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Influence of roadways on patterns of mortality and flight behavior of adult dragonflies near wetland areas

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ABSTRACT

The relatively low population size and long adult lifespan of dragonflies (Odonata, Anisoptera) makes them one of the few non-vertebrate groups likely to be impacted by direct roadway mortality. We studied adult dragonfly mortality and behavior associated with roadways for a number of species. Daily mortality rates for dragonflies were estimated from standardized surveys along predetermined lengths of roads. Relative abundance and flight behavior around and across roadways, a potentially important mortality factor, was determined from timed roadside observations. Observed flight behavior provided no evidence that roads act as significant barriers to dispersal for adult dragonflies. Estimated mean number killed ranged from 2 to 35 dragonflies/km/day. Species varied greatly in their susceptibility to motor vehicles. Two species (*Plathemis lydia* and *Libellula luctuosa*) made up more than 70% of the dead dragonflies collected, but only represented 14% and 31% of live dragonflies observed, respectively. The relatively low flight heights of these two species over roads (typically under 2 m) may explain their susceptibility; however, another common species (*Tramea lacerata*) also exhibited low flight height but did not experience high mortality, possibly because of its increased flight agility. Large numbers of adult dragonflies were killed over the entire flight season by motor vehicle collisions, exhibiting the need for assessing the long-term impact of roadway mortality on dragonfly population dynamics.

1. Introduction

Roadways can have a wide variety of impacts on nearby ecosystems. For example, by altering hydrology or introducing pollutants in the form of runoff (e.g. salt or silt), roadways can dramatically alter the structure of plant communities and their associated fauna in wetland areas (Atkinson and Cairns, 1992; Sriyariaj and Shutes, 2001; Houlahan et al., 2006). More subtle impacts can take the form of alterations in animal communities that occur because roadways represent barriers to dispersal (Keller and Largiadér, 2003; Waller and Servheen, 2005; McGregor et al., 2008) or significant sources of mortality for some species (Lodé, 2000; Aresco, 2005; Shepard et al., 2008), reducing and perhaps eventually eliminating them from habitats near roadways. Roadways can function as barriers even if there is no direct mortality because some animals avoid the disturbances created by moving vehicles (e.g. noise, lights, and wind currents), or because roadways alter the local microclimate around them creating hostile environments (Mader, 1984). Although these effects have important consequences, perhaps the greatest concern is that roadways may function as barriers simply because they can be a source of high mortality for species unable to avoid direct collisions with motor vehicles. Whether the effects of roadways are through avoidance, direct mortality, or both; for many species, they can potentially reduce population sizes and fragment relatively continuous habitat into a series of isolated habitat islands (Forman et al., 2003).

Although it is a common observation that vast numbers of insects die on the grills and windshields of motor vehicles, few studies have attempted to quantify mortality rates. Most studies on the effects of roadways on animal populations have concentrated on vertebrate taxa. When compared to other dominant taxa, such as insects and arachnids, vertebrates generally have relatively longer lives, lower fecundity, and lower population sizes; therefore, they are more likely to be sensitive to the effects of roadway mortality than other groups. For example, Hels and Buchwald (2001) estimated that approximately 25% of the reproductively active population of *Pelobates fuscus* (a common anuran) were killed attempting to cross the road.

Wetland areas support diverse insect assemblages in which many species depend on aquatic habitats for larval stages and terrestrial habitats for adult stages. In general, the adult stages of most wetland insects are relatively short-lived, with individual fe-

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males laying a large numbers of eggs, typically within a short period (often one night) after emerging. Many of these species exhibit mass emergence, forming large mating swarms and experiencing high rates of adult mortality from a variety of predators. These life history features mean that such wetland species are unlikely to show strong population declines due to increased mortality caused by the collisions with motor vehicles along roadways. However, not all wetland insects share these life history traits. Some species, especially predatory groups such as beetles and dragonflies, have relatively long-lived adult stages in which adults feed actively and the females produce eggs over an extended period of time.

