

THE EFFECTS OF ROADSIDE MOWING ON BUTTERFLIES (LEPIDOPTERA:
PAPILIONOIDEA AND HESPERIOIDEA) IN NORTH CENTRAL FLORIDA

By

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To my grandmother, Mathilde Halbritter

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LIST OF ABBREVIATIONS

FDOT Florida Department of Transportation

Abstract of Thesis Presented to the Graduate School
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By

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Studies on road ecology and vehicular collisions with animals have primarily focused on vertebrates, leaving invertebrate taxa rather underrepresented. The vegetation in roadside margins in north central Florida is routinely mowed to maintain both highway safety and aesthetics, yet margins have the potential to provide habitat for many invertebrate taxa. The effects of roads on butterflies have not been investigated in Florida.

The first objective of this study was to investigate how varying the mowing frequency affects butterfly (Lepidoptera: Hesperioidea and Papilionoidea) abundance and mortality in highway margins. The second objective was to investigate the effects of mowing frequency on flower abundance and species richness.

Three different mowing treatments were applied to sections of margin along highways in Alachua County, Florida: no mowing, mowing every 6 weeks, and mowing every 3 weeks. Live butterfly abundance was assessed using linear transects and presumably road-killed butterflies were collected from the roadside. Overall relative mortality was calculated and relative mortalities were calculated under each treatment.

Correlations between flower species richness and abundance and butterfly abundance were also investigated. Data were collected from April 29th, 2011 to November 1st, 2011.

Results indicate the mowing treatment had a significant effect on flower abundance and species richness, with the 3-week treatment yielding the lowest abundance and richness. Mowing treatment alone did not have a significant effect on any butterfly variable, but the treatment*time interaction had a significant effect on live butterflies. The data suggest that the no-mow treatment yielded more live butterflies from early August onward. This study offers tentative support for mowing at most every 6 weeks to facilitate greater floral resource abundance in roadside margins. Further research should focus on the population effects of mowing on butterflies and other important pollinators.

CHAPTER 1 LITERATURE REVIEW

Roads in the United States

The expansion of infrastructure in the United States has laid a grid of roads across a vast array of natural habitats. The total public road coverage in 1900 was 3,733,678 km and this figure has been gradually increasing over the past century. As of 2010, the total public road coverage in the United States was 6,572,188 km, with 4,796,618 km being classified as rural roads and the remainder as urban roads under the Federal Highway Administration's functional class system. Urban roads are those that pass through urbanized areas or through small municipalities that have populations of 5,000 or greater. Rural roads are those passing outside of the boundaries of urbanized areas and passing through areas with populations of less than 5,000 (Federal Highway Administration 2012).

Unlike the gradual increase of public road coverage, vehicle kilometers of travel per year have increased at a considerably higher rate than the former. The vehicle kilometers of travel in 2010 totaled 4,774,129 million km, with 1,583,833 million km being driven within the rural functional class (Federal Highway Administration 2012). Although habitats adjacent to roads in rural areas tend to be of higher quality, the narrow strips of land at road edges (i.e. margins) have the potential function as viable habitat in urban areas.

Road Ecology

Roads and vehicle traffic have been implicated in having negative impacts on a number of animal taxa (Ashley and Robinson 1996; Coffin 2007; Forman and Alexander 1998; Mader et al. 1990; McKenna et al. 2001; Smith et al. 1996; Spellerberg 1998;

Taylor and Goldingay 2010; Way 1977). Roads have also been considered to have positive impacts on some taxa by providing habitat or refuge (Coffin 2007; Hopwood 2008; Leach and Recher 1993; Spellerberg 1998; Tshiguvho et al. 1999).

Studies often examine the impacts of roads at localized scales and neglect the impacts on animals at the population level (Taylor and Goldingay 2010). For example, an allegedly positive impact would be increased abundance of animals in a roadside margin. However, it may turn out to be a negative impact on the population if mortality is greater than reproduction and immigration is greater than emigration. Studies that investigate the impacts of roads on nature are part of an emergent field of science known as road ecology.

Road ecology arose from both landscape and ecosystem ecology, and the initial focus was on the negative effects of roads on nature (Road Ecology Center, Davis, CA). The study of road ecology is defined as the biotic and abiotic interactions between roads and natural ecosystems. The infrastructure of roads and similar structures form a road system, and put broadly, road ecology addresses the relationship between road systems and the ecosystem (Forman et al. 2003).

The study has its roots as a more organized discipline in the 1980's. However, road impacts on animals have been addressed for some time through mortality surveys (Haugen 1944; Sperry 1933) and the effects of roadside fences on deer mortality have been investigated (Puglisi et al. 1974; Reed et al. 1982). Way (1976) points out that the first public mention of roads being important for conservation efforts was made in 1976. In the 1980's Florida took great initiative in installing wildlife crossing structures to facilitate safer animal movement (Smith et al. 1996). As long as motorized vehicles

remain the primary mode of transportation, the impacts of roads on wildlife will continually need to be addressed.

Forman and Alexander (1998) identify road ecology as both a “sleeping giant” and a “major frontier,” recognizing that integrating road construction planning and conservation is a great challenge to both science and civilization. They note that recent ecological understanding is nested within five topics: “(a) roadsides and adjacent strips; (b) road and vehicle effects on populations; (c) water, sediment, chemicals, and streams; (d) the road network; and (e) transportation policy planning.” Spellerberg (1998) notes that there are gaps in our understanding of the effects of habitat fragmentation and that many authors believe it will have the greatest impact on nature. Roads are likely to have effects on animal movement, and barrier effects may be the greatest ecological impact of roads on nature (Forman and Alexander 1998). Other effects include alterations to water flow, sediment movement and erosion rate alteration, and chemical pollutants from vehicles, road salts, and herbicides. This thesis focuses primarily on an ecological understanding of roadsides and adjacent strips.

Roadside Mortality

One of the most direct impacts roads can have on mobile animal species is mortality due to collisions with moving vehicles, i.e. roadkills. It is apparent in literature reviews that the majority of studies on roadkills to date have focused on vertebrates (Forman and Alexander 1998; Spellerberg 1998; Taylor and Goldingay 2010). There are comparably fewer studies that investigate invertebrate roadkills and only a handful that focus on butterflies (Bak et al. 1998; McKenna et al. 2001; Munguira and Thomas 1992; Ries and Debinski 2001; Ries et al. 2001; Saarinen et al. 2005; Wynhoff, et al. 2011). Vertebrate mortality is evident in a variety of taxa with varying sizes and movement

capabilities: Florida panthers (*Puma concolor coryi* Bangs 1899) (Maehr et al. 1991), deer (Gangon et al. 2007), reptiles and amphibians (Ashley and Robinson 1996), and sparrows (Hodson 1966).

Traffic volume and vegetative cover have been most often associated with higher roadside mortality of vertebrates (Taylor and Goldingay 2010). Other parameters such as road width, surface texture, and proximity to habitat would likely have varying impacts on different animals. Features of the landscape may also locally influence movement patterns. Areas of high mortality, i.e. roadkill “hot-spots”, are often targeted for mitigation (Taylor and Goldingay 2010). Smaller rural roads can be large contributors to roadkills because of the number of such roads that pass through more suitable habitat (Taylor and Goldingay 2010).

The numbers of roadkills reported for various animal taxa can seem astounding, but it is important to weigh them against estimated population sizes and other sources of mortality. A 6-week study in central Illinois reported 1,824 allegedly road-killed butterflies. This number was extrapolated to 20,000,000 individuals/week state-wide (McKenna et al. 2001), but estimates of the statewide population were not available for comparison. Butterfly roadkills in the United Kingdom were reported to be responsible for a mortality of 0.6-7% of the population, depending on the species (Munguira and Thomas 1992). They argued that roadkills were an insignificant source of mortality compared to natural causes. High numbers of sparrow (*Passer domesticus* Linnaeus 1758) mortalities were reported in Hodson (1966), yet roadkills were unlikely to have affected the population due to the sparrow’s rapid reproductive rate. However, roadkills can have much greater impacts on certain local populations or species in general. The

key deer, *Odocoileus virginianus clavium* Barbour & G. M. Allen 1922, was experiencing significant roadkill rates of approximately 16% of its population (Forman and Alexander 1998).

Habitat Loss and Fragmentation

Habitats that are either directly destroyed or altered by human activity are often rendered unsuitable for the resident biota. Roads can increase human accessibility to natural areas and Coffin (2007) notes that transportation geographers find a positive correlation between road infrastructure growth and economic development. McDonald et al. (2008) predict that urban growth will have localized but cumulatively significant negative effects on ecoregions (i.e. areas that have similar ecosystems), rare species, and protected areas. They find clear evidence that urban areas have increased the threats to survival of several vertebrate species. Gomes et al. (2011) found that relative abundances and species richness of small rodents were negatively affected by urbanization, but the effects varied with species. A long-term study in Rome found that urbanization substantially reduced species richness in the insect groups evaluated (Fattorini 2011a). Urbanization was also shown to increase endangerment of native fish species and the invasion of non-native species in California water sheds (Marchetti et al. 2006), thus the threats of urbanization are not limited to terrestrial environments.

A study in the Cape Floristic Region of South Africa considered intensive agriculture, urbanization, and invasive alien species to be threats to biodiversity (Rouget et al. 2003). They created a predictive model to determine the expanse of the latter three threats and found low overlap between them. Consequently, they argue in favor of a multi-threat approach to assessing conservation planning.

Although habitat alteration is generally regarded as harmful, it is important to consider that habitat alteration does not necessarily always translate to habitat loss. Essentially, when a habitat changes, it is not always the case that the species present are not able to survive the change (Speight et al. 2008). Some organisms are able to tolerate some degree of urbanization provided key resources are still available, as is the case with a skipper butterfly in a coastal sand dune habitat (Leidner and Haddad 2011). Skipper butterflies entered the adjacent urban matrix allegedly due to its low structural contrast with sand dune habitat and the butterflies utilized habitat patches in the matrix to aid in dispersal. Urban areas may even be favorable to certain species, as was the case with open-habitat spiders in Debrecen, Hungary (Magura et al. 2010). The spiders were associated with the higher ground and air temperature in urban areas. Most tenebrionid beetles in urban Rome are common, but urban areas can be important habitats for a few rare species (Fattorini 2011b).

Many organisms rely on dispersal within or between habitats to acquire resources, breed, or escape unsuitable environmental conditions. Hanski (2004) would argue that metapopulations, or groups of populations that interact and are spatially connected, are common in highly fragmented landscapes. Suitable habitat patches and connectivity between them do not persist indefinitely. Loss of the habitat patches increases local extinction rates and lack of connectivity reduces re-colonization, thereby negatively affecting the persistence of the metapopulation (Hanski 1999). It was noted in Wilcox and Murphy (1985) that most ecologists agree that habitat fragmentation poses the greatest threat to biological diversity and is the primary cause of increased extinctions.

The construction of roads not only adds a potential source of mortality that was not originally part of a habitat, but also directly removes and fragments formerly contiguous habitats. Forman and Alexander (1998) argue that the “barrier effect may emerge as the greatest ecological impact of roads with vehicles,” thus fragmentation can be more of a threat than roadkills. Habitat alteration also has the potential to proliferate beyond the road’s edge in the form of habitat degradation, which can result from the penetration of invasive species from the disturbed roadside, pollution of various forms, and higher plant mortality (Spellerberg 1998).

Roads have been shown to act as movement barriers and it is not so much the composition of the road’s surface as it is the width and traffic volume that form the barriers (Forman and Alexander 1998). The tendency of a road to form a barrier can vary, however. A mark-release-recapture study involving ground-dwelling carabid beetles showed that the beetles preferred to move parallel to a road rather than cross it at a ratio of 4.4:1, respectively (Mader et al. 1990). Thus the rate of road crossing was reduced. On the contrary, Ries and Debinski (2001) found that roads did not appear to impede the movement of a fritillary butterfly species in Iowa’s severely fragmented prairies. Munguira and Thomas (1992) found that roads had some impeding effects on the movement of less vagile (i.e. less prone to disperse) species of Lepidoptera, but roads had no effect on the movement of vagile species. These mixed findings suggest the need for assessment of the responses of specific taxa to roadsides.

Edge Interactions

The creation of edge habitat often associated with roads can have mixed effects. The edge habitat is essentially an ecotone between the natural habitat patch and the road itself. The probability of an organism encountering an edge will increase as the

edge to interior ratio increases (Ries and Debinski 2001). Laurance and Yensen (1991) cite a number of studies that investigated edge effects in fragmented habitats including invasion of weedy plants, greater exposure to climatic factors, and a greater presence of generalist predators. They developed an “edge function” that mathematically explains the factors associated with the distance an edge effect penetrates a habitat patch. Edge effects have a greater effect when patches are small or have large perimeter:area ratios. The “core-area” that does not experience the edge effects depends on the edge functions and shape of the patch. The “Core-Area Model” focuses on interior species conservation, suggesting that remaining habitat patches be kept as large and as circular as possible to maximize core-areas. Interior species tend to be more sensitive to edges.

Past edge studies have often tried to designate certain species as edge species, but Ries and Sisk (2010) suggest that species be labeled based on how sensitive they are to responding to edges. An edge response can be related to increased or decreased abundances near edges. Edge sensitivity can be related to extrinsic factors, such as edges having high structural contrast, e.g. vegetation height. Intrinsic factors affecting sensitivity are more tied to an organism’s life-history or ecological characteristics. Ries and Sisk (2004) present a model that suggests organisms will tend to avoid edges adjacent to unfavorable habitat and ignore edges between two equally suitable habitats. They also state that if edges have more resources, organisms may also tend to congregate there. This could be the case for butterflies in roadside margins with high floral abundance.

Edge responses have been shown to vary depending on the organism. The carabid beetles considered in Mader et al. (1990) were quite sensitive to the road edge,

while the fritillary butterflies considered in Ries and Debinski (2001) appeared to be insensitive. The latter found that road crossings did not differ from random movements for the fritillaries. Fry and Robson (1994) found that hedgerows along field margins impeded the crossing of certain butterfly species. Some were considered capable of crossing but did not apparently for behavioral reasons. The vagile butterfly species considered in Munguira and Thomas (1992) crossed roads more frequently than expected. These species are known to live in open mobile populations, while those less vagile species live in mostly closed populations.

