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ORIGINAL PAPER

Ecological investigations to select mitigation options to reduce vehicle-caused mortality of a threatened butterfly

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Abstract Whereas roads that bisect habitat are known to decrease population size through animal-vehicle collisions or interruption of key life history events, it is not always obvious how to reduce such impacts, especially for flying organisms. We needed a quick, cost-efficient and effective way to determine how best to decrease vehicle-caused mortality while maintaining habitat connectivity for the federally listed Oregon silverspot butterfly, *Speyeria zerene hippolyta*. Therefore, we gathered targeted ecological information that informed selection of a mitigation option prior to implementation. We sampled butterfly behavior and environmental conditions along a highway and conducted a small-scale experiment along a decommissioned road corridor used by these butterflies. Using our findings, we recommended vegetation management and helped managers eliminate options they were considering that would be ineffective such as increasing shade or wind in the road, and installing fencing or hedgerows aimed at directing flight above traffic. This quick and inexpensive approach of using ecological observations and small-scale experiments to evaluate the likely success of each available mitigation option can be used to determine effective, species-specific solutions for reducing traffic impacts on pollinators and other small, flying organisms of conservation concern.

Keywords Animal-vehicle collisions · Behavior · Habitat connectivity · Mitigation measures · Oregon silverspot butterfly

Introduction

Roads have been documented to cause population-level impacts from animal-vehicle collisions, interruption of key life history events, and barrier effects, yet management solutions to reduce such impacts for many species are lagging behind the science (Mader 1984; Mumme et al. 2000; Bhattacharya et al. 2003; McGregor et al. 2008; Fahrig and Rytwinski 2009; Clark et al. 2010; Patrick and Gibbs 2010; Karraker and Gibbs 2011; Kociolek et al. 2011; Lampe et al. 2014; Keret et al. 2015; Marsh and Jaeger 2015). Population-level effects of roads are especially a concern for organisms with small populations (Gibbs and Shriver 2002; Holderegger and Di Giulio 2010). Indeed, the demise of at least 10% of the federally listed threatened and endangered species in the US was attributed to road presence, construction and maintenance (Czech et al. 2000). Also, small animals are hit by vehicles much more frequently than large ones (Conover et al. 1995). Therefore, small animals with small population size may face the greatest risks. Similarly, animals that tend to fly low over roads may be particularly susceptible to collisions (Soluk et al. 2011; Grilo et al. 2014) and billions of pollinators are estimated to be hit annually in North America (Baxter-Gilbert et al. 2015). As a result, species management plans, including ones for threatened and

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endangered flying insects, include reduction of road kill as a goal (e.g. U.S. Fish and Wildlife Service 2001).

The effectiveness of mitigations to reduce road mortality can be specific to species or sites (Kociolek et al. 2011), and solutions such as under-road crossing structures with fencing implemented for larger vertebrates may not work effectively for flying animals (Jackson and Griffin 2000). Some birds have been found to be more likely to cross over the road via a vegetated, land-bridge style overpass than a nearby stretch of the road (Jones and Pickvance 2013; Kociolek et al. 2011). Hence, it is not clear which mitigation options are best for different types of flying animals in general and certainly not for smaller fliers such as butterflies.

Managers are seeking to reduce sources of mortality to preserve the Oregon silverspot butterfly (*Speyeria zerene hippolyta*; hereafter OSB), which is listed as threatened under the United States Endangered Species Act. OSBs cross a highway that separates ideal oviposition locations from primary nectaring and roosting sites at one of their five remaining populations, Rock Creek, Oregon. Not only do butterflies experience high road mortality rates in general (McKenna et al. 2001; Rao and Girish 2007), approximately 35 % of OSBs that attempted to cross the highway at the Rock Creek site were estimated to have fatal collisions with passing vehicles (Powers 1988, as cited by; Testa 1995). Vehicle turbulence may also cause butterfly mortality due to its strong, chaotic forces; turbulence even contributes to mortality of much less fragile fliers such as owls (Massemin and Zorn 1998; Ojeda et al. 2015). Hence, reducing vehicle-caused mortality is one of the management goals for OSBs (U.S. Fish and Wildlife Service 2001). The OSB Advisory Team identified several possible measures to reduce road mortality (Table 1) and asked our research team to determine which options under consideration would be most effective. The options required investigation to determine their feasibility overall, at the site, and for the species.

