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Roadside habitat impacts insect traffic mortality

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Abstract

Paved roadways, spanning 6.6 million kilometres across the continental United States, are often bordered by natural or restored habitats and could provide opportunities for pollinator conservation. Because insects are frequently killed by auto traffic, roadside habitats may be ecological traps that kill more pollinators than they produce. Here we compare insect traffic mortality when roadsides are bordered by woodlots, meadows, or lawns. We also compare study sites with and without restored medians to examine the impact of creating habitat that can only be accessed by crossing traffic. We confined our study to high speed roads (70–90 km h^{-1}) with heavy traffic volume. Both habitat type and the presence of a vegetated median affect vehicle strikes fatal to insects. Insect mortality in general, and its effect on bees and butterflies in particular, was consistently lower when roads were bordered by woodlots than when they were bordered by lawn or meadows. Which roadside habitats were associated with the highest insect mortality depended on the taxon in question and the presence or absence of a vegetated median. Butterfly and dragonfly mortality was highest on roads with meadow medians, while bee mortality was highest on roadsides with lawn medians. Across most site comparisons, vegetated medians significantly elevated fatal insect-vehicle strikes. Regardless of the habitat bordering roadsides, insect mortality was unacceptably high for areas being considered for conservation. We suggest four research directions that may lead to reduced insect mortality in roadside habitats.

Keywords Pollinators · Roadside restoration · Insect traffic mortality · Bees · Butterflies

Introduction

Paved roadways span over 6.6 million kilometres across the continental United States (U.S. Highway Adminstration 2013). Although road length in the U.S. only grew 2% between 1997 and 2007, traffic volume increased nearly 20% in that time period (Barthelmess and Brooks 2010; Wheeler and Beatley 2009). It is well-established that roads can negatively impact organisms in neighboring habitats in several ways (Skórka et al. 2013). Roads can fragment habitats, degrade local environments, increase edge effects, isolate breeding populations, reduce population sizes, and cause genetic bottlenecks (Forman and Alexander 1998; Bouchard et al. 2009; Ries et al. 2001; Munoz et al. 2014). Vehicle strikes are one of the greatest direct sources of mortality for vertebrates (Forman and Alexander 1998; Langevelde et al. 2008; Calvert et al. 2013) and there is increasing evidence that this is the case for insects as well (Baxter-Gilbert et al. 2015; McKenna et al. 2001; Skórka et al. 2013).

Most studies on road impacts have ignored arthropods entirely, and those that have measured arthropod mortality have focused on charismatic Lepidoptera (McKenna et al. 2001; Munguira and Thomas 1993) and Odonata (Furness 2014; Rao and Girish 2007). Traffic speed and volume have been shown to contribute to roadside insect mortality (Baxter-Gilbert et al. 2015; Skórka et al. 2013; McKenna et al. 2001), but there arguably has been an insufficient amount of work evaluating the impact of roadside habitat type and quality on insect vehicle strikes (but see Munguira and Thomas 1993; Ries et al. 2001). Moreover, we know of no study that has conclusively examined how the presence of attractive habitat in roadway medians impacts insect mortality across a broad range of taxa.

Here we compare the effects of high speed traffic on insect mortality when roads are bordered by different quality

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habitats to help determine whether roadside restorations can have conservation value or act as ecological traps for insects. Although we measured all insect taxa, we explicitly tested whether roads bordered with habitat attractive to foraging bees, butterflies, and dragonflies cause more insect mortality than those with lower quality habitat.

Materials and methods

In June of 2015 we selected 30 sites in Delaware, Maryland, and Pennsylvania with a posted speed limit of 70–105 km h^{-1} and similar intact habitat on both sides of the road. Sites were separated from each other by at least 400 m and while they varied in annual average daily traffic (AADT = 38,650 ± 32,144 SD), all had high traffic volumes.