Island Biogeography

MacArthur and Wilson (1967) developed a simple model (M-W) where they acknowledged islands both surrounded by water in the literal sense and islands of habitat surrounded by hostile or unsuitable habitat (i.e. matrix). Larger islands tend to be more specious as do islands that are closer in distance to a mainland or source habitat. Islands closer to the mainland see more immigration and larger islands see less extinction. There is an equilibrium rate of immigration and extinction known as the turnover rate.

Brown and Kodric-Brown (1977) modified the M-W model to account for the rescue effect: extinction rates are reduced on islands that are closer to the mainland due to increased immigration rates. Thus turnover rates may be higher on distant islands. Another modification involves the target effect, where larger islands would see higher immigration rates than smaller ones. Turnover rates may increase on large islands. Lomolino (1990) demonstrated this with mammals crossing ice between habitats. The main idea to take from island biogeography is that by their nature islands act as barriers to dispersal, and such movement would otherwise stabilize the birth and

death rate, reduce inbreeding depression, promote gene flow, increase colonization, and increase adaptive genetic variation (as reviewed in Rosenberg et al. 1997).

Forman and Alexander (1998) argue that allowing animal movements across certain sections of road, despite the possibility of increasing roadkills, would be the best solution to help populations imperiled by fragmentation. Thus managing roadside margins as suitable habitat may reduce the barrier effects of roads by allowing for habitat connectivity and effectively larger habitat islands. Edge interactions should still be studied, as they are not considered under island biogeography and are not universal across all taxa encountering the edge.

Roadside Margins as Corridors

One of the suggested ways to mitigate habitat loss and fragmentation is to create biological corridors. Rosenberg et al. (1997) consider a patch of land to be a corridor if it provides for animal movement between habitat patches. It does not necessarily need to provide resources needed for reproduction. As mentioned earlier, the movement of individuals between populations is beneficial to the persistence of metapopulations. Corridors have the potential to link populations and allow for home range dispersal. The latter may be especially important if the home range exceeds the size of the habitat patch (Rosenberg et al. 1997). For a corridor to be successful, an animal needs to find the corridor, use the corridor, and successfully pass through the corridor (Rosenberg et al. 1997). A lot will depend on how the animal responds to the edge and the matrix environment surrounding the corridor. Recent findings appear to offer support for corridors; however, additional research is needed to assess the benefits of corridors to populations and communities (Haddad and Tewksbury 2006).

There are a series of studies with butterflies in managed pine forests that suggest corridors are beneficial to open-habitat butterfly populations. A study involving two butterfly species showed that open corridors increase interpatch movement rates compared to no corridors (Haddad 1999). Butterfly populations within patches connected by corridors reached higher densities (Haddad and Baum 1999) and a genetic analysis revealed that corridor-facilitated dispersal promoted greater genetic variability in one species (Wells et al. 2009). It was also shown that corridors are more effective when the distance between two habitat patches is greater than the butterflies' ability to detect and reach the other patch through the matrix (Haddad 2000).

Roadside margins tend to be narrow, linear patches of land that can potentially connect larger patches. They may also function as stepping stone habitats. Haddad (2000) noted that one species of butterfly was likely using the open corridor as habitat. Even if certain roadside margins do not function as corridors, they are potentially important habitats.

Roadside Margins as Habitat

Rosenberg et al. (1997) consider a patch of land to be a habitat if it provides the resources needed to sustain survivorship, reproduction, and movement. A habitat patch is a source patch if it supports a stable population and yields emigrants while one that depends on immigrants is a sink patch. It is generally considered that the more heterogeneous a habitat is with its physical structure and resources, the greater species diversity it is able to support. Tews et al. (2004) noted that several studies reported a positive correlation between habitat heterogeneity and animal species diversity, with a particular emphasis of study on anthropogenically-influenced habitats. They point out that the scale of heterogeneity is important to consider and they identify a component

called the keystone structure. It is the resource that an organism (or group of organisms, potentially) relies on for survival. Heterogeneity at one spatial scale may benefit some organisms while to others it may act to fragment the habitat. Thus it is important to consider how the scale of habitat management will affect a variety of species and how each species would interact with the resources in its habitat.

Roadside margins can serve as habitat for a number of animal species. Small rodents were found to be breeding in roadside margins in the United Kingdom, suggesting that the margins supported populations (Bellamy et al. 2001) and were being used as a habitat. Way (1977) reports that roadsides in the British Isles function as breeding habitat for 40% of their mammal species, 100% of reptile species, 20% of bird species, 41.7% of butterfly species, 47% of bumblebee species, and 8.3% of amphibian species. If more thorough species inventories were conducted, it is likely that roadside margins would be found to support even more species than those documented.

In order for roadsides to function as habitat for butterflies, they need to provide resources for all life stages (Ries et al. 2001). Floral nectar is a major resource that roadside margins provide for butterflies. It is needed to sustain flight and provides the energy needed for courtship and dispersal. Roadside margins have been shown to support larval habitat as well (Munguira and Thomas 1992; Wynhoff et al. 2011). A study in the United Kingdom showed that butterflies were breeding in roadside margins, thus suggesting their value as habitat providing larval resources (Munguira and Thomas 1992). They also found that butterfly species richness was positively correlated with the width of the margin and diversity was correlated with the number of nectar sources, suggesting valuable habitat to the adult stage. Saarinen et al. (2005) also observed

butterflies using margins as habitat in Finland. They commented on how margins could function as reserves for butterflies that would utilize a similar natural habitat, in this case grassland habitats in Finland.

Similar studies have involved agricultural field boundaries and green lanes (similar structurally to roadside margins) between agricultural fields. In this case, the vegetation in the boundaries and green lanes offers a habitat surrounded by the unsuitable agricultural field matrix. Boundaries and green lanes have been shown to support butterfly populations and the abundance of nectar sources is one key factor in this (Dover 1989; Dover et al. 2000; Sparks and Parish 1995), as is the presence of larval host plants (Croxtton et al. 2005).

Ecological Succession

Habitat patches do not persist in one particular condition indefinitely. Ecological succession can be described as the change in natural community structure over time. Primary succession occurs when new earth is formed and colonized. Secondary succession occurs when a pre-existing community is removed by a disturbance. The initial colonists after a disturbance are typically poor competitors but are adapted to take advantage of ephemeral resources. In north central Florida, fire is a natural disturbance that maintains many open understory forb communities in pine flatwoods (Monk 1968). In the absence of fire, pine flatwoods will transition to a southern mixed hardwood forest. Way (1972) notes that roadside margins in the United Kingdom that were no longer mowed transitioned from herb-rich areas to areas of bramble and scrub. If left unattended, roadside margins in regions where succession progresses from open fields to forest will begin to fill in with shrubs and woody vegetation. Without some level of disturbance, roadside margins in Florida would also transition to woody vegetation.

Intermediate Disturbance Hypothesis

Grime (1973) postulated that low environmental stress, i.e. infrequent disturbance, tends to facilitate the proliferation of a few highly competitive species. He noted that competition was a significant factor in maintaining low species densities in roadside margins. At intermediate levels of disturbance, strong competitors are not as vigorous and less competitive species are able to coexist. Very high levels of disturbance would allow only a select few of the hardiest species to survive. Thus the intermediate disturbance hypothesis predicts that species diversity will be greatest at some intermediate level of disturbance. There are many other mechanisms that influence coexistence aside from competition.

Diversity in tropical dry forests in Ghana was found to be greatest at intermediate levels of disturbance, but disturbance explained little of the variation in wet forests (Bongers et al. 2009). Both ecosystems differ in climate, species biology, and especially in the nature of disturbance they typically receive. As a result the two communities respond differently to disturbance. Another study demonstrated that trade-offs between dispersal abilities and competitive abilities in response to between-patch disturbance had an effect on coexistence, with an intermediate disturbance favoring coexistence (Roxburgh et al. 2004). They noted a similar trend at the within-patch level: after the disturbance, the poor competitors' seed bank germinated first and eventually the better competitor replaced the growing stand of vegetation. When considering within-patch disturbances, both species can coexist at different times but not in the same area. With between-patch disturbances, both species can coexist at the same time but in different areas. Thus it is important to consider both the scale of the disturbance (Hiura 1995; Wilson 1994) and the generation time of the organisms in a community (Wilson 1994).

Mowing of Roadside Margins

Mowing of roadside margins may or may not encompass the entire margin habitat but it typically occurs at least annually. Way (1972) reported in a survey of Highway Departments in the United Kingdom that maintaining lines of sight at curves, a place to pull off the road, and aesthetics were all common reasons for maintaining (with either mowing or herbicides) roadside margins. Roadside margins are also thought to have additional benefits such as offering places for pedestrians and equestrians to travel. They also function to stabilize the road's surface and allow for water drainage away from the road. Way (1972) also reported that there were complaints of not enough mowing of margins in cities and too much mowing of margins in the countryside.

According to Gerald and Graham (1995), margins are mowed and maintained in Florida in order to beautify transportation corridors and maximize safety. Maintaining aesthetically pleasing roadsides is important to Florida's tourist-based economy. The FDOT is also concerned with maintaining the natural environment. Despite regional differences in mowing and other landscape maintenance practices, margins along rural highways should be free of trees for at least the first 9.1 m of margin.

Most margins along highways in Alachua County, Florida are mowed at a 3-week interval during the warmer months (Kenneth Campbell pers. comm.), primarily for safety and aesthetics. The FDOT will often hire private contractors to mow sections of highway. Mowing ensures vehicles have a place to pull over in highway emergencies and that a buffer is present when there is a loss of vehicle control. Regarding aesthetics, the FDOT in Alachua County has received complaints from the public about overgrown roadsides. However, the sowing of wildflower seeds in some margins under the state's Wildflower Program began largely from public admiration of a roadside

unintentionally seeded with crimson clover (Florida Department of Transportation 2012). Thus the public has an influence on roadside maintenance.

Objectives

Ries et al. (2001) mention that there are no studies prior to the year 2000 that address the effects of restoring roadsides to their original habitats on any animal species. Other roadside studies involving Lepidoptera have been conducted primarily in northern Europe and the upper midwestern United States. No studies involving roadside management and its impacts on butterflies or insects have been conducted in the southeastern United States.

The first objective of my study was to investigate how variations in the mowing frequency of roadside margins in north central Florida affects butterfly abundance and roadkill mortality. I investigated any differences in response to mowing frequency based on life history characteristics of different butterfly species. Additionally, I calculated overall relative mortality and relative mortality under each variation in order to test for differences. The second objective was to investigate how mowing frequency affects the abundance and richness of roadside flowering plants. I investigated correlations between butterfly abundance and floral resource abundance.

I used butterflies in this study because they are easy to identify and spot, and, because they utilize different resources during their development, they could be ecological indicators of a variety of other insects (especially pollinators and flower visitors). An ecological indicator is defined as a species or group of taxa that serves as indicators of the impact of environmental stressors on biotic communities (McGeoch 1998). The stressors in my project were disturbance from mowing and mortality from

roadkills. Understanding how anthropogenically-induced stressors affect the flora and fauna of a particular habitat will be essential to conservation efforts (McGeoch 1998).

The margins can provide larval host plants and adult nectar sources and thus represent true habitats for many species of butterflies and other pollinating insects. It is possible that, in addition to common or disturbance-tolerant species, margins can provide habitat for less common species. A long-term goal of projects like this would be to address FDOT offices with a mowing regime that would reduce relative butterfly mortality, provide a more suitable habitat, and still afford highway safety and aesthetic value.

CHAPTER 2 ROADSIDE MOWING EXPERIMENTATION

Introduction

Roads have a marked presence on the earth's surface and create a potential front of interactions with a variety of ecosystems. In the United States alone, roads spanned a distance of 6,572,188 km as of 2010. As noted in Coffin (2007), transportation geographers find a positive correlation between road infrastructure growth and economic development.

The study of road ecology, which addresses the relationship between road systems and the ecosystem, began in the 1980's (Forman et al. 2003). Spellerberg (1998) summarizes some of the recognized ecological effects of roads: direct loss of habitat during road construction, creation of edge habitat, habitat degradation near the road's edge, animal roadkill, habitat fragmentation and isolation of animal populations, and changes in species composition.

Habitat loss and habitat fragmentation are both serious threats to biological diversity. McDonald et al. (2008) predict that urban growth will have localized but cumulatively significant negative effects on ecoregions (i.e. areas that have similar ecosystems), rare species, and protected areas. Others have shown the negative effects of urban development on species richness (Fattorini 2011a; Gomes et al. 2011) and native species (Marchetti et al. 2006). Agriculture and invasive species are also threats to biological diversity (Rouget et al. 2003). Some species are able to utilize urban areas as habitat provided resources and conditions are suitable (Fattorini 2011b; Magura et al. 2010).

Metapopulations, or groups of populations that interact and are spatially connected, are considered common in fragmented habitats (Hanski 2004). Individual habitat patches do not persist indefinitely and community structure changes over time, especially after a disturbance. Dispersal is needed between habitat fragments to maintain stable metapopulation dynamics, and permanent loss of both habitat patches and connectivity would negatively affect the persistence of a metapopulation (Hanski 1998). Wilcox and Murphy (1985) note that most ecologists agree that habitat fragmentation poses the greatest threat to biological diversity. Forman and Alexander (1998) claim that the greatest ecological impact roads would have are barrier effects and that roadkills have minor impacts by comparison. This generalization must be used with caution, as the impacts of roads on different taxa can vary.

Although roads are generally considered to have negative impacts on the environment, the narrow strips of land adjacent to roads (i.e. margins) have the potential to serve as habitat. Way (1977) reports that margins in the British Isles function as breeding habitat for 40% of their mammal species, 100% of reptile species, 20% of bird species, 41.7% of butterfly species, 47% of bumblebee species, and 8.3% of amphibian species. Roadside margins may be important sources of habitat in areas where little natural habitat remains (Coffin 2007; Hopwood 2008). In addition to functioning as habitat, margins may function as dispersal corridors for both native (Eversham and Telfer 2004) and invasive species (Brown et al. 2006).

This project aimed to investigate how variations in the mowing frequency of roadside margins affect butterfly abundance and roadkill mortality and flower abundance and species richness. Routine mowing is used to manage roadside margins

in Florida. Margins are typically mowed every 3 weeks during the peak growing season in Alachua County (Kenneth Campbell pers. Comm.) and this disturbance regime maintains the margins as early successional open habitats. Arrangements were made with the FDOT for the mowing implementation and three experimental sites were selected along rural highways. Three different mowing frequencies were administered beginning on April 6th, 2011 and ending on November 2nd, 2011. Prior to this study, the effects of roadside mowing on butterfly abundance, species richness, and mortality in Florida were not known.