Our goals were (a) to provide an inexpensive, practical process that can be used to determine a course of action to reduce mortality of small flying organisms, (b) to use ecological data to evaluate mitigation options that were not yet implemented or tested (see Table 1), and (c) to demonstrate how we linked ecological measures to mitigation options for small, flying animals. Hence, we examined the ecology of our target organism, OSBs, in ways that would help us evaluate the potential impact of ‘No Mitigation’, ‘Reduced Verge Attractiveness’, ‘Altitude Guides’, ‘Reduced Road Attractiveness’, ‘Speed Reduction’ and ‘Virtual Flower Bridge’, the latter in lieu of an expensive ‘Wildlife Overpass’.

Resources along the verge can attract animals to the road corridor (Grilo et al. 2012) and, in some cases, increase road crossings (Orlowski 2008). Removing roadside hedgerows helped reduce vehicle collisions with birds in Poland (Orlowski 2008) and planting unpalatable plants adjacent to the road prism and preferred ones away from it reduced ungulate-vehicle collisions (Romin and Bissonette 1996). To determine whether ‘Reducing Verge Attractiveness’ might be a useful mitigation, we examined whether butterflies crossed the road to flowers on the verge.

In contrast, other studies have found that vegetation along the road can also promote safe crossing by guiding animals to fly above traffic (Erritzoe et al. 2003). We tested the hypothesis that a strategically placed diversion (e.g. fence or hedgerow) in the flight path would increase flight altitude without disrupting connectivity, the ‘Altitude Guide’ mitigation.

Table 1 Mitigation options linked to study questions and methods

Mitigation options	Ecological questions addressed	Method
No Mitigation	Does vehicle-caused mortality occur? At what frequency?	Surveyed road corridor for collisions with vehicles
Reduce Verge Attractiveness: Reduce attractiveness of roadside by removing resources along verge	Is roadside vegetation correlated with movement to or in the road?	Compared flowering plants and OSB numbers on the verge
Altitude Guides: Guide flight above road to preserve connectivity yet decrease mortality	Can movement patterns be used to locate guides (e.g., hedgerows)? Does a guide elevate flight above traffic or its turbulence?	Identified location of, height of, and behavior during road crossings; Quantified effect of a fence meant to increase flight altitude
Reduce Road Attractiveness: Reduce attractiveness of road by manipulating environmental conditions favored by OSBs	Do specific behaviors seen on the road indicate attraction (e.g. basking)? Is road use correlated with environmental differences?	Surveyed paired road and meadow plots to compare temperature, wind, and humidity to OSB use and behavior
	Do certain road traits (e.g. road cuts) provide wind shelter or ameliorate temperature? Are such areas preferentially used by OSBs?	…and among road sections (road cut versus not)
Speed Reduction: Reduce opportunities for vehicle caused mortality by reducing driver speed under certain conditions	How do environmental variables affect activity levels in the road and crossing?	Predicted OSB presence in the road using weather-based statistical models
Overpass or Flower Bridge: Provide a way for OSBs to cross over the road	Will OSBs fly higher to access a food resource?	Observed planters of nectar-rich flowers stepped at 1 m height intervals

Environmental conditions along roads can attract or repel organisms or promote or hinder connectivity and could be evaluated to inform the possible mitigation of 'Reducing Road Attractiveness'. Roads can absorb more solar radiation, providing a surface warmer than surrounding meadows that may attract poikilotherms (Shine et al. 2004; Dennis 2008). Therefore, changing shade levels and heat absorption could affect attraction of roads. Because coastal Oregon roads typically are not exposed to sun for long periods due to cloudy conditions, we examined whether OSBs were using the road in a way, such as basking, that would indicate increasing shade would decrease roadkill. Similarly, verge areas that are more sheltered from the wind are used more by some butterfly species (e.g., Soderstrom and Hedblom 2007) and therefore reducing earthen berms along a road could effectively increase wind on the road surface. We therefore compared wind velocity and OSB use in areas with and without berms to determine if reducing berms would alter the presence of OSBs in the road.

Speed reduction signs have been used for flying invertebrates (Soluk and Moss 2003; Bissonette et al. 2007), but constantly reduced speed is not a viable option for the coastal highway in question. Flashing speed reduction and warning signs (Sullivan et al. 2004) reduce collisions with ungulates under some conditions (Huijser et al. 2009). If such signs were triggered by environmental variables correlated with a flying organism crossing the road, they might reduce the likelihood of collision during periods of high risk; however, drivers may not respond to warning signs about butterfly collision. As a first step, we examined whether road use by the target species was predictable based on environmental conditions and therefore could be used to inform a 'Speed Reduction' mitigation.

