Reducing Mowing Frequency Increases Floral Resource and Butterfly (Lepidoptera: Hesperioidea and Papilionoidea) Abundance in Managed Roadside Margins

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Reducing mowing frequency increases floral resource and butterfly (Lepidoptera: Hesperioidea and Papilionoidea) abundance in managed roadside margins

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Abstract

Roads are common in natural landscapes and can have significant impacts on wildlife. Most studies have focused on vertebrates and primarily addressed the negative impacts of roads. However, roadside margins have the potential to support habitat for some taxa, such as pollinating insects. The purpose of this study was to determine whether changes in roadside vegetation management affect butterflies (Lepidoptera: Hesperioidea and Papilionoidea) and floral resources. Specifically, we investigated how mowing frequency affects both the abundance and mortality of butterflies and the abundance and species richness of herbaceous plants in bloom along highway margins. Three different mowing treatments were applied to sections of highway margin in Florida, USA: no mowing, mowing every 6 wk, and mowing every 3 wk. Butterfly and floral resource data were gathered at regular intervals for 6 mo during the peak growing season, from late spring through early fall. Correlations between floral species richness and abundance and butterfly abundance were calculated. The mowing treatment had a significant effect on floral resources, with the 3 wk treatment yielding the lowest abundance and species richness. The mowing treatment alone did not have a significant effect on any butterfly variable, but the mowing treatment*time interaction had a significant effect on live butterfly abundance. The no-mow treatment yielded the greatest numbers of live butterflies from late summer into early fall. This study suggests that reducing mowing during peak seasonal butterfly activity can increase butterfly numbers. Future studies in different regions would benefit from considering the effects of time of year of mowing in addition to the frequency.

Key Words: pollinator; habitat; management

Resumen

Las carreteras son comunes en los campos naturales y pueden tener un impacto significativo en la vida silvestre. La mayoría de los estudios se han centrado en los vertebrados y son dirigidos principalmente a los impactos negativos de las carreteras. Sin embargo, los márgenes de las carreteras tienen el potencial de apoyar el hábitat de algunos taxones, como los insectos polinizadores. El propósito de este estudio fue el determinar si los cambios en el manejo de la vegetación de los márgenes de las carretera afectan las mariposas (Lepidoptera: Hesperioidea y Papilionoidea) y los recursos florales. Específicamente, se investigó cómo la frecuencia de cortar la vegetación afecta la abundancia y la mortalidad de las mariposas y de la abundancia y riqueza de especies de plantas herbáceas en floración en los márgenes de la carretera. Se aplicaron tres tratamientos diferentes de cortar la vegetación a secciones del margen de la carretera en la Florida, EE.UU: sin cortar, cortar cada 6 semanas y cortar cada 3 semanas. Se recolectaron los datos sobre las mariposas y recursos florales a intervalos regulares durante 6 meses durante la temporada de crecimiento máximo, desde el final de la primavera hasta el principio de otoño. Se calcularon correlaciones entre la riqueza de especies y abundancia de flores y la abundancia de mariposas. Los tratamientos de cortar la vegetación tuvo un efecto significativo sobre los recursos florales, con el tratamiento de 3 semanas resultando en la abundancia y riqueza de especies más baja. El tratamiento de solo cortar no tuvo un efecto significativo sobre cualquier variable de la mariposa, pero la interacción del tiempo del tratamiento * tuvo un efecto significativo sobre la abundancia de mariposas vivas. El tratamiento de no-cortar produjo el mayor número de mariposas vivas desde el final del verano hasta el principio de otoño. Este estudio sugiere que una reducción en el corte de la vegetación durante la actividad máxima estacional de las mariposas puede aumentar el número de mariposas. Los estudios futuros en diferentes regiones se beneficiarían de considerar los efectos de la época del año del corte de la vegetación, además de la frecuencia.

Palabras Clave: polinizadores; hábitat; manejo

The expansion of global infrastructure is mirrored by numerous road networks across a vast array of natural habitats. As of 2012, the total public road coverage in the United States was 6,586,610 km (Federal Highway Administration 2014). Roads and vehicle traffic have been shown to negatively impact a number of animal taxa via mortality resulting from wildlife–vehicle collisions, habitat fragmentation, and environmental degradation (Way 1977; Mader et al. 1990; Ashley & Robinson 1996; Smith et al. 1996; Forman & Alexander 1998; Spellerberg 1998; McKenna et al. 2001; Coffin 2007; Taylor & Goldingay 2010). However, the narrow regions along road edges (i.e., margins) can positively impact some taxa by providing refuge habitat (Leach & Recher 1993; Spellerberg 1998; Tshiguvho et al. 1999; Coffin 2007; Hopwood 2008).

Road ecology was derived from landscape and ecosystem ecology and initially addressed the negative effects of roads on wildlife (Road

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Ecology Center 2014). The field has expanded to address population-level impacts of roads, but larger-scale studies at the community and landscape level are needed to understand complex and long-term ecological interactions (van der Ree et al. 2011). Forman & Alexander (1998) identified road ecology as both a "sleeping giant" and a "major frontier," recognizing that applying road ecology to road construction planning, management, and conservation is an issue for both science and civilization. As long as motorized vehicles remain the primary mode of transportation, the effects of roads on wildlife will continually need to be addressed.

Mortality due to collisions with moving vehicles (i.e., roadkill) is one of the most direct impacts roads can have on mobile organisms. It is apparent in literature reviews that the vast majority of studies on roadkills have focused on vertebrates (Forman & Alexander 1998; Spellerberg 1998; Taylor & Goldingay 2010). The impact of roadkills on animal populations tends to be influenced by behavior and population dynamics. For example, large mammals have fewer offspring and have much longer generation times compared with insects. The key deer, *Odocoileus virginianus clavium* Barbour and Allen (Artiodactyla: Cervidae), experienced roadkill rates of approximately 16% of the entire population. Reproduction and immigration rates were likely insufficient in mitigating the impact of roadkill mortality on the deer population (Forman & Alexander 1998). On the contrary, 4 million sparrow, *Passer domesticus* (L.) (Passeriformes: Passeridae), roadkills per year were estimated in the United Kingdom by Hodson (1966), but the roadkill rate was not considered high enough to affect the overall sparrow population. There are comparably fewer studies that investigate arthropod roadkills and only a handful that focus on butterflies (e.g., Munguira & Thomas 1992; Bak et al. 1998; McKenna et al. 2001; Ries & Debinski 2001; Ries et al. 2001; Saarinen et al. 2005). In the United Kingdom, roadkills were reported to be responsible for a direct loss of up to 7% of individuals from *Pieris rapae* (L.) (Lepidoptera: Pieridae) populations but were considered an insignificant source of mortality when compared with natural causes (Munguira & Thomas 1992).