Materials and Methods

Experimental Design

Three sections of highway were selected along the outskirts of Gainesville, FL (Alachua County) that served as experimental sites for this study: Highway 441 10.5 km northwest of the corner of University Avenue and Main Street (downtown), Northeast Waldo Road 16.5 km northeast of downtown, and Southeast Hawthorne Road 16.5 km southeast of downtown (Figure 2-1). At each site, the roads all have the same posted speed limits (105 km/h), similar traffic volumes (averaging 11,000 vehicles/d), and all are four-lane highways with a vegetated center median (Florida Department of Transportation 2009). The center median along Waldo Road was historically augmented with a wildflower mixture, but the medians at the other two sites also had wildflowers. The adjacent vegetation at each site was pine and mixed hardwood forest, although some sections at the Hawthorne Road site were adjacent to patches of cypress wetland. The woody vegetation extended back at least 600 m at each site. These sites were selected to have as similar an adjacent habitat structure as possible to minimize variability. The managed roadside margins spanned an average width of 13 m from the

road's edge to the established woody vegetation and were predominantly comprised of grasses and forbs (Figure 2-2).

The three sites were divided into blocks and each block consisted of a 600-m strip of margin parallel to one side of the road's outer edge. Three mowing treatments were administered in 200-m sections within each block. All blocks within each site were on the same side of the road. There was a 100-m buffer between each block. Site 1 (Highway 441) contained two blocks, Site 2 (Waldo Road) contained four blocks, and Site 3 (Hawthorne Road) contained two blocks. Sites 1 and 3 had a limited span of suitable margin compared to Site 2. In order to maximize replication of the treatments, the extra suitable margin at Site 2 was utilized despite the imbalance in the design.

The mowing treatments were no mowing (Treatment A, no-mow) during the course of the study, mowing every 6 weeks (Treatment B, 6-week), and mowing every 3 weeks (Treatment C, 3-week, standard practice) (Figure 2-3). These three treatments were randomly assigned within each of the eight blocks (Figure 2-4) using a random integer set generator (Haahr 2011). The mowing treatments were administered by the FDOT. An unintentional treatment was added to Site 2 toward the latter half of the study. The 6-week treatment was accidentally mowed after 3 weeks on August 31st, becoming the interrupted 6-week treatment (Treatment D).

Permanent signs demarcating the original three treatment levels and the buffer were placed at the woody vegetation line by the FDOT at the beginning and end of each 200-m treatment section within each block (Figure 2-5). The signs read: "A", "B", "C" or "Buffer". The FDOT informed its workers what the letters designated and they were made aware of the mowing specifications. Each site also had its endpoints marked with

larger signs to notify the public about the experiment. The signs read “Test site begins” and “Test site ends” and were placed at the experimental sites during the middle of the study.

To account for any overlap effects of adjacent treatments, butterfly and flower data were only collected in the middle 100 m of each 200-m treatment section. These sections were demarcated with orange lines spray painted onto the asphalt. The FDOT was made aware of these in order to prevent any confusion during mowing.

Treatment Specifications

The first 1.5 m along the road’s immediate edge, i.e. clear zone, was mowed every 3 weeks once active growth began. A clear zone is maintained to allow space for correction of an errant vehicle or for a vehicle to safely pull off the paved surface of the road in case of emergency (Gerald and Graham 1994). Mowing of the clear zone did not start until after July 20th due to slow growth at the road’s immediate edge and dry conditions. The remaining margin that extended back to the established woody vegetation received the three designated mowing treatments (Figures 2-2 and 2-3).

A John Deere Ztrack mower (Model 797, Deere & Company, Moline, Illinois) was used to administer the treatments. It had three spinning blades that spanned a width of 1.8 m. The height of the mower’s blades was set at 14 cm. Although the type of machine used was not expected to be a variable of concern, the same mower was used on all three sites. Parr and Way (1988) reported that as long as the height of cutting remains constant, the type of mowing machine should not have a significant effect on the margin’s vegetation structure or species composition.

The FDOT administered the mowing treatments beginning on April 6th, 2011 and ending on November 2nd, 2011 (Table 2-1). The peak growing season for north central

Florida occurs during the wetter months of June, July, August, and September. The greatest abundance of flower blooming typically peaks in the spring and fall (Jaret Daniels pers. comm.). Mowing treatments were administered on the Wednesday of each treatment week. All sites were mowed on Wednesdays according to treatment level specifications; however, weather-related issues or logistical problems led to some sites being mowed the next day or the previous day. The FDOT sent me documentation forms with each mowing cycle to allow me to verify that treatments were administered correctly.

The 100-m buffer was originally assumed to receive mowing as needed. It was predicted to receive a somewhat different mowing frequency than the three treatments, but it turned out to be easier for the FDOT to administer the 3-week treatment (Treatment C). In any case, the buffer served to separate the blocks and made it more convenient to recognize the blocks in the field. Data were not gathered from the buffer.

Live Butterfly Sampling

Live butterflies were counted once every 2 weeks (Table 2-2) by walking a linear transect running parallel to the road. The width of the transect was the width of the margin. Since most butterfly species have an average life span of several weeks as adults, the 2-week sampling interval was deemed an appropriate use of limited sampling time. These counts occurred on Fridays or at least 24 h after a mowing treatment (e.g. a mowing postponed to a Friday would lead to data collection on a Saturday). Linear transects similar to those used in Feber et al. (1996), McKenna et al. (2001), Munguira and Thomas (1992), Ries et al. (2001), and Saarinen et al. (2005) were used at all three sites. Considering how narrow the treatment sections were, a

linear transect seemed suitable to capture the majority of butterfly activity during the sampling interval.

An observer walked the transect at approximately 1 m/s and a recorder followed in the clear zone. The recorder kept an eye on the transect markers and recorded butterfly species counts on a table as the observer spotted them. The observer walked down the middle of the transect each time for consistency. Some butterflies were unintentionally flushed out as the observer walked. As sections receiving the no-mow treatment grew taller and more difficult to traverse, the transect was walked as close to the original path as possible to maintain consistency. The field of vision of the observer roughly spanned the width of the margin and was maintained at roughly 2 m out ahead of the observer. Butterflies were identified on the wing or while perched on exposed vegetation; however, some smaller species that were difficult to identify were netted, photographed, and released. If a netting attempt failed, the individual was documented at the most specific taxonomic level of certainty.

All field work (live butterfly sampling, dead butterfly sampling, and flower sampling) was primarily conducted between the hours of 9 am and 2 pm. The order in which the three sites were visited alternated between the six permutations of the three sites: 1-2-3, 3-2-1, 2-1-3, 3-1-2, 1-3-2, and 2-3-1 (Table 2-2). These orders were repeated during the course of the study and they ensured that there was not a bias for sampling a butterfly species that either prefers late morning or early afternoon at any particular site. It ensured that each site was sampled at different times during the sampling period. Late afternoon temperatures during the summer months in Florida can be dangerous for

prolonged field work and sampling at those times was avoided. Additionally, butterflies tend to peak in activity between 10 am and 2 pm (personal observation).

Shade temperature was recorded with a digital thermometer (Water Resistant Pen Shape Stem Thermometer, Carolina Biological Supply Company, Whitsett, NC). Wind speeds were visually estimated to the nearest 8 km/h and cloud cover was visually estimated on a qualitative scale: sunny, mostly sunny, partly cloudy, mostly cloudy, and cloudy. Persistent rain, cloudy skies combined with forecasted maximum daytime temperatures below 18 °C, and winds over 32 km/h warranted a rescheduling or postponing of data collection.

Dead Butterfly Sampling

Presumably road-killed (dead) butterflies found along the roadside of each treatment section were collected, counted, and identified once weekly (Table 2-2). Each collection day theoretically represented 7-d-worth of road-killed butterflies. Collecting occurred on Fridays or at least 24 h after a mowing treatment. The first 1 m of paved surface at the road's edge and the first adjoining 1 m of clear zone were examined carefully by two observers with overlapping fields of vision. The observers carefully walked parallel paths and made sure that any shadows cast were not falling on each other's viewing area. Walking was done against the flow of traffic for safety concerns since both observers were very close to moving traffic.

Data from the first collection (week 0) were discarded as they potentially included dead butterflies that had been accumulating before the treatments were administered. Dead butterflies seen outside the 2-m-wide viewing zone were removed but not counted. Intact butterfly corpses and butterfly wings were collected with forceps and placed in labeled glassine envelopes for temporary storage. Wings and wing fragments

were still counted as one individual. It was deemed unlikely that four wings from one butterfly were counted as four butterflies, as wings and wing fragments typically lie fairly close to each other in the grassy thatch (Figure 2-6).

Flower Sampling

Flower abundance and species richness data in the margins were gathered the Tuesday before or the day before each mowing treatment (i.e. every 3 weeks) (Table 2-2). Five randomly placed 1-m² quadrats per 100 m of treatment section were used to acquire the data. This 3-week interval seemed appropriate as most plant species encountered would be expected to bloom over such a period rather than solely on a single day. The 100-m sections were divided into 80 rectangles and a random integer generator was used to pick five rectangles (Haahr 2011). Careful pacing of the observer was used as an estimated measurement to locate the five rectangles on an imaginary grid. The recorder followed and instructed the observer where to drop the quadrat. The observer dropped the quadrat into the rectangle without looking directly into it to avoid sampling bias. Each rectangle was 10 m², so the dropping of the quadrat was haphazard at that scale.

Abundance was determined by counting the number of flowers and/or inflorescences seen growing within the quadrat. If flowers were less than 1 mm in diameter and part of an inflorescence, the inflorescence was counted as a flower. Tall flowers that were folded over by the quadrat and appeared to be in the 1-m² sampling area were not counted if they were rooted outside the area. When large numbers of small flowers were present, counts were made in clusters and estimated to the nearest five flowers. Species were assigned a descriptive name in the field and were later identified from collected specimens and photographs. Only flowers that were open and

viable, i.e. receptive to pollinators, were counted. Flowers from grasses (Poaceae) were not counted.

Statistical Methods

The experimental set-up resembled an unbalanced split-plot design. The high plot level, the sites, had no treatment structure. Although the three sites were not selected at random, it was assumed that if numerous such sites existed, those selected would have been representative of such sites. The small plot level, the eight blocks, had a randomized complete block design and the treatment structure was simple. It had one factor (mowing) with up to four levels (the no-mow treatment, 6-week treatment, 3-week treatment, and eventually the interrupted 6-week treatment). The experimental units were the sections within each block that received a mowing treatment. The random independent variables were site and block. The fixed independent variables were treatment and time (data collected weekly, every 2 weeks, or every 3 weeks). The dependent variables were the live butterfly counts, the dead butterfly counts, the relative mortality ratio, flower density, and flower species richness. Analyses were made using SAS version 9.2 for Windows. Significance was considered for p-values less than or equal to 0.05.

In order to determine whether or not the interrupted 6-week treatment was an effect I could ignore, I tested a carryover effect for significance. A new variable was defined in SAS, $PRIORTRT_i = TRT_{i-1}$ (Littell 2006). It represented the treatment conditions a specific treatment section had during the prior week. Thus *PRIORTRT* was not assigned a value for the first week. The data were analyzed with a split-plot design using PROC GLIMMIX. The data analyzed included everything up through September. The explanatory variables were *TRT*, *TIME*, *TRT*TIME* (interaction), and *PRIORTRT*.

The live and dead butterfly data and flower density data were $y'=\log(y+1)$ transformed for this analysis. This analysis was run 3 weeks after the mowing error and this transformation satisfied the normality assumption. The flower species data were not transformed.

The live butterfly data and the dead butterfly data did not appear to meet the assumption of having normal distributions with the final data, despite attempting a $y'=\log(y+1)$ transformation. There appeared to be no other transformation that could make the data meet the normality assumption necessary for the main analyses. Several other distributions were used in an attempt to fit the model, including Poisson and over-dispersed Poisson; however, the results did not converge using the basic split-plot model. The zero-inflated Poisson distribution had results that converged but the diagnostic tests showed the data did not fit the distribution.

The live and dead butterfly data were quite sparse, and in order to best retain the variability structure, the two-parameter Gamma distribution was chosen. It turned out to be a better fit for the data. A spline structure was given to the *TIME* variable in order to decrease the number of coefficients to be estimated, thereby avoiding the convergence problems. Splines are typically designated by dividing the whole interval into equal sections. However, the data did not have uniform variations over time. Knots were chosen to divide the data into sections such that a quadratic curve would adequately capture the pattern within each spline section of the live butterfly data and a cubic curve would adequately capture the pattern within each spline section of the dead butterfly data. The live butterfly data had knots on July 8th, August 19th, September 16th, and October 14th (Figure 2-7). The dead butterfly data had knots on June 3rd, August 26th,

and September 23rd (Figure 2-8). Although these selections may bring biases in the estimates, they outweighed the costs of using the standard equal divisions (i.e. lack of convergence).

The relative mortality ratio for each treatment section was calculated as the sum of dead butterflies divided by the sum of both dead and live butterflies: $\text{dead}/(\text{dead}+\text{live})$. The ratio was calculated in 3-week intervals in order to permit future linear regression analysis with the 3-week interval of the flower sampling data. There were 3 dead butterfly counts in each interval and these were averaged. Because of the 2-week interval of live butterfly counts, some of the ratios had two live counts and these were averaged. Logistic regressions are typically used to model proportions; however, the results did not converge using this method. The beta distribution in PROC GLIMMIX was selected since it supports proportion values between 0 and 1. To maintain consistency, a spline structure was used but with only one knot on August 26th (Figure 2-9). A cubic curve was fit to each spline section.

A split-plot analysis was used on the flower data. Flower species that were known to be favorable nectar sources for butterflies were also analyzed as a separate group (nectar). Thus there were four groups of flower variables: flower density of all species (all), flower density of nectar species, species richness of all flowers, and species richness of nectar flowers. Flower density data (all and nectar) were $y'=\log(y+1)$ transformed and fit to the split-plot model with a normal distribution. Flower species (all) data did not need to be transformed to meet the normality assumptions. Flower species (nectar) data could not be transformed to meet the normality assumptions, so they were left untransformed and fit using a Poisson distribution. PROC GLIMMIX was used for

the analyses. The interrupted 6-week treatment was selected as the baseline for assessing differences between treatments since it was not one of the original treatments. Pairwise comparisons (least squares means) were made between the no-mow, 6-week, and 3-week treatments.

