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ORIGINAL PAPER

The potential for elevated soil salinity to enhance the ecological trap effect of roadside pollinator habitat

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Abstract

The management of roadside habitat may be an important component of the conservation of declining pollinators, but insect mortality along roadsides can be high, creating a potential "ecological trap." Runoff from winter applications of deicing salt can increase soil salinity along roadsides, and if this results in higher sodium levels in floral nectar, it could increase the attractiveness of roadside plants to pollinators, possibly accentuating the ecological trap effect. We compared the soil salinity in a highway median to soil collected from nearby fields and compared the Na^+ concentrations in nectar from common milkweed (*Asclepias syriaca*) from these two habitats. We also manipulated soil salinity in field populations of *A. syriaca* by adding brine solution to document changes in nectar Na^+ and pollinator visitation. We found that soil salinity in the median of a highway in Clarke County, VA was 2.3 times higher than the salinity of field soil, however nectar from *A. syriaca* in the two habitats did not differ significantly in Na^+ concentration. Addition of brine to field soil increased soil salinity 17-fold and significantly increased the level of Na^+ in *A. syriaca* nectar. Pollinators visited *A. syriaca* umbels that received the brine treatment twice as frequently as controls. Implications for insect conservation: We conclude that elevated soil salinity is capable of increasing nectar Na^+ and the attractiveness of *A. syriaca* flowers to insect pollinators, but roadside soil salinity in our study was not high enough to enhance an ecological trap effect of roadside vegetation.

Keywords *Asclepias syriaca* · Deicing salt · Ecological trap · Nectar · Pollinator · Sodium

Introduction

In 2020, there were approximately 4.19 million miles of public roads in the United States (U.S. Department of Transportation Highway Statistics 2020). Areas along the shoulders and medians of these right of ways are particularly suitable for grassland habitat, and many researchers have advocated for managing these areas as part of a conservation effort to mitigate arthropod biodiversity declines (Hopwood 2008; Hanley and Wilkins 2015; Hanula et al. 2016; Kasten et al. 2016; New et al. 2021; Twerd et al. 2021). Improved roadside habitat through the planting of native species is regarded as especially attractive to pollinators (Phillips et al. 2021). Roadside habitat can also benefit insects by increasing connectivity between habitat fragments (Forman et al. 2003). Despite the potential benefits that such habitat improvements might offer, there are concerns about elevated mortality to pollinators attracted to roadsides.

Roadside habitat restorations could act as "ecological traps" for insects, wherein a preferred habitat actually reduces fitness (Hale and Swearer 2016). Direct insect mortality through collisions with automobile traffic along highways can take a significant toll on insects using adjacent habitat (Baxter-Gilbert et al. 2015; Zielin et al. 2016; Keilsohn et al. 2018; Martin et al. 2018; Phillips et al. 2019; Fitch and Vaidya 2021; Campioni et al. 2022). Roadside habitat can also affect insect fitness indirectly. For example, due to pollution from engine combustion, plants growing along roadsides can have elevated levels of heavy metals

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(e.g., lead and zinc) that can be toxic to their herbivores (Mitchell et al. 2020).

One of the most widespread road pollutants in parts of the United States and other temperate areas is the residue from deicing salt, sodium chloride (Tiwari and Rachlin 2018; Szklarek et al. 2022). Although most salt applications occur outside the growing season, the cumulative effect of deicing applications can leave soils highly saline (Thompson et al. 1986a, b; Beaton and Dudley 2013). Soil salinity tends to peak in early spring when deicing applications cease, but soil salinity can remain elevated throughout the growing season (Thompson et al. 1986a; Olofsson and Lundmark 2009). Salt in the soil can be taken up by plants and stored in leaf tissue (Bryson and Barker 2002; Marosz 2011; Snell-Rood et al. 2014; Luckzak et al. 2021), where it is capable of reaching levels toxic to insect herbivores (Mitchell et al. 2020).

Whether roadside plants have elevated nectar sodium levels has never been examined. Nectar is the primary carbohydrate source for most pollinators, but nectar contains other important micronutrients, including sodium (Hiebert and Calder 1983). Sodium, in particular, is often a limiting resource for insects (Lynn et al. 2022). Using experimental sodium additions to floral nectar, Finkelstein et al. (2022) found that the number of insect pollinators attracted to five different species of plants (*Achillea millefolium*, *Echinacea purpurea*, *Geranium sanguineum*, *Monarda didyma*, and *Penstemon digitalis*) nearly doubled relative to controls. If high soil salinity results in higher nectar sodium in roadside plants, making them more attractive to pollinators, this common roadside pollutant has the potential to enhance the ecological trap effect of roadside pollinator habitat.

In this paper we evaluate whether pollution from deicing salt has the potential to alter nectar chemistry and increase the attractiveness of flowers to pollinators in plants growing in high sodium environments. Specifically we will test the following hypotheses: (1) roadside soil is higher in sodium than soil collected from fields away from roadsides, (2) sodium in nectar is higher in plants growing along roadsides compared to plants growing in fields away from roadsides, (3) addition of a sodium chloride into the root zone of a plant will result in elevated nectar sodium relative to controls, and (4) pollinators will preferentially visit plants that received sodium chloride solution in their root zones relative to controls. We will also compare nectar sugar concentrations between roadside and field plants and between plants receiving root zone sodium chloride additions relative to controls. We expect sugar concentrations to be unaltered by habitat or sodium chloride addition. If roadside nectar is found to have higher sodium and higher sodium nectar makes plants more attractive to pollinators, we can conclude that the residue from road deicing salt has the potential to enhance any ecological trap phenomenon in roadside plantings by drawing a disproportionate number of insects.