Dragonflies (order Odonata; suborder Anisoptera) are one of the top predators within many aquatic food webs, especially when fish are absent. Many dragonfly species are viewed as being of special conservation interest because they are threatened by human activities (Clausnitzer et al., 2009). In the United States, Bried and Mazzacano (2010) reported that 277 of the 441 dragonfly species are "species of greatest conservation need" in at least part of their range, and 37 species are listed as either threatened or endangered on the IUCN redlist. The larval (aquatic) stage of the dragonfly life cycle is typically on the order of months to years (Anholt, 2009) and the life span of adult dragonflies can range from weeks to months (Corbet, 1999). They have smaller population sizes, lower fecundity, and longer reproductive life spans than most other wetland insect groups. Additionally, many species travel extensively as adults searching for food, mates, and new oviposition sites, or while routinely traveling between noncontiguous breeding and foraging sites, and thus they may frequently cross over roads (Riffell, 1999; Foster and Soluk, 2006). Combined, these characteristics suggest that dragonflies are more likely to be negatively affected from deaths by collisions with motor vehicles compared to other wetland insect types.

Few studies have investigated patterns of roadway fatalities in adult Odonata, and those that have been published are generally part of larger studies focusing on diverse taxa (e.g. Rao and Girish, 2007; Siebert and Conover, 1991) or are anecdotal observations without quantification (e.g. Beckemeyer, 1996). In a study assessing insect casualties over busy roadways in India, 1269 individual insects were collected as roadkills, 61% of which were various species of dragonflies (Rao and Girish, 2007). Riffell (1999) also investigated roadway mortality, documenting up to 256 dead dragonflies/km in a single day in northern Michigan. Such sustained high rates of mortality could potentially impact sensitive dragonfly populations near roadways; however, before we can assess the sensitivity of dragonfly populations to roadways, we need to better understand the responses of dragonflies to roadways and the factors that contribute to their vulnerability.

This study examines patterns of adult dragonfly behavior near roadways and assesses rates of mortality from vehicle collisions for a number of dragonfly species associated with wetland areas in northern Illinois. Specifically, we assessed whether roadways act as significant barriers to the movement of adult dragonflies, quantified the death rates along a series of roads in suburban Chicago, and evaluated the extent to which variation in flight behaviors make some species more vulnerable to collisions with motor vehicles.

2. Methods

2.1. Study area

To estimate the rate at which dragonflies are killed when crossing roads, we conducted roadside surveys for dead dragonflies along segments of four roadways in the Des Plaines River Valley near Joilet, Illinois that varied greatly in traffic volume (Fig. 1).

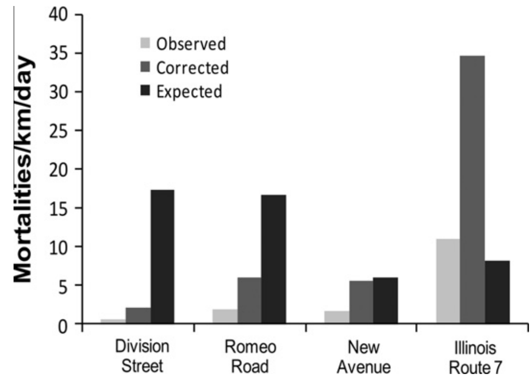

Fig. 1. Comparison of mean observed, corrected, and expected mortality rates of adult dragonflies/km/day in order of traffic volume at Division Street (DS), Romeoville Road (RR), New Avenue (NA), and Illinois Route 7 (IR) sites. Expected species mortality rates were calculated using Eq. (2).

The study areas were: Division Street within Lockport Prairie Nature Preserve (DS), Romeo Road adjacent to Romeoville Prairie Nature Preserve (RR), New Avenue along Long Run Seep Nature Preserve (NA), and the Illinois Route 7 west side approaches to the Lockport Bridge (IR).