Correlations between the transformed live butterfly counts and each of the four groups of flower variables were calculated. There were ten site and treatment combinations (1A, 1B, 1C, 2A, 2B, 2C, 2D, 3A, 3B, and 3C), and Pearson's correlations were computed using pairs of the $y'=\log(y+1)$ transformed live butterfly data (from each of the ten site and treatment combinations) and each of the four flower variables. Thus there were a total of 40 correlations. The more stringent Spearman's rank correlation was utilized in the same manner for comparative purposes.

Live butterfly data and dead butterfly data were separated by species based on whether or not they are migratory, whether they utilize open or wooded habitat, and their different wing spans (Small <20 mm, 21 mm < Medium < 45 mm, and Large > 46 mm) (Scott 1986). I hypothesized that migratory species would be less sensitive to the variants of margin structure since they fly in fairly directed paths. The effects of the mowing treatments on the butterfly data were analyzed. The same model and specified spline knots from the collective butterfly data were used. Group sums over all treatments were also calculated (i.e. mowing treatment and time were not considered a variable of concern in this context). A Chi-square test was used to determine whether migratory tendency, habitat utilization, or wing span had an effect on relative mortality. Standardized residuals were calculated for the wing span group to examine where the differences lie.

Results

The average temperature during butterfly data collection hours from April 29th, 2011 to October 28th, 2011 was $28.8\text{ }^{\circ}\text{C} \pm 0.487\text{ }^{\circ}\text{C}$ (standard error). The minimum temperature during which data were recorded was $14.8\text{ }^{\circ}\text{C}$ on the morning of October 21st and the maximum temperature during which data were recorded was $36.1\text{ }^{\circ}\text{C}$ on July 29th. Most sampling days had temperatures close to the average. Butterflies were seen flying on cloudy days and even during light drizzle. Data collection was temporarily postponed during the rare and brief instances of heavy rain.

Carryover Effect

There was evidence that the erroneous mowing constituted an effect I could not ignore. The mowing interruption caused a change in the transformed live butterfly data and the flower species data ($p < 0.05$). There was no evidence that the erroneous mowing had an effect on the transformed dead butterfly data and the transformed flower densities. Even though the carryover effect was significant for two of the four variables of interest, it was considered to be significant for all variables to avoid complications in future analyses that use combinations of variables for which the carryover effect was both significant and not significant. Thus all of the treatment sections in Site 2 that received the 6-week treatment were relabeled as receiving the interrupted 6-week treatment from September 2nd to the end of the study. The drop in the number of live butterflies in the interrupted 6-week treatment after September 2nd reflects the carryover effect (Figure 2-7).

Butterfly Data, All Species

There were a total of 258 live butterflies recorded and 184 dead butterflies collected. This translates to an overall relative mortality of 0.416. With 2.4 km of

roadside sampled repeatedly over the course of 27 weeks, there were approximately four live butterflies per km per week. There were approximately three road-killed butterflies per km per week. These values only apply to one side of the road.

There were 29 butterfly species identified in five families (Table 2-3). The numbers of live and dead butterflies and the relative mortalities, regardless of mowing treatments, differed depending on the species (Table 2-4). Butterfly numbers, both live and dead, increased greatly after mid-late August (Figures 2-7 and 2-8).

The spline effect on time ($p=0.003$; $df=6, \infty$) and the mowing treatment *spline interaction ($p=0.012$; $df=14, \infty$) were both statistically significant for the live counts, but the mowing treatment alone did not have a significant effect on the counts. This reflects the changes in butterfly numbers between each of the spine sections and the treatment effects becoming more apparent in the later spline sections (Figure 2-7). The spline effect on time was statistically significant for the dead counts ($p=0.049$; $df=6, \infty$), but the mowing treatment*spline interaction did not have a significant effect on the counts. This reflects the changes in butterfly numbers between each of the spine sections but no apparent treatment effects (Figure 2-8). None of the aforementioned treatments or their interaction had a significant effect on relative mortality (Figure 2-9).

Flower Data

A total of 12,699 flowers and inflorescences were recorded with an average of 11.76 flowers per square meter across the nine samplings (May 13th through November 1st). There were 57 flower species identified in 30 families and 16 morphospecies that were not able to be identified to species. Of the identified flower species, 38 are known to be nectar sources utilized by butterflies (Table 2-5). The remaining 19 flower species

are not known to be nectar sources, but that does not exclude them from influencing butterfly behavior (Table 2-6). Most of the identified flower species are native to Florida, with only 10 non-native species recorded.

The mowing treatment had a significant effect on each of the four flower variables (Table 2-7). The results of the pairwise comparisons indicated the no-mow treatment and 6-week treatment were not significantly different from each other (Figure 2-10). They both had significantly greater densities and numbers of species compared to the 3-week treatment. Contrasts in mowing treatments became more visually evident later in the summer as the no-mow treatment (Treatment A) grew taller (Figure 2-5). There were no treatment*time (spline was not used here) interactions for the flower data and there did not appear to be a net increase in flower density over time (Table 2-7). The number of species in bloom and the density tended to fluctuate over time.

Butterfly and Flower Correlations

Only two of the 40 correlations (Pearson's) tested were found to be significant (Table 2-8). This is exactly what would be expected to occur with a Type I error, thus I would conclude there is no evidence of significant correlations. None of the site and treatment combinations were found to have any significant correlations when using Spearman's rank correlation.

Butterfly Groups

The non-migratory live butterfly data and the large dead butterfly data were the only two groups that gave minimally significant convergence estimates. None of the fixed effects or interactions (i.e. treatment, spline, treatment*spline) were statistically significant. Due to the marginally significant convergence of the models and the much

smaller sampling sizes of the groups, the results of the group analyses with respect to the fixed effects are inconclusive.

When looking at the groups regardless of the fixed effects, habitat utilization did not significantly affect the relative mortality of butterflies. The migratory tendency had a significant effect on the relative mortality ($p < 0.001$, $df = 1$), with migratory butterflies experiencing higher relative mortalities compared to non-migratory butterflies (Figure 2-11). The size of the butterflies also had a significant effect on the relative mortality ($p < 0.001$, $df = 2$). Small butterflies had the greatest numbers seen alive and medium butterflies the least. Based on the standardized residuals, the relative mortality of the small butterflies was less than the expected value and the relative mortality of the large butterflies was greater than the expected value (Figure 2-11).

Discussion

It is evident that the frequency of roadside mowing in Alachua County has a profound effect on floral composition in the margins over the course of one field season. The effects of mowing frequency on butterflies are recognized but not as clear. Certain aspects of each species' life history affect their respective relative mortality due to roadkill. Statistical quandaries precluded further analyses of block and site effects.

I have reason to believe there may have been some site effect. There were qualitative differences between the three sites, namely the cardinal orientation and the side of the road each site was located on. Site 1 along Highway 441 and Site 2 along Waldo Road were both on the south side of the road. The tall woody vegetation would shade the experimental units during times with low sun angles. Site 1 was oriented northwest-southeast and it received more direct morning sun. Site 2 was oriented southwest-northeast and it received more direct afternoon sun. Butterfly activity was

typically low until a site was exposed to sun by late morning. Site 3 received continuous full sun since it was on the north side of the road and was oriented west-east. It also appeared to be the driest of the three sites, with some experimental units having patches of bare topsoil. The difference in site exposure to the sun was a primary reason for systematically altering the order in which the sites were sampled.

The blocks within Sites 1 and 3 did not appear to differ too drastically from one another and overall I do not believe there was a block effect. Site 2 was twice the length of the other sites and there were some differences between its blocks. Those closest to the northeast end of Site 2 were narrower and received less full sun than those closest to the southwest end. These differences likely reflect a best case scenario of minimal roadside margin variability. Margins can vary quite considerably with vegetation structure and composition. The experimental design aimed to minimize site and block differences yet replicate the treatment in different areas.

Carryover Effect

Because of the treatment*spline interaction, it is difficult to state how the mowing interruption affected live butterfly numbers. Trends in the graph would suggest the interruption resulted in fewer live butterflies recorded in those experimental units until October 14th, where numbers suddenly climb (Figure 2-7). Flower species counts and densities also dropped in three out of four of the experimental units after the interruption. The reduction in floral resources coincides with an apparent reduction in live butterflies for the first two samplings after the mowing error. The lack of significance of the carryover effect on the flower densities is due to the fluctuating nature of the data both before and after the mowing interruption.

Butterfly Data, All Species

The U.S. Drought Monitor classifies drought with the following increasing order of severity: abnormally dry, moderate drought, severe drought, extreme drought, and exceptional drought. Alachua County experienced extreme drought conditions beginning in mid-December of 2010 and continued to experience severe to extreme drought conditions up to mid May 2011. Moderate to occasionally severe drought conditions continued up to early August 2011, and then abnormally dry to moderate drought conditions prevailed for the remainder of the study (U.S. Drought Monitor).

The drought likely affected butterfly populations leading to lower than expected numbers gathered over the 27-week study. There were many zero counts in the butterfly data sets and this led to the statistical problems. The increase in live butterfly numbers nicely reflected the improving drought conditions in August (Figure 2-7). The increase in numbers may also be attributed to the influx of migratory species toward late summer; however, there were roughly equal numbers of combined live and dead migratory and non-migratory individuals (228 migratory and 214 non-migratory). The roadside vegetation at all three sites would occasionally dry out and turn brown near the immediate road's edge where water does not tend to collect. There was seldom any standing water in the lower contours of the margins, even during the summer wet season.

The total live butterfly count of 258 individuals (or four per km per week) is a huge underestimate of the number of butterflies in the margins over the course of the study. Saarinen et al. (2005) counted 5,964 butterflies over 17 sites between early June and late August for two years in a Finnish study. Each site was sampled over 3.25 km. One would expect approximately four and a half butterflies per km per week, which was

similar to my findings. The duration and frequency of my transect sampling method only gave a snapshot of butterfly activity the margins, especially regarding migratory species. Each 100 m of experimental unit sampled occurred over a span of about 1 min 40 sec every 2 weeks. It was assumed that any resident butterflies of the margin would be detectable during the 1 min 40 sec interval. However, there were likely many butterflies resting in nearby vegetation and non-migratory species can have larger ranges of which the roadside margins are only a part of. Many butterflies were observed passing through the margins when data were not being recorded.

I did not quantitatively sample for butterflies or floral resources in the adjacent habitats, thus it was impossible to analyze whether or not butterflies and resources were more abundant in the roadside margins than in the surrounding habitats. However, I have often noted that roadside margins, forest edges, and other ecotone habitats contain more floral resources and greater insect activity. Based on the model developed in Ries and Sisk (2004), it is possible that butterflies would congregate in the margins because the latter offered high concentrations of resources compared to nearby habitats. Roadside margins have been considered by others to function as habitat for butterflies (Munguira and Thomas 1992; Ries et al. 2001; Saarinen et al. 2005; Way 1977; Wynhoff et al. 2011), but there is an increased mortality factor associated with vehicular traffic.

Behavior at the road's edge was not recorded, but there were instances of butterflies coming to the road's edge and either turning around or turning and flying parallel to it. This could be interpreted as a barrier effect to movement perpendicular to the road. On the other hand, all of the migratory species crossed the road quite readily.

Ries and Debinski (2001) found that roads did not appear to impede the movement of *Speyeria idalia* Drury 1773, a non-migratory species in prairies. It is possible that intrinsic factors such as flight behavior may have an effect on edge responses.

If the margins can offer resources between separated habitats parallel to the road, they have potential to function as corridors in that dimension. Eversham and Telfer (2004) found evidence for roadside margins serving as corridors for carabid beetles, but concluded that margins more likely functioned as breeding refugia. The invasive cane toad *Bufo marinus* Linnaeus 1758 was shown to be using roads and cleared fence lines as dispersal corridors in Australia, but thicker margin vegetation appeared to impede dispersal (Brown et al. 2006).

Understanding the source-sink dynamics of roadside margins will be helpful in evaluating their efficacy in conservation efforts. Pulliam (1988) defines a sink habitat as one in which reproduction undercompensates for local mortality. The latter argues that dispersal from source populations can sustain large sink populations. A 9-yr study involving Florida scrub-jays *Aphelocoma coerulescens* Bosc 1795 found that habitat adjacent to a highway served as a sink, in which mortality exceeded reproduction and persistence only occurred as a result of immigration (Mumme et al. 2000). Using designated sections of roadside margin in conservation efforts would be far more appealing if they could be shown to function as source habitat or dispersal corridors for a variety of taxa.

If roadside margins are sink habitats for some species they can still be more beneficial than having no suitable habitat. In areas where surrounding habitats have been destroyed, roadside margins have been suggested as important habitat (Coffin

2007; Hopwood 2008). I observed at least two species of open habitat butterflies in copula in my experimental units, but I did not search for larvae (the larval host plants were present). Although it is logical to assume reproduction was occurring in the margins, my project did not evaluate the potential of the margins to be a source habitat for those species. Munguira and Thomas (1992) noted that butterflies were breeding in roadside habitats in the United Kingdom.

The total dead butterfly count of 184 individuals (or three per km per week) is also an underestimate of the total road-killed per week along the roads. McKenna et al. (2001) found 1,824 allegedly road-killed butterflies over 6 weeks, but they sampled both sides of the road over 2 days each week. I only sampled on one side of the road one day a week. Although each sampling in my study theoretically included a week of accumulating mortality, it is likely that butterflies also remained stuck to the fronts of vehicles or were carried off by scavengers. There were a few instances when a struck butterfly was observed falling farther into the margin than the sampling area.

Munguira and Thomas (1992) found that only one out of 50 butterfly corpses placed at the side of the road disappeared after 2 weeks. However, the abundance of red imported fire ants along the immediate edge of the road likely resulted in a much shorter persistence time of intact butterfly corpses in my study. Ants were observed dismembering recently struck butterflies that were still moving (i.e. less than 1 h post impact). The wings were the only parts that remained after the ants had finished. Wings tended to stay in the short grass within 1 m of the body and there was never believed to be an instance where two wings from one individual were counted as two different individuals.

My study found an overall relative mortality of 41.6% of butterflies observed. This is likely due to the nature of the data collection. Dead butterfly numbers were representative of a greater time interval compared to live butterfly numbers. Munguira and Thomas (1992) found relative mortality to be in the range of 0.6-7% of the butterfly populations. They conducted mark-release-recapture studies to assess population densities and argued that roadside mortalities were minimal compared to natural causes. More thorough sampling techniques employed on the live butterflies would have allowed for a better estimate of the population densities of butterflies in my study. At present it is difficult to determine how detrimental roadkill mortality was on butterfly populations in my experimental units.