Methods

Study site and study species

This study was conducted in the northern Shenandoah Valley of Clarke County, VA, USA in June and July 2022. Study sites were on or near the University of Virginia's Blandy Experimental Farm (hereafter, Blandy). Highway plots were located along a 1.64 km segment of US 17/50 (hereafter, US 50) west of Blandy's main entrance (center of the segment: 39.073818° N, 78.069425° W, elevation ~ 180 m). This segment of highway has two eastbound and two westbound lanes, separated by a 15 m-wide median of exotic grasses and native and exotic wildflowers. It is one of the two main east-west highways through the county connecting the city of Winchester, Clarke, and Frederick Counties (total population based on 2020 census: 134,322) to the Washington, D.C. metro area. Soil types in this section of the median included Poplimento silt loam, Swimley-Hagerstown silt loam, and Weaver silt loam (USDA 1982).

For comparison to the highway samples, we sampled from an early succession field at Blandy that parallels US 50 in plots that were at least 120 m away from the nearest road. The center of the area was at 39.066481° N, 78.058884° W (elevation ~ 180 m), about 1.3 km from the center of the US 50 study area. The field was last disturbed in 2009 and was dominated by exotic grasses and native and exotic wildflowers. Soil types in this area of the field included Poplimento silt loam and Timberville silt loam (USDA 1982). To match field soil samples to the same soil types found in the highway median, we also sampled soil from a field on a private property adjacent to Blandy and US 50 (centered at 39.072037° N, 78.068644° W).

The preceding winter in Clarke County brought approximately ten snow and ice events that resulted in the application of deicing salt to US 50 (Virginia Department of Transportation, Stephens City, VA, pers. comm.). Typically, deicing salt is applied prior to the event as a 23% brine solution that dries on the pavement. Depending on the severity of the event, this initial brine application may be followed by multiple applications of coarse, granular salt.

We focused on common milkweed, *Asclepias syriaca* (Apocynaceae), a species ideal for this study for several reasons. First, it is one of the most common native plants along US 50 in Clarke County, and it is a common roadside plant throughout its native range (e.g., Kasten et al. 2016). Common milkweed is a perennial herb that overwinters as an underground rhizome. A single rhizome may produce multiple ramets that emerge in April or May. In Virginia, flowering typically begins in June and usually ends in July. The flowers are arranged in umbels (20–100 flowers/umbel; Howard and Barrows 2014) and produce copious amounts nectar. Milkweed pollen is packaged in pollinia (Wyatt and Broyles 1994), which cannot be utilized as food by pollen-foraging insects, so nectar is the only reward for the many generalist pollinators that visit milkweed umbels. Common milkweed is also a critical host plant for the declining monarch butterfly (*Danaus plexippus*), and conservation biologists have advocated for increasing milkweed plantings to create oviposition and nectaring opportunities, including along roadsides (Kasten et al. 2016; Daniels et al. 2018; Cariveau et al. 2019).

Soil salinity comparisons: highway versus field

We identified five plots along US 50. We did not select plots randomly. Instead, we dispersed them relatively evenly (about 100–200 m apart) along the 1.64 km length of the site to minimize spatial autocorrelation. We intentionally selected areas where milkweed was growing abundantly and that were at a slightly lower grade than the road, avoiding raised areas and limestone rock outcrops. We felt that these lower areas were the most likely to receive runoff from the road and were therefore more likely to experience elevated salinity (verified by preliminary sampling). Our highway sample should therefore be regarded as a "worst case scenario" from this stretch of highway. Coring sites ranged from 4.2 to 5.5 m from the edge of the roadway. On 10 June, we collected three 2 cm diameter soil cores at each plot from a depth of 0–10 cm (15 cores total). Coring locations within a plot were separated by at least 10 m. Cores were stored in Ziplock® bags and placed in a cooler until they were brought to the lab.

For comparison to the highway samples, we collected 15 cores from the Blandy field site on the same date. We selected five plots and sampled three cores from each as described above. Because the soil types in the field did not include all of the soil types found along the road, we collected samples from Poplimento silt loam, Swimley-Hagerstown silt loam, and Weaver silt loam at locations on an adjacent private property on 15 June to test whether soil type explained the observed differences in salinity between habitats.

We obtained an initial mass and dried the soil samples at 60° C for 24 h (preliminary work demonstrated that samples reached a constant mass within this time) before obtaining the dry mass of the soil. We calculated soil moisture as the percent mass loss from the initial to dried samples. Each dry soil sample was mixed in a beaker with distilled water at a 1:1 ratio by mass and placed in a shaker incubator for 60 min. We then poured each sample into a 50 ml centrifuge tube and centrifuged for three minutes to pellet the soil solids. We measured the salinity (ppm Na^+) of the supernatant using a Hanna Instruments Portable EC Meter.

Nectar comparisons: highway versus field

Beginning on 21 June 2022 and continuing through 1 July 2022, we collected nectar samples from at least three *A. syriaca* plants from each of the US 50 and Blandy plots described for the soil salinity comparison. We collected nectar only on mornings following a rainless night. The day before a nectar collection, we placed 10 × 15 cm white satin bags (Uline, Pleasant Prairie, WI, USA) over umbels that had about 75% or more of their flowers open but showed no signs of senescence. The satin bags minimized nectar evaporation and collection by insects. We collected nectar using 10 µl capillary tubes (Drummond Scientific Company) the next morning, starting at about 7 h am and ending at about 10 h am. Once the capillary tube was about 75% full, we used a Drummond Microcap Bulb Dispenser to deposit the nectar into a 0.5 ml microcentrifuge tube. We collected as much nectar as possible from each plant, with total volumes of usable samples ranging from 70 to 190 µl. Samples were placed in a cooler in the field and stored in a -20° C freezer until they could be analyzed for sodium.