Understanding the relationship between volume of traffic and death rates is important for interpreting patterns of mortality and disturbance. We estimated traffic volume at RR by counting the number of vehicles passing the observers for six 5-min segments during each observation session. Due to the high volume of traffic at NA and IR, we obtained average daily traffic counts from the Illinois Department of Transportation. DS is in a nature preserve and receives only very small volumes of slowly moving traffic, so we were able to directly estimate traffic volume. Survey lengths at each site varied, as they were determined by the length of road directly adjacent to wetland areas. The lengths of the survey areas and mean traffic volumes for the sites are as follows: DS = 1.205 km, <10 vehicles/day; RR = 0.567 km, 880 vehicles/day; NA = 0.898 km, 7300 vehicles/day; IR = 0.146 km, 25,500 vehicles/day.

2.2. Mortality along roadways

Mortality surveys required two teams of three people each; one person observed oncoming traffic, while the remaining two walked slowly side by side, scanning the road surface and the non-vegetated or sparsely vegetated shoulder of the roadway for dead insects. To maximize search intensity, teams followed one another while surveying each side of the roadway, moving against the flow of traffic. The traffic observer's role was solely to warn the surveyors about oncoming traffic and they did not participate in the scanning of the roadway for dead dragonflies. The width of the roadway area searched varied somewhat depending upon growth of vegetation on the shoulder of the road, but on average was about 5 m. To establish a rate of mortality for adult dragonflies over a 24-h period, each roadside survey required that two surveys be conducted. The first survey essentially was a prescreening of the roadway and served to remove all dead dragonflies and other insects from the roadside area. After 24 h, the second survey then removed all dragonflies (species identified and location recorded) that had been killed and remained on the roadway in the period between the surveys. We then calculated mean daily mortality rate per kilometer for each site and species to gain a better understanding of how traffic volume, population density, and dragonfly behavior affect roadway mortality.

Surveys were conducted generally during warm clear weather that represented good flight conditions for dragonflies in general.

Any rain events during the 24 h assessment period would cause that survey to be canceled since dragonfly carcasses are easily washed off roadway surfaces during rain events. All surveys were conducted between July 7 and August 8, 1995.

2.3. Calibration of roadway mortality estimates

Dead dragonflies are relatively light and are a potential source of food for some species; therefore, it was important to account for the possibility that carcasses may have been blown off the road or removed by scavengers during the 24-h study interval. In order to account for this, we determined rate of loss of dragonfly carcasses from the roadway within a 24-h period. To do this, we haphazardly placed 15–20 dead dragonflies of assorted species along the roadway in the afternoon (1400–1600 CST) and then surveyed for them after 24 h using the methodology described above. All dragonfly carcasses used in this part of the study were discreetly marked so that when collected we could separate them from any natural road kills. This study was carried out on five separate days along both NA and DS. To determine whether losses occurred primarily during the day or night, we performed additional road walks on three mornings (700–1400 CST). These studies were carried out along DS and NA between August 7 and September 3, 1996. Results were used to adjust observed mean daily mortality rates from the main roadway surveys.

2.4. Relative abundance and behavior along roadways

We assessed relative abundance and behavior of adult dragonflies over or near roadways at the four sites (DS, RR, NA, and IR) within the areas surveyed for dragonfly road kills. Six to eight trained researchers made flight behavior observations of dragonflies in the area. The observers were spaced at 20 m intervals along the shoulder of the roadway facing outward from the center. Observers recorded the behavior of all dragonflies approaching the road within a 10 m radius bounded on each side by the observation zone of the adjacent observer. All stations and boundaries of observation zones were marked with numbered flagging along roadside vegetation or fencing. Each observation session proceeded for ten minutes, during which the observer recorded all dragonfly activity by speaking into a handheld voice recorder.

The information recorded for each observation included: species and/or distinguishing marks, direction of approach, estimated flight height, time spent over roadway, behavior, general pattern of flight, direction taken when leaving observation zone or roadway, and sex (if possible). For each session, observers were assigned to stations by randomly drawn numbers. We conducted observation sessions in sets of three for each direction facing out from the roadway (e.g., three observation sessions facing south followed by three facing north). Flight height is an especially important measure since individuals flying at traffic level have the most potential to be impacted. An average vehicle height of 1.8 m was determined by randomly measuring vehicles in a large parking lot.

