 0.047
	Sod farm	0.916 ± 0.089	0.637 ± 0.058	2.052 ± 0.160	0.493 ± 0.043
	t, df	0.3, 18	-0.4, 18	0.8, 18	-0.3, 18
	P	0.741	0.728	0.441	0.748
August 2020	Lawn	1.127 ± 0.066	0.669 ± 0.043	2.653 ± 0.193	0.497 ± 0.048
	Sod farm	0.943 ± 0.097	0.691 ± 0.042	2.266 ± 0.246	0.574 ± 0.042
	t, df	1.6, 18	-0.4, 18	1.2, 18	-1.2, 18
	P	0.135	0.724	0.231	0.243

Means among the rows with the same letters are not significantly different as determined by the Tukey–Kramer test ($P < 0.05$)

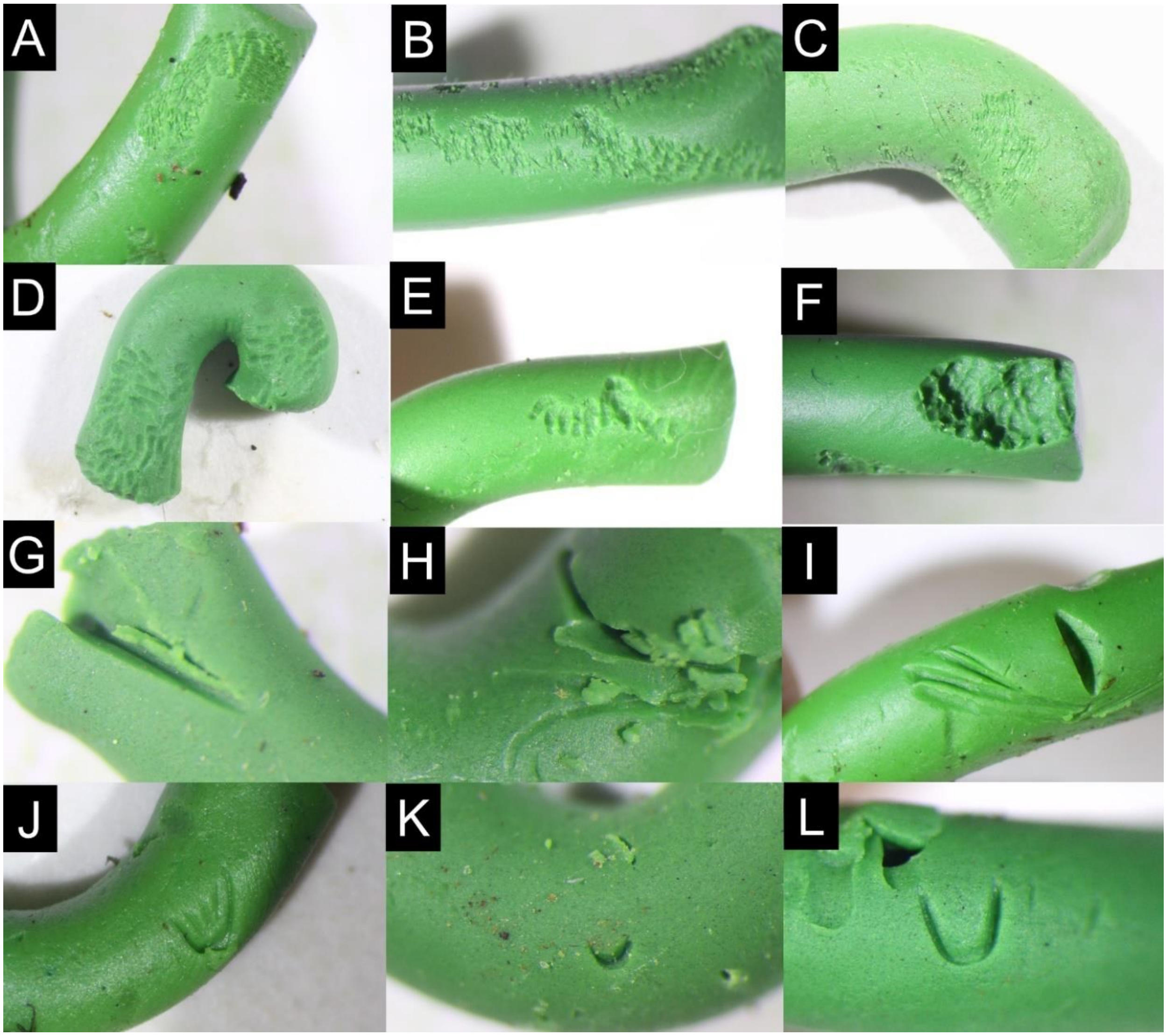

Fig. 5.1. New impression types recorded from residential lawns (RL) and sod farms (SF): (A-C) stacked surface marks [A-C recorded from RL], (D-F) scooped marks [all from RL], (G-I) deep cut marks [G from RL and H-I from SF], and (J-L) U-shaped marks [J-K from RL and L from SF].

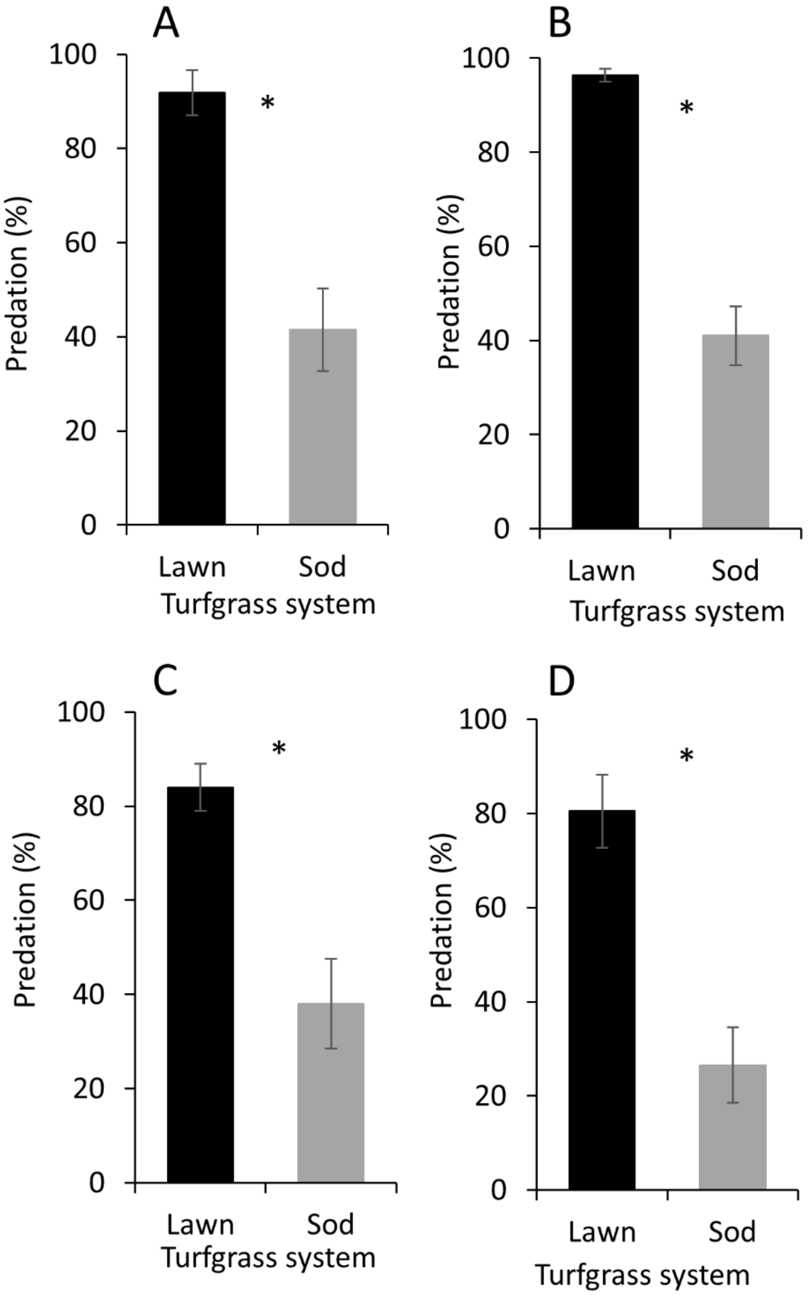

Fig. 5.2. Mean (±SE) percentages of predation on live sentinel *S. frugiperda* larvae during (A) June 2019, (B) August 2019, (C) June 2020, and (D) August 2020. Asterisks above the pairs of bars indicate significant differences (independent sample *t* test, $P < 0.05$).