On 21 July 2022, we measured Na^+ concentrations of the nectar samples using a Thermo Scientific Dionex™ ICS-3000 IC (ion chromatography) system. Ion chromatography separates cations passing through an ion exchange column and provides sensitive, high-resolution measurements for the low Na^+ concentrations that we expected in milkweed nectar. Samples needed to be diluted in order to have sufficient volume for the IC instrument. Each sample included 70 µl of nectar and 1930 µl of distilled water. We chose this dilution ratio to include the greatest number of samples possible while remaining above the detection limit (0.9 µeq/l) of the IC method. We were able to analyze a total of 23 nectar samples from along US 50 and 27 samples from Blandy.

We also estimated sugar concentration for each sample using a Bausch and Lomb® (range 0–32%) refractometer (Kearns and Inouye 1993). A test for the effect of sodium chloride on refractometer readings showed that even the highest level of Na^+ that we detected in nectar had no measurable effect. A total of 18 and 25 nectar samples had adequate volume for sugar analysis for US 50 and Blandy plants, respectively.

Salinity manipulations: nectar and pollinator effects

In our salt manipulation experiments, we used a population of *A. syriaca* from the same early succession field at

Blandy that we used for the soil salinity and nectar comparisons described above. This location ensured that control plants had low salinity soil. We established three plots in this field, within which we marked thirty *A. syriaca* ramets with orange flags, randomly assigning 15 to a salt treatment and 15 to a control treatment. Ramets included in the study were isolated from the next nearest ramet by at least 1 m, and ramets assigned to a salt or control treatment were separated by at least 5 m to avoid treatment contamination and to help ensure that we were sampling different genets in this clonal plant.

Plots were treated sequentially, one plot per week over the course of three weeks, beginning the week of 28 June and continuing through the week of 11 July. On day one, plants assigned a salt treatment received 500 ml of salt brine (20 parts water and 1 part Morton® Table Salt) within a 50 cm diameter circle around the stem. Plants assigned to control treatments received 500 ml of distilled water poured within a 50 cm radius circle around the stem. On day two, we bagged 1–2 umbels on all 30 plants in the plot. From approximately 7 h am until 10 h am on day three, we collected nectar from bagged umbels on 7–9 plants from each treatment group. On day four, we recorded pollinators at plants for 15-minute intervals beginning at approximately 8.5 h am until approximately 12 h noon. For the first observation period, one observer was assigned randomly to a "salt" plant and another to a control plant, and observers alternated between salt and control plants thereafter. We monitored a total of 7–12 plants per treatment per plot. Observers categorized floral visitors into one of six groups: honey bees (*Apis mellifera*), bumble bees (*Bombus* spp.), small bees (mostly Halictidae and Megachilidae), wasps (Vespidae), beetles (Coleoptera), flies (Syrphidae and Muscidae), and skippers (Hesperiidae). We commonly observed milkweed beetles (*Tetraopes tetrophthalmus*), thrips (Thysanoptera), and ants (Formicidae) on umbels, but we did not include these in our analyses. On day five, we collected 2 cm diameter × 10 cm deep soil cores from the root zone of each ramet from which we collected a nectar sample on day three.

We measured soil salinity and soil moisture for salt additions and control samples as described earlier. We measured Na^+ levels in the nectar with the HPIC system on 21 July, as described earlier. We obtained a total of 13 nectar samples with an adequate volume of nectar for Na^+ analysis for each treatment. We measured sugar concentration (%) of the nectar with a Bausch and Lomb® refractometer, as described earlier. A total of 14 and 17 nectar samples had adequate volume for sugar analysis for control and salt addition plants, respectively.

Data analysis

All analyses were conducted with SAS 9.4. We report least-squares means in all cases and 95% confidence intervals derived from the models. To compare mean soil salinity, soil moisture, nectar Na^+ concentration, and nectar sugar concentration between samples along US 50 and control sites, we used a mixed model ANOVA with "habitat" (US 50 or Blandy) as a fixed effect. We included "plot" (1–5) nested within the habitat as a random effect to account for non-independence. All data met homogeneity of variance and normality assumptions.

To compare the mean soil salinity and soil moisture adjacent to the manipulated plants at Blandy, we used a generalized linear mixed model with a log-normal distribution and a log link function. The model included the "salt treatment" (brine or distilled water control) as a fixed effect and the plot (1–3) as a random effect. Because nectar Na^+ concentrations in salt-manipulated plants showed a bimodal distribution, we compared "salt" plants to control plants with a non-parametric Wilcoxon 2-sample test. Nectar sugar concentration was compared with a mixed model ANOVA with "salt treatment" (brine or distilled water control) as a fixed effect and plot as a random effect.

Differences in pollinator visitation between "salt" and "control" plants were analyzed with a generalized linear mixed model with a Poisson distribution and a log link function. Salt treatment (brine or distilled water) was treated as a fixed effect and plot as a random effect. We recorded the number of umbels open on each plant with the intention of using this as a covariate, but umbel number was uncorrelated with the number of insect visitors in either control or salt addition plants and was therefore omitted from the model. Separate analyses were run for the total number of pollinators, the number of bumblebees (*Bombus* spp.), the number of honeybees (*A. mellifera*), and the number of small bees (mostly Halictidae and Megachilidae).