McKenna et al. (2001) found that butterfly mortality actually appeared to decline on roads with very high traffic rates. They suggested a higher per capita mortality which could be attributed to smaller population densities in roadside margins with higher traffic speed and volume. A study in central Iowa showed that butterflies were more likely to exit a non-native grassy roadside than a weedy or native prairie roadside (Ries et al. 2001). Relative mortality was found to be higher along the grassy roadsides. Abundance was highest in the restored prairie roadsides. This implies a greater tendency for the butterflies to leave the grassy roadside, perhaps because they found no resources there.

There are a handful of studies that demonstrate a correlation between mowing frequency and local butterfly activity. Roadside margins in urban areas of Finland that received the heaviest mowing regimes had significantly decreased butterfly abundance (Saarinen et al. 2005). Likewise, another study reported lowest butterfly densities in

roadside margins that received the highest mowing frequency, which also reduced the availability of nectar sources (Bak et al. 1998). Feber et al. (1996) showed that mowing in agricultural margins affected butterfly abundance, with plots cut in the spring, fall, or not cut at all attracting more butterflies and more species than plots cut in the summer. These studies were all conducted in more northern latitudes that experience shorter growing seasons. Thus the frequency of mowing will likely have different effects on plant growth depending on the climate.

Considering the abundance of zeros and the small sample size, it was not surprising to find no statistical significance of the mowing treatments in my study. The significance of the spline effect for both the live and dead counts indicates that the response variables changed between each of the spline sections. Thus there was some effect of time on numbers since the spline is based on time intervals. The significance of the treatment*spline interaction on the live counts indicates that the effects of mowing treatments on the response variables changed between each of the spline sections. Because of this interaction, it is difficult to separate out the treatment effects.

The mowing treatment also did not have a significant effect on the response variable. However, based on the trends on the line graph, it appears that the no-mow treatment yielded the greatest number of live butterflies from August onward (Figure 2-7). None of the independent variables were significant for the relative mortality analysis; however, the line graph suggests the 3-week treatment yielded the greatest relative mortality in the final spline section (Figure 2-9). The aforementioned European studies all had very low mowing frequencies more comparable to my no-mow or 6-week treatment.

Flower Data

The quadrat sampling method likely missed several species of flowers. Over the course of the study, the random sampling covered the majority the treatment sections but species compositions changed and not all species were captured in the quadrats. Plants not in flower and grasses were not sampled. Many of these could potentially serve as larval host plants, especially grasses for the Hesperidae.

The results of the quantitative analyses corroborate the qualitative observations. As would be expected, the highest level of mowing (i.e. disturbance) held flower species richness and density at lower levels. The vertical differences in the vegetation were quite apparent after a mowing treatment, but these were not measured. It is interesting to note that, although not significant, the 6-week treatment appeared to yield the greatest number of flower species (Figure 2-10). It is possible that pre-existing differences in blocks contributed to the results of the flower analysis. A reassignment of treatments to each experimental unit over the course of several years would help reduce the effect of that variable.

Feber et al. (1996) showed that plant species richness was lower on uncut swards in field margins compared to swards that were cut in the spring or fall (outside the main summer growing season). They argue that no mowing would promote unfavorable succession of the habitat and that mowing is necessary but should not coincide with peak blooming periods. Feber et al. (1994) showed that summer mowing removed nectar sources and larval host plants, greatly reducing the abundance of the meadow brown butterfly, *Maniola jurtina* Linnaeus 1758. Another study showed that some routine mowing increased plant species richness, but again only when the mowing did not coincide with times of peak growth (Parr and Way 1988).

The above studies were conducted over multiple years. The experimental units in my study that remained unmown tended to have the greatest abundance of flowering plants and greater species richness than the frequent 3-week treatment units. However, the former were only left unmown for one season. The early successional habitats in those units would transition to hardwood-dominated habitats and the forb understory richness would decline if left unmown for multiple years. Thus, like in the European studies, some routine mowing would also benefit margins in Florida. Since there was no significant difference between the no-mow treatment and the 6-week treatment in my study, mowing every 6 weeks or less could be employed. Knowledge of the phenologies of keystone flower species that would be beneficial to the greatest diversity of butterflies and other insects should be used as a guide for mowing.

Butterfly and Flower Correlations

Because the mowing treatment did not have a significant effect on butterfly numbers, it is not surprising that there were generally no significant correlations between live butterfly counts and the flower variables. One would expect that greater flower densities and/or more species of flowers present would support higher butterfly densities. Ries et al. (2001) noted a clear trend of increasing butterfly richness and abundance in concert with increasing flower species richness in roadside margins. However, they found that flower density had no effect on the butterflies. Croxton et al. (2004) also found a positive correlation between species richness of butterflies and of vascular plants in green lanes (both nectar sources and larval host plants). Feber et al. (1996) found that there was a greater abundance of butterflies in field edges that had greater a greater abundance of key nectar source species. Thus it would appear that a

greater assemblage of flower species that are useful to butterflies would be more beneficial than higher densities of flowers in general.

Butterfly Groups

Significance of the fixed effects (i.e. treatment, spline, treatment*spline) on the butterfly groups was not expected. The issues of sparse data and zero counts were amplified by splitting the butterflies into groups. The significantly higher relative mortality of the migratory species in the analysis ignoring the fixed effects is likely due to the fact that those species crossed the road far more frequently. They maintained fairly straight flight paths and several species, including *Agrualis vanillae* Linnaeus 1758, *Phoebis sennae* Linnaeus 1758, and *Urbanus proteus* Linnaeus 1758, are known to fly with a 142-156 degree heading during fall migrations (Walker and Littell 1994). McKenna et al. (2001) noted a peak in *Danaus plexippus* Linnaeus 1758 mortality coinciding with their southward migration. Munguira and Thomas (1992) found that roadkills were responsible for killing a greater percentage of species living in open, mobile populations compared to those in closed, sedentary populations. The non-migratory species in my study likely spent more time in the margins and/or had fewer encounters with moving traffic.

Ries et al. (2001) grouped butterflies into a category that I did not consider. They sorted species into groups that were either disturbance-tolerant or habitat-sensitive and found that average abundance of both groups was affected by margin structure (either grassy, weedy, or prairie). Margin structure had no effect on average species richness of the disturbance-tolerant group but it had an effect on the average richness of the habitat-sensitive group. Margins with prairie vegetation were considered more favorable

for the butterflies than margins with non-native grasses. There were more habitat-sensitive butterflies, on average, found in the prairie margins.

Butterfly size likely introduced a sampling bias in my study, as large butterflies are more likely to be seen than small butterflies. It was less likely to spot a dead small butterfly than a live and moving one. This likely resulted in the low relative mortality for small butterflies in the analysis ignoring the fixed effects.

Conclusions

This project examined the effects of altering the frequency of mowing in roadside margins on butterflies and flowering plants. The mowing treatment did not have a significantly distinguishable effect on butterfly abundance in roadside margins. However, the significance of the treatment*spline interaction for the live butterfly data indicates the effect of mowing on live butterfly numbers depends on the time of the year. Frequent mowing after early August appears to limit butterfly numbers. Butterfly mortality was not significantly affected by the mowing treatment. Overall, migratory species of butterflies suffered higher relative mortalities compared to non-migratory species. Smaller butterfly species suffered less relative mortality than larger species. However, these differences may have been heightened by increased detectability of larger road-killed butterfly species.

Changing the frequency of mowing has a significant effect on the abundance and species richness of flowering plants in roadside margins. FDOT standard practice in Alachua County is mowing every 3 weeks. Compared to no mowing and mowing every 6 weeks, the 3-week interval yielded significantly fewer flowers and species per square m. Thus it appears that the FDOT could mow every 6 weeks or less, especially after August when considering butterflies. The roadside margins supported a generous

species richness of flowering plants, with at least 57 identified species of flowering plants. There were likely more species that were not sampled. Surprisingly, only 10 species identified were not native to Florida.

The outcome of this study will facilitate a better understanding of how roadside management affects butterflies that utilize the margins. Since butterflies rely on different resources at different life stages, they are good ecological indicators for a broader array of taxa. It is clear that margins in Alachua County have the potential to support butterflies given the assemblages of flowering plants. It is also clear that margin management affects the composition and availability of flowering plants. If correctly managed, roadside margins have the potential to be habitat to many common insect species, especially pollinators and flower visitors. Even rare species may potentially utilize the margin habitat. There is also the potential for margins to function as dispersal corridors or stepping stone habitats for some species. Margins adjacent to agricultural fields can also be sources of pollinators, benefitting agricultural production. Under circumstances when preserving large habitats is no longer an option, the conservation value of roadside margins should not be overlooked.

Table 2-1. Mowing treatment timeline for the 2011 season.

Week of	Treatment B	Treatment C
April 6 th	x	x
April 27 th		x
May 18 th	x	x
June 8 th		x
June 29 th	x	x
July 20 th		x
August 10 th	x	x
August 31 st	x*	x
September 21 st	x	x
October 12 th		x
November 2 nd	x	x

“Week of” indicates the week during which the mowing treatment(s) were administered, with the date being Wednesday of that week. Each “x” indicates which treatment(s) were administered for each week. Treatment B= 6-week. Treatment C= 3-week. The “x*” was unintentionally administered to the Waldo Road site (Site 2) only, thereby beginning the interrupted 6-week treatment (Treatment D).

Table 2-2. Data sampling interval for the 2011 season.

Month	Sampling Date	Site Order	Sampling Type		
APR	29	3-1-2	Dead	Live	
MAY	6	2-1-3	Dead		
	13	2-3-1	Dead	Live	Flower (17)
	20	1-3-2	Dead		
	27	1-2-3	Dead	Live	
JUN	3	3-2-1	Dead		Flower (7)
	10	3-1-2	Dead	Live	
	17	2-1-3	Dead		
	24	2-3-1	Dead	Live	Flower (28)
JUL	1	1-3-2	Dead		
	8	1-2-3	Dead	Live	
	15	3-2-1	Dead		Flower (19)
	22	3-1-2	Dead	Live	
	29	2-1-3	Dead		
AUG	5	2-3-1	Dead	Live	Flower (9)
	12	1-3-2	Dead		
	19	1-2-3	Dead	Live	
	26	3-2-1	Dead		Flower (30)
SEP	2	3-1-2	Dead	Live	
	9	2-1-3	Dead		
	16	2-3-1	Dead	Live	Flower (20)
	23	1-3-2	Dead		
	30	1-2-3	Dead	Live	
OCT	7	3-2-1	Dead		Flower (11)
	14	3-1-2	Dead	Live	
	21	2-1-3	Dead		
	28	2-3-1	Dead	Live	
NOV					Flower (1)

“Dead” indicates when dead butterflies were collected. “Live” indicates when live butterflies were counted. “Flower” indicates when both the number of flowers and the number of species in flower were counted. The dates in parentheses correspond to a sampling date on the Tuesday(s) of the corresponding month.

Table 2-3. Identified species of butterflies recorded or collected from April 29th, 2011 to October 28th, 2011.

Family	Species and Author	Habitat	Size	Migrate
Hesperiidae	<i>Copaeodes minima</i> Edwards 1870	O	S	N
	<i>Erynnis horatius</i> Scudder & Burgess 1870	W	M	N
	<i>Hylephila phyleus</i> Drury 1773	O	S	Y
	<i>Polites vibex</i> Geyer 1832	O	S	Y
	<i>Pyrgus oileus</i> Linnaeus 1767	O	S	N
	<i>Urbanus proteus</i> Linnaeus 1758	O	M	Y
Lycaenidae	<i>Calycopis cecrops</i> Fabricius 1793	W	S	N
	<i>Hemiargus ceraunus</i> Fabricius 1793	O	S	N
	<i>Strymon melinus</i> Hübner 1818	O	S	N
Nymphalidae	<i>Agraulis vanillae</i> Linnaeus 1758	O	L	Y
	<i>Danaus gilippus</i> Cramer 1775	O	L	Y
	<i>Danaus plexippus</i> Linnaeus 1758	O	L	Y
	<i>Junonia coenia</i> Hübner 1822	O	M	Y
	<i>Limenitis archippus</i> Cramer 1775	W	L	N
	<i>L. arthemis astyanax</i> Fabricius 1775	W	L	N
	<i>Phyciodes phaon</i> Edwards 1864	W	S	N
	<i>Vanessa virginiensis</i> Drury 1773	O	M	N
Papilionidae	<i>Battus philenor</i> Linnaeus 1771	W	L	N
	<i>Eurytides marcellus</i> Cramer 1777	W	L	N
	<i>Papilio glaucus</i> Linnaeus 1758	W	L	N
	<i>Papilio palamedes</i> Drury 1773	W	L	N
	<i>Papilio polyxenes</i> Fabricius 1775	W	L	N
	<i>Papilio troilus</i> Linnaeus 1758	W	L	N
Pieridae	<i>Abaeis nicippe</i> Cramer 1779	O	M	N
	<i>Colias eurytheme</i> Boisduval 1832	O	M	N
	<i>Eurema दौरा</i> Godart 1819	O	S	Y
	<i>Nathalis iole</i> Boisduval 1836	O	S	N
	<i>Phoebus sennae</i> Linnaeus 1758	O	L	Y
	<i>Pontia protodice</i> Boisduval & Le Conte 1830	O	M	N

The authors are cited in Pelham (2008). The Habitat column indicates whether each species tends to occupy open (O) habitats or wooded (W) habitats. The Migrate column indicates whether or not (Y or N, respectively) a given species tends to migrate. These two classes were based on Scott (1986). The Size column is based on average wing span for each species: S < 20 mm, 21 mm < M < 45 mm, and L >46 mm.

Table 2-4. Number of live and dead butterflies per species recorded or collected from April 29th, 2011 to October 28th, 2011.