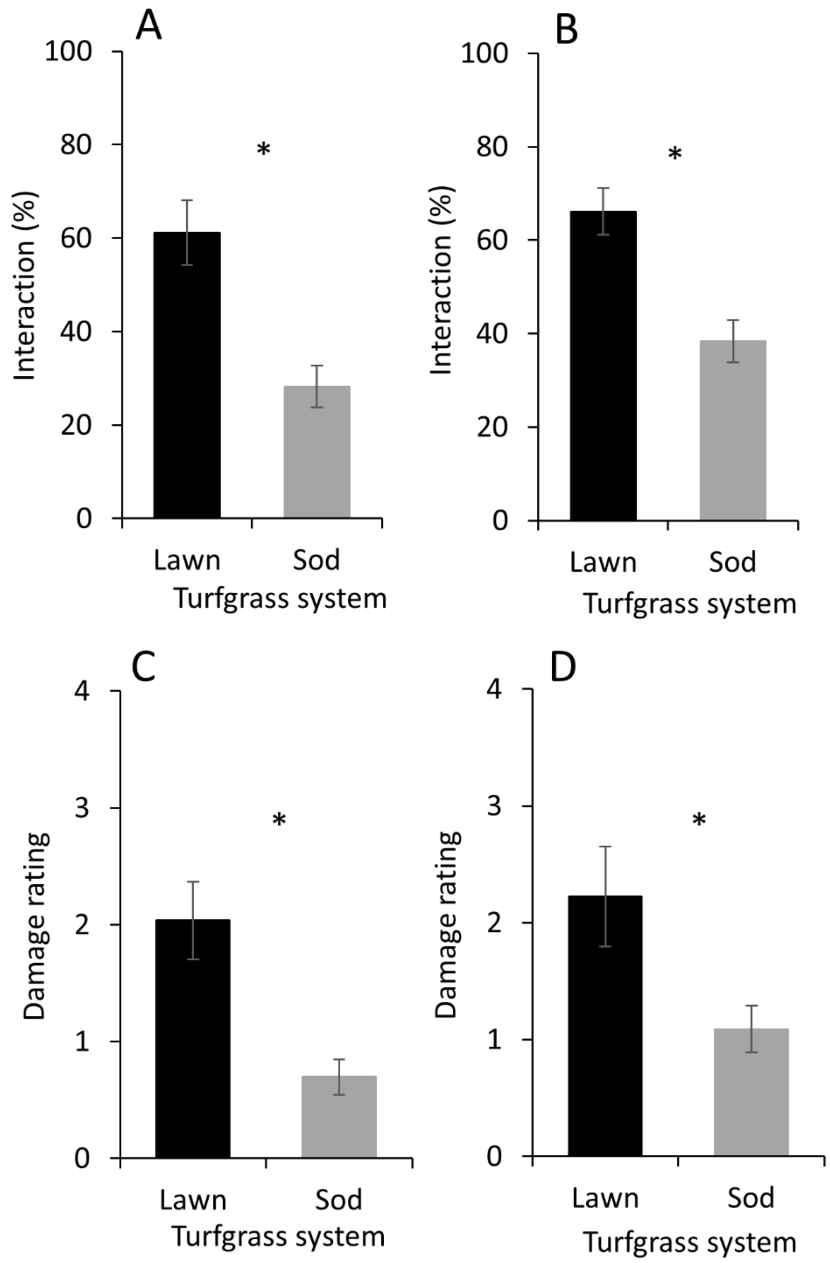

Fig. 5.3. Mean (±SE) percentages of attacks on clay models during (A) June 2019 and (B) August 2019 and damage ratings during (C) June 2019 and (D) August and September 2019. Asterisks above pairs of bars indicate significant differences (independent sample *t* test, $P < 0.05$).

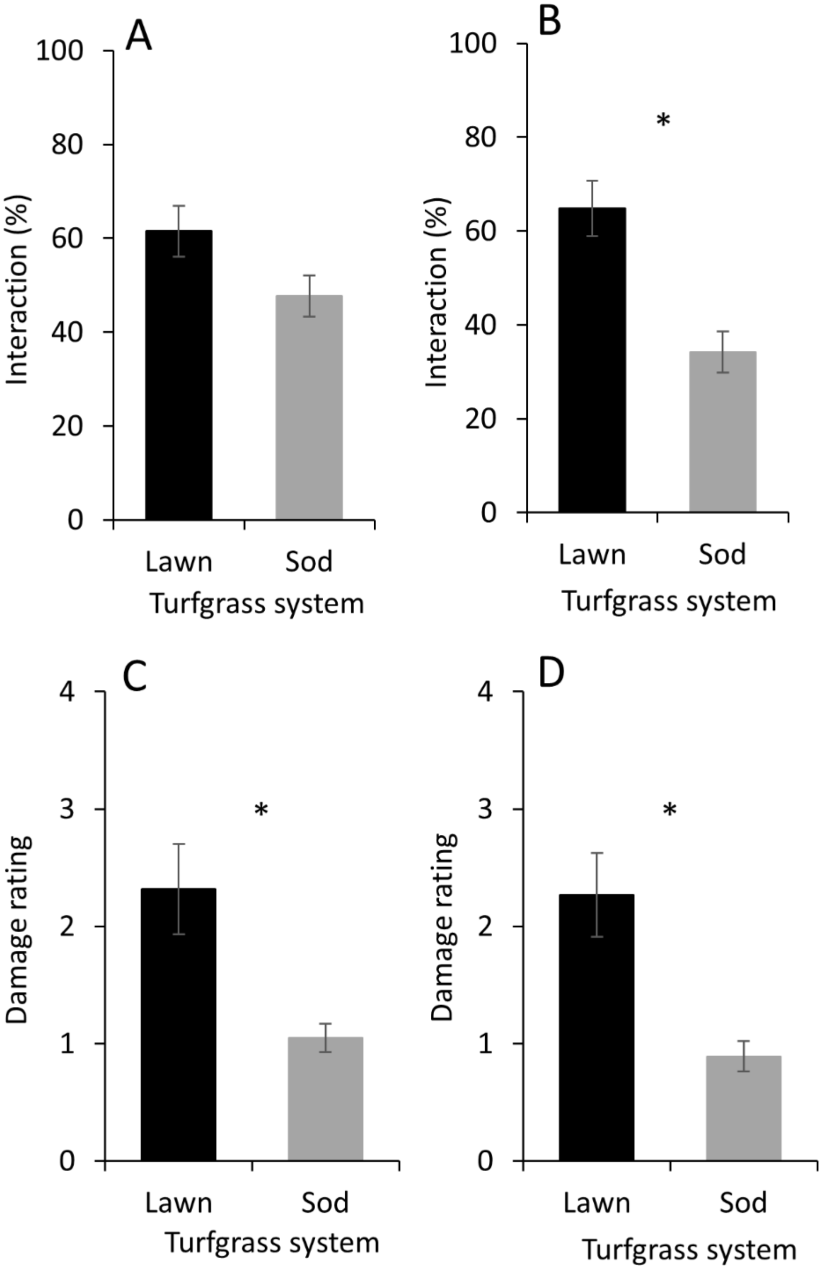

Fig. 5.4. Mean (±SE) predatory activity on clay model cards during (A) June 2020 and (B) August 2020; mean (±SE) damage rating during (C) June 2020 and (D) August 2020. Asterisks above pairs of bars indicate significant differences (independent sample *t* test, $P < 0.05$. Non-significant data lack asterisks.