Results

The mean soil salinity along US 50 was 2.3 times higher than in the field at Blandy ($F_{1,8} = 129.39, p < 0.0001$; Fig. 1). The percent soil moisture did not differ between Blandy (18.6%, 95% CI: 17.2–20.1%) and the highway (19.6%, 95% CI: 18.1–21.1%; $F_{1,8} = 1.18, p = 0.3086$). Soil samples collected from a field on an adjacent property that matched the soil types on US 50 had a mean soil salinity (62.0%, 95% CI: 46.0–78.0%) that was similar to the samples collected on Blandy and that differed significantly from the highway samples ($F_{1,4} = 100.86, p = 0.0006$). This suggested that the

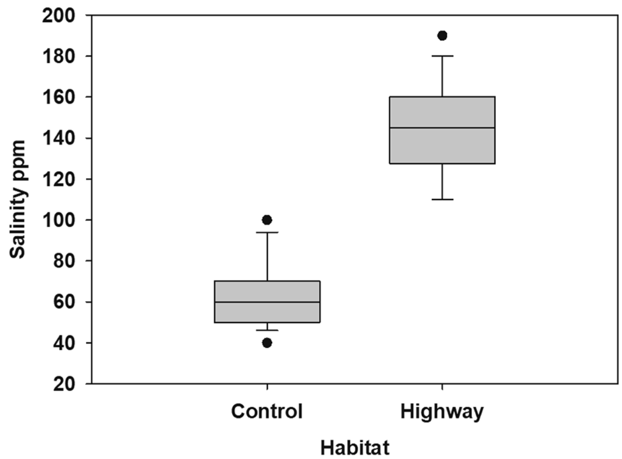

Fig. 1 Box and whisker plots for soil salinity (ppm) from samples collected from the US 50 highway and Blandy Experimental Farm control sites. The box represents the span of the upper and lower quartiles, and the horizontal line within the box indicates the median. Whiskers represent 1.5 times the interquartile range. The mean (and 95% confidence interval) for the control and highway sites are 62.7 ppm (51.1–74.3 ppm) and 145.0 ppm (133.0–177.0 ppm), respectively

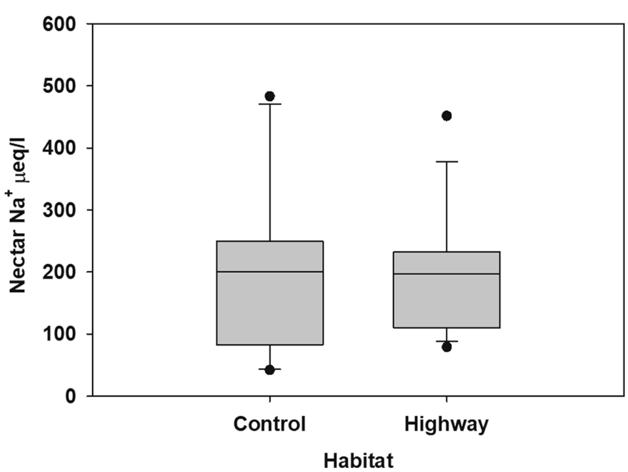

Fig. 2 Box and whisker plots for nectar salinity (Na^+ µeq/l) from samples collected from common milkweed at the US 50 highway and Blandy Experimental Farm control sites. The box represents the span of the upper and lower quartiles, and the horizontal line within the box indicates the median. Whiskers represent 1.5 times the interquartile range. The mean (and 95% confidence interval) for the control and highway sites are 200.9 µeq Na^+/l (109.7–292.1 µeq Na^+/l) and 193.3 µeq Na^+/l (110.2–276.4 µeq Na^+/l), respectively

higher sodium level along the highway was due to the roadside environment rather than the soil type.

Despite the difference in soil salinity, the mean Na^+ concentration in nectar collected from *A. syriaca* along the highway did not differ from the nectar collected from Blandy ($F_{1,8} = 0.02$, $p = 0.8906$; Fig. 2). The mean sugar concentration in nectar collected from *A. syriaca* along the highway (17.1%, 95% CI: 13.8–20.3%) did not differ significantly

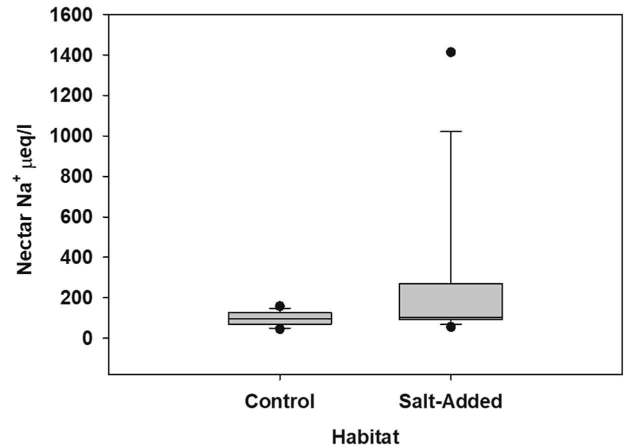

Fig. 3 Box and whisker plots for nectar salinity (Na^+ µeq/l) from samples collected from the control and salt-added common milkweed. The box represents the span of the upper and lower quartiles, and the horizontal line within the box indicates the median. Whiskers represent 1.5 times the interquartile range. The mean (and 95% confidence interval) for the control sites and salt-added plants are 94.1 µeq Na^+/l (-72.0–260.3 µeq Na^+/l) and 263.3 µeq Na^+/l (97.6–429.1 µeq Na^+/l), respectively

from the nectar collected at Blandy (20.5% CI: 17.6–23.3%; $F_{1,7} = 3.36$, $p = 0.1051$).