Despite the potential danger of roadkills, roadside margins can serve as habitat for a number of animal species and can be especially beneficial if the surrounding habitats are inhospitable or absent (Coffin 2007; Hopwood 2008). Way (1977) reported that roadsides in the British Isles functioned as breeding habitat for 40% of the islands' mammal species, 100% of reptile species, 20% of bird species, 42% of butterfly species, 47% of bumblebee species, and 8% of amphibian species. Others have shown that roadside margins function as habitat for butterflies (Munguira & Thomas 1992; Ries et al. 2001; Saarinen et al. 2005; Wynhoff et al. 2011). If more thorough species inventories are conducted, roadside margins could support even more species than those currently documented. Tews et al. (2004) highlighted a positive correlation between habitat heterogeneity and animal species diversity in the literature, noting a particular focus on vertebrates in anthropogenically influenced habitats. Heterogeneity at one spatial scale (e.g., spacing of host plants or variations in vegetation height) may benefit some species while it may act to fragment the habitat of others (Spitzer et al. 1997). Therefore, it is important to consider how the temporal and spatial scales of habitat management will affect a variety of species and how each species would interact with the resources in its habitat.

Our study aimed to reduce the knowledge gap for invertebrates in road ecology by testing whether or not simple changes in roadside management can impact butterflies utilizing roadside margins in Alachua County, Florida, USA. According to Gerald & Graham (1995), margins are mowed and maintained in Florida to beautify transportation corridors and maximize safety. Mowing ensures that vehicles have a place to pull over in highway emergencies and that a cleared buffer is present if there is a loss of vehicle control. Additionally, maintaining aesthetically pleasing roadsides is important to Florida's tourist-based economy. Most margins along highways in Alachua County, Florida, are mowed at a 3 wk interval during the growing season, primarily for safety and aesthetics (Campbell K, Florida Department of Transportation, Alachua County, Florida, USA, personal communication).

We tested the hypothesis that altering the mowing frequency changes the number of butterflies and floral resources found in roadside margins. Butterfly presence in disturbed habitats is often positively correlated with floral resource availability (Dover 1989; Munguira & Thomas 1992; Sparks & Parish 1995; Dover et al. 2000). The roadside margins in Florida are disturbed areas that are maintained in an early successional state, supporting an assemblage of grasses and forbs. Consequently, we measured floral species richness and abundance under different mowing frequencies and analyzed their correlations to butterfly numbers. Our study offers insights to the butterfly species utilizing margins and those that are susceptible to roadkill, and presents suggestions for more effective management practices. Studies such as ours aim to reach a compromise between management and conservation.

Materials and Methods

STUDY DOMAIN AND EXPERIMENTAL DESIGN

Three highway sites were selected within a 19 km radius of Gainesville, Alachua County, Florida, USA. All sites had a high degree of similarity to minimize the effects of confounding environmental variables. Each highway had a posted speed limit of 105 km/h, a similar traffic volume (averaging 11,000 vehicles/d), and all were 4-lane highways with a vegetated center median (Florida Department of Transportation 2009). Site selection based on ecological properties was made using satellite imagery and verified by ground truthing. The managed roadside margins at each site, composed of shared species of grasses and forbs, spanned an average width of 8 m (ranging from 4–10 m) from the road's edge to the established woody vegetation. The latter was primarily pine and mixed hardwood forest at each site, although some sections of the State Route 20 site were adjacent to patches of cypress wetland. The roadside soils at each site were sandy. The woody vegetation extended back at least 600 m from the road at each site. These sites are fairly representative of rural highways in North Central Florida.

Eight blocks were distributed between the 3 sites. Each block consisted of a 600 m strip of margin parallel to one side of the road's outer edge (i.e., the center medians were not used). All blocks within each site were located on the same side of the road. There was a 100 m buffer between each block that served to aid in spatial and visual separation of the blocks. Site 1 (Highway 441) contained 2 blocks on the south side of the road, Site 2 (State Route 24) contained 4 blocks on the southeast side of the road, and Site 3 (State Route 20) contained 2 blocks on the north side of the road. Site 2 had the longest stretch of continuous margin and was divided into 4 blocks to maximize replication of the treatments.

The designed explanatory variable was the mowing treatment, which had 3 levels: no mowing (no-mow) during the course of the study, mowing every 6 wk, and mowing every 3 wk (standard practice). The 3 mowing treatments were assigned randomly to 200 m sections within each block such that each treatment occurred once in each block. This distance was selected to provide a standardized snapshot of butterfly activity and allow all sections to be sampled within the same day. Treatments were administered to each assigned section for the duration of the study.

TREATMENT SPECIFICATIONS

The mowing treatments were administered by the Florida Department of Transportation (FDOT). A John Deere Ztrack mower (Model 797, Deere & Company, Moline, Illinois, USA) was used to administer the mowing treatments. It had 3 spinning blades that spanned a total width of 1.8 m. The entire width of the margins was mowed during each treatment. The height of the mower's blades was set at 14 cm. Parr & Way (1988) found that if the height of cutting remained constant, the type of mowing machine did not have a significant effect on roadside plant species richness. We nonetheless ensured the same mower was used on all 3 sites.

The mowing treatments began on 6 Apr 2011 and ended on 2 Nov 2011, covering the peak growing season for North Central Florida. We intended for all sites to be mowed on the same day of each week 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 provided documentation forms with each mowing cycle to verify that all treatments were administered correctly. An unintentional treatment was added to Site 2 during the 19th week of the study. All sections at Site 2 receiving the 6 wk treatment were accidentally mowed on 31 Aug 2011 after only 3 wk of a cycle, each becoming the interrupted 6 wk treatment.

A clear zone covering the first 1.8 m from the road's immediate edge was 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 & Graham 1995). The clear zone was mowed every 3 wk, but mowing did not start until after 20 Jul 2011 due to slow plant growth associated with a prolonged early-season drought. The 100 m buffers were mowed every 3 wk, and data were not gathered from the buffers.

SAMPLING DESIGN

Data in the form of live butterfly counts, butterflies found dead near the road's edge, and floral resource counts were gathered primarily from the blocks between the hours of 9:00 AM and 2:00 PM. Persistent rain, cloudy skies combined with forecasted maximum daytime temperatures below 18 °C, and/or winds over 32 km/h warranted a rescheduling of data collection. To account for any spillover effects from adjacent treatments within each block, data collection was restricted to the middle 100 m of each 200 m treatment section. The order in which the 3 sites were visited alternated between the 6 permutations of the 3 sites: 1-2-3, 3-2-1, 2-1-3, 3-1-2, 1-3-2, and 2-3-1. The permutation orders were repeated as necessary. This method of alternating orders aimed to minimize temporal sampling bias compounded by travel time between sites. Blocks within sites were always visited in the same order.