We divided sites into three categories: *Meadow*; those containing wildflowers and tall grasses as their dominant vegetation; *Wooded*; those containing trees and shrubs as their dominant vegetation; and *Lawn*, those that were frequently mowed and contained short non-native grass as their dominant vegetation. Sites were further classified into those with median strips containing habitats and those without median strips. Permits to collect dead insects on roadsides were obtained for some sites due to state laws. At each site 400 m transects (200 m on each side of the road) were established and GPS coordinates were taken via Google Maps™ to mark location. Site size (the depth of the habitat bordering the road multiplied by the 200 m length of the transect) was obtained using Google Maps. Before the trials began, we removed insects that had been previously killed by traffic from the surface of the road edge along each transect. From mid-June to mid-July we collected all dead insects on the road shoulder within the transect approximately once per week for 4 weeks resulting in five collections per site. On each sample date, we also counted all flowers between 2 and 3 m from the road on each side. After insects were collected, they were labeled and returned to the lab for identification to the least taxonomic unit.

Statistical analysis

To compare the relationship between habitat variables and insect mortality, we used a generalized linear model with negative binomial distribution for over dispersed count data (MASS package: Venables and Ripley 2002; O'Hara and Kotze 2010). Each model included mortality as our response variable and habitat type (lawn, meadow or wooded) and the presence of a median (yes or no) as fixed effects in the model. To account for the possible impact of flower density at each site as well as calendar date of the collection we used these data as covariates. To reduce skew, we log transformed our covariate for number of flowers. We evaluated the performance of our error distribution and also compared the full model with nested models with/without covariates or interactions using likelihood ratio tests. Lastly, we checked fit of our final model by visually confirming a normal distribution to the residuals, and a dispersion parameter of 1, and that a Chi square test on the residual deviance and degrees of freedom was > 0.05. We present our regression coefficients here in terms of incidence rate ratios (IRR) which represent the percent change in insect mortality when comparing one habitat type to another while holding other factors in the model constant. For example, an IRR of 2.0 means the habitat type has 2 times the mortality of the reference habitat. An IRR of 0.5 means it has half the mortality. We determined IRR by taking the exponential function of each model's β coefficients. Complete model results are presented in Supplementary Table 2.

We assessed all pairwise comparisons in our generalized linear models using the function "glht" within the package "multcomp" (Hothorn et al. 2008). We used a Tukey's comparison to determine confidence intervals and significant difference between the means of our habitat types at $\alpha = 0.05$. All analyses were performed in program R version 3.3.3 (R Core Team 2017). Total insect mortality was highly correlated with the number of beetles (Coleoptera) collected ($r = 0.97$), thus, we removed beetles from our total insect count and ran this order separately (see Supplementary Information for beetle analyses). Our final models included total insect mortality (without beetles), dragonflies (Odonata), butterflies (Lepidoptera: Papilionoidea) and bees (Hymenoptera: Apoidea) mortality (Table 1).

Results

We collected 6371 dead insects during his study representing 106 taxa (Supplementary Table 1). Scarabaeidae (3007), Bombus (850) and Libellulidae (239) were the most abundant taxa killed by vehicles. Coleoptera (3480), Hymenoptera (1734), and Lepidoptera (500) were the most abundant orders.

Total insects (without beetles)

Our final model for total insects included only our fixed factors and no interactions. All of our habitats were significantly different from one another (habitat type: $F_{2,116} = 10.13$, $p < 0.001$; Fig. 1). Meadows caused significantly more mortality than lawns (meadow–lawn: IRR 1.68, β 0.52 ± 0.17; CI 0.11, 0.93, $p = 0.003$), while wooded areas killed fewer insects than both lawns (wooded–lawn: IRR 0.46, β − 0.78 ± 0.18, CI − 1.21, − 0.36, $p < 0.001$) and meadows (wooded–meadow: IRR 0.27, β − 1.30 ± 0.18, CI − 1.72, − 0.88, $p < 0.001$). Across all habitat types there were