Varying physical circumstances required that there be some flexibility in how observation stations were determined among the five sites. The Division Street (DS) site in Lockport Prairie Nature Preserve consisted of eight observation stations, with the first station located just outside the entrance gates and the others sequentially running east. Observation stations along Romeoville Road (RR) were laid out in the same manner, with the eighth station located just east of the bridge and the remaining seven running west. The New Avenue (NA) site also had eight observation sites; however, all observations were made from the east side of NA because of the restricted view on the west side. Thus, we conducted one set of observation sessions while facing east and one while facing west (across NA). Similarly, eight stations were also set out along the south side of the Route 7 approach to the Lockport Bridge (IR); however, the embankment severely restricted the northwest view and thus observations were made facing southeast only.

3. Results

3.1. Mortality along roadways

A total of 36 roadway surveys were conducted, with 5 at DS, 9 at RR, 12 at NA, and 10 at IR, resulting in the collection of 49 identifiable dragonfly carcasses. Mean number of dead adult dragonflies collected per kilometer per day varied substantially among sites: DS = 0.66, RR = 1.93, NA = 1.76, IR = 10.96 (Fig. 1).

Nine species of dragonflies were identified from the 24-h roadside surveys of the four sites. Of all species found, three species (*Plathemis lydia*, *Libellula luctuosa*, and *Anax junius*) represented 71% of the dead dragonflies collected. Less than four carcasses were found for each of the remaining six species (*Libellula pulchella*, *Perithemis tenera*, *Dromogomphus spinosus*, *Sympetrum sp.*, *Erythemis simplicicollis/Pachydiplax longipennis*, and *Celithemis eponina*).

3.2. Calibration of roadway mortality estimates

A total of 80 marked dragonfly carcasses were placed along NA and 71 were placed along DS. Mean percent returns of dragonflies over 24 h were similar at both NA (35% ± 3.8) and DS (28% ± 2.8). The proportion of marked dead dragonflies recovered after 24 h did not differ significantly between the sites (univariate ANOVA, $p = 0.5600$). This indicates that approximately two thirds (68.4%) of dead dragonflies along the roadway will be removed over a 24-h period and that our roadside surveys underestimate 24-h death rates by a factor of 3.12. Of the dragonfly carcasses removed over 24 h, the mean overnight removal rate (1600–0800) was 61.7% (±11.2). Mean removal rates over the daylight hours from 0800 to 1600 were 34.5% (±4.3). Taken together, this data indicates that removal rates are relatively constant, with roughly one third of the dead dragonflies being blown away or removed by scavengers over any particular 8 h period. There was no indication that removal rates differed amongst the species set out along the roadways. Using this information, we calibrated the observed mean daily mortality rate for losses at each site. Corrected estimates of mean dragonfly mortality/day/km ranged between 2.1 and 34.6, with DS showing the lowest rate and IR the highest (Fig. 1).

3.3. Behavior along roadways

A total of 1995 adult dragonflies were observed and 16 species were identified during the behavioral observation sessions, with many species observed at least once at all sites. The frequency of species observed provides a measure of the relative abundance of species across all four sites. *Tramea lacerata* was the most frequently observed species, accounting for 24.97% of all identified dragonflies. *E. simplicicollis* and *P. longipennis* look similar to each other and exhibit similar flight behavior, thus they were not reliably distinguished during the observation sessions. Data for these species are treated as an aggregate. Data from the six most frequently observed species (*T. lacerata, L. pulchella, P. tenera, L. luctuosa*, *P. lydia*, and *A. junius*) were used for further analysis of flight heights over and near roads to compare relative abundance with expected and observed mortality rates (Table 1).

For all species reported in this study, 57.7% of individuals in flight were observed over the road, and 47.1% actually crossed to the other side. Interestingly, dragonflies observed at IR, the site

Table 1
Comparison of relative abundance and observed, corrected and expected species mortality rates of the six most frequently identified species in behavioral observations. Expected species mortality rates were calculated using Eq. (1).