Live butterflies seen in the treatment sections were counted and identified on the same day every 2 wk. Butterflies were identified mostly on the wing or while perched on vegetation, but efforts were made to net and photograph individuals that were difficult to identify. If a netting attempt failed, the individual was documented at the lowest taxonomic level of certainty. Considering how narrow the margins were, a linear transect parallel to the road and spanning the width of the margin (~ 8 m) was suitable to document the species of butterflies present. Our transect methods reflected those used by Munguira & Thomas (1992), Feber et al. (1996), McKenna et al. (2001), Ries et al. (2001), and Saarinen et al. (2005), but our methods were not intended to quantify total abundance. Rather, we intended to document relative abundance of each species for comparative purposes and to determine whether roadkilled butterflies were representative of those seen flying in the margins.

Roadkilled butterflies found near the road's edge within each treatment section were removed, counted, and identified once weekly. 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 2 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. Shadows would otherwise reduce the visibility of butterfly corpses in clear zone vegetation. Walking was done against the flow of traffic for safety concerns because both observers were very close to moving traffic.

Data from the 1st 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 or wing fragments were still counted as an individual. It was unlikely that 4 wings from 1 butterfly were counted as 4 butterflies, as wings and wing fragments typically remained within 15 cm of each other in the short clear zone vegetation.

Floral abundance and species richness sampling was done on the day before each mowing treatment. Data were gathered within 5 randomly placed 1 m^2 quadrats per 100 m treatment section. Each 100 m treatment section was divided into 80 cells, and 5 cells were selected randomly for quadrat placement on each sampling day in each section. Careful pacing of the observer was used as an estimated measurement to locate the 5 cells on an imaginary grid. The recorder followed and instructed the observer where to drop the quadrat. Because each cell was approx. 10 m^2, the observer dropped the quadrat into the cell without looking directly at the ground to minimize sampling bias.

Floral resource abundance was determined by counting the number of flowers and/or inflorescences within each quadrat. If flowers were less than 1 mm in diameter and part of a larger inflorescence (approx. 2.5 cm or less in diameter), the inflorescence was counted as a single flower. Tall flowers that were folded over by the quadrat and appeared to be in the 1 m^2 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 5 flowers. Species were identified visually in the field when possible. Any unknown species 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 ANALYSES

The experiment was modeled as an unbalanced split-plot design. The high plot level, the sites, had no treatment structure. Although the 3 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 8 blocks, had a randomized complete block design. The random independent variables were site and block. The fixed independent variables were mowing treatment, time (i.e., mowing frequency), treatment*time interaction, a butterfly species' migratory tendency, a butterfly species' natural habitat, and butterfly wing span category (size) (Scott 1986). Consequently, mixed models were utilized. The dependent variables were live and dead butterfly abundance, relative butterfly mortality, and density and species richness of floral resources. With one exception, analyses were conducted using SAS version 9.2 for Windows (SAS Institute Inc., Cary, North Carolina, USA). Significance was considered for *P*-values less than or equal to 0.05.

To determine whether or not the interrupted 6 wk treatment was an effect we could ignore, we tested a carryover effect for significance before analyzing the final datasets. 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 1st week. The data were analyzed with a split-plot design using Proc GLIMMIX. The data analyzed included everything up through Sep (i.e., up to 3 wk after the mowing error). The explanatory variables were treatment, time, treatment*time (interaction), and $PRIORTRT$. The live and dead butterfly data and flower density data were $y' = ln(y + 1)$ transformed for this analysis, but the flower species richness data were not transformed.

The live and dead butterfly data did not appear to meet the assumptions of normality, despite attempting a $y' = ln(y + 1)$ transformation. Because the live and dead butterfly data were quite sparse, and in order to best retain the variability structure, we utilized the 2-parameter Gamma distribution. A spline structure was given to the time variable in order to decrease the number of coefficients to be estimated, thereby avoiding convergence problems. Knots were chosen to divide the data into spline sections such that the pattern in each section would be captured adequately by a cubic polynomial approximation. Although these selections may bring biases in the estimates, they outweighed the costs of using standard equal divisions (i.e., lack of convergence).

The relative mortality for each treatment section was calculated as the sum of dead butterflies divided by the sum of both dead and live butterflies: Relative Mortality = Dead / (Dead + Live). This ratio was calculated in 3 wk intervals to permit future linear regression analyses with the 3 wk sampling interval of the floral resource data. There were 3 dead butterfly counts in each interval and these were averaged. Because of the 2 wk interval of live butterfly counts, some of the ratios had 2 live counts and these were averaged. The beta distribution in Proc GLIMMIX was selected because it supports proportion values between 0 and 1. To maintain consistency, a spline structure was utilized.

A split-plot analysis was used on the floral resource data. Based on our observations and prior field experience, flower species that were known to be favorable nectar sources for butterflies were analyzed as a separate group. Thus, there were 4 groups of floral resource variables: floral density of all species (floral density), floral density of nectar species (nectar density), total floral species richness (floral richness), and richness of floral nectar species (nectar richness). Density data were $y' = ln(y + 1)$ transformed and fit to the split-plot model with a normal distribution. Floral richness data did not need to be transformed to meet the normality assumptions. Nectar richness 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. Pair-wise comparisons (least squares means) were made between the no-mow, 6 wk, and 3 wk treatments. Non-transformed means were presented in figures.

Correlations between the live butterfly counts and each of the 4 groups of floral resource variables were calculated using R version 3.0.2 (R Core Development Team, Vienna, Austria). There were 10 site and treatment combinations (Site 1: no-mow, 6 wk, and 3 wk; Site 2: no-mow, 6 wk, 3 wk, and interrupted 6 wk; Site 3: no-mow, 6 wk, and 3 wk), and Spearman's rank correlations were computed using pairs of the live butterfly data (from each of the 10 site and treatment combinations) and each of the 4 floral resource variables. Thus, there were 40 correlations.

Live and dead butterfly data were separated by species into groups based on whether or not they are migratory, whether they utilize open or wooded habitat, and their different wing spans (size: small ≤ 20 mm, 21 mm ≤ medium ≤ 45 mm, and large ≥ 46 mm) (grouping decisions

were based on Scott 1986). The effects of the mowing treatments on the butterfly groups were analyzed. The same model and specified spline knots from the unseparated butterfly data were used. Group sums over all treatments also were calculated (i.e., mowing treatment and time were not variables of concern in this context). In this case, a chi-square test was used to determine whether migratory tendency, habitat utilization, or wing span had an effect on relative mortality ratios. Standardized residuals were calculated for the wing span group to examine where the differences lie.