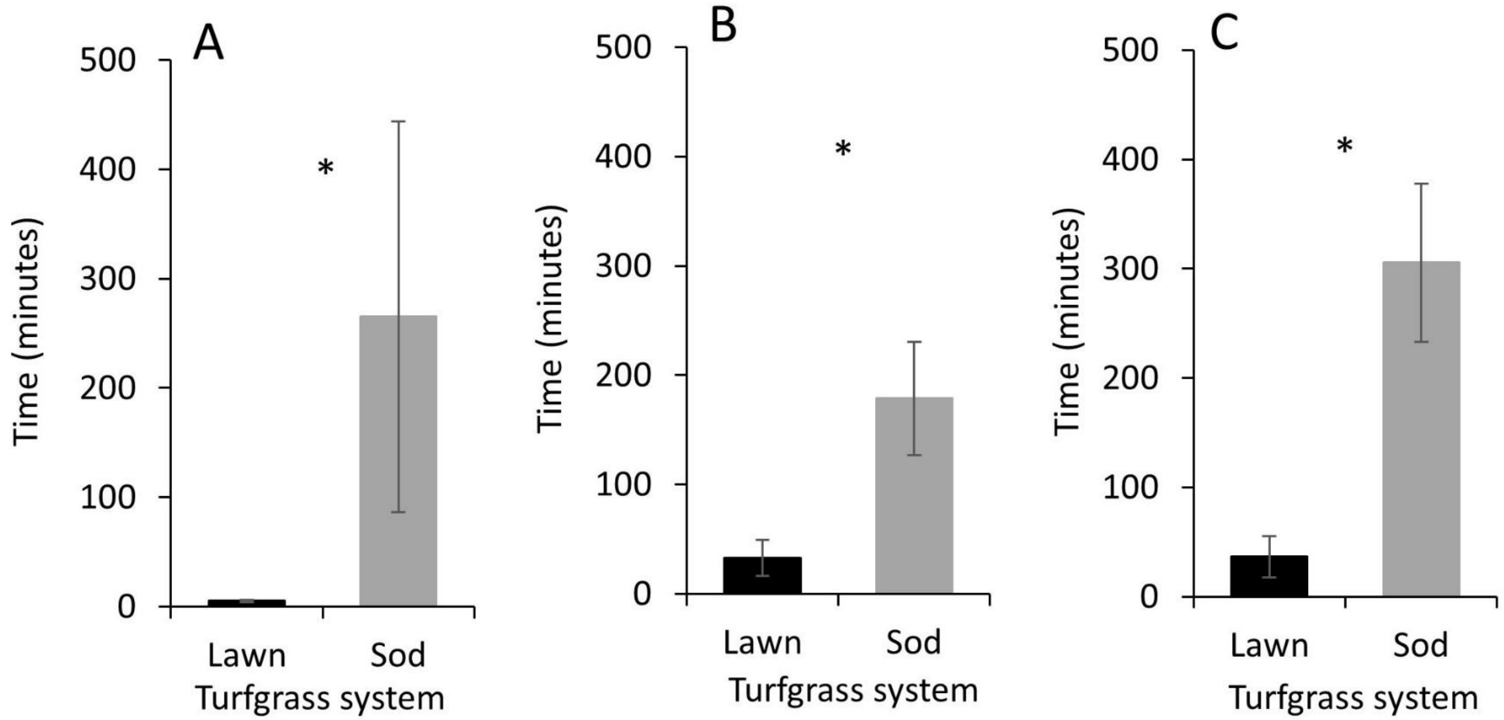

Fig. 5.5. Mean (± SE) time in minutes to first predatory event on live sentinel larvae recorded using time-lapse cameras during (A) October 2019, (B) June 2020, and (C) August 2020. Asterisks above pairs of bars indicate significant differences (independent sample *t* test, $P < 0.05$).

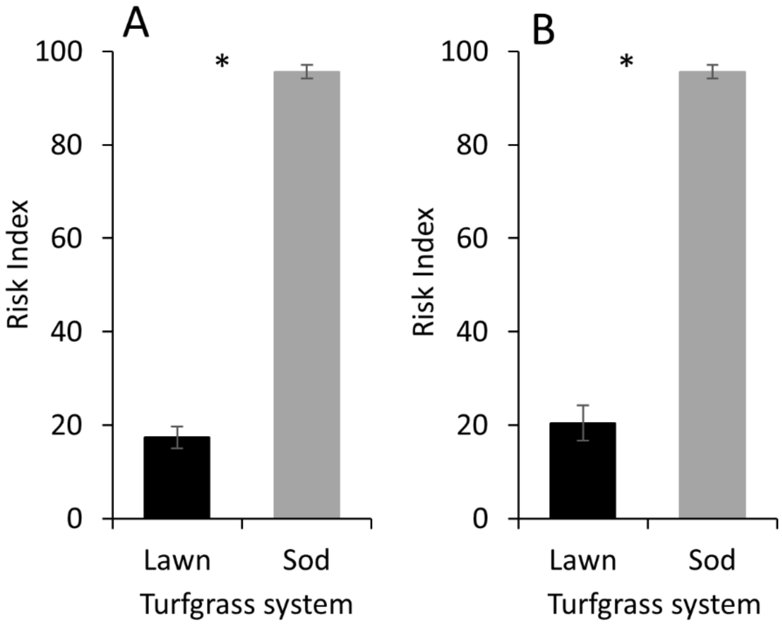

Fig. 5.6. Risk index values for residential lawns and sod farms during (A) April-October 2019 and (B) April-October 2020. Asterisks above pairs of bars indicate significant differences (independent sample *t* test, $P < 0.05$).

CHAPTER 6

EFFECTS OF WATER-DEPRIVED TURFGRASS ON FALL ARMYWORM AND ITS PREDATOR, INSIDIOUS FLOWER BUG

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ABSTRACT Turfgrass, being a water-demanding plant, is susceptible to changes in levels of water content. Climate-change-mediated prolonged droughts can potentially affect plants, herbivores, and predators. Thus, it is important to understand how herbivores, such as fall armyworm *Spodoptera frugiperda* (JE Smith) (Lepidoptera: Noctuidae) and its predator, *Orius insidiosus* (Say) (Hemiptera: Anthocoridae), respond to changing levels of water deprivation. The objective of the study was to determine the effects of water deprivation on *S. frugiperda* and *O. insidiosus* when feeding on drought-tolerant bermudagrass (*Cynodon* spp.) 'TifTuf' and drought-susceptible 'Tifway.' Three levels of water-deprived conditions were created by adding 60, 36, and 18 mL per 1.5 L pot in a greenhouse. The neonates of *S. frugiperda* and adults *O. insidiosus* were caged on turfgrass pots in a three-way factorial design. The treatments were three levels of water deprivation, two levels of the predator (present or absent), and two levels of turfgrass. The percentage larval mortality weight, length, and head capsule width were measured. The results showed that a significantly greater larval mortality was observed in the presence of *O. insidiosus* across all water levels than during its absence. The larval weight of *S. frugiperda* was significantly greater for the fully and moderately watered treatments than for the sparsely watered treatment. Overall, predaceous activity of *O. insidiosus* remained unaffected at various water levels and the bermudagrass cultivars, whereas the performance of *S. frugiperda* deteriorated with an increase in water deprivation regardless of bermudagrass cultivar.

KEYWORDS: water deprivation, turfgrass, herbivore, predator, predator-prey interactions

Turfgrass covers 1.9% of urban and rural landscapes in the US and offers various aesthetic, economic, and functional benefits (Beard and Green 1994, Monteiro 2017). The expanding urbanization is expected to increase the turfgrass area in the US (Robbins and Birkenholtz 2003). Currently, the turfgrass industry in Georgia contributes $7.8 billion USD annually (Wolfe and Stubbs 2020). Turfgrass requires a continuous supply of water for normal growth and development (Kopp and Jiang 2015). The water usage for turfgrass maintenance could be indicated by the residential outdoor water use, accounting for 22–67% of the total household water consumption depending on the weather conditions (Mayer et al. 1999). Municipalities or local government entities impose water use restrictions during drought periods, especially outdoor water use, to manage domestic water consumption. These restrictions can compound the need for water and can negatively affect the normal growth and development of turfgrass (Hejl et al. 2021).

Although turfgrass morphology and physiology are severely affected when deprived of water, turfgrass copes with water scarcity periods with elevated water potential by increasing water uptake and decreasing water loss, referred to as dehydration avoidance mechanism (Zhou et al. 2012). Bermudagrass [*Cynodon dactylon* (L.) Pers.] has higher water use efficiency than other warm-season turfgrass species, such as centipedegrass [*Eremochloa ophiuroides* (Munro.) Hack.], St. Augustinegrass [*Stenotaphrum secundatum* (Walt.) Kuntze], and zoysiagrass (*Zoysia* spp.) and can tolerate water-scarce conditions for a prolonged period (Zhou et al. 2012, 2013, Katuwal et al. 2020). Previously, Jespersen et al. (2019) showed that ‘TifTuf’ bermudagrass maintained relatively lower canopy temperatures and greater retention of osmolytes than other bermudagrass cultivars suggesting that ‘TifTuf’ bermudagrass is more tolerant to drought conditions (Jespersen et al. 2019). Thus, the ability to tolerate drought conditions varies across bermudagrass cultivars.

Water deprivation-mediated effects on plant biology can carry over to the dependent herbivores and affect their survival and development (Huberty and Denno 2004). Studies have shown variable responses to water-stressed plants for sucking and chewing herbivores. On piercing and sucking insects, such as aphids, studies showed that host selection and feeding performance of aphids is reduced on water-stressed plants, possibly due to the increased plant defenses and decreased phloem pressure (Kansman et al. 2020, 2021, Leybourne et al. 2021). On chewing herbivores, the results are mixed where water-stressed plants induced favorable, unfavorable, or no effects on their biology (Huberty and Denno 2004, Duan et al. 2021). Moreover, water-deprived conditions of the plant affect the feeding behavior and survival of the herbivore insect (Marín et al. 2020, Leybourne et al. 2021).