Family	Species and Author	Dead	Live	D/(D+L)
Hesperiidae	<i>Copaeodes minima</i> Edwards 1870	0	22	0.00
	<i>Erynnis horatius</i> Scudder & Burgess 1870	3	10	0.23
	<i>Hylephila phyleus</i> Drury 1773	4	2	0.67
	<i>Polites vibex</i> Geyer 1832	1	3	0.25
	<i>Pyrgus oileus</i> Linnaeus 1767	1	25	0.04
	<i>Urbanus proteus</i> Linnaeus 1758	1	0	1.00
	Unidentified species, likely Hesperinae	0	16	0.00
Lycaenidae	<i>Calycopis cecrops</i> Fabricius 1793	0	3	0.00
	<i>Hemiargus ceraunus</i> Fabricius 1793	0	17	0.00
	<i>Strymon melinus</i> Hübner 1818	0	3	0.00
Nymphalidae	<i>Agraulis vanillae</i> Linnaeus 1758	60	36	0.63
	<i>Danaus gilippus</i> Cramer 1775	2	0	1.00
	<i>Danaus plexippus</i> Linnaeus 1758	5	3	0.63
	<i>Junonia coenia</i> Hübner 1822	1	22	0.04
	<i>Limenitis archippus</i> Cramer 1775	4	1	0.80
	<i>L. arthemis astyanax</i> Fabricius 1775	1	0	1.00
	<i>Phyciodes phaon</i> Edwards 1864	0	21	0.00
	<i>Vanessa virginiensis</i> Drury 1773	1	3	0.25
Papilionidae	<i>Battus philenor</i> Linnaeus 1771	2	1	0.67
	<i>Eurytides marcellus</i> Cramer 1777	4	3	0.57
	<i>Papilio glaucus</i> Linnaeus 1758	6	0	1.00
	<i>Papilio palamedes</i> Drury 1773	14	0	1.00
	<i>Papilio polyxenes</i> Fabricius 1775	3	2	0.60
	<i>Papilio troilus</i> Linnaeus 1758	4	0	1.00
Pieridae	<i>Abaeis nicippe</i> Cramer 1779	25	8	0.78
	<i>Colias eurytheme</i> Boisduval 1832	1	1	0.50
	<i>Eurema daira</i> Godart 1819	2	22	0.08
	<i>Nathalis iole</i> Boisduval 1836	0	3	0.00
	<i>Phoebus sennae</i> Linnaeus 1758	37	18	0.67
	<i>Pontia protodice</i> Boisduval & Le Conte 1830	2	13	0.13

The relative mortality was calculated as Dead/(Dead+Live). The unidentified species within Hesperidae were grouped together. They all appeared to have morphological features characteristic of the Hesperinae.

Table 2-5. Identified flowering plant species that are known to be nectar sources for butterflies recorded from April 29th, 2011 to November 1st, 2011.

Family	Nectar Plant Species and Author	Native
Alismataceae	<i>Sagittaria lancifolia</i> Linnaeus 1759	Y
Apiaceae	<i>Eryngium baldwinii</i> Sprengel 1825	Y
Asteraceae	<i>Acmella oppositifolia</i> (Lamarck) R. K. Jansen 1985	Y
	<i>Bidens alba</i> (Linnaeus) de Candolle 1836	Y
	<i>Erigeron strigosus</i> Muhlenberg ex Willdenow 1803	Y
	<i>Eupatorium album</i> Linnaeus 1767	Y
	<i>Mikania scandens</i> (Linnaeus) Willdenow 1803	Y
	<i>Pluchea rosea</i> (Miller) Pruski 2005	Y
	<i>Symphotrichum simmondsii</i> (Small) G. L. Nesom 1995	Y
	<i>Lepidium virginicum</i> Linnaeus 1753	Y
Brassicaceae	<i>Lobelia feayana</i> A. Gray 1877	Y
Campanulaceae	<i>Lobelia feayana</i> A. Gray 1877	Y
Clusiaceae	<i>Hypericum mutilum</i> Linnaeus 1753	Y
Commelinaceae	<i>Tradescantia ohiensis</i> Rafinesque 1814	Y
Fabaceae	<i>Aeschynomene viscidula</i> Michaux 1803	Y
	<i>Chamaecrista fasciculata</i> (Michaux) Greene 1897	Y
	<i>Desmodium incanum</i> de Candolle 1825	N
	<i>Medicago lupulina</i> Linnaeus 1753	N
	<i>Melilotus albus</i> Medicus 1787	N
	<i>Trifolium repens</i> Linnaeus 1753	N
Gentianaceae	<i>Sabatia angularis</i> (Linnaeus) Pursh 1814	Y
Iridaceae	<i>Sisyrinchium angustifolium</i> Miller 1769	Y
	<i>Sisyrinchium rosulatum</i> E. P. Bicknell 1899	N
Lamiaceae	<i>Hyptis alata</i> (Rafinesque) Shinnars 1962	Y
	<i>Stachys floridana</i> Shuttleworth ex Bentham 1848	Y
Onagraceae	<i>Ludwigia peruviana</i> (Linnaeus) H. Hara 1953	N
	<i>Oenothera laciniata</i> Hill 1767	Y
Oxalidaceae	<i>Oxalis stricta</i> Linnaeus 1753	Y
Plantaginaceae	<i>Bacopa caroliniana</i> (Walter) B. L. Robinson 1908	Y
	<i>Bacopa monnieri</i> (Linnaeus) Pennell 1946	Y
Portulacaceae	<i>Portulaca pilosa</i> Linnaeus 1753	Y
Rubiaceae	<i>Diodia virginiana</i> Linnaeus 1753	Y
	<i>Richardia brasiliensis</i> Gomes 1801	N
	<i>Spermacoce remota</i> Lamarck 1792	Y
Tetrachondraceae	<i>Polypremum procumbens</i> Linnaeus 1753	Y
Verbenaceae	<i>Phyla nodiflora</i> (Linnaeus) Greene 1899	Y
	<i>Verbena brasiliensis</i> Vellozo 1829	N
Xyridaceae	<i>Xyris ambigua</i> Beyrich ex Kunth 1843	Y

The species authors and the native classification (Y= native and N= not native to Florida) are cited in Wunderlin and Hansen (2008).

Table 2-6. Other identified flowering plant species that are not known to be nectar sources for butterflies recorded from April 29th, 2011 to November 1st, 2011.

Family	Species and Author	Native
Apiaceae	<i>Ptilimnium capillaceum</i> (Michaux) Rafinesque 1830	Y
Araliaceae	<i>Hydrocotyle verticillata</i> Thunberg 1798	Y
Asteraceae	<i>Conyza canadensis</i> (Linnaeus) Cronquist 1943	Y
	<i>Eupatorium capillifolium</i> (Lamarck) Small ex Porter & Britton 1894	Y
Clusiaceae	<i>Hypericum gentianoides</i> (Linnaeus) Britton et al. 1888	Y
Cyperaceae	<i>Rhynchospora colorata</i> (Linnaeus) H. Pfeiffer 1935	Y
Eriocaulaceae	<i>Eriocaulon compressum</i> Lamarck 1789	Y
Euphorbiaceae	<i>Chamaesyce hypericifolia</i> (Linnaeus) Millspaugh 1909	Y
Hydroleaceae	<i>Hydrolea quadrivalvis</i> Walter 1788	Y
Lamiaceae	<i>Clinopodium brownei</i> (Swartz) Kuntze 1891	Y
Lythraceae	<i>Cuphea carthagenensis</i> (Jacquin) J. F. Macbride 1930	N
Melastomataceae	<i>Rhexia mariana</i> Linnaeus 1753	Y
Molluginaceae	<i>Mollugo verticillata</i> Linnaeus 1753	N
Onagraceae	<i>Gaura angustifolia</i> Michaux 1803	Y
	<i>Ludwigia octovalvis</i> (Jacquin) P. H. Raven 1962	Y
Plantaginaceae	<i>Lindernia grandiflora</i> Nuttall 1818	Y
Polygalaceae	<i>Polygala lutea</i> Linnaeus 1753	Y
Polygonaceae	<i>Polygonum punctatum</i> Elliott 1817	Y
Urticaceae	<i>Boehmeria cylindrica</i> (Linnaeus) Swartz 1788	Y

The species authors and the native classification (Y= native and N= not native to Florida) are cited in Wunderlin and Hansen (2008).

Table 2-7. Effects of the fixed independent variables on the four flower response variables.

Site/Trt	Flower density, all	Flower density, nectar	Flower species, all	Flower species, nectar
1A	0.775	0.594	0.561	0.254
1B	0.618	0.214	0.094	0.104
1C	0.244	0.558	0.198	0.643
2A	0.140	0.077	0.402	0.461
2B	0.540	0.378	0.478	0.259
2C	0.604	0.868	0.276	0.525
2D	0.026*	0.007*	0.345	0.338
3A	0.652	0.136	0.336	0.193
3B	0.276	0.229	0.382	0.293
3C	0.205	0.384	0.740	0.177

The p-values are indicated under the three fixed independent variable columns. The numerator, denominator degrees of freedom apply to each column. The "Treatment" column includes the no-mow, 6-week, 3-week, and interrupted 6-week treatment levels. *Significant at $\alpha= 0.05$, **Significant at $\alpha< 0.01$.

Table 2-8. Outcomes of the Pearson's correlation analyses between the four flower variables and ten site*treatment combinations.

Response	Treatment*Time; df= 18,162	Time; df= 8,162	Treatment; df= 3,17
Flower density, all species	0.6475	0.4820	0.0330 *
Flower density, nectar species	0.1527	0.0019 **	0.0390 *
Flower species, all species	0.0931	0.2958	0.0036 **
Flower species, nectar species	0.2458	0.0239 *	0.0052 **

The p-values are listed in each column. * Significant at $p<0.05$.

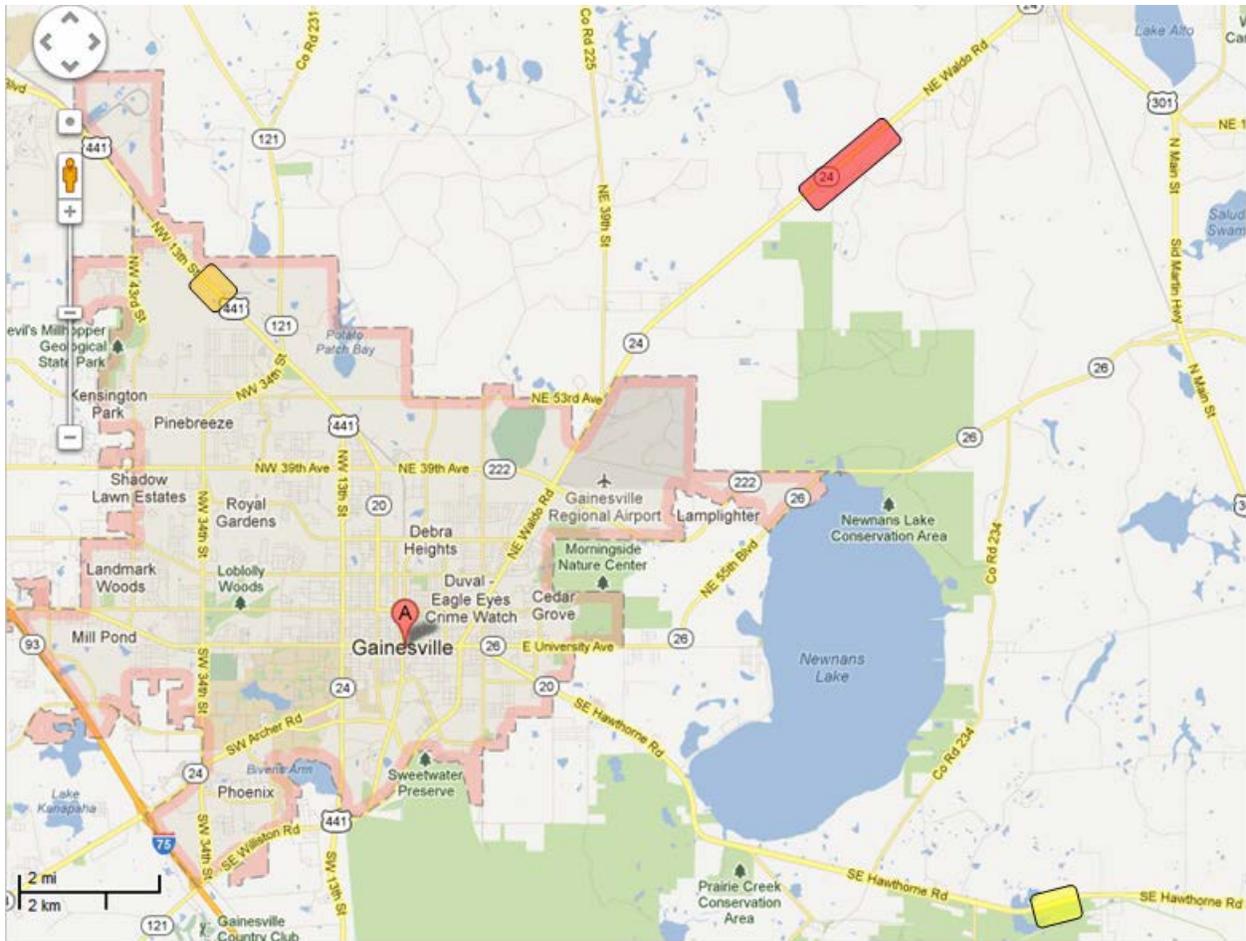


Figure 2-1. Approximate locations of the three experimental sites represented by the colored boxes, with downtown Gainesville, Florida as the central reference point. Site 1 (orange, upper left) lies between Alachua and Gainesville along Highway 441. Site 2 (red, upper right) lies between Gainesville and Waldo along Northeast Waldo Road. Site 3 (yellow, lower right) lies between Gainesville and Hawthorne along Southeast Hawthorne Road. Map courtesy of Google.



Figure 2-2. A freshly mowed section of roadside margin along Southeast Hawthorne Road (Site 3). Each experimental unit begins 1.5 m in from the road's edge and extends back to where the woody vegetation begins.

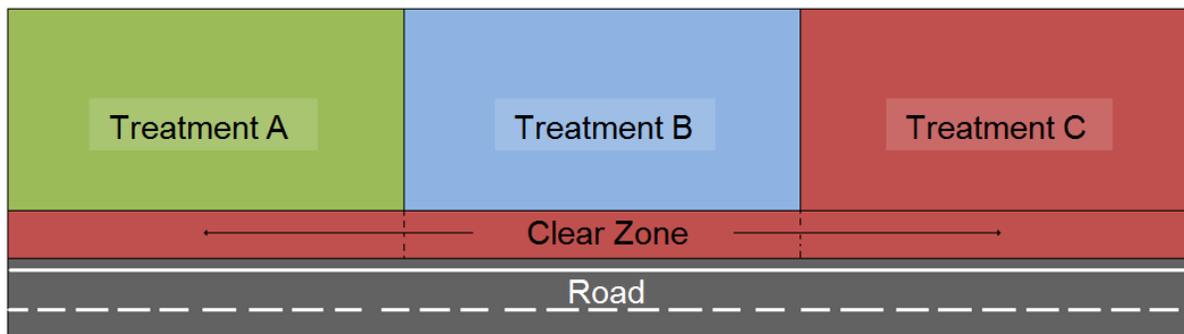


Figure 2-3. Hypothetical mowing regime schematic for a block. Treatment A= no-mow, Treatment B= 6-week, and Treatment C= 3-week (standard practice). The 1.5-m-wide clear zone was mowed every 3 weeks at all blocks. An entire block was 600 m long and each treatment section was 200 m long. The schematic is not to scale.