Overpasses planted with flowering plants would probably be an effective mitigation because butterflies could follow the plants over the road to avoid traffic, as has been found for birds using vegetated wildlife overpasses (Jones and Pickvance 2013). Overpasses are expensive so the Advisory Team was interested in finding effective but simpler or less expensive options. One possible option along the lines of an overpass but much smaller scale would be to make a thin bridge of flowers over the highway or a virtual bridge of flowers leading upwards to promote flight over the highway. A project for bee connectivity used a similar approach (The Guardian 2015). Hence, we piloted a 'Virtual Flower Bridge.'

Below we describe a case study of a process that can be followed by others wishing to use data to identify the best mitigation options before implementation. We also share the ecological data we gathered and used to assess the likely success of the six mitigation options.

Methods

Study sites

We studied OSBs at two sites along the Oregon central coast, Rock Creek and Mt. Hebo, that provide the larval food plant *Viola adunca* and nectar plants. Rock Creek is located south of Waldport (44.17835° N, −124.11494° W) in a salt spray meadow (~8 ha). The meadow is mowed to prevent overgrowth of *V. adunca* by invasive grasses and woody species. It is intersected by Highway US 101, the coastal highway, which has a posted speed limit of 88.5 km/h (55 m/h). In 2008, the average annual daily traffic (AADT) on a stretch of Highway US 101 near Rock Creek was 2100 vehicles (Testa, unpublished data).

The Mt. Hebo site occupies ~15 ha and comprises nine meadows separated by forest (Hammond 2013, Appendix Fig. S1). We used a decommissioned road on Mt. Hebo (Siuslaw National Forest), for the 'Altitude Guide' experiment that examined the effect of a diversion, in this case fencing, on connectivity and the likelihood of mortality from vehicle collision and for the 'Flower Bridge' observations aimed at determining if placing flowers on ever-higher poles would attract OSBs to fly higher over roads. We used Mt. Hebo for this part of the research because the highway through Rock Creek (US 101) is dangerous for researchers and butterflies alike and because the larger Mt. Hebo population facilitated a larger sample size. Weekly estimates summed across the 8-week flight season in 2009 totaled 423 OSBs (including potential recounts of individuals across weeks) at Rock Creek and 1411 at Mt. Hebo, though in some years the latter is up to 5,000 OSBs.

Field methods

We conducted a suite of observations and an experiment to evaluate the different potential mitigation options (Table 1). Adult OSBs can live for 3 weeks, typically during July through late September. OSBs do not fly in the rain or other inclement weather (Haughton et al. 2003) so we only conducted surveys when weather was suitable for flight during these months.

Observations to address 'No Mitigation'

Two observers surveyed road plots for OSBs at the Rock Creek site from 17 August to 19 September 2009. We selected a 1.2 km section of Highway US 101 and divided it into sixteen 75×8 m^2 plots. Each plot was then subdivided into five marked 15×8 m^2 subplots, for a total of 80 subplots (Appendix Fig. S2) to allow more precise location data and clean lines of sight.

We performed instantaneous scan sampling (Lehner 1996) by systematically surveying each component subplot until a whole plot was scanned and recording all collisions as well as vehicle headings. We then repeated the survey for the plot. Three or four randomly selected plots were surveyed each observation day. Four replicates were conducted for each of the 16 plots (16 plots × 5 subplots × 10 scans × 4 replicates) for a total of 3,200 scans and 32 h of observation per plot. We also conducted all-occurrence surveys (Lehner 1996) during which we recorded all OSB activity in the road and all occurrences of OSB flight paths crossing vehicles during 15-min intervals. We observed each road plot four times throughout the season (totaling 64 15-min observation periods, 16 h). We recorded the same variables included in the scan surveys plus flight direction and flight altitude. Finally, we opportunistically watched the road for possible OSB-vehicle collisions for ~60 min each observation day at Rock Creek for a total of 16 h.

Observations to address the need for 'Reducing Verge Attractiveness'

To determine whether OSBs crossed the road to access flowering plants on the verge we first counted the number of flowering plants in six randomly placed 1 m^2 quadrats along the verge (within 1 m of the road) of each of 15 of the road subplots. The subplots were selected with a stratified random design, randomly selecting five subplots from each of three levels of OSB crossing (none observed, 1–2 OSBs, or 3–7 OSBs observed crossing in the subplot). We quantified plants by counting the number of nectar plants in flower that grew at 100 intersection points of a gridded 1 m^2 quadrat. We then summed the number of OSBs crossing the road in each of the corresponding 15 × 8 m road subplots.