Species	Relative abundance (%)	Mean daily mortality (km)	Corrected mean daily mortality (km)	Expected daily mortality (km)
T. lacerata	24.97	0.00	0.00	12.07
L. pulchella	14.01	0.67	2.12	6.77
L. luctuosa	10.01	2.91	9.19	4.84
P. tenera	8.05	0.97	3.06	3.89
P. lydia	7.04	4.62	14.60	3.40
A. junius	6.77	1.93	6.11	3.27

with the highest volume of traffic, were much less likely to cross the road than expected when compared to the other three sites ($\chi^2_3 = 200.70$, $p < 0.0001$). Species did vary significantly in tendency to cross roads ($\chi^2_5 = 14.66$, $p = 0.0119$). Cellwise Chi-square statistics indicated that *T. lacerata* had a lower crossing rate than expected (cellwise-$\chi^2 = 1.85$), while *L. luctuosa* crossed more frequently than expected (cellwise-$\chi^2 = 3.79$).

Patterns of minimum observed flight height over the roadway varied significantly amongst species ($F(1,5) = 14.08$, $p < 0.0001$). *L. luctuosa* and *E. simplicollis*/*P. longipennis* were the lowest fliers with over 79% of the flights below 1.8 m. *L. quadramaculata* and *P. lydia* were also low fliers with over 70% of their flights under 1.8 m. The species with the highest proportion of flights above 1.8 m was *P. tenera* (80.3%) followed by *A. junius* (55.2%).

3.4. Predicted vs. expected mortality

By combining estimates of relative abundance of live dragonflies active near the roadway with estimates of total number of carcasses, we generated a simple neutral model to predict roadway mortality for individual species:

$$D_{pi} = D_t \cdot O_i / O_t \quad (1)$$

where D_{pi} is the predicted rate at which species "*i*" will be found dead on the roadway, D_t is the sum of death rates across all species, O_i is the mean number of live observations of species "*i*", and O_t is the sum of live observations of all dragonflies. Differences between the model prediction and actual mortality (Table 1) were tested using a Chi-square analysis. Relative abundance of living dragonflies was not an adequate predictor of species specific death rate ($\chi^2_5 = 23.65$, $p = 0.0003$). Minimum flight height ($r = -0.50$, $p = 0.3074$) and percent crossing the road ($r = -0.66$, $p = 0.1530$) were also poorly correlated with corrected death rates for each species (Fig. 2).

By using the total number of dragonflies observed we were able to calculate total expected dragonfly death rate for specific roadways using the following equation:

$$D_{ps} = D_x \cdot O_s / O_a \quad (2)$$

where D_{ps} is the predicted mortality rate for all species at site "*s*", D_x is the sum of death rates across all species and sites, O_s is the mean number of observations of all species observed at site "*s*", and O_a is the sum of observations of all dragonflies at all sites (Fig. 1). Interestingly, when species were grouped this way overall number of dragonflies observed over the road was highly correlated with corrected death rates ($r = -0.97$, $p = 0.0231$), followed by volume of traffic ($r = 0.97$, $p = 0.0293$) (Fig. 3).

4. Discussion

There was no evidence in this study that roadways acted as strong behavioral barriers to adult dragonflies. If roadways functioned as significant barriers, then it seems likely that fewer individuals seen flying near the roadway would cross them; however, we found that approximately 58% of observed dragonflies did cross or fly directly over the roadway. Dennis (1986) found much higher levels of crossing avoidance in the orange tip butterfly (*Anthocharis cardamines*) where at least 88% of the individuals observed approaching the motorway did not attempt to cross it. Despite this, he still determined that it was unlikely that the roadway had much of an effect on the population as a whole. Our observations suggest it is unlikely that dragonflies avoid roads; in fact, extensive observation of flight behavior in some species such as the endangered Hine's emerald dragonfly (*Somatochlora hineana*) suggests that they often appear to use them as corridors when they connect two noncontiguous habitats (Soluk personal observation). Although dragonflies do not appear to treat roadways as behavioral barriers, it is important to keep in mind that they can still function to restrict movements since dragonflies actively attempting to cross roadways do not always succeed in making it to the other side.