Water deprivation can also influence the well-being of the higher trophic levels, such as predators, by inducing positive or negative effects on the predatory insects. For example, the larch ladybird *Aphidecta obliterata* (L.) (Coleoptera: Coccinellidae) and two-spotted lady beetle *Adalia bipunctata* (L.) (Coleoptera: Coccinellidae) demonstrated increased consumption of green spruce aphid, *Elatobium abietinum* (Walker) (Hemiptera: Aphididae) when feeding on water-stressed Sitka spruce [*Picea sitchensis* (Bong.) Carr.] saplings (Banfield-Zanin and Leather 2016). On the contrary, *Macrolophus pygmaeus* Rambur (Hemiptera: Miridae) demonstrated a decrease in the egg consumption of Mediterranean flour moth, *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae), and a reduced longevity when fed on water-stressed tomato (*Solanum lycopersicum* L.) plants (Han et al. 2015). Thus, it is critical to understand how predators handle their diet under the water-deprived condition of the host plants.

The fall armyworm *Spodoptera frugiperda* (JE Smith) (Lepidoptera: Noctuidae) is a serious turfgrass pest in the US. It is unclear how drought condition affects the larval stages of *S. frugiperda* population and their common predators. Many anthocorid predators, including insidious flower bug, *Orius insidiosus* (Say) (Hemiptera: Anthocoridae), occur in the turfgrass system and can devour young instars of *S. frugiperda* (Joseph and Braman 2009). Thus, the objective of the study was to determine the effects of water-deprivation on the neonates of *S. frugiperda* and adults of *O. insidiosus* under the drought-tolerant and susceptible bermudagrass cultivars.

Materials and Methods

Plants and general methods

Two bermudagrass cultivars, drought-susceptible ‘Tifway’ and drought-tolerant ‘TifTuf’ were planted and maintained in a greenhouse at the University of Georgia Griffin campus, Griffin, Georgia, U.S. in 2019 and 2020. The turfgrass plugs were obtained from certified turfgrass plots. The turfgrass plots were not exposed to insecticides but irrigated daily. The plugs of turfgrass cultivars were planted in 1.5 L plastic nursery pots in white, 0.125-0.25 mm sand medium (topdressing sand, Butler Sand Company, Butler, Georgia, USA). The eight drain holes in the bottom of the pot were covered using a 14 × 14 cm nylon mesh (length × width) to prevent the loss of the sand particles from the pot. Each pot was filled with ~2250 g of sand; however, some sand was lost from pots during the routine irrigation and fertilizer applications. The potted plants were maintained in a greenhouse. Turfgrass plants were irrigated daily using a water shower wand. The potted turfgrass was fertilized at weekly intervals with 20:20:20 N:P:K (Plant Foods, Inc., Vero Beach, Florida, USA) at 5.93 g/L of water. Each pot received 100 mL of the fertilizer solution. Turfgrass blades were clipped each week at ~6 cm height from the sand media. The potted turfgrasses were maintained for nine months before initiating the first round of the trial and three months before repeating the same experiment the second time.

Insects

The first instars of *S. frugiperda* were used in the experiment. *S. frugiperda* eggs were purchased from a commercial insectary (Benzon Research Inc., Carlisle, Pennsylvania, USA). The eggs laid on the paper towels were carefully put into the clear, round 18.4 × 7.4 cm plastic container (diameter × height) and were sealed using parafilm (Bemis Company Inc., Oshkosh, Wisconsin, USA). The eggs were incubated in an environmentally controlled chamber (Model I-36LL, Percival Scientific, Perry, Iowa, USA) at 28 °C, 40% relative humidity, and L16:D8 photoperiod for 48 h. First instars of *S. frugiperda* were used in the experiment.

O. insidiosus adults were purchased from commercial insectary (Insidiosus-System®, Biobest USA Inc., Romulus, Michigan, USA), and viability of adult bugs was checked upon arrival. The adults were temporarily stored in an insulated Styrofoam box for 24 h at ~7 °C after adding a couple of ice cubes to maintain their survival.

Water regimes

Three water deprivation regimes were generated, 1) fully watered, 2) moderately watered, and 3) sparsely watered by adding 60, 36, or 18 mL of water daily. The amount of water required for fully-watered treatment was determined after adding a known amount until pots dripped excess water. This process was repeated with six pots, and the average amount of water was determined. The water requirement for moderately and sparsely watered treatments was determined by calculating 60% and 30% of 60 mL, respectively. The net weight gain of pots was also determined after measuring the weights at pre-and post-water application to pots for each water deprivation treatment. A 1000 mL plastic container 13.9 × 21.6 cm (diameter × height) with 21 holes (0.3 cm diameter) was used to evenly deliver water to the potted grass by holding the container above the grass canopy.

Cages

Cages were built to prevent *S. frugiperda* larvae and *O. insidiosus* adults from escaping from the turfgrass canopy. A 0.05 × 60 × 10.2 cm (height × length × width) transparent acrylic sheet (Cat. # AF.0202448, ePlastics, San Diego, California, USA) was cut and rolled lengthwise so that both ends overlapped to form 15.2 × 10.2 cm (diameter × height) hollow cylinder (Fig. 6.1A). The overlap region was stapled together. A 22.9 × 22.9 cm white polyester no-see-um mesh (Cat. #7250NSW, BioQuip Inc., Rancho Dominguez, California, USA) (Fig. 6.1B) was cut and attached to the open end of the hollow cylinder using a clear heavy-duty packaging tape (3M Co., Saint Paul, Minnesota, USA). The resulting cylindrical cage was inserted on the top of the pot, forming a cage.

Experimental setup

Twenty first-instars of *S. frugiperda* were transferred into each pot using a paintbrush. For those pots that received predators, 10 *O. insidiosus* adults were introduced to the pots. The pots were covered with the cage immediately after introduction (Fig. 6.1C-D). The *S. frugiperda* and *O. insidiosus* introductions were conducted at 21 °C, and the pots were transferred to the greenhouse at 28 °C and natural 14:10 light: dark period during July. The *O. insidiosus* adults were starved for 6 h at 21 °C before introduction into the pots using aspirators.

First, the water treatments were initiated for 7 d. On the 8th day, *S. frugiperda* neonates and *O. insidiosus* adults were introduced and retained in the cages for seven more days with daily water. The experiment was arranged in a factorial design. The factors were water deprivation at three levels (fully, moderately, and sparsely watered), predator at two levels (present or absent), and turfgrass cultivar at two levels (‘TifTuf’ and ‘Tifway’). The factor-level combinations were replicated nine times.

Evaluation

After 7 d of post-introduction, the cages were removed, and the pots were held upside down over a 27.9 × 21.6 cm white paper. The turfgrass was gently brushed 20 times by hand to recover *S. frugiperda* larvae then pots were closely inspected under an incandescent lamp to ensure all the *S. frugiperda* larvae were recovered. The number of *S. frugiperda* larvae recovered from each pot was documented and were individually transferred to plastic vials. The larval head capsule width and body length were measured using Vernier caliper (model #1468417, General UltraTech, Friendswood, Texas, USA), and the weight was recorded using a digital balance (model #AX423/E, Ohaus Co., Parsippany, New Jersey, USA).

Statistical analyses

The statistical analyses for all of the experiments were conducted using SAS software (SAS Institute 2012). To calculate the percentage larval mortality, the number of recovered *S. frugiperda* larvae was subtracted from the total number of larvae introduced in each replication. Then the number of missing larvae was divided with 20 larvae introduced and multiplied by 100. The data representing percentage mortality data, weight, length, and head capsule width were subjected to three-way analysis of variance (ANOVA) using the PROC GLIMMIX procedure to observe the individual effects as well as the two- and three-way interaction effects of the treatments, water deprivation levels, turfgrass cultivars, presence or absence of predator, on the larval mortality, weight, length, and head capsule width.

To determine the effects of water deprivation and cultivar, the larval mortality, weight, length, and head capsule width data were subjected to one-way ANOVA using the PROC

GLIMMIX procedure in SAS. This procedure used a generalized linear mixed model with Gamma distribution for percentage larval mortality and Poisson distribution for larval weight, length, and head capsule width, along with log link function. The data were sorted by cultivar using the PROC SORT statement. Means were separated using the Tukey-Kramer HSD posthoc test at α = 0.05.

Pearson's correlation analyses were performed between weights of pots, larval mortality, weight, length, and head capsule width using the PROC CORR procedure in SAS.

Results

Trial 1

The larval weight was significantly greater for moderately watered treatment than the fully and sparsely watered treatments (Fig. 6.2B, Table 6.1). However, the larval length and head capsule width were not significantly different among water deprivation treatments (Fig 6.2, Table 6.1). The larval mortality, weight, length, and head capsule width were not significantly different between turfgrass cultivar treatment (Fig. 6.2, Table 6.1). The percentage mortality of *S. frugiperda* larvae was significantly greater with adult *O. insidiosus* than without *O. insidiosus* (Table 6.1; Fig. 6.3A). The larval weight (Table 1; Fig. 3B), length (Table 1; Fig. 3C), and head capsule width (Table 1; Fig. 3D) were significantly lower with adult *O. insidiosus* than without *O. insidiosus*.