Results

CARRYOVER EFFECT

The mowing interruption caused a change in the live butterfly, floral richness, and nectar richness data from Site 2 ($P < 0.05$). There was no evidence that the errant mowing event had an effect on the dead butterfly, floral density, and nectar density data. Even though this carryover effect was significant for 2 of the 4 floral resource 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 wk treatment were relabeled as receiving the interrupted 6 wk treatment from 2 Sep to the end of the study. The drop in the number of live butterflies in the interrupted 6 wk treatment after 2 Sep reflects the carryover effect (Fig. 1a).

BUTTERFLY DATA, ALL TAXA

There were in total 258 live butterflies recorded and 187 dead butterflies collected. This translates to an overall relative mortality of 0.420. There were 30 butterfly taxa (27 species, 2 species groups, and 1 subfamily group) identified in 5 families (Table 1). The numbers of live and dead butterflies, regardless of mowing treatments, differed depending on the taxon (Table 1). Live and dead butterfly counts increased greatly after mid–late August (Figs. 1a and b).

The spline structure on time (df = 6, ∞; $P = 0.003$) and the mowing treatment *spline interaction (df = 14, ∞; $P = 0.012$) were statistically significant for the live counts, but the mowing treatment alone did not have a significant effect on the counts. Live butterfly counts changed between spline sections, and the treatment effects became more apparent in the later spline sections (Fig. 1a). The spline structure on time was statistically significant for the dead counts (df = 6, ∞; $P = 0.049$), but the mowing treatment*spline interaction did not have a significant effect on the counts. The dead butterfly counts changed between each of the spline sections, but there were no apparent treatment effects (Fig. 1b). None of the aforementioned treatments or their interactions had a significant effect on the relative mortality ratio (Fig. 1c).

FLORAL RESOURCE DATA

Approximately 12,700 flowers and inflorescences were recorded with an average of 11.76 flowers per m^2 across the 9 sampling periods (13 May through 1 Nov). There were 72 flower species identified in 32 families, of which 41 species are known to be nectar sources utilized by adult butterflies (Table 2). The remaining 31 species are not typically known to be nectar sources, but that does not exclude them from influencing adult butterfly foraging behavior (Table 3). Most of the identified flower species are native to Florida, with 15 non-native species recorded.

Table 1. Identified roadside margin butterfly taxa and their attributes.

Family, species, and author	Habitat	Migrate	Size	Dead	Live
Hesperiidae					
Copaeodes minima Edwards	O	N	S	0	22
Erynnis horatius Scudder & Burgess	W	N	M	3	10
Hylephila phyleus Drury	O	Y	S	4	2
Polites vibex Geyer	O	Y	S	1	3
Pyrgus oileus/albescens L./Plötz	O	N	S	1	25
Urbanus proteus L.	O	Y	M	1	0
Unknown Hesperiidae, likely Hesperiinae	—	—	—	0	16
Lycaenidae					
Calycopis cecrops F.	W	N	S	0	3
Hemiargus ceraunus F.	O	N	S	0	17
Strymon melinus Hübner	O	N	S	0	3
Nymphalidae					
Agraulis vanillae L.	O	Y	L	63	36
Danaus gilippus Cramer	O	Y	L	2	0
Danaus plexippus L.	O	Y	L	5	3
Junonia coenia Hübner	O	Y	M	1	22
Limenitis archippus Cramer	W	N	L	4	1
L. arthemis astyanax F.	W	N	L	1	0
Phyciodes phaon/tharos Edwards/Drury	O	N	S	0	21
Vanessa virginiensis Drury	O	N	M	1	3
Papilionidae					
Battus philenor L.	W	N	L	2	1
Eurytides marcellus Cramer	W	N	L	4	3
Papilio glaucus L.	W	N	L	6	0
Papilio palamedes Drury	W	N	L	14	0
Papilio polyxenes F.	W	N	L	3	2
Papilio troilus L.	W	N	L	4	0
Pieridae					
Abaeis nicippe Cramer	O	N	M	25	8
Colias eurytheme Boisduval	O	N	M	1	1
Eurema daira Godart	O	Y	S	2	22
Nathalis iole Biosduval	O	N	S	0	3
Phoebis sennae L.	O	Y	L	37	18
Pontia protodice Boisduval & LeConte	O	N	M	2	13

The species authorities 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 (Y = yes) or not (N = no) a given species tends to migrate in Florida. The Habitat and Migrate 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. The genera *Pyrgus* and *Phyciodes* each contained 2 species with very subtle wing pattern differences. Because not all individuals could be captured for proper identification, the species were lumped into their respective genera. Similarly, unidentified individuals within Hesperiidae were grouped together. They all appeared to have morphological features characteristic of the Hesperiinae.

The mowing treatment had a significant effect on each of the 4 floral resource variables (Table 4). The results of the pair-wise comparisons indicated the no-mow and 6 wk treatments were not significantly different from each other (Fig. 2). They both had significantly greater densities and numbers of species compared with the 3 wk treatment. Contrasts in mowing treatments became more visually evident later in the summer as vegetation in the no-mow treatment grew taller, but there were no significant treatment*time interactions (a spline structure on time was not used here). There was evidence suggesting the density of nectar species changed over time (Table 4).

BUTTERFLY AND FLORAL RESOURCE CORRELATIONS

Only 3 of the 40 correlations tested were found to be significant. This is considerably close to what would be expected to occur with a Type I error using α = 0.05 (i.e., a 5% Type I error rate), thus we would conclude there is no evidence of significant correlations.