Although a few studies have examined dragonflies as roadkill (Siebert and Conover, 1991; Riffell, 1999; Rao and Girish, 2007), we are the first to systematically compare abundance and behavior of individual species with the likelihood of those species being killed while crossing the road. Our results clearly show that some species (e.g. *P. lydia* and *L. luctuosa*) were especially vulnerable to road traffic, while others (e.g. *T. lacerata*) were killed much less frequently than expected given their high frequency of observation. This indicates that relative frequency alone is not an adequate predictor of death rate, and that factors such as flight behavior must

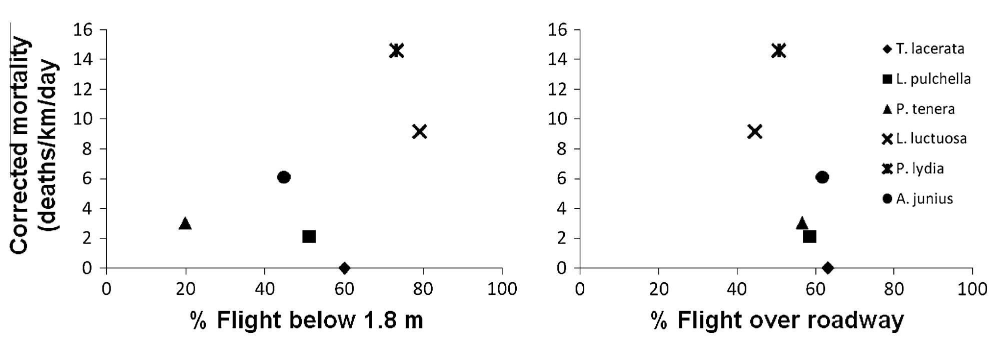

Fig. 2. Comparison of corrected mortality with flight behaviors of the six most frequently identified species in behavioral observations.

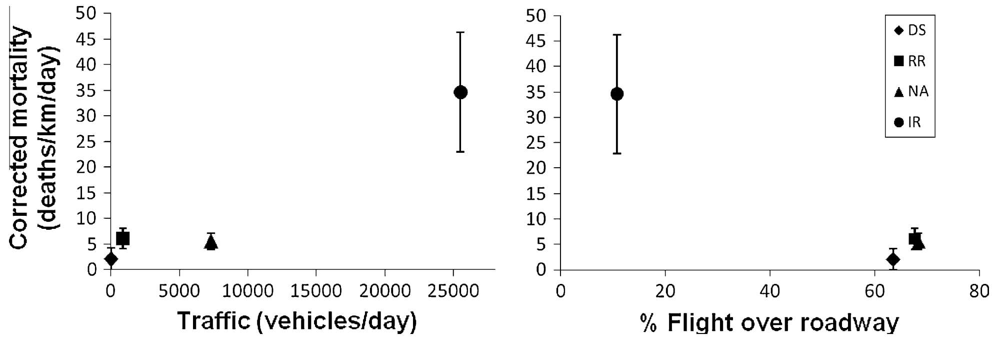

Fig. 3. Comparison of corrected mortality with traffic volume and observed flight behaviors at each site where road walks and behavioral observations were conducted.

be considered. *L. luctuosa* and *P. lydia* had the lowest recorded flight heights of all species, both with the average of 1.8 m and a median of 1.2 m. This makes them vulnerable to the bulk of traffic which consists of typical passenger cars and trucks which are generally less than 2 m tall. In contrast, *P. tenera* had an average flight height of 4.2 m and only a moderately low death rate. Although flight height is a reasonable predictor of risk of mortality from motor vehicles, it can be offset by other components of flight behavior. For example, in our study *T. lacerata* was the most commonly observed dragonfly and 60% of its flights were below 1.8 m; however, not a single carcass was found during roadway surveys, probably because this species is an extremely adept flier with the ability to make rapid vertical movements with ease (Soluk personal observation).

When compared across species, tendency to cross the road was poorly correlated with mortality; however, contrasting dragonfly behavior by site reveals a strong correlation. Volume of traffic is inversely related to the tendency of dragonflies to cross the roadway. Not surprisingly, sites with large volumes of traffic had larger rates of mortality, so although fewer dragonflies attempted to cross the road in these areas, mortality of those that did attempt to cross is increased. This was particularly apparent at the Illinois Route 7 (IR) roadway, which was the only site where corrected death rate was actually higher than the estimated rate based on dragonfly abundance. Previous studies have had mixed results when correlating traffic volume and roadway mortality (Carr and Fahrig, 2001; McGregor et al., 2008), and although this is only one factor affecting death rates, it is one that seems to be of importance for dragonflies.