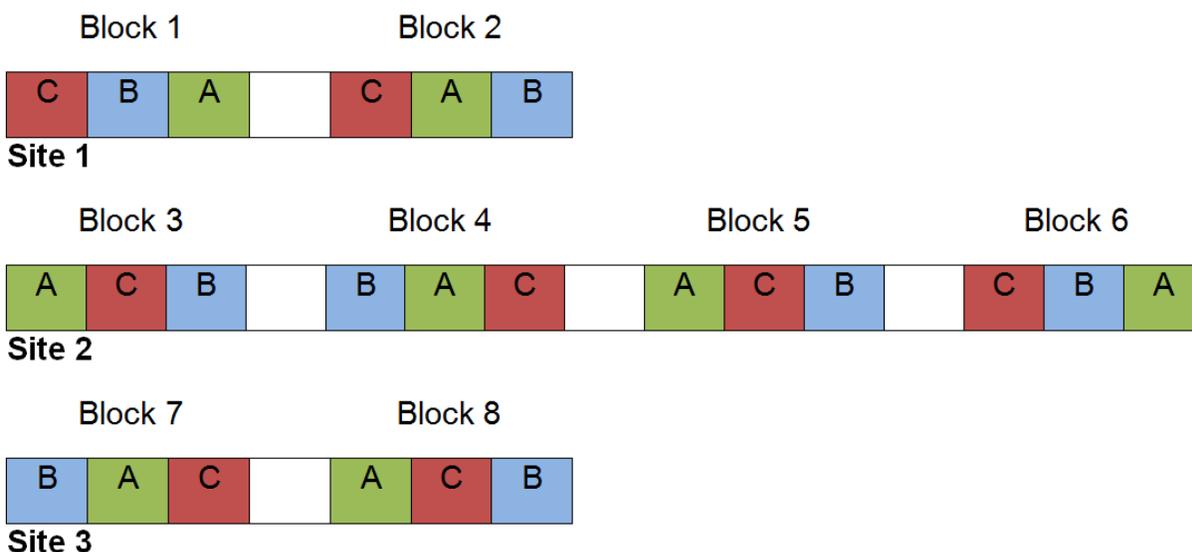


Figure 2-4. Mowing treatment randomization pattern implemented throughout the course of the study. The white spaces are the 100-m buffers between blocks, with the next block continuing after the buffer. Treatment A= no-mow, Treatment B= 6-week, and Treatment C= 3-week (standard practice). After August 31st, the Treatment B's for Site 2 were replaced with Treatment D= interrupted 6-week.



Figure 2-5. The dividing line between two mowing treatments indicated by large differences in vegetation structure to the left and to the right of the semi-permanent sign installed by the Florida Department of Transportation. "A"= no-mow treatment and "C"= 3- week treatment.



Figure 2-6. Wing remnants of *Abaeis nicippe* Cramer 1779 in the grassy thatch at the road's immediate edge. This would be counted as one individual.

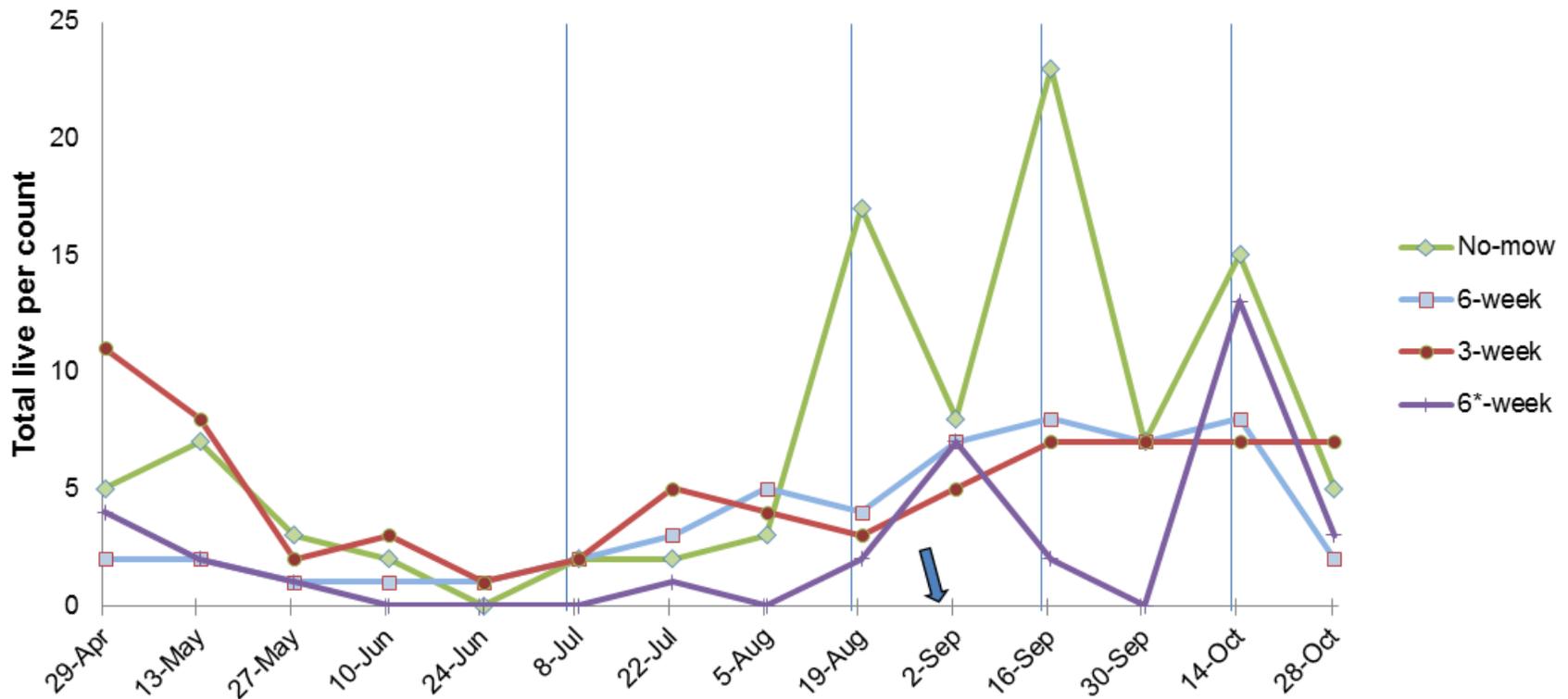


Figure 2-7. Line graph of the total live counts of butterflies (made every 2 weeks) under each mowing treatment at each sampling date over the course of the study. The 6*-week treatment (interrupted 6-week) was split from the 6-week treatment for the whole time period for longitudinal reasons, i.e. to avoid an unnatural drop in the 6-week treatment after the former arose (arrow). The vertical lines indicate the location of the spline knots.

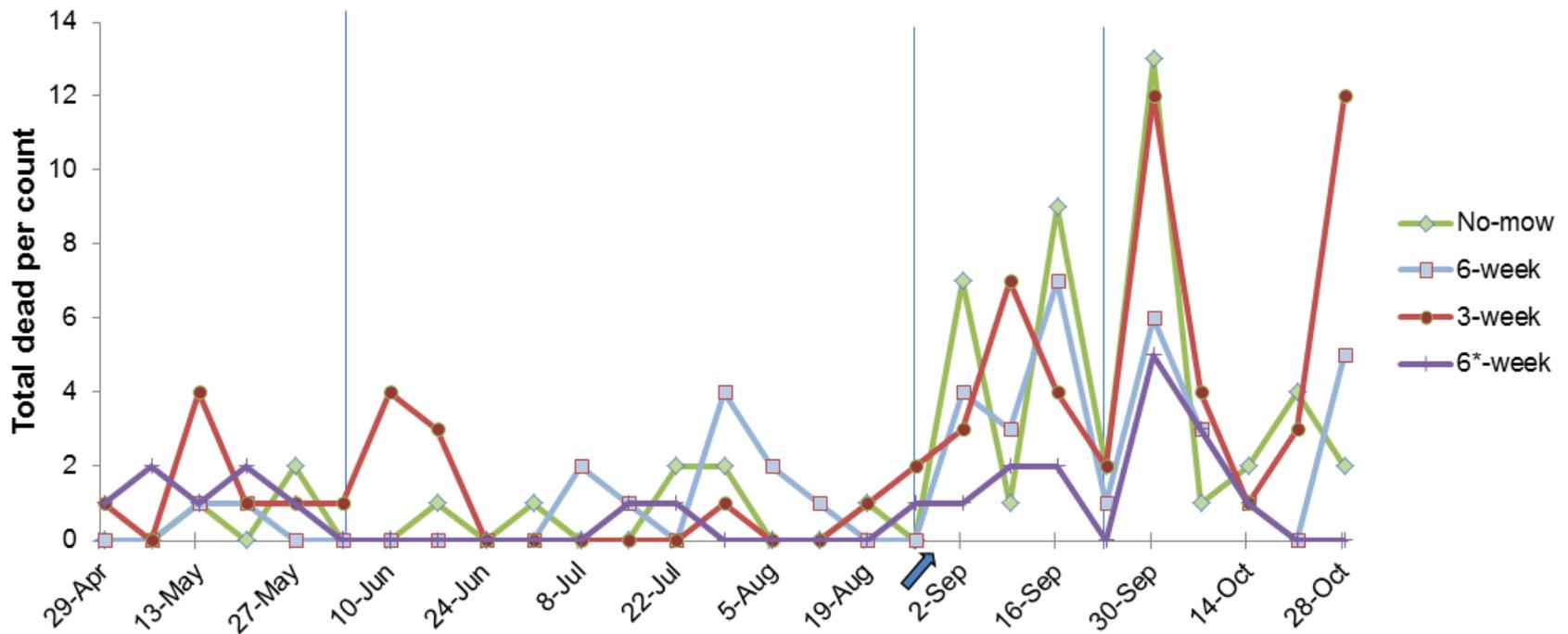


Figure 2-8. Line graph of the total dead counts of butterflies (made weekly) under each treatment at each sampling date over the course of the study. The 6*-week treatment (interrupted 6-week) was split from the 6-week treatment for the whole time period for longitudinal reasons, i.e. to avoid an unnatural drop in the 6-week treatment after the former arose (arrow). The vertical lines indicate the location of the spline knots.

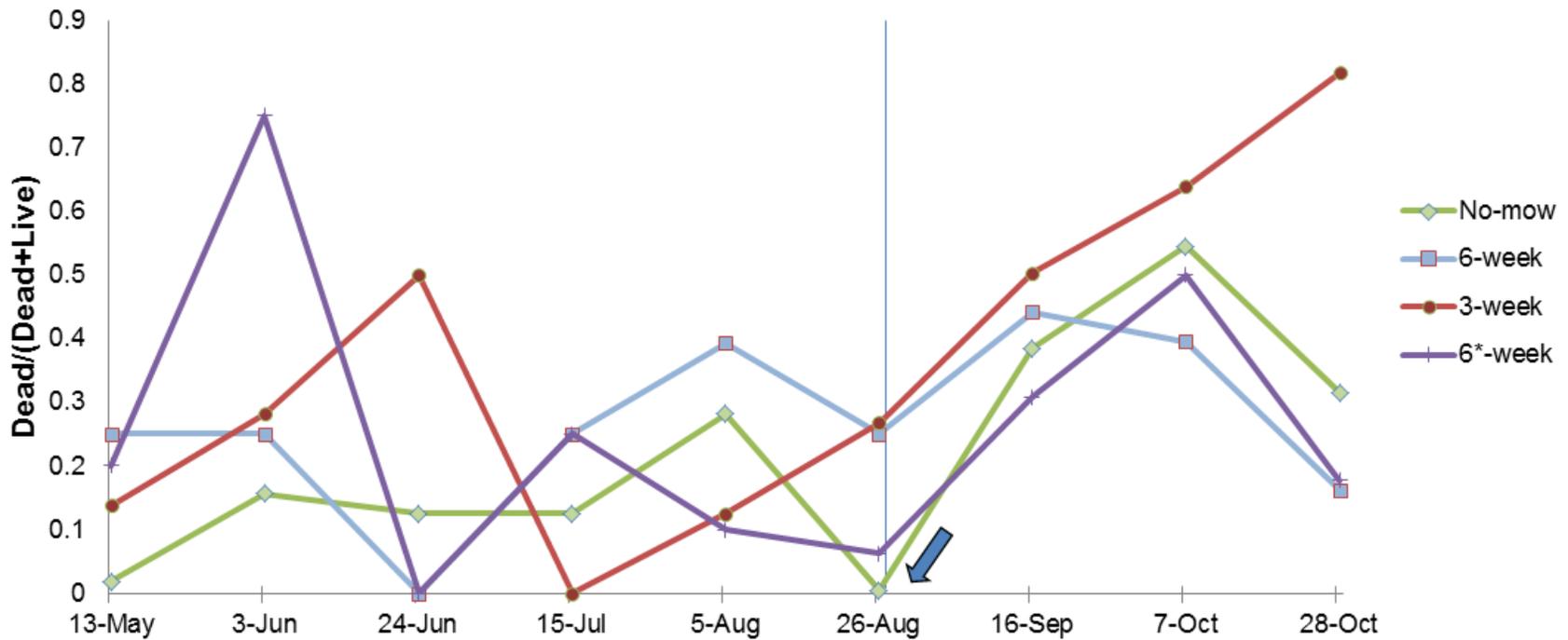


Figure 2-9. Line graph of the relative mortalities of butterflies (calculated every 3 weeks) under each treatment over the course of the study. The 6*-week treatment (interrupted 6-week) was split from the 6-week treatment for the whole time period for longitudinal reasons, i.e. to avoid an unnatural drop in the 6-week treatment after the former arose (arrow). The vertical line indicates the location of the spline knot.