BUTTERFLY GROUPS

None of the fixed effects or interactions (i.e., treatment, spline, treatment*spline) was statistically significant when considering mowing treatment. 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 we looked at the groups regardless of the fixed effects, habitat utilization had a significant effect on the relative mortality of butterflies (df = 1; $P < 0.001$). Wooded-habitat butterflies had a higher relative mortality (0.67) compared with open-habitat butterflies (0.375). The migratory tendency had a significant effect on relative mortality (df = 1; $P < 0.001$), with migratory butterfly species experiencing higher relative mortalities (0.596) compared with non-migratory species (0.224). Size also had a significant effect on relative mortality (df = 2; $P < 0.001$). Based on the standardized residuals, the relative mortality of the small butterflies (0.055) was less than the expected value, and the relative
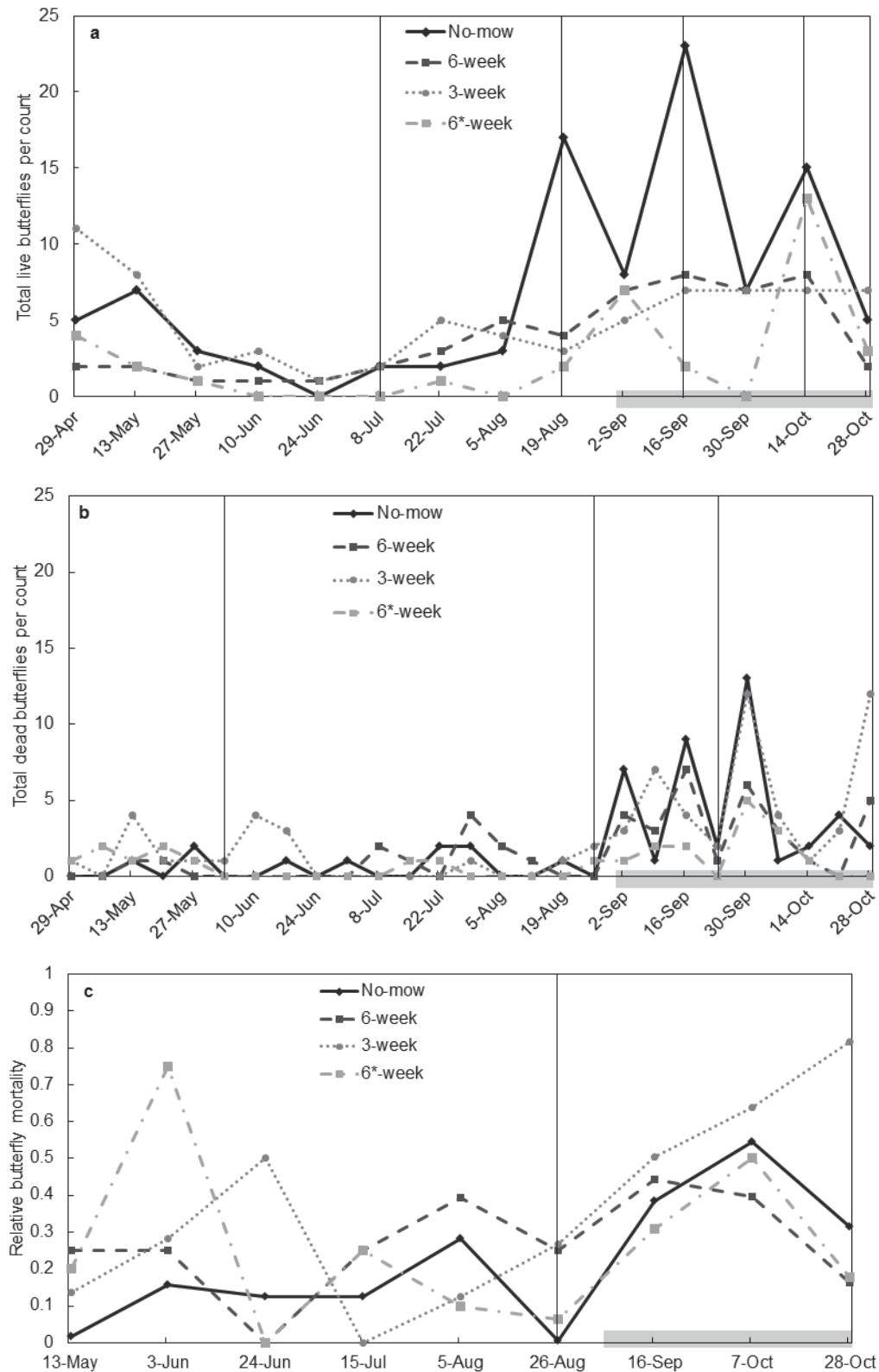
Fig. 1. Effects of mowing treatment (no mowing, mowing every 6 wk, and mowing every 3 wk) on butterfly abundance and mortality. (a) Live butterflies were counted every other week and summed for the section replicates of each mowing treatment. (b) Dead butterflies were counted weekly and summed for the section replicates of each mowing treatment. (c) The relative butterfly mortalities were calculated every 3 wk as $\Sigma_{Dead} / (\Sigma_{Dead} + \Sigma_{Live})$ for the section replicates of each mowing treatment. The gray box on each x-axis indicates when the interrupted 6 wk treatment (6* wk) was added due a mowing error in the 6 wk treatment sections in Site 2. The 6* wk treatment was split from the 6 wk treatment for the whole time period in all sites for longitudinal reasons, i.e., to avoid an unnatural drop in the 6 wk treatment after the mowing error. The 6* wk treatment was split after the mowing error in Site 2 in the statistical analysis. Black vertical lines represent the knots that separated the data into spline sections for the statistical analyses.

Table 2. Identified roadside margin flowering plant species known to be nectar sources for butterflies, based on our experience and observations.

Family	Nectar plant species and author	Native
Alismataceae	*Sagittaria lancifolia* L., 1759	N
Apiaceae	*Eryngium baldwinii* Sprengel, 1825	N
Asteraceae	*Acmella oppositifolia* (Lamarck) R. K. Jansen, 1985	N
	Bidens alba (L.) de Candolle, 1836	N
	Erigeron annuus (L.) Persoon, 1807	N
	Erigeron strigosus Muhlenberg ex Willdenow, 1803	N
	Eupatorium album L., 1767	N
	Mikania scandens (L.) Willdenow, 1803	N
	Pluchea rosea (Miller) Pruski, 2005	N
	Symphyotrichum simmondsii (Small) G. L. Nesom, 1995	N
Brassicaceae	*Lepidium virginicum* L., 1753	N
Campanulaceae	*Lobelia feayana* A. Gray, 1877	N
	Triodanis biflora (Ruiz & Pavon) Greene, 1894	N
Clusiaceae	*Hypericum mutilum* L., 1753	N
Commelinaceae	*Tradescantia ohiensis* Rafinesque, 1814	N
Fabaceae	*Aeschynomene viscidula* Michaux, 1803	N
	Chamaecrista fasciculata (Michaux) Greene, 1897	N
	Desmodium incanum de Candolle, 1825	
	Medicago lupulina L., 1753	
	Melilotus albus Medicus, 1787	
	Trifolium repens L., 1753	
Gentianaceae	*Sabatia angularis* (L.) Pursh, 1814	N
Iridaceae	*Sisyrinchium angustifolium* Miller, 1769	N
	Sisyrinchium rosulatum E. P. Bicknell, 1899	
Lamiaceae	*Hyptis alata* (Rafinesque) Shinners, 1962	N
	Stachys floridana Shuttleworth ex Bentham, 1848	N
Onagraceae	*Ludwigia octovalvis* P. H. Raven, 1962	
	Oenothera laciniata Hill, 1767	N
Oxalidaceae	*Oxalis stricta* L., 1753	N
Plantaginaceae	*Bacopa caroliniana* (Walter) B. L. Robinson, 1908	N
	Bacopa monnieri (L.) Pennell, 1946	N
Portulacaceae	*Portulaca pilosa* L., 1753	N
Rubiaceae	*Diodia virginiana* L., 1753	N
	Richardia brasiliensis Gomes, 1801	
	Spermacoce remota Lamarck, 1792	N
Tetrachondraceae	*Polypremum procumbens* L., 1753	N
Verbenaceae	*Phyla nodiflora* (L.) Greene, 1899	N
	Verbena brasiliensis Vellozo, 1829	
	Verbena officinalis halei Barber, 1982	N
	Verbena scabra Vahl, 1798	N
Xyridaceae	*Xyris ambigua* Beyrich ex Kunth, 1843	N

The species authorities and the native classification (N = native to Florida) are cited in Wunderlin & Hansen (2008).

mortality of the large butterflies (0.689) was greater than the expected value. Medium butterflies had a relative mortality of 0.374.