The addition of brine to the root zone of *A. syriaca* resulted in mean soil salinity 17 times higher than control soil (1061.7 ± 152.1 ppm versus 60.0 ± ppm; $F_{1,48} = 245.28$, $p < 0.0001$). The mean salinity of control soil was similar to what was seen in the same field earlier in the summer. The addition of brine increased soil moisture by 11.6% in the root zone of salt-addition (18.7%, 95% CI: 17.9–19.4%) relative to control milkweed (16.8%, 95% CI 16.0–17.5%; $F_{1,49} = 13.78$, $p = 0.0005$).

Nectar Na^+ levels from salt addition plants were much more variable than for control plants ($s^2 = 1.29$ for controls, $s^2 = 161.28$ for salt addition nectar). Nectar from control plants ranged from 1.56 µeq Na^+/l to 5.51 Na^+/l, while nectar from salt addition plants ranged from 1.93 µeq Na^+/l to 49.47 Na^+/l (Fig. 3). A Wilcoxon 2-sample test showed higher Na^+ concentrations in the distribution of nectar samples from the salt addition relative to controls ($z = 1.74$, 1-tailed $p = 0.0406$). We found no significant difference in nectar sugar concentrations between control plants (20.6%, 95% CI: 15.5–25.7%) and salt addition plants (21.8% CI: 16.8–26.8%; $F_{1,27} = 0.66$, $p = 0.4247$).

We observed a total of 231 insect visitors to *A. syriaca* umbels during a total of 55 15-minute observation periods. Honey bees were by far the most common visitors (127), with beetles (37) a distant second, followed by bumble bees (24) and small bees (23). Insects visited salt-treated plants at a rate twice as high as control plants ($F_{1,52} = 24.54$, $p < 0.0001$; Fig. 4). Honey bees accounted for much

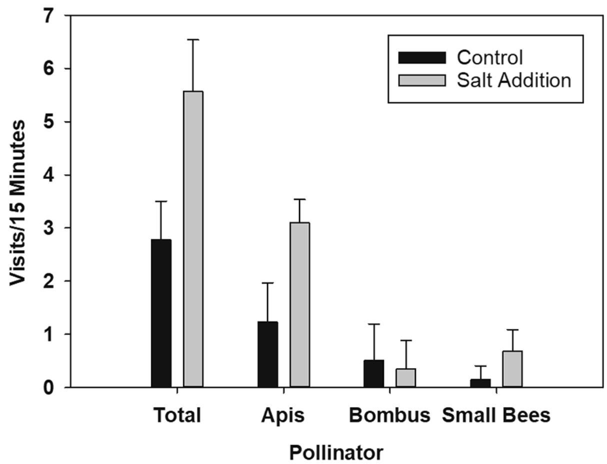

Fig. 4 Mean number of pollinator visits per 15-minute session (and 95% confidence intervals) to common milkweeds treated with salt brine or control plants. Data are reported for the total number of pollinators as well as the number of honey bees (*Apis*), bumble bees (*Bombus*), and the number of small bees (Halictidae and Megachilidae)

of this difference ($F_{1,52} = 21.65$, $p < 0.0001$), averaging 2.5 times more visits to salt-treated plants relative to controls. Small bees also showed a strong preference ($F_{1,51} = 7.65$, $p = 0.0079$), with 4.5 times as many observations on salt-treated plants. The mean number of bumble bee visits did not differ between treatments ($F_{1,52} = 0.74$, $p = 0.3924$).

Discussion

A focus on improved land management is essential to mitigate global pollinator declines (Dicks et al. 2021). Managing roadside vegetation to enhance its value to pollinators might be a particularly effective tool (Hopwood 2008; Hanley and Wilkins 2015; Hanula et al. 2016; Kasten et al. 2016; New et al. 2021; Phillips et al. 2021; Twerd et al. 2021). However, roadside habitat is often associated with high insect mortality due to collisions with traffic (Baxter-Gilbert et al. 2015; Zielin et al. 2016; Keilsohn et al. 2018; Martin et al. 2018; Fitch and Vaidya 2021; Campioni et al. 2022), creating a concern that roadside plantings may function as “ecological traps” (Hale and Swearer 2016). Because of the attraction of pollinators to high-sodium nectar (Finkelstein et al. 2022), the application of deicing salt could enhance the ecological trap effect of roadside habitat.

We found that soil salinity in the highway median was over twice what we saw in control sites, but this did not result in higher levels of sodium in the floral nectar of *A. syriaca* along roadsides. Experimental addition of brine into the root zone of *A. syriaca* was able to increase nectar sodium levels, at least in some individuals, and this salt treatment doubled the number of insect pollinators visiting umbels. However, the increase in soil salinity after brine addition was much higher than we observed in the soil along the highway. Our study therefore suggests that road deicing applications in this region of Virginia are unlikely to enhance any ecological trap effect of roadside plantings for pollinators.

The ability of deicing salt to enhance nectar salinity could vary geographically (Thompson et al. 1986a). Salinity along Canadian highways in the spring can reach 5.49 mg/g (Beaton and Dudley 2013), equivalent to 5490 ppm and well above even the highest soil salinity we produced with our brine applications (3060 ppm). Our experimental brine applications demonstrate that soil salinities in this range could increase nectar salinity and the attractiveness of plants to pollinators. Similarly, soil salinity can vary annually (Thompson et al. 1986a), depending on the severity and frequency of winter storms, resulting in large annual differences in the sodium uptake of roadside plants (Mitchell et al. 2020). Soil salinity also tends to be higher earlier in the growing season (Thompson et al. 1986a). Further exploration of the effects of roadside salt, especially at more northern latitudes or earlier in the growing season within the “salt belt” would be warranted.