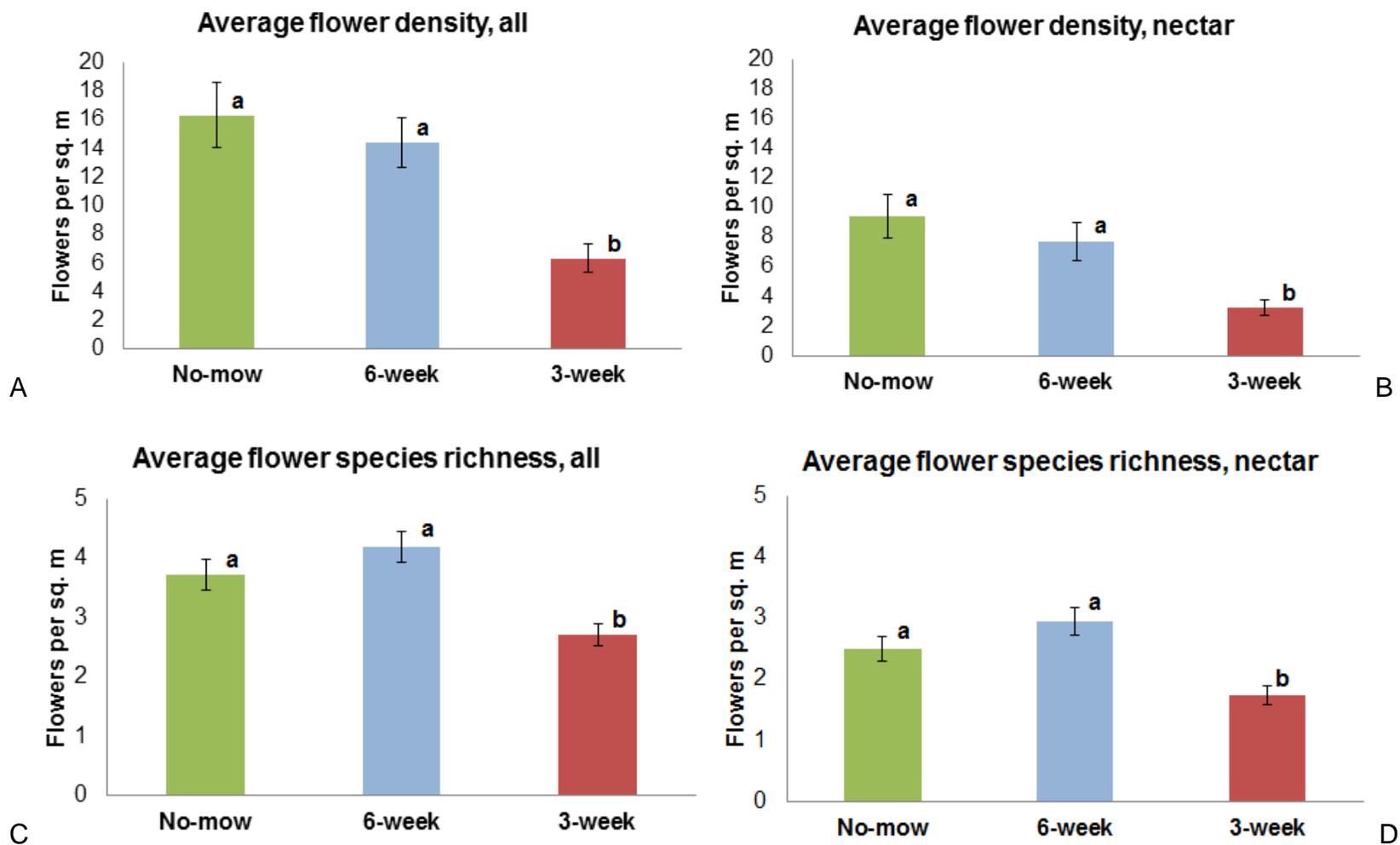


Figure 2-10. Effects of the three mowing treatments on the four flower response variables. The interrupted 6-week treatment is not included because it was used a baseline for comparison. Bar values and standard error brackets are calculated from the raw data. Different letters above the bars indicate means that are significantly different. A) density considering all species, B) density considering only known nectar species, C) richness considering all species and D) richness considering only known nectar species.

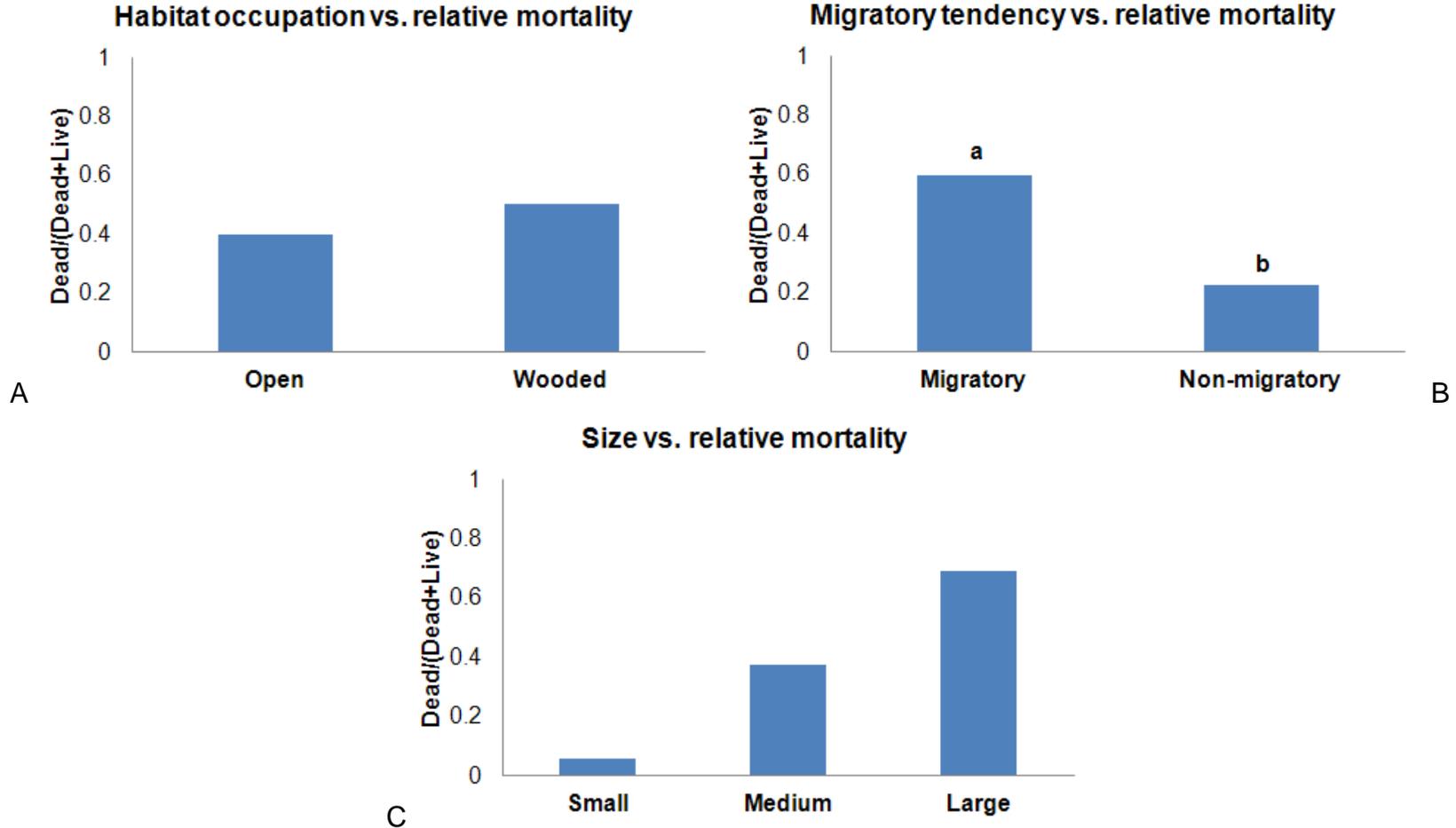


Figure 2-11. Effects of butterfly groups on relative mortality, $Dead/(Dead+Living)$. Mowing treatment and time were not considered in this analysis. Groupings are based in Scott (1986). Different letters above the bars indicate means that are significantly different. A) habitat occupation indicates whether or not the butterfly species tends to occupy open or wooded habitats, B) migratory tendency indicates whether or not the butterfly species tends to migrate at any point and C) size refers to wing span: Small <20 mm, 21 mm < Medium < 45 mm, and Large > 46 mm.

CHAPTER 3 CONCLUSIONS AND SUGGESTIONS FOR FUTURE RESEARCH

It would be premature to recommend the FDOT drastically reduce its mowing frequency to benefit butterfly populations. Although there is evidence from this one-year study that less frequent mowing yields a greater abundance and species richness of flowering plants in roadside margins, the benefits to butterflies at the population level could not be assessed. The data suggest that not mowing the margins supports greater numbers of butterflies, especially from August onward. The fact that the treatment*spline interaction was significant for the live butterfly counts is suggestive of the ecological significance of mowing. Without an understanding of the source-sink dynamics associated with these roadside margins, managing them to have more plentiful resources for butterflies may not be the most sound conservation strategy.

Sink habitats can receive an influx of immigrants from source habitats and can have far more individuals than source habitats (Pulliam 1988). The source habitats of the migratory species would be scattered at a scale impractical for effective sampling. However, many of the non-migratory species found in this study could be adequately sampled for. If dispersal ranges are known for a species, it can be sampled for in habitats surrounding roads. Mark-release-recapture methods or more frequent transect walks would give better population estimates than a single transect walk once every 2 wks. Abundances could then be compared between margin and surrounding habitat. Mark-release-recapture would also offer insight to immigration and emigration patterns. Larval sampling could be used as an indicator of reproduction in the habitat. Unfortunately, it would be nearly impossible to sample mortality in surrounding habitats.

It is also possible that margins could be source habitats for some species. Further research should focus on a greater variety of insect orders. As mentioned in Coffin (2007) and Hopwood (2008), margins could be important habitat if the surrounding habitats are uninhabitable. In that case, even if margins were sinks, they would still be better than not having any habitat in the first place. The persistence of populations in such margins would depend on re-colonization from dispersing individuals from adjacent habitats. If the distance between two habitat patches exceeds the dispersal capabilities of the species, corridors may be helpful in facilitating dispersal (Haddad 2000).

Some species of butterflies may tend to stay in margins that have more resources and avoid crossing the road. Thus the margins have potential to serve as linear dispersal corridors between habitats parallel to roads. By staying in the margins, the butterflies experience lower relative mortality. However, in this sense roadside margins may act as barriers to dispersal perpendicular to roads. A trade-off between minimizing mortality and encouraging dispersal becomes evident. Forman and Alexander (1998) argue in favor of making roads permeable to dispersal, despite the risk of roadkill mortality. Although I observed some butterfly species avoid crossing the road, I cannot confirm that they never crossed the road. Munguira and Thomas (1992) showed through mark-release recapture studies that 10-30% of closed population (i.e. non-migratory) butterflies crossed the road. They claimed this would not constitute a barrier to gene flow.

Further research should investigate the barrier effects of roads on butterflies and other insects that appear to avoid crossing the road. If dispersal is not severely

hampered, then creating resource-rich margins would reduce mortality and still permit dispersal between habitat fragments. A combination of behavioral observation, mark-release-recapture, and genetic analysis would be an effective way to evaluate successful dispersal (Leidner and Haddad 2011).

It is possible that the outcomes of this project would have been more conclusive had there not been such anomalous weather conditions. Repetition of this experiment over multiple seasons would make results more convincing. If weather patterns fluctuate between experiments, insight to how the butterflies respond to disturbance under different abiotic stressors could be gained. This could offer some predictive power to deciding the best management strategies for a particular season.

Roadside margins adjacent to agricultural fields may prove to be source habitat for pollinators that could enter the fields and provide pollination services. Dover (1989) found that there were more butterflies in fields with conservation headlands (i.e. managed margins) than in fields that had their margins sprayed with the same pesticides used in the field crop. Agricultural fields in the United States tend to be monocultures and poor habitat for supporting a diversity of insects. Managing margins to be resource-rich habitats could provide a source of pollinators. Verifying the efficacy of such a technique could be done by comparing pollinator abundance and richness between fields adjacent to resource-rich margins and fields adjacent to resource-poor margins.

Since roadside margins are already routinely managed in many areas, considering their use in conservation efforts may be a good alternative to adding land area to reserves or setting aside additional reserves (Ries et al. 2001), be it for corridors or

habitat. Roadside compensatory restoration should be focused at potential bottlenecks, i.e. regions where fragmentation and mortality is severe (Bohemen 1995). Munguira and Thomas (1992) suggest that margins could be improved to function as butterfly habitat by encouraging native vegetation growth, planting native seed mixtures, varying the topography, and by making the margin habitat as wide as possible.

Wildflower augmentation is an aspect of management that should be considered for its ecological value. The FDOT supports the Wildflower Program, in which wildflower seeds are sewn along select sections of highway. The seed mixtures typically contain species that are attractive and self-sustaining. While practical economically, these may be not be ecologically ideal. Further research should focus on which species of flowers and seed mixtures would be beneficial to insects and economical.

Margins should be maintained as a heterogeneous habitat to benefit the greatest number of species. One study of field margins found that hedgerows act as barriers to movement for some species, but also serve as perching sites and resources for other species (Fry and Robson 1994). The latter also suggested a varied approach in margin design, with a variation in hedge heights and openings in areas that would benefit from dispersal. McKenna et al. (2001) noted a high mortality of monarch butterflies and attributed it to the close proximity of their larval host plants to the road's immediate edge. In this case, maintaining a clear zone near the road's edge may reduce monarch mortality if the host plants are farther from traffic. Experiments that investigate a mosaic pattern of margin management would provide insights to benefits of habitat heterogeneity. Ultimately, the best management practices for roadside margins will depend on how the natural community in question responds to them.

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BIOGRAPHICAL SKETCH

Dale Halbritter was born in 1988 in Torrance, California. He grew up with his parents in the small high desert town of Palmdale, California. As a child, he loved playing outside and spent a lot of his free time collecting insects in his neighborhood. By middle school, he had his parents taking him on frequent outings to the nearby San Gabriel Mountains to go hiking and insect collecting. He enjoyed collecting butterflies the most and made a hobby out of raising spiders in captivity. The Halbritter homestead was always filled with terrariums of live arthropods. In high school, Dale joined the Lorquin Entomological Society based in Los Angeles and began making connections with amateur and professional entomologists. He attended the University of California, Riverside for his Bachelor of Science in entomology. He graduated summa cum laude in 2010 and moved to Gainesville to attend the University of Florida for his Master of Science in entomology.