The water deprivation and turfgrass cultivar interaction was significantly different for *S. frugiperda* larval length and head capsule width (Table 6.1). However, the same interaction was not significantly different for larval mortality, weight, and head capsule width. The one-way ANOVA result was conducted for water deprivation treatment by turfgrass cultivar for larval length. The larval length was significantly greater for the sparsely watered and moderately watered treatments than for the fully watered treatment in ‘TifTuf’(*F* = 5.1; 2, 50, *P* = 0.010; Fig. 6.4A), whereas in ‘Tifway,’ the larval length was significantly greater for fully watered and moderately watered treatments than for sparsely watered treatment (*F* = 6.7; 2, 50, *P* = 0.003; Fig. 6.4A). The head capsule width was not significantly different for ‘TifTuf’ (*F* = 0.2; 2, 50, *P* = 0.799) or ‘Tifway’ (*F* = 0.8; 2, 50, *P* = 0.0.475; Fig 6.4B).

There were no significantly different interactions between turfgrass cultivar and *O. insidiosus* status as well as between water deprivation and *O. insidiosus* status (Table 1) on *S. frugiperda* larval mortality, weight, length, and head capsule width. The three-way interaction among water deprivation, turfgrass cultivar, and *O. insidiosus* was not significantly different for larval mortality, weight, length, and head capsule width (Table 6.1).

Trial 2

The larval mortality was significantly greater for sparsely watered treatment than moderately and fully watered treatment (Table 6.1; Fig. 6.2A). The larval weight was significantly lower for sparsely watered treatment than moderately watered treatment followed by fully watered treatment (Table 6.1; Fig. 6.2B). The larval length was significantly greater for fully and moderately watered treatments than for the sparsely watered treatment (Table 6.1; Fig. 6.2C). The larval head capsule width was not significantly different among water deprivation treatments (Table 6.1; Fig. 6.2D). The turfgrass cultivar treatment was not significantly different for larval mortality, weight, length, and head capsule width (Table 6.1). The percentage mortality of *S. frugiperda* larvae was significantly greater with adult *O. insidiosus* than without *O. insidiosus* (Table 6.1; Fig. 6.3A). The larval weight (Table 6.1; Fig. 6.3B), length (Table 6.1; Fig. 6.3C), and head capsule width (Table 6.1; Fig. 6.3C) were significantly lower with adult *O. insidiosus* than without *O. insidiosus*.

The water deprivation and turfgrass cultivar interaction was only significantly different for larval head capsule width but not significantly different for larval mortality, weight, and length (Table 6.1). The one-way ANOVA was conducted for water deprivation treatment by turfgrass cultivar for larval head capsule width and there were no significant differences among water deprivation treatments for 'TifTuf' (*F* = 2.1; 2, 50, *P* = 0.129) or 'Tifway' (*F* = 0.1; 2, 50, *P* = 0.955; Fig 6.5). The turfgrass cultivar and *O. insidiosus* status interaction was not significantly different for *S. frugiperda* larval weight, length, and head capsule width (Table 6.1).

The water deprivation and *O. insidiosus* status interaction was significantly different for larval mortality, weight, and length but not for larval head capsule width (Table 6.1). The one-way ANOVA was conducted for water deprivation treatment by *O. insidiosus* status for larval mortality, weight, and length. The larval mortality was not significantly different among water deprivation treatments when *O. insidiosus* adults were present (*F* = 0.6; 2, 50, *P* = 0.556; Fig. 6.6A), whereas in the absence of *O. insidiosus* adults, *S. frugiperda* larval mortality was significantly greater for sparsely watered treatment than for fully and moderately watered treatments (*F* = 6.6; 2, 50, *P* = 0.003; Fig. 6.6A). The *S. frugiperda* larval weight was significantly greater for fully and moderately watered treatments than for sparsely watered treatment with *O. insidiosus* adults present (*F* = 56.5; 2, 50, *P* < 0.001; Fig. 6.5B); whereas, in the absence of *O. insidiosus* adults, larval weight was significantly greater in fully watered treatment than moderately watered treatment followed by sparsely watered treatment (*F* = 309.8; 2, 50, *P* < 0.001; Fig. 6.6B). When *O. insidiosus* adults were present, the larval length was significantly greater for moderately watered treatment than for fully and sparsely watered treatments (*F* = 5.4; 2, 50, *P* < 0.001; Fig. 6.6C), whereas the larval length was significantly greater for fully and moderately watered treatments than for scarcely watered treatment (*F* =

17.4; 2, 50, *P* < 0.001; Fig. 6.6C).The larval mortality, larval weight, length, and head capsule width were not significantly different on water deprivation, turfgrass cultivar, and *O. insidiosus* three-way interaction (Table 6.1).

In trial 1, Pearson's correlation analysis showed that *S. frugiperda* larval mortality was negatively correlated with weight, length, and head capsule width (Table 6.2). Significant positive correlations were observed between the larval weight, length, and head capsule width. There was a significantly positive association between larval length and head capsule width. In trial 2, a significantly negative correlation was observed between *S. frugiperda* larval mortality and pot weight (Table 6.2). The pot weight was significant, positively associated with larval weight. There were significant negative correlations between larval mortality and weight, length, and head capsule width. A positive correlation was found between larval weight and larval length, as well as larval weight and head capsule width. The larval length showed a significantly positive association with head capsule width (Table 6.2).

Discussion

Climate change-driven extreme precipitation patterns, such as frequent or intensive rainfall and prolonged drought, are expected to cause reduced soil moisture and decreased water availability to plants (Knapp et al. 2008, Post and Knapp 2020). Water deprivation can lead to dramatic changes in plant physiology, which could affect multiple trophic levels, especially the dependent invertebrate communities on plants (Huberty and Denno 2004, Barnett and Facey 2016, Post and Knapp 2020). The results from the current study showed that the development of *S. frugiperda* larvae was greater on turfgrass when water is moderately or abundant available than when scarce. The mortality of *S. frugiperda* larvae was more severe on turfgrass when water availability was scarce than moderately available. *O. insidiosus* adults cause greater levels of *S.*

frugiperda larval mortality on turfgrass regardless of turfgrass cultivar or water availability, which indicates the predation of *O. insidiosus* is neither affected by water deprivation nor turfgrass cultivar. The current study provides a novel, important evidence of the effect of water deprivation on the herbivore and predators in turfgrass.

The survival and bodyweight of *S. frugiperda*, was greater on the treatments with full and moderate water availability than the sparsely watered treatments. This supports the plant vigor hypothesis where well-watered plants improve herbivore performance on vigorous or nonstressed plants (Price 1991). However, the performance of lepidopteran herbivores varies by plant stress status. When the feeding performance of two lepidopterans was studied on well-watered and stressed *Alliaria petiolata* (M.Bieb.) Cavara & Grande plants, *Pieris brassicae* (L.) consumed more leaves of healthy plants than leaves of stressed plants. In contrast, the *Spodoptera littoralis* (Boisduval) caused more feeding damage on the stressed plants than on the healthy plants (Gutbrodt et al. 2011). Similarly, the performance of a nymphalid, *Danaus plexippus plexippus* (L.), was better on the previously damaged and water-stressed *Asclepias syriaca* L. (Apocynaceae) plants than relative less damaged and water-stressed plants (Hahn and Maron 2018). These contrasting development patterns of lepidopteran larvae on stressed and non-stressed plants vary by herbivore species and their feeding choices (Gutbrodt et al. 2011).

Adults of *O. insidiosus* demonstrated high levels of predation of *S. frugiperda* larvae across all three water deprivation levels and two bermudagrass cultivars, indicating its potential to manage early instars of *S. frugiperda* under water-deprived conditions. Water stress could also induce bottom-up effects on the omnivorous predator. Han et al. (2015) showed that the life span and egg predation of *E. kuehniella* Zeller was reduced when exposed to omnivorous predator, *Macrolophus pygmaeus* Rambur (Hemiptera: Miridae) on water and nitrogen stressed tomato plants. The negative bottom-up effects from plant to predator can also depend on the ability to tolerate plant stress. Many studies have shown that bermudagrass genotypes are tolerant to water-deprived conditions compared to other warm-season turfgrass species, including centipedegrass, St. Augustinegrass, and zoysiagrass (Zhou et al. 2012, 2013, Katuwal et al. 2020). Thus, in the current study, it is a possibility that the superior predaceous performance of *O. insidiosus* under varied water deprivation conditions was related to superior tolerance traits of bermudagrass to water deprivation. However, the survival of *O. insidiosus* adults was not recorded in the current study. Therefore, more detailed and longer-term follow-up studies are required to understand the survival and life cycle parameters under water-deprived turfgrass.

In summary, the results showed that water deprivation has direct, negative effects on *S. frugiperda* larval survival and development. The current study highlights the potential of *O. insidiosus* to manage early instars of *S. frugiperda* under fully-watered and water-deprived turfgrass cultivars. More studies are warranted to understand the survival and development of the *O. insidiosus* in different turfgrass species and their cultivars grown at varied water deprivation levels, which could help improve the integrated pest management programs in various turfgrass systems.