Table 1 Mean ± standard error for each habitat type and median treatment for insect groups of ecological importance

Habitat type	Median	Beetles	Butterflies	Bees	Odonata	Other insects	Total mortality
Lawn	Yes	75.95 ± 41.06	3.90 ± 1.26	19.30 ± 3.66	1.75 ± 0.54	18.15 ± 4.54	117.30 ± 48.69
Lawn	No	30.60 ± 7.75	0.95 ± 0.41	5.60 ± 1.73	0.15 ± 0.08	2.70 ± 0.59	39.85 ± 9.02
Meadow	Yes	40.25 ± 9.70	9.95 ± 2.54	11.25 ± 2.20	9.05 ± 3.47	30.50 ± 7.31	91.95 ± 17.46
Meadow	No	10.90 ± 2.70	2.90 ± 1.25	11.90 ± 3.99	2.00 ± 0.65	7.60 ± 2.00	33.30 ± 7.90
Wooded	Yes	10.30 ± 1.37	0.75 ± 0.27	1.10 ± 0.32	0.75 ± 0.26	11.55 ± 1.14	23.70 ± 2.14
Wooded	No	6.00 ± 1.29	0.25 ± 0.12	2.00 ± 0.81	0.25 ± 0.10	4.20 ± 0.62	12.45 ± 1.70

"Other insects" includes Dermaptera, Diptera, Ephemeroptera, Hemiptera, Hymenoptera (excluding Apidae), Isoptera, Lepidoptera (excluding butterflies), Mantodea, Neuroptera, and Orthoptera

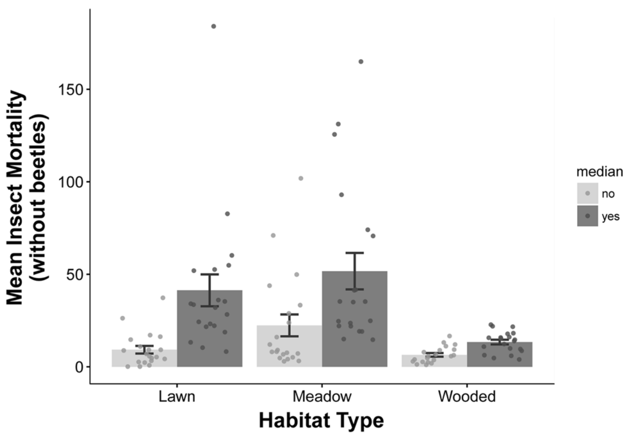

Fig. 1 Mean insect mortality (not including beetles) on roadsides bordered by lawn, meadow, or woods with and without median strips. The most mortality occurred in meadows and the least mortality occurred in wooded areas. The presence of a median significantly increased the insect mortality detected for all sites. Error bars indicate standard error of the mean

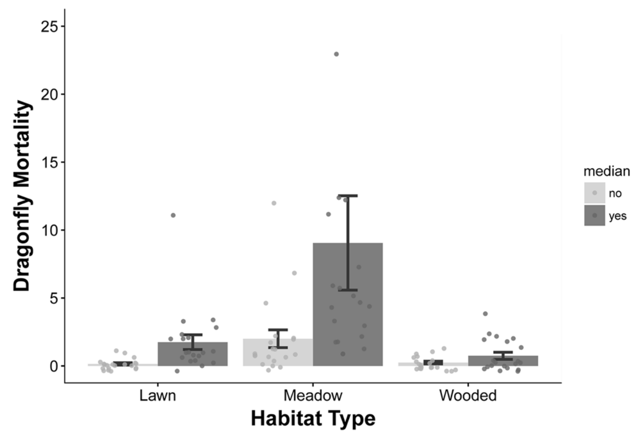

Fig. 2 Dragonfly mortality on roadsides bordered by lawn, meadow, or woods with and without median strips. The most mortality occurred in meadows and the least mortality occurred in wooded areas. The presence of a median significantly increased dragonfly mortality for both meadows and lawn habitats. Error bars indicate standard error of the mean. One high observation of 71 individuals is not included in the graph in order to clearly show relationships; however, this value was included in the model

significantly more dead insects when a median was present (median: IRR 2.77, β 1.02 ± 0.15, CI 0.74, 1.31, $p < 0.001$).