'Altitude Guide' experiment

We conducted a small experiment to determine if nets placed in the flight path of OSBs would guide them to fly over the height of vehicles. In 2012, we divided a stretch of decommissioned road at Mt. Hebo into ten 8 × 7 m^2 sections. These sections spanned the width of the roadway plus 2 m on either side and were placed to include the sunniest area, the predominant butterfly flight path. Six trials were conducted, each in a different randomly selected section. Each section had two sets of pole-crossings placed 7 m apart (Appendix Fig. S4). Each trial consisted of four consecutive 15-min observation periods that alternated between periods in which a 3-m tall net (2 cm polypropylene mesh bird netting) was stretched between the poles to ideally guide OSBs to fly at higher altitude, and periods in which no net was hung. The starting order (net or no net) was random.

Observations to address the mitigation options of 'Reducing Road Attractiveness,' and 'Speed Reduction'

The methods informing both the 'Reducing Road Attractiveness' and 'Speed Reduction' mitigation options included the surveys of butterflies in road plots described above for the evaluation of 'No Mitigation' and, for comparison, also identical surveys in nearby meadow plots at the Rock Creek site. Each road plot was paired with a plot of the same dimensions in the surrounding meadow. We placed each meadow plot at the same latitude as the road plot but at a random distance and direction (east or west) from the highway centerline. Upon completing 10 replicate surveys of a road or meadow plot, we surveyed its paired plot using the same protocol. Four replicates were conducted for each of the 16 pairs of plots yielding 3,200 scans and 32 h of observation for each of the meadow plots in addition to the same effort for road plots described above. For each survey we counted the number of butterflies engaged in any of seven behaviors and recorded whether a collision occurred (Arnold 1988; Appendix Fig. S3). We also recorded date, time, wind speed, temperature, and humidity per plot using a Kestrel 4500 Pocket Weather Tracker (Kestrel Meters, Kestrelmeters.com) held 1 m above the ground, which was the typical flight altitude of OSBs in our early observations.

Most stretches of the road at the site were subject to strong cross-road winds that could affect OSB flight and usage. In contrast, the typical west wind passed higher above the road in stretches where the terrain had been cut away to lay the road (road cut). Hence, another aspect of evaluating 'Reducing Road Attractiveness' entailed comparing OSB usage and conditions of road plots in the road cut to road plots just north and south of the road cut where the road was flush with the surrounding terrain (Table 1). If we found evidence of lower crosswinds in the road cut promoting butterfly use, the surrounding terrain could be modified to increase wind at road level.

We created a measure of detection probability in meadow plots by determining the number of OSBs that were not recorded during an instantaneous survey, as follows. Immediately after each of the 42 scans the observer zigzagged back through the plot toward the initial subplot to flush and record any butterflies missed during the initial scan. We were unable to zigzag through 18 subplots because of dense brush and our observations suggest it was unlikely many OSBs were roosting in this dense brush. Detection probability was always >97 %, suggesting the results of scan surveys were representative of OSB presence and behaviors across plots. We estimated observer bias by having the two observers conduct scans simultaneously. Observers recorded the same number of OSBs in 31 of 34 plots (91 %) during initial surveys and in 33 of 34 plots during zigzag surveys.

'Virtual Flower Bridge' pilot observations

To determine whether OSBs would fly up to an attractant that may be able to serve as a stepping stone to a higher one, effectively creating a virtual bridge above the highway, we observed flight to a 1 m high pole that was either topped with a bright color (red: n = 3, yellow n = 2) or flowers (n = 2) on two days when OSBs were active, 25 August and 1 September 2012, for a total of 90 min observation.

Statistical analyses

Summary statistics are reported as mean ± standard error (SE) of untransformed data, unless otherwise noted. Opportunistic sampling data were used in summary counts of OSB-vehicle collisions and crossings but were excluded from statistical analyses as these were not collected with a random sampling method, which violated assumptions of statistical tests. R was used for all statistical analysis (R Development Team). We determined if transformed data met the assumptions of parametric analyses using the Shapiro–Wilk test of normality and Variance Inflation Factor (VIF) and F-tests for equal variance.