Discussion

The frequency of roadside mowing in Alachua County, Florida, USA, had a profound effect on floral diversity in the margins over the course of 1 field season. The effects of mowing frequency on butterflies were detectable but not as clear. Certain aspects of each butterfly species' behavior may affect their respective relative mortality due to roadkill. The lack of statistical significance of the fixed effects (i.e., treatment, spline, treatment*spline) on the butterfly groups (i.e., migration, habitat, and size) was expected because the issues of sparse data and zero counts were amplified by splitting the butterflies into groups. Statistical analyses of correlations between butterfly and floral resource abundance were inconclusive possibly due to the sparse butterfly data at each sampling interval.

BUTTERFLY DATA

Our results suggest that seasonal abundance of live butterflies was affected by changes in roadside vegetation management. Because of

Table 3. Identified roadside margin flowering plant species that are not known to be nectar sources for butterflies but may influence foraging behavior.

Family	Species and authority	Native
Apiaceae	*Ptilimnium capillaceum* (Michaux) Rafinesque, 1830	N
Araliaceae	*Hydrocotyle verticillata* Thunberg, 1798	N
Asteraceae	*Boltonia diffusa* Elliott, 1823	N
	Conyza canadensis (L.) Cronquist, 1943	N
	Cotula coronopifolia L.	
	Eclipta prostrata (L.) L., 1771	N
	Eupatorium capillifolium (Lamarck) Small ex Porter & Britton, 1894	N
	Pectis prostrata Cavanilles, 1797	N
Campanulaceae	*Wahlenbergia marginata* (Thunberg) Alph. de Candolle, 1830	
Clusiaceae	*Hypericum gentianoides* (L.) Britton et al., 1888	N
Cyperaceae	*Rhynchospora colorata* (L.) H. Pfeiffer, 1935	N
Eriocaulaceae	*Eriocaulon compressum* Lamarck, 1789	N
Euphorbiaceae	*Chamaesyce hypericifolia* (L.) Millspaugh, 1909	N
Fabaceae	*Desmodium triflorum* (L.) de Candolle, 1825	
	Kummerowia striata (Thunberg) Schindler, 1912	
Hydroleaceae	*Hydrolea quadrivalvis* Walter, 1788	N
Lamiaceae	Clinopodium brownei (Swartz) Kuntze, 1891	N
Loganiaceae	*Mitreola petiolata* (J. F. Gmelin) Torrey & Gray, 1841	N
Lythraceae	*Cuphea carthagenensis* (Jacquin) J. F. Macbride, 1930	
Malvaceae	*Melochia corchorifolia* L., 1753	
Melastomataceae	*Rhexia mariana* L., 1753	N
Molluginaceae	*Mollugo verticillata* L., 1753	
Onagraceae	*Gaura angustifolia* Michaux, 1803	N
	Ludwigia octovalvis (Jacquin) P. H. Raven, 1962	N
Plantaginaceae	*Gratiola pilosa* Michaux 1803	N
	Lindernia grandiflora Nuttall, 1818	N
	Mecardonia acuminata (Walter) Small, 1903	N
Polygalaceae	*Polygala lutea* L., 1753	N
	Polygala leptocaulis Vellozo, 1829	N
Polygonaceae	*Polygonum punctatum* Elliott, 1817	N
Urticaceae	*Boehmeria cylindrica* (L.) Swartz, 1788	N

The species authorities and the native classification (N = native to Florida) are cited in Wunderlin & Hansen (2008).

the spline (i.e., time) interaction with mowing treatment, it is difficult to separate out the mowing treatment effects. However, based on graphical trends, it appears that the no-mow treatment yielded the greatest number of live butterflies from Aug onward (Fig. 1a). This suggests that avoiding or reducing mowing during times of peak butterfly activity would be most beneficial. Similarly, mowing frequency has been shown to impact butterfly activity in northern Europe. Roadside margins in urban areas of Finland that received the heaviest mowing regimes had significantly decreased butterfly abundance (Saarinen et al. 2005). Likewise, Bak et al. (1998) reported lowest butterfly densities in roadside margins that received a high mowing frequency, which also reduced the availability of nectar sources. 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 indicate that the timing and frequency of mowing are important factors associ-

Table 4. Responses of the 4 floral resource variables to mowing treatment (no mowing, mowing every 6 wk, and mowing every 3 wk) and time (29 Apr to 1 Nov 2011).

Response	Treatment*Time df = 18,162	Time df = 8,162	Treatment df = 3,17
Density, all species	0.6475	0.4820	0.0330*
Density, nectar species	0.1325	0.0029*	0.0331*
Species richness, all species	0.0931	0.2958	0.0036*
Species richness, nectar species	0.1283	0.0757	0.0029*