Plants growing on soil experimentally enriched in salt (Kaspari et al. 2017) or growing along roadsides (Bryson and Barker 2002; Marosz 2011; Snell-Rood et al. 2014; Mitchell et al. 2020; Luckzak et al. 2021) have been shown to have increased foliar Na^+, but ours is the first study to show that elevated soil salinity can result in elevated nectar salinity. Our observation that salt addition to the soil doubled the number of pollinators visiting *A. syriaca* umbels was similar to the increase in pollinator visitations after the addition of sodium directly to floral nectar in five different species of wildflowers in Vermont (Finkelstein et al. 2022). Because salt additions had no effect on the sugar concentration of the nectar in our study, we infer that pollinators were attracted directly to the higher levels of sodium. Sodium limitation is common in terrestrial herbivores, including insects (Kaspari et al. 2017; Borer et al. 2019; Welti et al. 2019; Kaspari 2020), and our observations on pollinating insects, most of which have plant-based diets (e.g., the diets of most bees comprise only nectar and pollen), further underscores the importance of sodium in terrestrial food webs.

Bees accounted for 75% of all visits to *A. syriaca*, with honey bees (*A. mellifera*) the most common visitor. Honey bees showed a strong bias for visiting salt-treated plants. Sodium is known to be an essential nutrient for honey bees (Brodschneider and Crailsheim 2010), and foragers are known to collect saline water for the hive (Lau and Nieh 2016). Small bees were much less common, but they showed an even stronger response (4.6-fold increase) to the salt treatment. Most of these small bees were sweat bees

(Halictidae), which are well known for their attraction to sodium chloride (Roubik 1989). Bumble bees (*Bombus* spp.), on the other hand, were about as numerous as small bees but showed no preference for salt-treated plants. We could find no information in the literature on salt or sodium collection by this important group of pollinators.

In our salt addition experiment, the highest level of nectar sodium that we observed in control plants was 157.4 μeq Na^+/l. Although six of the nectar samples taken from salt-treated plants exceeded this level (190.9–1413.5 μeq Na^+/l), seven of the nectar samples fell below (55.3–101.7 μeq Na^+/l). The wide range of nectar sodium levels in the salt-treated plants suggests that our root-zone application of brine was not equally effective across plants. Weather undoubtedly played an important role in this variation. There was heavy rainfall prior to nectar collection from plot three, and the maximum nectar sodium level among the four samples from salt treated plants was only 101.7 μeq Na^+/l. Rainfall cannot account for all of the variation in response, however. The addition of brine caused a modest increase in soil moisture in the root zone. Greater water availability has been shown to increase nectar secretion (Zimmerman 1983; Carroll et al. 2001; Waser and Price 2016) but usually not sugar secretion on a per inflorescence basis (Mueller et al. 2020; Chabert et al. 2022; but see Petanidou et al. 1999). Salt uptake is a complex function of soil moisture, transpiration flux, and soil salinity (Shah et al. 2022), and the interplay of these three variables may have contributed to the variability in response of the nectar Na^+ that we observed.

In conclusion, our study demonstrates that elevated soil salinity is capable of increasing the Na^+ concentration in floral nectar, and this resulted in twice as many insect pollinators visiting salt-treated plants. Although our study did not find elevated nectar Na^+ concentrations in plants growing along the highway, soil salinity at our highway study site was much lower than levels seen in our manipulative experiment. Soil salinities comparable to our manipulations can be common in roadside habitats, however, especially in areas with more severe winter weather. Although we found no evidence that the "ecological trap" effect would be enhanced by saline nectar in our area, we cannot exclude the possibility that such an effect would operate in areas with greater road salt application or during years or seasons with higher soil salinity.

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Author contributions Both authors conceptualized and designed the study. Both authors conducted field, laboratory work, and statistical analyses. David H. Lovett wrote the first draft of the manuscript and commented on David E. Carr's revisions.

Data availability The datasets generated during the current study are available on Figshare, https://doi.org/10.6084/m9.figshare.20442780, https://doi.org/10.6084/m9.figshare.20442738.

Declarations

Competing interests All authors certify that they have no affiliations with or involvement in any organization or entity with any financial interest or non-financial interest in the subject matter or materials discussed in this manuscript.

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References

Baxter-Gilbert JH, Riley JL, Neufeld CJH, Litzgus JD, Lesbarrères D (2015) Road mortality potentially responsible for billions of pollinating insect deaths annually. J Insect Conserv 19:1029–1035. https://doi.org/10.1007/s10841-015-9808-z

Beaton LL, Dudley SA (2013) Tolerance of roadside and old field populations of common teasel (*Dipsacus fullonum* subsp. *sylvestris*) to salt and low osmotic potentials during germination. AoB PLANTS 5. https://doi.org/10.1093/aobpla/plt001

Borer ET, Lind EM, Firn J, Seabloom EW, Anderson TM, Bakker ES, Bierderman L, La Pierre KJ, MacDougall AS, Moore JL, Risch AC, Schultz M, Stevens CJ (2019) More salt, please: global patterns, responses and impacts of foliar sodium in grasslands. Ecol Lett 22:1136–1144. https://doi.org/10.1111.ele.13270

Brodschneider R, Crailsheim K (2010) Nutrition and health in honey bees. Apidologie 41:278–294. https://doi.org/10.1051/apido/2010012