Acknowledegments

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Table 6.1. Analysis of variance showing the effect of the water deprivation, turfgrass cultivar, predator, and their interactions on percentage *S. frugiperda* larval mortality and larval weight, length, and head capsule width in trial 1 and 2.

Trial	Treatment	Mortality			Weight			Length			Head capsule width		
		F	df	*P*	*F*	df	*P*	*F*	df	*P*	*F*	df	*P*
1	Water[a]	1.7	2, 88	0.194	4.4	2, 95	0.015	0.8	2, 95	0.459	0.6	2, 95	0.568
	Turfgrass[b]	0.1	1, 88	0.812	3.8	1, 95	0.056	0.8	1, 95	0.384	2.3	1, 95	0.136
	Predator[c]	70.8	1, 88	<0.001	15.8	1, 95	<0.001	31.3	1, 95	<0.001	36.5	1, 95	<0.001
	Water × Turfgrass	0.7	2, 88	0.484	2.5	2, 95	0.085	3.6	2, 95	0.030	3.2	2, 95	0.046
	Turfgrass × Predator	0.0	1, 88	0.919	0.0	1, 95	0.984	0.1	1, 95	0.830	0.5	1, 95	0.494
	Water × Predator	2.8	2, 88	0.064	0.1	2, 95	0.948	0.3	2, 95	0.764	0.7	2, 95	0.499
	Water × Turfgrass × Predator	2.3	2, 88	0.102	0.7	2, 95	0.502	1.6	2, 95	0.216	2.7	2, 95	0.073
2	Water	6.7	2, 88	0.002	12.4	2, 95	<0.001	5.3	2, 95	0.007	2.8	2, 95	0.069
	Turfgrass	0.4	1, 88	0.508	2.4	1, 95	0.126	0.0	1, 95	0.859	0.0	1, 95	0.836
	Predator	382.7	1, 88	<0.001	63.7	1, 95	<0.001	101.3	1, 95	<0.001	104.1	1, 95	<0.001
	Water × Turfgrass	2.5	2, 88	0.088	2.8	2, 95	0.069	2.6	2, 95	0.082	3.2	2, 95	0.047
	Turfgrass × Predator	0.6	1, 88	0.449	0.0	1, 95	0.956	0.1	1, 95	0.754	0.1	1, 95	0.706
	Water × Predator	6.9	2, 88	0.002	5.9	2, 95	0.004	3.3	2, 95	0.040	3.1	2, 95	0.052
	Water × Turfgrass × Predator	0.9	2, 88	0.399	0.2	2, 95	0.820	0.4	2, 95	0.662	0.6	2, 95	0.557

[a] Water deprivation = Three levels – fully watered (60 mL), moderately watered (36 mL), and sparsely watered (18 mL)
[b] Turfgrass cultivar = Two levels – 'TifTuf' and 'Tifway' bermudagrass
[c] Predator = Two levels – presence and absence of adult *O. insidiosus* with *S. frugiperda* neonate

Table 6.2. Pearson's correlation between pot weight, larval mortality, weight, size, and head capsule width during 2020 and 2021

Year	Variable	Pot weight (g)	Mortality (%)	Weight (mg)	Length (mm)	Head capsule width (mm)
1	Pot Weight (g)					
	Larval mortality (%)					
	Body weight (mg)		-0.398***			
	Body length (mm)		-0.504***	0.899***		
	Head capsule width (mm)		-0.504***	0.842***	0.961***	
2	Pot Weight (g)					
	Larval mortality (%)	-0.194*				
	Body weight (mg)	0.345***	-0.626***			
	Body length (mm)		-0.729***	0.907***		
	Head capsule width (mm)		-0.745***	0.850***	0.979***	

The notations indicate the correlation (*P*: *, <0.05; **, <0.01; and ***, <0.001) between different variables

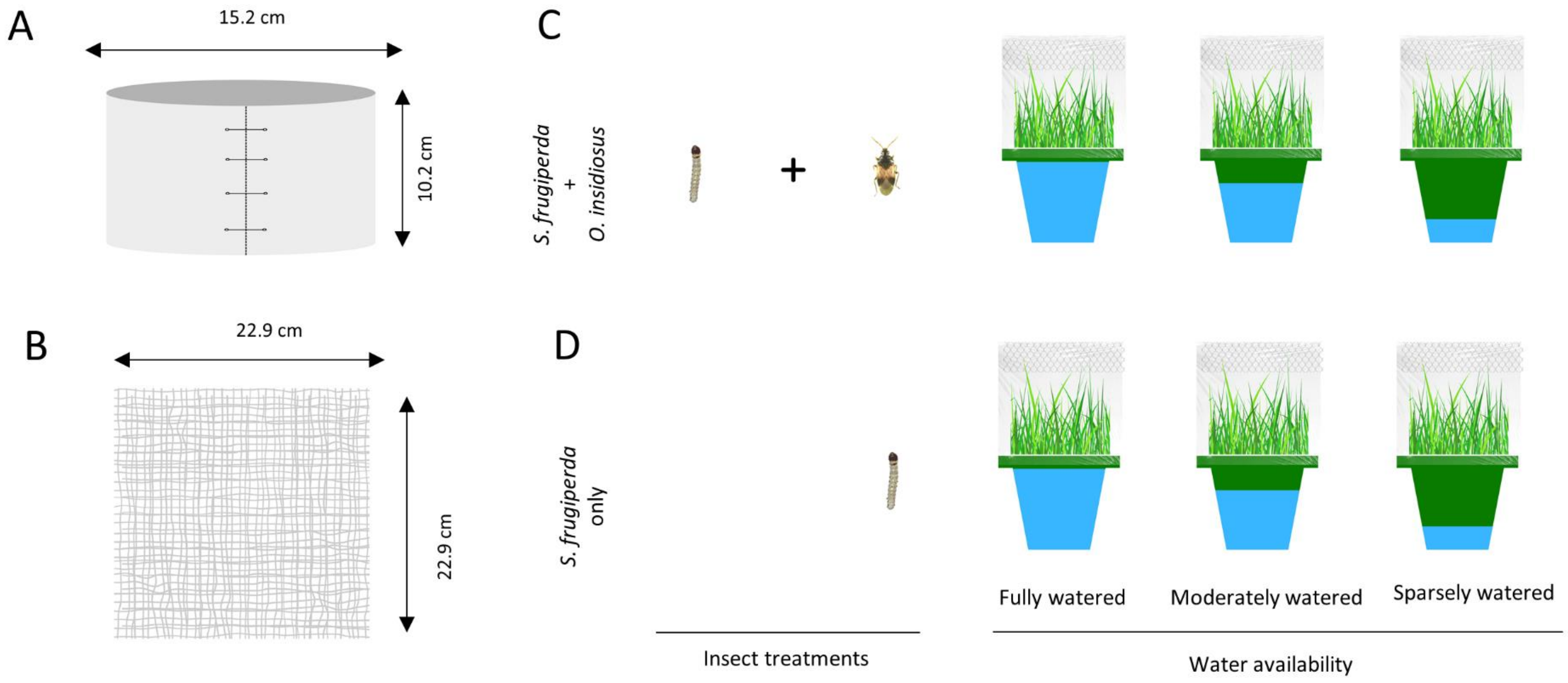

Fig. 6.1. Schematic diagram of experimental setup: (A) *S. frugiperda* + *O. insidiosus*, (B) *S. frugiperda* only treatments released on turfgrass pots at fully, moderately, and sparsely watered treatments (C) rolled hollow cylinder of transparent acrylic sheet and (D) white polyester no-see-um mesh.