Dragonflies

Our dragonfly model included our fixed effects of habitat type and median with no interactions. Dragonfly mortality was higher when a median was present (median: IRR 5.05, β 1.62 ± 0.28, CI 1.09, 2.18, $p < 0.001$, Fig. 2); however, this effect did not occur at wooded sites (wooded [yes]–wooded [no], IRR 3.00, β 1.10 ± 0.60, CI − 0.60, 2.80, $p > 0.1$). The habitat types were significantly different from one another ($F_{2, 116} = 7.00$, $p = 0.001$) with meadows having more mortality than both lawns (Meadow–Lawn: IRR 6.42, β 1.86 ± 0.31, CI 1.14, 2.58, $p < 0.001$) and wooded areas (Wooded–Meadow: IRR 0.09 β − 2.39 ± 0.34, CI − 3.18, − 1.59, $p > 0.001$, Fig. 2). Wooded areas and lawn were not different from one another (Wooded–Lawn: IRR 0.59, β − 0.53 ± 0.38, CI − 1.41, 0.36, $p > 0.1$).

Butterflies

Our model for butterflies included only calendar date as a covariate and no interactions. Butterfly mortality was positively related to calendar date (calendar date: IRR 1.06, β 0.06 ± 0.01, CI 0.04, 0.08, $p < 0.001$, Supplementary Fig. 2). Accounting for calendar date, there was significantly more butterfly mortality when a median was present for all sites (median: IRR 3.19, β 1.16 ± 0.27, CI 0.64, 1.68, $p < 0.001$, Fig. 3). Mean butterfly mortality was also significantly different among the sites ($F_{2, 115} = 12.72$, $p < 0.001$, Fig. 3), with wooded areas having less butterfly mortality than both lawns (wooded–lawn: IRR 0.20, β − 1.62 ± 0.38, CI − 2.50, − 0.74, $p < 0.001$) and meadows (wooded–meadow: IRR 0.08, β − 2.57 ± 0.37, CI − 3.43, − 1.72, $p < 0.001$), but meadows having more mortality than lawns (meadow–lawn: IRR 2.59, β 0.95 ± 0.29, CI 0.28, 1.62, $p = 0.003$).

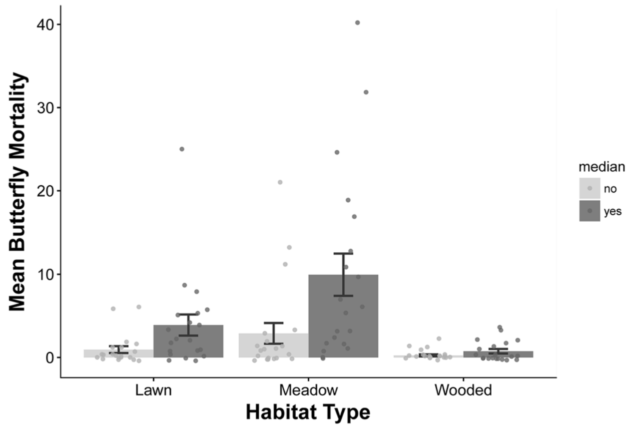

Fig. 3 Butterfly mortality on roadsides bordered by lawn, meadow, or woods with and without median strips. The most mortality occurred in meadows and the least mortality occurred in wooded areas. The presence of a median significantly increased the butterfly mortality detected for all sites. Error bars indicate standard error of the mean