Type III tests for fixed effects for the GLIMMIX procedure, SAS version 9.2 for Windows (SAS Institute Inc., Cary, North Carolina, USA). The *P*-values are listed in each column. *Significant at $P < 0.05$.
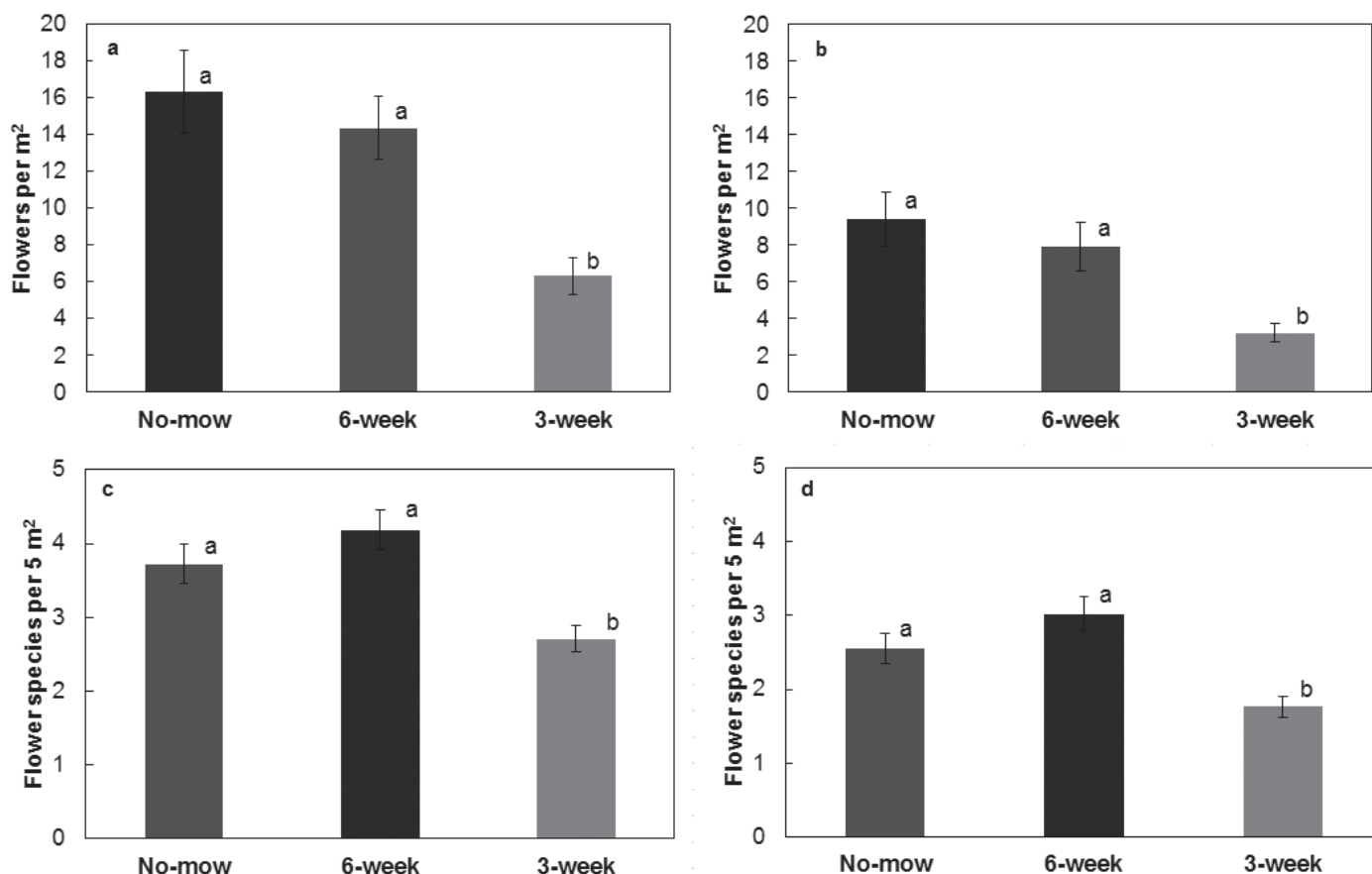
Fig. 2. Effects of the 3 mowing treatments on the 4 floral resource response variables. (a) Density of all species, (b) density of known nectar species, (c) species richness of all species, and (d) species richness of known nectar species. The graphs depict the raw means. Different letters above the bars indicate means that are significantly different.

ated with butterfly abundance in more northern latitudes that experience shorter growing seasons. The impacts of frequency and timing of mowing will likely vary depending on the region, climate, and year-to-year variations in weather.

A persistent drought likely affected butterfly source populations leading to our lower than expected sample sizes. Alachua County experienced extreme drought conditions beginning mid-Dec 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 Aug 2011, and then abnormally dry to moderate drought conditions prevailed for the remainder of the study (National Drought Mitigation Center 2014). The increase in live butterfly numbers coincided with the improving drought conditions in Aug (Fig. 1) and more abundant floral resources. The increase in numbers was attributed to the influx of migratory species toward late summer and the build-up of resident populations later in the season. The total live butterfly count of 258 individuals was not an estimate of the actual population sizes in the margins and surrounding habitats. The duration and frequency of our transect sampling gave standardized snapshots of live butterfly activity and roadkill, allowing us to compare relative mortalities and to see if roadkill butterfly diversity was representative of live butterfly diversity in the margins.

Although there were roughly equal numbers of combined live and dead migratory and non-migratory individuals (231 migratory and 214 non-migratory), the significantly higher overall relative mortality of migratory species was likely due to the fact that these species crossed the road more frequently. McKenna et al. (2001) noted a peak in *Danaus*

plexippus L. (Lepidoptera: Nymphalidae) roadkill mortality coinciding with their southward migration. The 2 most abundant migratory species in our study, *Agraulis vanillae* L. (Lepidoptera: Nymphalidae) and *Phoebis sennae* (L.) (Lepidoptera: Pieridae) are known to fly with a 142 to 156 degree heading during fall migrations (Walker & Littell 1994). This heading is nearly parallel to our Site 1, perpendicular to Site 2, and nearly perpendicular to Site 3. Thus, butterflies would be crossing the road at Sites 2 and 3 more frequently than at Site 1. Interestingly, the combined number of dead *A. vanillae* and *P. sennae* found at Sites 1, 2 (normalized to the length of Sites 1 and 3), and 3 were 8, 32, and 28, respectively. Munguira & Thomas (1992) found that roadkills were responsible for killing a greater percentage of species living in mobile populations compared with those in sedentary populations. The non-migratory species in our study likely spent more time in the margins and traveled shorter distances, thereby reducing their susceptibility to roadkill. We did not formally document whether these butterflies completed their life cycle in the margin, but at least 2 species, *Hemiargus ceraunus* (F.) (Lepidoptera: Lycaenidae) and *Pyrgus oileus/albescens* L./Plötz (Lepidoptera: Hesperiidae), were seen in copula. The higher relative mortality of wooded-habitat butterflies compared with open-habitat butterflies may be the result of them moving more frequently between patches of forest on either side of the road.

The total dead butterfly count of 187 individuals was not an estimate of the actual number road-killed butterflies per week. McKenna et al. (2001) found 1,824 dead butterflies over 6 wk in Illinois, but they sampled both sides of the road and along center medians at some sites. Munguira & Thomas (1992) found that only 1 out of 50 butterfly

corpses placed at the side of the road disappeared after 2 wk in the United Kingdom. Although each sampling period in our study theoretically included a week of accumulating mortality, it is likely that the residency time of the corpses was less than a week. Red imported fire ants *Solenopsis invicta* Buren (Hymenoptera: Formicidae) were abundant in the margins, and ants were observed dismembering recently disabled butterflies that were still alive (i.e., less than 1 h post-injury). Birds also likely fed on butterfly corpses, and butterflies may have adhered to the front of moving vehicles, but neither was documented. It is unlikely that mortality resulted directly from the mower because butterflies would have ample time to escape. Butterfly size likely introduced a sampling bias to our study, because large butterflies were 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 lower than expected relative mortality for small butterflies.