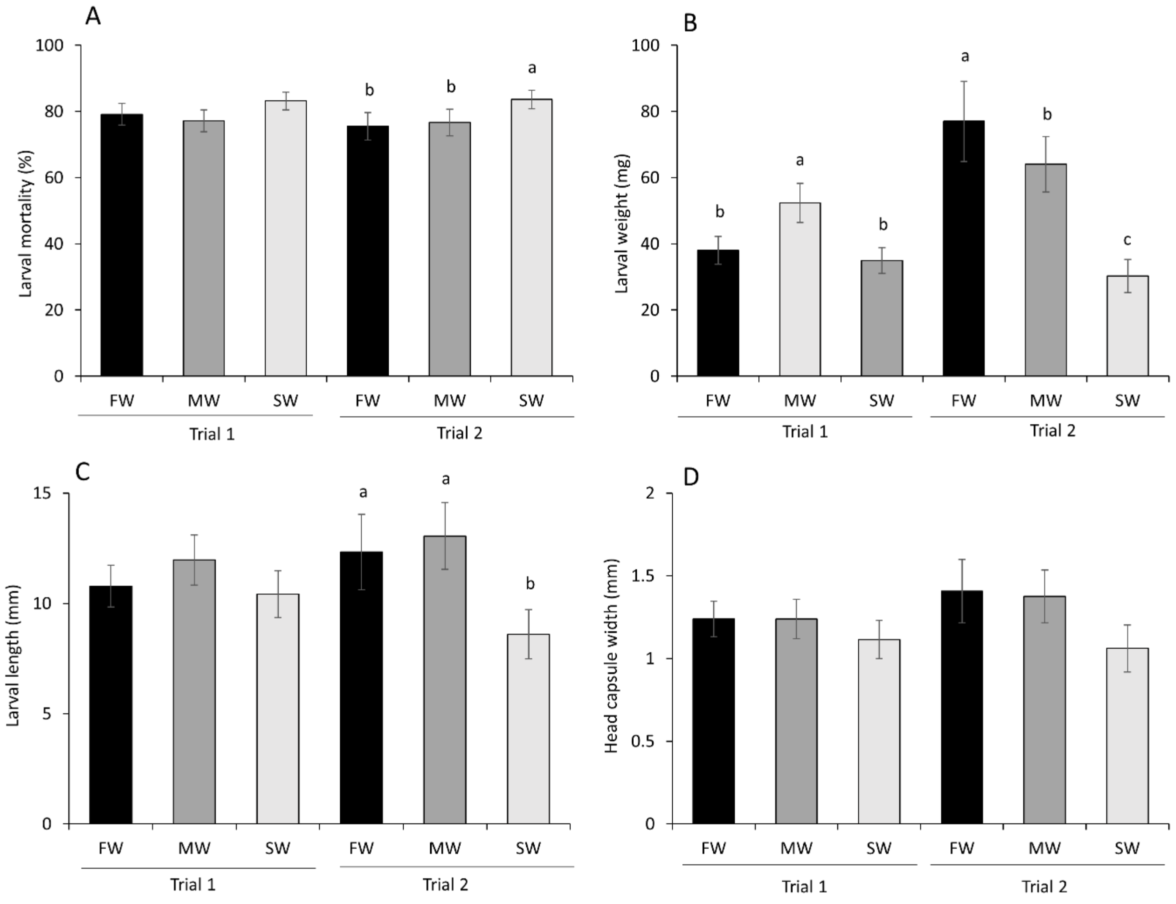

Fig. 6.2. Mean (±SE) *S. frugiperda* larval (A) mortality (B) weight (mg) (C) length (mm) and (D) head capsule width (mm) for fully (FW), moderately (MW), and sparsely watered (SW) treatments, in trial 1 and 2. Bars within a trial with the same letters are not significantly different (Tukey’s test, α = 0.05).

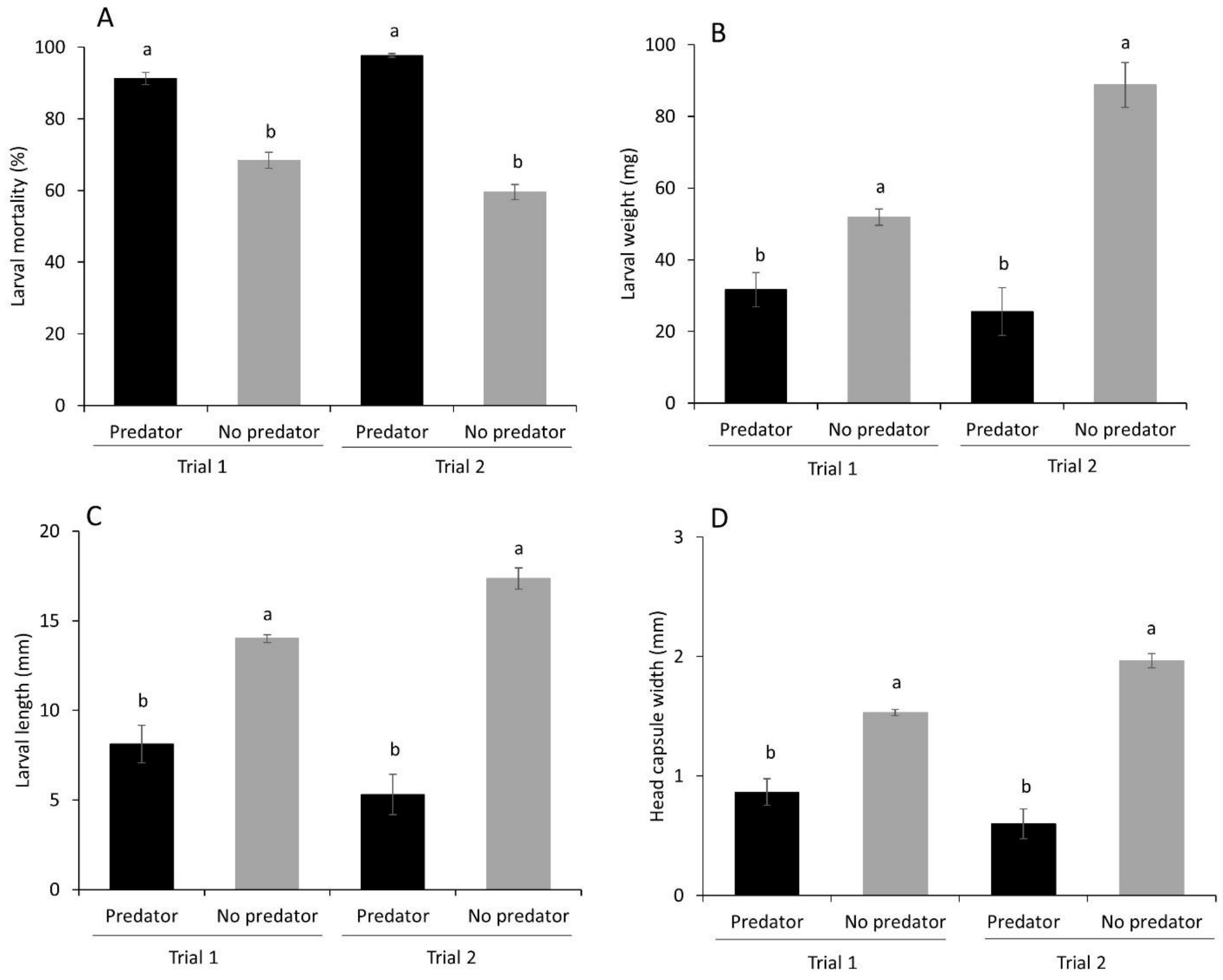

Fig. 6.3. Mean (±SE) *S. frugiperda* larval (A) mortality (%) (B) weight (mg) (C) length (mm) and (D) head capsule width (mm) for with and without adult *O. insidiosus* (predator) treatments in trial 1 and 2. Bars within a trial with the same letters are not significantly different (Tukey's test, α = 0.05).

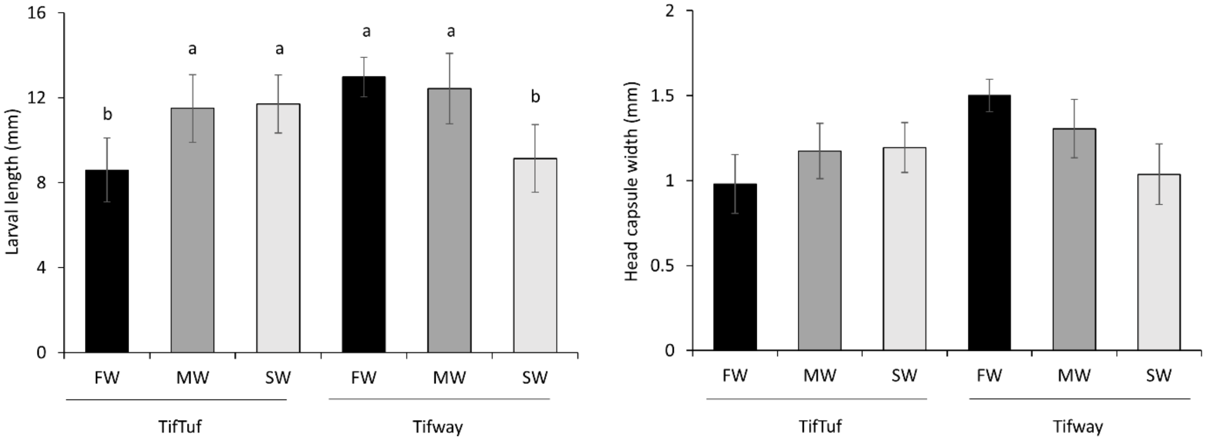

Fig. 6.4. Mean (±SE) *S. frugiperda* larval length recovered from two turfgrass cultivars maintained at fully (FW), moderately (MW), and sparsely watered (SW) treatments in trial 2. Bars within the turfgrass cultivar withthe same letters are not significantly different (Tukey's test, α = 0.05).