A linear regression determined if the number of OSBs crossing the road (log transformed) at the subplot level was a function of the number of flowering plants adjacent to the road.

A Pearson's Chi square test with Yates' correction was used to evaluate the frequency distribution of flight path behavior in the flight altitude analysis. A Spearman's rank correlation was used to evaluate the tendency for condition variables (temperature, wind, relative humidity) to vary together with flight altitude in the middle of the pole-crossings.

Paired t-tests compared road versus meadow plots (n = 16, for sampling periods closest to seasonal peak abundance of OSBs) to determine whether OSB presence (log) and environmental variables differed between habitats for mitigations related to 'Reducing Road Attractiveness'. We used student's *t*-tests to compare the number of OSBs, wind speed, or temperature in subplots within the road-cut area to values in an equal number of subplots to the immediate north (subplots 52–66) and south (subplots 23–36) of the road-cut. A lag test of spatial autocorrelation of the plots for values 1 through 4 indicated no linear relationships. A partial Box and Jenkins ACF test on the residuals of the linear model, plotting the relationship between OSB presence and plot number, indicated there was no strong spatial dependence among plots.

We used logistic regression (following Gotelli and Ellison 2004) to determine if any of the measured environmental variables could be predictive of flight across the road. Observations were pooled across subplots each day, yielding 320 scans (16 plots × 5 subplots × 4 replicates). The percentage of the observations correctly classified by the logistic regression models ranged from 58 to 72 % and the explanatory power over random (kappa) was always <0.2.

Results

Road mortality—informing 'No Mitigation' option

One confirmed OSB-vehicle collision, a female, occurred 19 August 2009. Nine instances of likely OSB-vehicle collisions (apparent mortality) were recorded in which butterflies were not seen exiting the roadway after the vehicle passed. Mortality could not be confirmed because the vehicles were moving away from the observer. Thus, between 1.0 and 10.5 % of the 95 observed road crossings resulted in a vehicle-caused mortality.

Evaluating need for 'Reducing the Attractiveness of the Verge'

Four behaviors were observed in the road: nectaring, basking, flying, and interactive (Appendix Fig. S3). The one account of nectaring in the road occurred where a flowering plant was hanging over the guardrail and pavement. Moreover, OSB presence in the road was positively correlated with flowering plants along the roadside ($r^2 = 0.51$, n = 15, $t = 3.71$, $p = 0.003$, y = 0.126X + 0.245). More OSBs were found flying in the road in subplots that had more flowering plants adjacent to them (Fig. 1).

Evaluating the potential for effective 'Altitude Guides'

Five main locations of OSB road crossing, encompassing about half the plots, were apparent at the Rock Creek site (Fig. 2). Although the road surface was often lower than

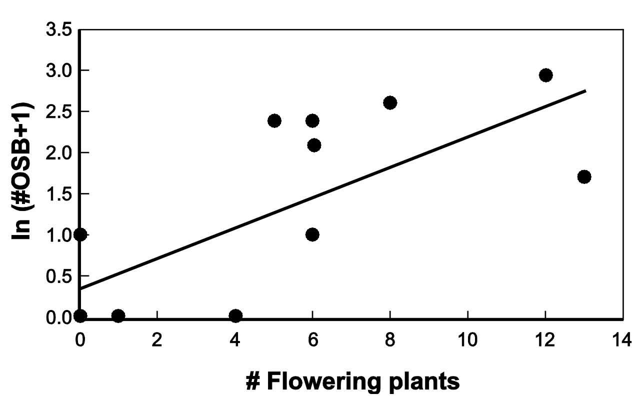

Fig. 1 Linear regression of Oregon silverspot butterfly presence in the road and flowering plants along the verge. Y = 0.126X + 0.245; $r^2 = 0.52$