Our study indicates that large numbers of dragonflies are killed along roadways and that species vary widely in their susceptibility. This is especially significant when considering that approximately 63% of species found in the United States are indicated as being "species of greatest conservation need" in at least part of their range (Bried and Mazzacano, 2010), and worldwide estimates indicate that perhaps 15% of all Odonata species are threatened with extinction (Clausnitzer et al., 2009).

Overall, few studies have attempted to quantify insect mortality rates along roadways, and little is known about whether roadway mortality has significant long term effects on insect populations adjacent to roadways. A study on butterfly and burnet moth populations in different habitats concluded that although death rates differed between species, vehicles killed only a small portion of any particular population (Munguira and Thomas, 1992). This project did not directly assess whether there are any short or long-term impacts on dragonfly populations near roadways. Such an assessment requires a better understanding of large scale movement patterns of adults and the structure of dragonfly metapopulations than is currently available.

Even if only a small proportion of dragonfly populations are killed by motor vehicles, there can be short and long-term consequences for populations. This is especially true if the composition of the dead differs in age or sex ratio from the general adult population. Riffell (1999) compared the sex ratio of dragonflies found dead along a stretch of road and concluded that species of the genus *Somatochlora* had higher female casualties than males by a ratio of 8 males to 19 females. Such sex-skewed mortality could have a severe impact on reproductive output, greatly influencing the ability of small or isolated populations to persist or altering patterns of genetic exchange within a population. This question is particularly important for species such as the federally listed endangered Hine's emerald dragonfly, *S. hineana,* which experiences significant mortality from motor vehicles in some parts of its range (Soluk and Moss, 2003). In this species, the tendency of females to forage away from wetland areas (Foster and Soluk, 2006) may make them more likely to cross roadways situated near wetlands. Unfortunately, in this study sex ratio was not assessed consistently for specimens, often because of the extremely mutilated condition of the dragonfly carcasses found on busy roadways.

Assessing the impact of roadways on dragonfly populations is difficult and our methodology for estimating mortality due to vehicle collisions likely underestimates actual mortality rates. Although we corrected for losses that occurred over a 24-h period, we could not account for carcasses that had been carried off-site on vehicles following collisions (e.g. windshields or front grills of vehicles). Additionally, some dragonflies hit by vehicles do not land on the pavement or graveled shoulder at which point our methodology would have failed to detect them.

The overall impacts of roadways on adult dragonflies are complex. We know little about the recruitment dynamics of dragonflies or the dispersal rates of adult dragonflies among wetland areas. Future studies combining dragonfly population estimates, roadside attributes, and genetics will be essential in truly understanding the effects that roads have on Odonata species, especially the extent to which roadway mortality may fragment populations. Roadway attributes such as number of lanes, length along wetlands, traffic speed, traffic density, and predominant vehicle types may all play a role. These factors must be combined with species attributes such as life history traits, density, activity level, behavior, and tendency to cross the road in order to predict mortality and its impact on animal populations. The location of new roads, especially near sensitive ecosystems, should be researched thoroughly before construction to ensure that they do not fragment habitats in a manner that would increase animal crossings and generate subsequent mortality. Roads near wetlands are known to have strong impacts on larger fauna such as reptiles and amphibians (Hels and Buchwald, 2001; Aresco, 2005; Clark et al., 2010). Our study contributes to the growing body of evidence indicating that small and often overlooked taxa should be a significant concern as well. The larval stages of dragonflies play important roles in maintaining the structure of aquatic ecosystems through direct predation and behavioral modification of prey species including fish and amphibians. If the population structure and species composition of dragonflies and other Odonata is being altered as a consequence of roadways, then it is likely that there will be wider consequences for the conservation of wetlands and other aquatic ecosystems.

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