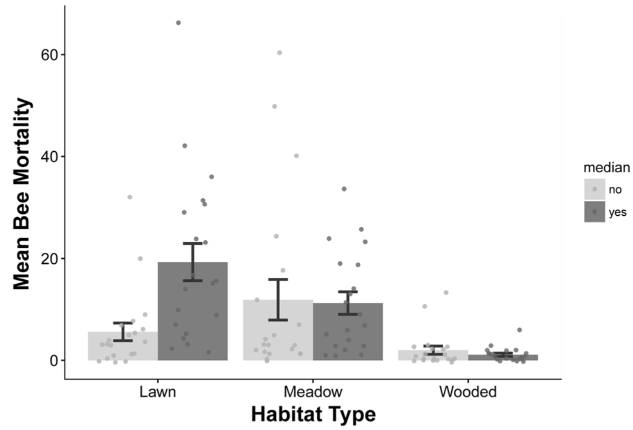

Fig. 4 Bee mortality on roadsides bordered by lawn, meadow, or woods with and without median strips. The most mortality occurred in meadows and lawns and the least mortality occurred in wooded areas. The presence of a median significantly increased bee mortality for only lawns. Error bars indicate standard error of the mean

Bees

Our model for bees included the logarithmic transformation of flowers as a covariate and an interaction between habitat type and median. Bee mortality was positively related to flower abundance (log flowers: IRR 1.31, β 0.27 $\pm$ 0.07, CI 0.12, 0.41, $p < 0.001$, Supplementary Fig. 3). Accounting for flowers and habitat, there was more bee mortality when a median was present (median: IRR 3.10, β 1.13 $\pm$ 0.34, CI 0.44, 1.81, $p = 0.001$); however, the effect of a median was only apparent at lawn sites (lawn [yes]–lawn [no], IRR 3.10, β 1.13 $\pm$ 0.34, CI 0.15, 2.10, $p = 0.01$). There was no difference in mortality between sites with and without medians for either meadows or wooded areas ($p > 0.1$).

Mean bee mortality was significantly different among the treatments ($F_{2, 113} = 5.54$, $p < 0.01$; Fig. 4); yet only wooded areas had lower mortality than meadows (wooded–meadow: IRR 0.33, β − 1.10 $\pm$ 0.40, CI − 2.04, − 0.15, $p = 0.02$). Confidence intervals of the differences overlapped zero when comparing meadows to lawns (meadow–lawn: IRR 1.34, β 0.29 $\pm$ 0.36, CI -0.55, 1.13, $p > 0.1$) and wooded areas to lawns (wooded–lawn: IRR 0.45, β − 0.80 $\pm$ 0.38, CI − 1.70, 0.09, $p > 0.1$).

Discussion

Our results reveal two important variables that affect vehicle strikes fatal to insects: (1) the type of habitat bordering the road, and (2) the presence or absence of a vegetated median. Insect mortality from vehicles in general, and its effect on bees and butterflies in particular, was consistently and significantly lower (less than half) when roads were bordered by woodlots than when they were bordered by lawns or meadows (Fig. 1). Which roadside habitats were associated with the highest insect mortality depended on the taxon in question and on whether or not a vegetated median was present. Butterfly mortality was highest on roads with meadow medians, while bee mortality was highest on roads with lawn medians (Figs. 3, 4). Across all habitat types, medians significantly elevated fatal insect-vehicle strikes.

Although high bee mortality where roadsides are bordered by lawn may seem counter-intuitive, we offer two explanations. First, many of our lawn transects were infused with clover (*Trifolium* spp.) that was variably in bloom, depending upon the time elapsed since they were last mowed. Both honeybees and bumblebees forage regularly on clover, and its presence near roads brings these bees into the danger zone throughout the foraging season. Second, it is possible that bees seeking forage fly across lawn sites when they are poor in flower resources and into passing traffic more frequently than they do when the abundant forage of well-designed meadows is present (Hill and Webster 1995). We believe insect-vehicle strikes are reduced when woodlots border roads because there are fewer diurnal insects active in this type of habitat. We were surprised that more nocturnal insects, particularly moths, were not found along roads bordered by woods. It is possible that vertical complexity in vegetation may facilitate successful road crossing for nocturnal insects using wooded habitats.