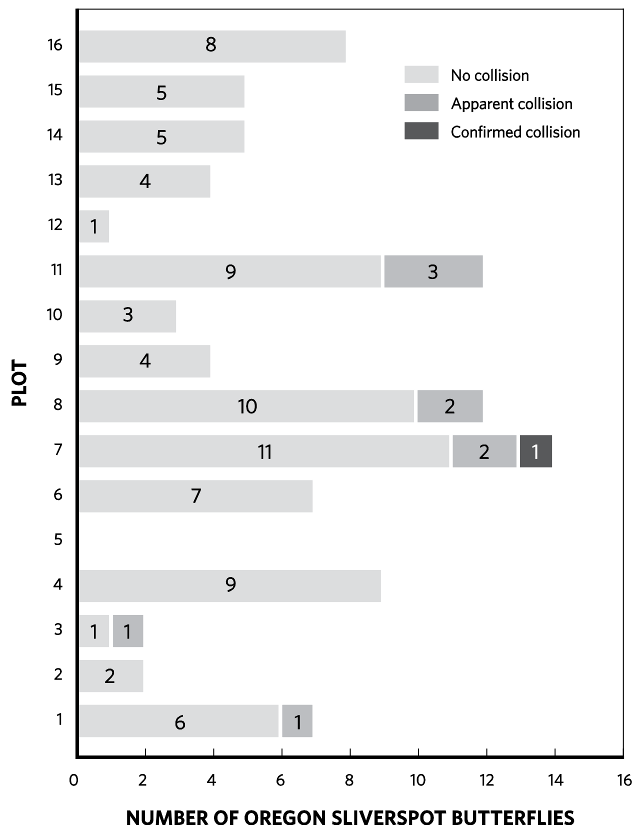

Fig. 2 Crossing locations and risk per location (no collision, apparent collision, confirmed collision) of Oregon silverspot butterflies crossing highway 101 at Rock Creek (49 observations from instantaneous scan sampling, 24 from all-occurrence surveys, and 22 from opportunistic sampling)

the surrounding habitat, OSB flight altitude above the road surface ranged from 0.5 to 4.5 m, averaging 1.6 ± 0.8 m (mean ± SD, n = 91), with flight lower in areas where the vegetation was lower and higher over bushes. A majority of OSBs (55/95) flew directly across the road without lingering. A third of the remaining 40 flew along the road but eventually returned to their road corridor entry points.

The experimental data did not support a conclusion that altitude diversions intended to guide flight altitude well above vehicles would improve butterfly safety while crossing a road. Less than 20 % (10/54) of approaching OSBs flew over the nets; the others flew around the nets (54 %), walked through them (4 %), or turned around (24 %). In contrast, 58 % of butterflies (35/60) passed between the pole crossings when no nets were present and only 15 % turned around. No individuals flew 3 meters or higher over both pole crossings, and only four butterflies (7 %) flew 2.5 m over both crossings. Moreover, 26 % (10 of 39) of the butterflies that flew over or around a net subsequently landed in the road between the nets and basked. The number of butterflies that landed after flying around or over the nets was significantly different ($\chi^2 = 8.26$, $p = 0.0161$) from the number of butterflies that landed after turning around or walking through the nets (1/16), and from the number that landed in the no-net treatment (4/60). Flight altitude did not significantly co-vary with temperature (Spearman rank correlations, all p's > 0.2).

Evaluating need for 'Reducing the Attractiveness of the Road'

Over three times more OSBs were detected in meadow plots (178) during scans than in road plots (paired t-test: $t = -2.82$, $df = 15$, $p = 0.013$). OSBs did not preferentially bask in the road (6.1 %) as compared to the meadow (12.9 %; Appendix Fig. S3). Basking behavior was only observed three times in road plots, always within 75 min of 12:00PM. The predominant behavior was flying, accounting for 86.4 % of observations in the road. The measured environmental variables varied much more across sampling days than across habitats and none differed significantly between habitats (all p's ≥ 0.1).

The average wind speed in road-cut subplots (0.90 ± 0.04 m/sec) was significantly lower ($t = 3.59$, $n = 45$, $p = 0.0006$) than in the subplots immediately adjacent to the north and south (1.06 ± 0.03 m/sec). Similarly, warmer temperatures ($t = -4.76$, $n = 45$, $p < 0.0001$) existed in road-cut plots (18.6 ± 0.24 °C) than outside of road-cuts (17.1 ± 0.17 °C). Nonetheless, no difference ($t = -0.27$, $n = 45$, $p = 0.7884$) was detected between OSB presence (ln) in the road-cut subplots (1.2 ± 0.45 OSBs) versus subplots to the immediate north and south (1.3 ± 0.32 OSBs). OSB flight was higher over the road surface in the road cut areas (2.1 ± 0.21, n = 18) than in the areas where the road was not sunk below the surrounding landscape (1.5 ± 0.09, $n = 73$; $t = 2.71$, $p = 0.0080$), suggesting that deep road cuts could help reduce mortality.