Our study found an overall relative mortality of 42% of all butterflies combined. This is likely due to the considerably more substantial underestimate of live butterfly numbers compared with dead butterfly numbers. Munguira & Thomas (1992) determined relative mortality to be in the range of 0.6 to 7% of the butterfly populations in their study. They conducted mark–release–recapture studies to assess population densities. More thorough sampling techniques employed on the live butterflies in our study would have allowed for an estimate of butterfly population densities. Future studies on roadside management also should consider long-term sampling to determine population-level impacts on butterflies or other insect pollinators.

FLORAL RESOURCE DATA

The highest mowing frequency resulted in the lowest floral species richness and densities. It is likely the frequency of disturbance was such that only the most disturbance-tolerant plant species were able to rapidly produce new flowers within 3 wk. It is interesting to note that, although not statistically significant, the interrupted 6 wk treatment appeared to yield the greatest number of flower species (Figs. 2c and d). The intermediate disturbance hypothesis posits that diversity is highest in systems that receive intermediate levels (i.e., frequency and magnitude) of disturbance (Connell 1978). Mowing every 6 wk may be close to the frequency of disturbance that maximizes species richness. Alternatively, it is possible that pre-existing differences in block diversity contributed to these results. A reassignment of treatments to each experimental unit over the course of several years would help control for this potentially confounding variable. The mower did not produce any noticeable disturbance to the soil or groundcover.

Research on routinely managed margin vegetation in northern Europe emphasizes the importance of timing and frequency of mowing. 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* L. (Lepidoptera: Nymphalidae). Feber et al. (1996) showed that plant species richness was lower on uncut swards in field margins compared with swards that were cut in the spring or fall outside the main summer growing season. They argued that not mowing would promote unfavorable succession of the habitat and that mowing is necessary but should not coincide with peak blooming periods. Another study showed that some routine mowing increased plant species richness, but again only when the mowing did not coincide with peak growth (Parr & Way 1988). The timing of seed setting also should be considered when planning a long-term mowing regime. Mowing after seed set and varying the timing of mowing from year to year would help maximize plant diversity (Leng et al. 2011).

The experimental units in our study that were not mowed tended to have the greatest abundance of flowering plants and greater species

richness than units mowed most frequently (i.e., every 3 wk). However, if roadside margins in Florida were never mowed, the diversity of herbaceous floral resources would be replaced by woody vegetation as ecological succession progressed. Thus, like in the European margins, some routine mowing is needed to keep roadside margins in an early successional state where floral resources would be most available to pollinators. Because there was no significant difference between the no-mow treatment and the 6 wk treatment in our study, mowing every 6 wk or less could be employed. Additional 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 the timing and frequency of mowing.

BUTTERFLY AND FLORAL RESOURCE CORRELATIONS

Mowing treatment alone did not have a significant effect on butterfly numbers, and it is not surprising that there were generally no significant correlations between live butterfly counts and the floral resource variables. One would expect that greater floral 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 floral species richness in roadside margins. However, they found that floral density had no effect on the butterflies. Croxton et al. (2005) 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 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.

ADDITIONAL IMPACTS OF ROADS ON ECOSYSTEMS

In addition to the paradox of roads creating mortality sinks and habitat, roads and adjacent managed areas can also act as barriers to dispersal and dispersal corridors. These processes affect population and community structure. Forman & Alexander (1998) argued that the barrier effect is potentially the most significant ecological impact of roads on wildlife. The tendency of a road to form a barrier varies with the behavior and mobility of the animal encountering the road's edge. 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 & Debinski (2001) found that roads did not appear to impede the movement of *Speyeria idalia* Drury (Lepidoptera: Nymphalidae) in Iowa's severely fragmented prairies. Munguira & 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. We did not formally quantify butterfly behavior at the road's edge, but there were instances of butterflies coming to the edge and either turning around or turning and flying parallel to it. In contrast, the migratory species tended to cross the road quite readily. These mixed findings reflect the need to assess the behavioral responses of taxa relative to different road types and road margins.

The goal of a corridor is to facilitate organismal dispersal between fragmented habitats. For a corridor to be successful, an animal needs to find the corridor, enter the corridor, and successfully pass through the corridor (Rosenberg et al. 1997). A study involving 2 butterfly species showed that creating corridors of suitable habitat increased move-

ment rates between larger patches of habitat (Haddad 1999). Butterfly populations within patches connected by corridors reached higher densities (Haddad & Baum 1999), and a genetic analysis revealed that corridor-facilitated dispersal can promote greater genetic variability (Wells et al. 2009). There is a general consensus for the efficacy of corridors; however, additional research is needed to assess the benefits of corridors to populations and communities (Haddad & Tewksbury 2006).

CONCLUSIONS AND FUTURE DIRECTIONS

Our study examined the effects of mowing frequency in roadside margins on butterflies and flowering plants. Frequent mowing appeared to limit butterfly numbers after early Aug. Changing the frequency of mowing had a significant effect on the abundance and species richness of floral resources in roadside margins. Compared with not mowing, or mowing every 6 wk, mowing every 3 wk yielded significantly lower floral resource abundance and species richness per unit area. Butterflies associated with the large southward migrations in the fall potentially would benefit from an abundant and diverse source of available nectar, as has been shown to be true with migrating monarch butterflies (Brower et al. 2006).

The outcome of this study aims to facilitate a better understanding of how roadside management in Florida affects butterflies that utilize the margins as either breeding habitat or corridors. The results suggest a less frequent mowing regime would increase butterfly numbers in roadside margins. Butterflies are good ecological indicators of a broader array of pollinator taxa, because they rely on a variety of resources at different life stages. Although documenting immature stages was not a part of this study, larval host plants for several open-habitat butterflies were observed. Further study is needed to assess the long-term ecological impacts of reduced mowing in Florida's roadside margins. If correctly managed, roadside margins have the potential to provide diverse floral resources and/or function as habitat for many insect species, especially pollinators and other flower visitors. Even rare species may potentially utilize margin habitats, although they were not observed in this study. There is also the potential for margins to function as dispersal corridors or stepping stone habitats for some species, especially migratory species. The domain of this study should be expanded by investigating roadside management impacts at a variety of latitudes, climates, and ecosystems. In regions where preserving large habitats is no longer an option, the conservation value of roadside margins should not be overlooked.

Acknowledgments

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