Bryson GM, Barker AV (2002) Sodium accumulation in soils and plants along Massachusetts roadsides. Commun Soil Sci Plant Anal 33:67–68. https://doi.org/10.1081/CSS-120002378

Campioni L, Marengo I, Román J, D'Amico M (2022) Mud-puddling on roadsides: a potential ecological trap for butterflies. J Insect Conserv 26:131–134. https://doi.org/10.1007/s10841-021-00367-y

Cariveau AB, Anderson E, Baum KA, Hopwood J, Lonsdorf E, Nootenboom C, Tuerk K, Oberhauser K, Snell-Rood E (2019) Rapid assessment of roadsides as potential habitat for monarchs and other pollinators. Front Ecol Evol 7. https://doi.org/10.3389/fevo.2019.00386

Carroll AB, Pallardy SG, Galen C (2001) Drought stress, plant water status, and floral trait expression in fireweed, *Epilobium angustifolium* (Onagraceae). Am J Bot 88:438–446. https://doi.org/10.2307/2657108

Chabert S, Sénéchal C, Fougeroux A, Pousse J, Richard F, Nozières E, Geist O, Guillemard V, Leylavergne S, Malard C, Benoist A, Carré G, Caumes E, Cenier C, Treil A, Danflous S, Vaissière BE

(2022) Effect of environmental conditions and genotype on nectar secretion in sunflower (*Helianthus annuus* L). OCL 27. https://doi.org/10.1051/ocl/2020040

Daniels J, Kimmel C, McClung S, Epstein S, Bremer J, Rossetti K (2018) Better understanding the potential importance of Florida roadside breeding habitat for the monarch. Insects 9. https://doi.org/10.3390/insects9040137

Dicks LV, Breeze TD, Ngo HT, Senapathi D, An J, Aizen MA, Basu P, Buchori D, Galetto L, Garibaldi LA, Gemmill-Herren B, Howlett BG, Imperatriz-Fonesca VL, Johnson SD, Kovács-Hostyánzki A, Kwon YJ, Lattorff HMG, Lungharwo T, Seymour CL, Vanbergen AJ, Potts SG (2021) A global scale expert assessment of drivers and risks associated with pollinator decline. Ecol Evol 5:1453–1461. https://doi.org/10.1038/s41559-021-01534-9

Finkelstein CJ, CaraDonna PJ, Gruver A, Welti EA, Kaspari M, Sanders NJ (2022) Sodium-enriched floral nectar increases pollinator visitation rate and diversity. Biol Lett 18:1–4. https://doi.org/10.1098/rsbl.2022.0016

Fitch G, Vaida C (2021) Roads pose a significant barrier to bee movement, mediated by road size, traffic and bee identity. J Appl Ecol 58:1177–1186. https://doi.org/10.1111/1365-2664.13884

Forman R, Sperling D, Bissonette J, Clevenger A (2003) Road ecology: Science and solutions. University of Chicago Press, Chicago, IL

Hale R, Swearer SE (2016) Ecological traps: current evidence and future directions. Proc Roy Soc B-Biol Sci 28. https://doi.org/10.1098/rspb.2015.2647

Hanley ME, Wilkins JP (2015) On the verge? Preferential use of road-facing hedgerow margins by bumblebees in agro-ecosystems. J Insect Conserv 19:67–74. https://doi.org/10.1007/s10841-014-9744-3

Hanula JL, Ulyshen MD, Horn S (2016) Conserving pollinators in north american forests: a review. Nat Areas J 36:427–439. https://doi.org/10.3375/043.036.0409

Hiebert SM, Calder WA (1983) Sodium, potassium, and chloride in floral nectars: energy-free contributions to refractive index and salt balance. Ecology 64:399–402. https://doi.org/10.2307/1937086

Hopwood JL (2008) The contribution of roadside grassland restorations to native bee conservation. Biol Conserv 141:2632–2640. https://doi.org/10.1016/j.biocon.2008.07.026

Howard AF, Barrows EM (2014) Self-pollination rate and floral-display size in *Asclepias syriaca* (common milkweed) with regard to floral-visitor taxa. BMC Evol Biol 14 http://www.biomedcentral.com/1471-2148/14/144

Kaspari M (2020) The seventh macronutrient: how sodium shortfall ramifies through populations, food webs, and ecosystems. Ecol Lett 23:1153–1168. https://doi.org/10.1111/ele.1351

Kaspari M, Roeder KA, Benson B, Weiser MD, Sanders NJ (2017) Sodium co-limits and catalyzes macronutrients in a prairie food web. Ecology 98:315–320. https://doi.org/10.1002/ecy.1677

Kasten K, Stenoien C, Caldwell W, Oberhauser KS (2016) Can roadside habitat lead monarchs on a route to recovery? J Insect Conserv 20:1047–1057. https://doi.org/10.1007/s10841-016-9938-y

Kearns CA, Inouye DW (1993) Techniques for pollination biologists. University Press of Colorado, Niwot, CO

Keilsohn W, Narango DL, Tallamy DW (2018) Roadside habitat impacts insect traffic mortality. J Insect Conserv 22:183–188. https://doi.org/10.1007/s10841-018-0051-2

Lau PW, Nieh JC (2016) Salt preferences of honey bee water foragers. J Exp Biol 219:790–796. https://doi.org/10.1242/jeb.132019

Luckzak K, Czerniawska-Kusza I, Rosik-Dulewska C, Kusza G (2021) Effect of NaCl road salt on the ionic composition of soils and Aesculus hippocastanum L. foliage and leaf damage intensity. Sci Rep 11:5309. https://doi.org/10.1038/s41598-021-84541-x