'Virtual Flower Bridge' pilot

Most butterflies that flew in the area flew right above the level of the flowers growing on the ground. We observed 100 OSBs pass the general area, including 41 that flew within 1 m of the pole with attractant, but none ascended to the color or flowers at the top of the pole.

Evaluating potential for environmentally triggered flashing 'Speed-Reduction Signs'

Both temperature and humidity were correlated with OSB activity. OSBs were detected in the road at ambient temperatures above 13.9 °C (survey range: 9.7–25.4 °C) and more were seen at warmer temperatures (road: $z = 2.349$, $df = 318$, $p = 0.0188$; meadow: $z = 4.711$ $df = 319$, $p < 0.0001$). The threshold temperature determined for prediction of OSB activity was 19.0 °C. OSBs were detected from 56.5 to 84.3 % relative humidity (survey range: 47.7–95.2 %), with more OSBs found at lower humidities (road: $z = -2.68$, $df = 318$, $p = 0.0073$; meadow: $z = -4.390$, $df = 319$, $p < 0.0001$). The threshold humidity value was 65.0 %. Wind was not correlated with OSB activity in this study (road $p = 0.498$; meadow $p = 0.758$), but OSBs were only observed flying at wind speeds under 7.5 m/s (16.8 mph; survey range 0–10.1 m/s).

Discussion

Presented with multiple mitigation options of unknown effectiveness, we targeted small-scale ecological investigations to determine which options to decrease OSB-vehicle collisions but maintain connectivity would be useful to implement or to research further. We verified that some OSBs were hit by vehicles. Any 'take' is considered actionable for this threatened species so 'No Mitigation' was not an option. We found OSBs flew over the road more often toward areas of the verge with more nectar flowers than areas with fewer flowers, suggesting flowers attract them to cross the road to these low areas. Some OSBs would fly above 3 m tall nets, but when they did clear a net they often landed between the nets in what would be the road surface if these were employed to guide their flight above traffic. These and other such observations from our studies informed the mitigation measures under consideration by the management team for this species, as discussed below.

Resources along the verge can attract animals to the road corridor (Grilo et al. 2012) and in some cases increase road crossings (Orlowski 2008). Our data were consistent with such findings and suggest it would be useful to follow a mitigation of 'Reducing Verge Attractiveness'. Reducing the attractiveness of the verge via low-cost vegetation manipulation was considered a high priority based on our observations of OSB nectaring in the road and more frequently entering road plots that contained higher densities of flowering plants. One approach is to clear the verge of flowering plants prior to the period of OSB flight. A study conducted at this site after the verge was mowed showed that OSBs that crossed the road flew higher than in our study and typically over the height of traffic (Bennett 2010), suggesting the mitigation of mowing the verge was effective.

Mowing the verge to eliminate flowers next to the road is controversial because verges can provide food and habitat as well as dispersal linkages connecting habitat for butterflies (Munguira and Thomas 1992; Pryke and Samways 2001; Ries et al. 2001; Saarinen et al. 2005; Valtonen et al. 2006; Noordijk et al. 2009; Skórka et al. 2013) and other animals (e.g., Kociolek et al. 2011; Ruiz-Capillas et al. 2013). Also, mowing verges can directly and indirectly harm pollinator species (Noordijk et al. 2009; Humbert et al. 2010). Mowing has even prompted some butterflies to cross the road in search of food resources and may increase collisions with vehicles (Valtonen et al. 2006; Skórka et al. 2013). Conversely, the verge in our study was narrow and surrounded by relatively extensive meadows, many of which slope down to the road. For butterflies flying across the road to access needed habitat, as with OSBs that primarily accessed emerging females and *Viola* on one side or nectar options on the other, flowers next to the road may lower their flight or cause them to linger in the road. Therefore, verge mowing could be considered when road mortality is high, surrounding habitats promote crossing, and verges do not provide the major source for nectar plants. Testing whether verges serve as an ecological trap for butterflies and other pollinators would also be valuable (Mumme et al. 2000).

The timing and regime of mowing is often a key consideration in managing the verge for butterflies (Valtonen et al. 2007; Noordijk et al. 2009; Wynhoff et al. 2011). The timing of verge mowing at the Rock Creek site was subsequently coordinated with meadow mowing so the verge would not have greater flowering plant diversity or more patches of flowering plants per unit area than the meadow.