Our results should be considered conservative for at least four reasons. First, when vehicles strike insects, many of these victims stick to the grill, side mirrors, car hood, or other car parts. These bodies would not have been counted by our approach (Skórka 2016). Second, when insects that are struck do fall to the pavement, many are immediately smeared beyond recognition on the road surface by traffic. Only some unknown proportion of the insects killed by vehicles are blown to the road edge in a recognizable state. Third, many of those ending up on the edge are then carried off by birds such as gray catbirds, mockingbirds, various sparrows, and bluebirds (Tallamy pers. obs.). Even more frequently, insect bodies are dismembered and carried away by ants. In fact, a recent study by Skórka (2016) suggests that traffic may actually increase such scavenging during night hours. Thus, since our trials occurred over several days, we likely lost many dead insects to scavenging. Finally, rain events often flush insect bodies into surrounding vegetation where they are difficult to detect. With this in mind, it is doubtful that recording insect mortality once per week is actually a record of a 7-day accumulation of vehicle strikes. More likely it is a partial record of only what has been killed over recent hours. Future studies should account for imperfect detection of scavenged carcasses in order to estimate true mortality.

Constraints in our sampling rendered our results conservative for two additional reasons. First, our measures of insect mortality on roadways built with medians may represent only half of the actual mortality levels. Due to it being unlawful to walk the edges of highway median strips, we only measured insect mortality on the two lateral edges of roads with medians. Insects killed as they left median vegetation were unaccounted for. Second, our data were gathered along relatively high-speed urban/suburban roadsides. Although slow and infrequent traffic may reduce insect kill rate for some taxa (Furness 2014; Skórka 2016), it is possible that rural roads built for slower moving traffic actually kill even higher numbers of insects because insect populations are generally higher in rural settings and slower traffic (48–73 km h^{-1}) still moves fast enough to cause fatal collisions with insects.

Despite the conservative nature of our study, we found high levels of insect mortality from vehicle strikes, particularly when lawns and meadows bordered our transects. These results are consistent with past studies of roadside insect mortality (McKenna et al. 2001; Skórka et al. 2013; Munoz et al. 2014) but are orders of magnitude lower than other estimates (Berenbaum 2015). In all cases, however, our data suggest that insect mortality from vehicle strikes is unacceptably high and ways to reduce such mortality should be investigated before wide-scale roadside pollinator plantings are encouraged.

Roadsides are tempting sites for restoring habitat favorable to pollinators and other insects that serve essential ecosystem functions described by Wilson (1987). Roadsides comprise millions of acres of land that historically have not been designed with ecosystem function in mind. They could serve to fuel complex food webs and boost populations of many forms of biodiversity. Roadsides could also connect isolated habitat fragments with each other and thus reduce local extinction due to losses from small population effects (Lande 1988). Yet our study suggests an imperative for research on several fronts to ensure that roadside restorations do not function as ecological traps for the very species they are designed to conserve. The following four questions should be considered: (1) To what degree are vehicle strikes related to the distance that restoration plantings are situated from the road edge? Keeping meadows just a few meters from the road edge may significantly reduce vehicle strikes. (2) What type of roadway should be targeted for conservation plantings? Understanding exactly how traffic volume and speed interact to increase or decrease vehicle strikes is essential. (3) Is it possible to reduce vehicle strikes by erecting inexpensive barriers separating roadside habitat from traffic and if so, what is the most effective design of such barriers? And finally, (4) how extensive does a restoration planting have to be before it produces more insects than it kills? This may be the most critical question of all, but it also will be one of the most difficult questions to answer.

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Compliance with ethical standards

Conflict of interest There is no conflict of interest.

Research involving human and animal participants No animals were harmed by this study. Insects and animals that died on roads were not a result of this study's manipulation, rather we looked for animal and insects that were already killed by existing traffic.

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