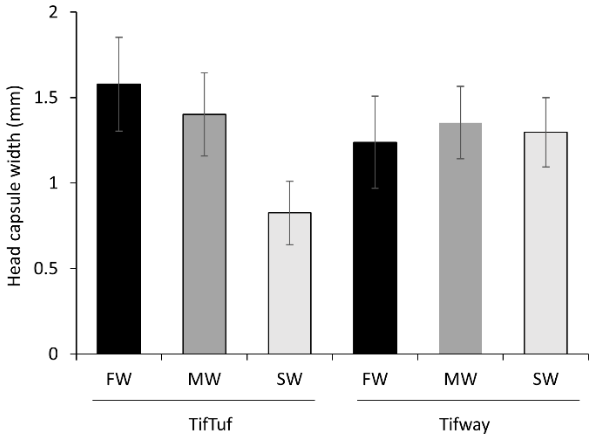

Fig 6.5. Mean (±SE) *S. frugiperda* larval head capsule width (mm) recovered from two turfgrass cultivars maintained at fully (FW), moderately (MW), and sparsely watered (SW) treatments in trial 2. Bars with the same letters are not significantly different (Tukey's test, α = 0.05).

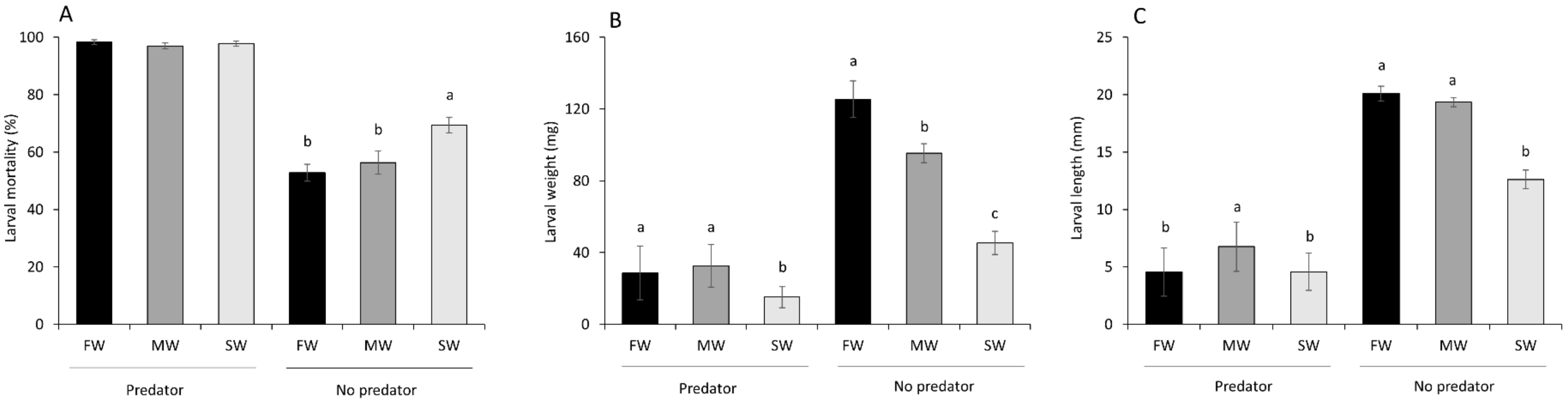

Fig. 6.6. Mean (±SE) *S. frugiperda* larval (A) mortality (%) (B) weight (mg) and (C) length (mm) for with and without adult *O. insidiosus* (predator) treatments recovered from two turfgrass cultivars maintained at fully (FW), moderately (MW), and sparsely watered (SW) treatments in trial 2. Bars within presence or absence of predator with the same letters are not significantly different (Tukey's test, α = 0.05).

CHAPTER 7

SUMMARY

The fall armyworm, *Spodoptera frugiperda* (JE Smith), is a serious lepidopteran pest of turfgrass (Poaceae) in the U.S. Many predators are known to attack larval stages of *S. frugiperda* in turfgrass systems. Because predators hardly leave any evidence of their activity, their role in the various turfgrass system is poorly understood. Although predatory activity can be studied using multiple techniques, clay models were rarely employed in turfgrass. Thus, assays were conducted to determine the types of impressions that common turfgrass arthropods leave on caterpillar-shaped clay models. Nine impression types were characterized after exposing 16 arthropod taxa, and they were scratches, paired marks, pricks, deep distortions, disturbed surfaces, detached segments, granulated surfaces, dents, and elongated scratches. Most arthropods produced scratches and paired marks, whereas granulated surfaces and elongated scratches were produced by only a few selected arthropods. To ensure that the impressions were correctly identified, nonexpert volunteers reviewed the impressions, and they identified those impression types with > 85% accuracy. Video recordings of arthropod interactions were captured to determine the behavior of the arthropods during their first interaction with the clay models. Most arthropods first interacted with the terminal rather than the middle regions of the models. There were no differences between their interactions with the large or small models, and they used their mouthparts as often as their legs. Knowledge of the impression types caused by common arthropods was subsequently used in the field studies in turfgrass.

Although the impressions created by common arthropods were characterized, little is known about the attributes of clay models, such as color, shape, and size, that influence arthropod interactions or are preferred by arthropods in the turfgrass field conditions. Thus, clay models were prepared with varied colors, shapes, and sizes and were exposed during daytime and nighttime in a turfgrass field. The results showed that arthropods interacted with clay models, and various types of impressions were recorded, including paired marks, scratches, cuts, and pricks. Although the color of the clay model had no significant effects on arthropod interactions during the night, significantly greater numbers of impressions were noticed on the blue and green models than on the yellow models during the daytime. The caterpillar-shaped models captured significantly greater densities of impressions than the beetle-shaped models. Additionally, the number of impressions significantly increased with an increase in the size of the model regardless of shape.

The turfgrass is maintained under varying heights, and little is known on how the predator-prey interactions are vertically distributed within the turfgrass canopy. This information can refine the cultural management strategies to enhance and conserve predatory services. Thus, the vertical distribution of predator-prey interactions within the turfgrass canopy was studied. The choice and no-choice experiments were conducted by placing clay models at lower (on soil), intermediate, and upper canopy of turfgrass. The results showed that incidence and severity of impressions were significantly greater on clay models placed at a lower level than those placed at the intermediate and upper levels in the choice and the no-choice experiments. These results would help develop clay models to monitor predators and improve the integrated pest management strategies for key pests, such as *S. frugiperda* in turfgrass.

The occurrence and abundance of predatory fauna in turfgrass systems have been reported; however, the activity of predators was not well documented. Thus, a study was conducted to determine (1) the incidence and (2) the severity of predation in less intensively managed residential lawns and intensively managed sod farms. The percentage of predation on live *S. frugiperda* sentinel larvae and the percentage of interaction and its severity on clay models were significantly greater in the residential lawns than in the sod farms. Among the seven impression types recorded on clay models, paired marks were the most abundant. Four new impression types, deep cut marks, stacked surface marks, scooped marks, and U-shaped marks, were observed on clay models in both turfgrass systems. Formicids were documented at significantly greater densities than were other predatory groups, such as carabids. Thus, the results show the need for enhanced predatory activity in sod farms by developing integrated pest management strategies and adopting measures to conserve natural enemies.

Turfgrass being a water-demanding plant, is susceptible to changes in levels of water content. Climate-change-mediated prolonged droughts can potentially affect plants, herbivores, and predators. Thus, it is important to understand how herbivores, such as *S. frugiperda* and its predator, *Orius insidiosus* (Say) (Hemiptera: Anthocoridae), respond to changing levels of water deprivation. Thus, the study was conducted to determine the effects of water deprivation on neonates of *S. frugiperda* and *O. insidiosus* adults when feeding on drought-tolerant bermudagrass ‘TifTuf’ and drought-susceptible ‘Tifway.’ Three levels of water-deprived conditions were created by adding 60, 36, and 18 mL per 1.5 L pot in a greenhouse. The neonates of *S. frugiperda* and adults *O. insidiosus* were caged on turfgrass pots in a three-way factorial design. The treatments were three levels of water deprivation, two levels of the predator (present or absent), and two levels of turfgrass. The percentage larval mortality weight, length, and head capsule width were measured. The results showed that a significantly greater larval mortality was observed in the presence of *O. insidiosus* across all water levels than during its absence. The larval weight of *S. frugiperda* was significantly greater for the fully and moderately watered treatments than for the sparsely watered treatment. Overall, predaceous activity of *O. insidiosus* remained unaffected at various water levels and the bermudagrass cultivars, whereas the performance of *S. frugiperda* deteriorated with an increase in water deprivation regardless of bermudagrass cultivar. More field studies are warranted in the future to understand the survival and development of the *O. insidiosus* in different turfgrass species and their cultivars grown at varied water deprivation levels, which could help to improve the integrated pest management programs in the turfgrass systems.