Hedgerows or other barriers can encourage some butterflies and birds to stay longer in a habitat (Severns 2008) and others to fly at a safe altitude above the road (Erritzoe et al. 2003). Our initial findings suggested guides to increase flight altitude such as netting or hedgerows might be effective for OSBs. OSBs basked less in the road and were observed much less there than in the surrounding habitat. They generally flew higher over the road where they first had to fly over higher terrain or vegetation, which was also reported by Bennett (2010). The majority of crossings occurred in five road segments, suggesting that strategic placement of guides to increase flight altitude effectively promote high crossings while still allowing drivers many views of the scenic coastline. We therefore investigated this option of 'Altitude Guides' further.

Our follow-up experiment with poles and netting across the flight path versus no-net poles proved an important step in this process, revealing that guides to increase flight altitude could increase road mortality. A majority of the OSBs encountering nets flew around them or turned around. More importantly, one quarter of the butterflies that crossed a net then landed in the (decommissioned) roadway between the nets. Consequently, we suggested that this mitigation measure be excluded. In contrast, Hines emerald dragonflies (*Somatochlora hineana*) were found to successfully fly higher over 3 m high nets spaced 6 m apart (though not 12 m apart,) than a no-net treatment (Furness and Soluk 2015), suggesting this option is suitable for stronger flyers.

The other mitigation options under consideration, which we grouped under 'Reducing Road Attractiveness' and

'Speed Reduction' were found to be discountable as effective solutions to vehicle-caused mortality. The removal of earthen berms or other manipulations that might influence wind or temperature of the road were eliminated as mitigation measures because no "sheltering" effect or preferential basking of OSBs was detected in the road-cut or elsewhere on the road. Uncertain effectiveness, inconvenience to travelers, and high cost may hinder feasibility of using a sign to encourage speed reduction. Linking speed reduction to the timing and environmental conditions typical of flight, as indicated by empirically based models, would reduce impacts to traffic compared to a constantly reduced speed limit. However, animal detection systems have not yet been used for and may not be effective for virtually invisible animals or ones whose impact does not endanger drivers.

A 'Virtual Flower Bridge' will not work though a contiguous bridge has potential. We aimed to mimic an alternate to an overpass with a virtual bridge of color or flowers, but OSBs were not attracted to fly up to our 1 m high planter of flowers during our pilot test. In addition, we found that OSB movement is not focused narrowly enough to identify a single overpass location so several crossing spots would be needed. An inexpensive version of a wildlife overpass could offer an effective solution; an example of such is a contiguous flower bridge from an art project for urban sustainability (environmental health clinic, http://www.environmentalhealthclinic.net/civicaction/butterfly-bridge).

In summary, we found evidence suggesting flowers on the verge attracted OSBs across the road. Hence, a mitigation 'Reducing Verge Attractiveness' was adopted: the Rock Creek site's verges are now mown every July to minimize road mortality (personal communication, Anne Walker, US Fish and Wildlife Service). At Rock Creek, the mowing mitigation is being complemented by a second mitigation: *Viola adunca*, the food for OSB larvae, is being planted on the side with many nectar plants with a goal of minimizing butterfly road crossings (Pers. Comm, A. Walker). Our data suggested the other mitigations were unlikely to be feasible or to achieve the goal of reduced road mortality. Nonetheless, the approaches and the possible mitigations may work well for other species.

If vehicles continue to be a concerning source of mortality, speed reduction and flower bridges could be further explored. For the former, it is important first to evaluate driver reaction to speed reduction signs aimed at butterfly protection and to determine the vehicle speed that would decrease vehicle lethality. Perhaps the best alternate mitigation is a continuous flower bridge or fully vegetated overpass. A more contiguous run of flowers with just gradual rise would not require these low fliers to change altitude without the immediate possibility of a nectar reward. This option requires further exploration for butterflies and other small flyers, as wildlife overpasses and other over-road crossings have been found to at least partially restore connectivity and reduce roadkill for other animals, including small birds (Jones and Pickvance 2013; Sawaya et al. 2013; Soanes et al. 2013; Teixeira et al. 2013).

By gathering information on the behavioral ecology of the target organism and following up on findings that looked promising, we evaluated several possible mitigation measures that probably will also be options for many other species. Using ecological observations linked to the underlying rationale of available mitigation options was an effective technique identifying what future research was most needed and which mitigation option might be pursued. Because roads are already having large effects on some populations and probably will have greater impacts with continued change in land use, especially in light of increasing demands on organisms having to respond to climate change, effective and inexpensive approaches are needed to determine how to mitigate consequences of vehicles on small, flying organisms.

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