Lynn JS, Fridley JD, Vandvik V (2022) More than what they eat: uncoupled biophysical constraints underlie geographic patterns of herbivory. https://doi.org/10.1111/ecog.06114. Ecography 2022

Marosz A (2011) Soil pH, electrical conductivity values and roadside leaf sodium concentration at three sites in central Poland. Dendrobiology 66:49–54

Martin AE, Graham SL, Henry M, Pervin E, Fahrig L (2018) Flying insect abundance declines with increasing road traffic. Insect Conserv Diver 11:608–613. https://doi.org/10.1111/icad.12300

Mitchell TS, Agnew L, Meyer R, Sikkink KL, Oberhauser KS, Borer ET, Snell-Rood EC (2020) Traffic influences nutritional quality of roadside plants for monarch caterpillars. Sci Total Environ 724. https://doi.org/10.1016/j.scitotenv.2020.138045

Mueller AL, Berger CA, Schittenhelm S, Stever-Schoo B, Dauber J (2020) Water availability affects sugar production and insect visitation of the cup plant *Silphium perfoliatum* L. (Asteraceae). J Agron Crop Sci 206:529–537. https://doi.org/10.1111/jac.12406

New TR, Sands DPA, Taylor GS (2021) Roles of roadside vegetation in insect conservation in Australia. Austral Entomol 60:128–137. https://doi.org/10.1111/aen.12511

Olofsson B, Lundmark A (2009) Monitoring the impact of de-icing salt on roadside soils with time-lapse resistivity measurements. Environ Geol 57:217–229. https://doi.org/10.1007/s00254-008-1302-4

Petanidou T, Goethals V, Smets E (1999) The effect of nutrient and water availability on nectar secretion and nectary structure of the dominant Labiatae species of phrygana. Syst Geogr Pl 68:233–244. https://doi.org/10.2307/3668604

Phillips BB, Gaston KJ, Bullock JM, Osborne JL (2019) Road verges support pollinators in agricultural landscapes but are diminished by heavy traffic and summer cutting. J Appl Ecol 56(10) 2316–2327. https://doi.org/10.1111/1365-2664.13470

Phillips BB, Wallace C, Roberts BR, Whitehouse AT, Gaston KJ, Bullock JM, Dicks LV, Osborne JL (2021) Enhancing road verges to aid pollinator conservation: a review. Biol Conserv 250. https://doi.org/10.1016/j.biocon.2020.108687

Roubik DW (1989) Ecology and natural history of tropical bees. Cambridge University Press, Cambridge, UK

Shah SHH, Wang J, Hao X, Thomas BW (2022) Modeling soil salinity effects on salt water uptake and crop growth using a modified denitrification-decomposition model: a phytoremediation approach. J Environ Manage 301. https://doi.org/10.1016/j.jenvman.2021.113820

Snell-Rood EC, Espeset A, Boser CJ, White WA, Smykalski R (2014) Anthropogenic changes in sodium affect neural and muscle development in butterflies. Proc Natl Acad Sci 111:10221–10226. https://doi.org/10.1073/pnas.1323607111

Szklarek S, Góreka A, Wojtal-Frankiewicz A (2022) The effects of roadsalt on freshwater ecosysterms and solutions for mitigating chloride pollution – a review. Sci Tot Environ 805:150289. https://doi.org/10.1016/j.scitotenv.2021.150289

Thompson JR, Rutter AJ, Ridout PS (1986a) The salinity of motorway soils I. Variation in time and between regions in the salinity of soils on central reserves. J Appl Ecol 23:251–267. https://www-jstor-org.proxy1.library.virginia.edu/stable/2403095

Thompson JR, Rutter AJ, Ridout PS (1986b) The salinity of motorway soils II. Distance from the carriageway and other sources of local variation in salinity. J Appl Ecol 23:269–280. https://www-jstor-org.proxy1.library.virginia.edu/stable/2403096

Tiwari A, Rachlin JW (2018) A review of road salt ecological impacts. Northeast Nat 25:123–142. https://doi.org/10.1656/045.025.0110

Twerd L, Sobieraj-Betlińksa A, Szefer P (2021) Roads, railways, and powerlines: are they crucial for bees in urban woodlands? Urban for Urban Green 61. https://doi.org/10.1016/j.ufug.2021.127120

USDA (1982) Soil survey of Clarke County Virginia. Soil Conservation Service

U.S. Department of Transportation (2020) Highway statistics 2020. Office of Highway Policy Information. https://www.fhwa.dot.gov/policyinformation/statistics/2020/vmt421c.cfm

Wasser NM, Price MV (2016) Drought, pollen and nectar availability, and pollination success. Ecology 97:1400–1409. https://doi.org/10.1890/15-1423.1

Welti EAR, Sanders NJ, de Beurs KM, Kaspari M (2019) A distributed experiment demonstrates widespread sodium limitation in grassland food webs. Ecology 100. https://doi.org/10.1002/ecy2600

Wyatt R, Broyles SB (1994) Ecology and evolution of reproduction in milkweeds. Annu Rev Ecol Syst 25:423–441. https://www.jstor.org/stable/2097319

Zielin SB, Littlejohn J, de Rivera CE, Smith WP, Jacobson SL (2016) Ecological investigations to select mitigation options to reduce vehicle-caused mortality of a threatened butterfly. J Insect Conserv 20:845–854. https://doi.org/10.1007/s10841-016-9916-4

Zimmerman M (1983) Plant reproduction and optimal foraging: experimental nectar manipulations in *Delphinium nelsonii*. Oikos 41:57–63. https://www.jstor.org/stable/i283091