

POLLINATION SUBSIDIES BETWEEN WETLAND AND DRY MEADOW HABITATS

SUSAN K. DUNKLEE

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**Advisor: Rebecca Irwin
Undergraduate Honors Thesis
Department of Biological Sciences
Dartmouth College, Hanover, New Hampshire**

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SUSAN K. DUNKLEE

Thesis Advisor: Rebecca Irwin

Dartmouth College

Hanover, New Hampshire

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Examining committee:

name, degree

name, degree

name, degree

ABSTRACT

Productive habitats can provide subsidies to neighboring habitats in the form of resources and services; however, little is known about whether subsidies operate in pollination systems. I studied wetland and dry meadow habitats in a subalpine system to assess whether wetlands provide neighboring pollinators with resource subsidies, or if wetlands facilitate the pollination of nearby dry meadows. I measured flower production and observed pollinator visitation in three types of meadows: wetlands, near dry meadows, and far dry meadows. Additionally, I assessed pollinator similarity between meadow types and tracked pollen flow using fluorescent dye. I found no significant differences in overall floral density or pollinator visitation between meadow types. Pollinator similarity was high for both wetlands compared to near dry meadows, 85.9%, and wetlands compared to far meadows, 82.6%. More dye movement was observed in dry meadows than in wetlands, and there was no evidence of inter-habitat pollen movement. Concerning the two major assumptions underlying the subsidy hypothesis, my results question the assumption that wetlands provide higher floral rewards than dry meadows and confirm the assumption that wetlands and dry meadows share pollinators. I found no evidence supporting the potential for a wetland-dry meadow subsidy in this system. Given the fundamental importance of pollination services in natural systems, this study provides needed research on the pollination biology of wetland and dry meadow species in subalpine ecosystems.

INTRODUCTION

Natural systems often contribute energy, resources, and services to neighboring systems as subsidies. Subsidies can either be material, such as a surplus of resources spilling over into a neighboring system (e.g., Polis and Hurd 1996), or functional, such as one organism providing a service to neighboring systems (e.g., Polis et al. 1997). Some of the best-known examples of subsidies come from aquatic systems and from aquatic-terrestrial system linkages (e.g., Nakano and Murakami 2001, Baxter et al. 2005). For example, salmon that migrate upstream to spawn provide material subsidies in the form of food and nutrients to both the aquatic system and riparian zones (Wipfli et al. 2003), and migratory fishes in tropical ecosystems can provide functional subsidies via their activities and behaviors in head-water streams, which can affect in-stream nutrient cycling (Taylor et al. 2006). Subsidies across terrestrial habitats may also be common, although they are less-well studied. For example, wild bees, birds, flies, as well as other invertebrates and mammals from surrounding habitats can contribute to the pollination of agricultural crops (Kremen et al. 2007). Pollinators provide flowers with a service by transferring pollen, and they can impact the level of gene flow via pollen transfer among plant populations (Govindaraju 1988). Up to 90% of angiosperm species rely on pollinator services for pollen transfer and successful seed production (Buchmann and Nabhan 1996); however, little is known about subsidies operating in non-agricultural pollination systems.

One neighboring habitat could provide pollination subsidies to another in at least two ways. First, from the pollinator's perspective, pollen and nectar from flowers in a productive system could provide pollinators from an outside system with a resource

subsidy. For example, bees require habitat that contains both suitable floral resources and suitable nesting sites (Cane 2001). Solitary bees have foraging ranges from 150 m to 600 m, depending on their size (Gathmann and Tschardtke 2002). Within that range, a variety of habitat types may occur, such as forests, meadows, and wetlands. If one area, such as a wetland, contains particularly nectar and pollen-rich floral patches, it may subsidize food resources to bees (which often nest in dry meadows) and support higher bee densities within neighboring habitat compared to if wetlands were not nearby.

Second, from the plant's perspective, if floral rewards are more abundant in wetlands and support larger populations of pollinators, plants in dry meadows may benefit via facilitation of pollination (Waser and Real 1979), assuming that dry-meadow species are pollen-limited for seed set (Ashman et al. 2004) and pollinators often switch between wetland and dry meadow habitat. For example, following the discovery of a favorable nectar reward, a pollinator is likely to pollinate another nearby flower of the same species, regardless of the second flower's nectar reward. Successful wetland visits may be followed by visits to nearby dry meadow flowers, even if the dry meadow flowers have less nectar and pollen. This could occur in situations with constant pollinators, which do not switch flower species very often (Chittka et al. 1999). Nearby meadows could also benefit from wetlands in the case of non-constant pollinators. If a pollinator runs out of its preferred flower species, the cost of searching may outweigh the cost of sampling other nearby species, so even if flower species vary between wetlands and dry meadows, nearby meadows may benefit from wetland pollinators if they spill over to dry meadow species when their preferred food items become unrewarding (Chittka et al. 1999).

The goal of this study was to determine if wetland habitats subsidized pollinators and pollination services to dry meadow habitats. In the Rocky Mountains of Colorado, many flowers grow in dry meadow habitat, a number of which experience pollen-limitation of seed set (e.g., Campbell and Halama 1993, Zimmerman and Pyke 1988,). Dry conditions, which are typical of these subalpine meadows, can reduce both the number of flowers and per-flower rewards produced (e.g., Zimmerman 1983, Zimmerman and Pyke 1988, Carroll et al. 2001). Wetlands and dry meadows also share some species of flowers, such as *Castilleja sulphurea* and *Vicia americana* (S. Dunklee, personal observation), and may share pollinators as well. I predicted that wetland systems would support more pollinators than dry meadow habitat on a per-flower basis. In addition, I predicted that wetlands would facilitate the pollination of neighboring dry meadows, assuming that water availability limits flower and floral reward production (Zimmerman 1983, Zimmerman and Pyke 1988, Carroll et al. 2001) and that pollinators frequently switch between habitat types. Alternatively, wetland systems may not subsidize pollination in dry meadow habitat if, for example, pollinators avoid dry habitat flowers due to poor nectar or pollen rewards (Thomson 1988), if wetland and dry meadow habitat don't share the same pollinator species, plants in different habitats compete for pollinators (Thomson 1980), or if predators of pollinators (such as dragonflies), which are common in wetlands, consume pollinators (Knight et al. 2005).

Previous studies have investigated pollination subsidies using a variety of approaches. Pollinator spillover, or the diffusion outwards of pollinators from one foraging grounds into another, has often been cited in agriculture settings based on observations of non-native honey bees pollinating wild plants and observations of wild

pollinators visiting crops (e.g. Gross 2001, Ricketts 2004). However, the introduction of honey bees can displace native pollinators (Thomson 2004), and the net subsidy of pollen flow between habitat types isn't well understood. Other studies have found notable overlap in the geographic range of upland pollinators and their favored wetland flower species, suggesting a link between habitat types (Thorp and Leong 1998). Kremen et al. (2004) found a positive correlation between pollen deposition in watermelon fields and proportion of riparian land within a 1200 m radius of their field sites. This suggests that wetlands may facilitate higher levels of pollination in neighboring agricultural fields, although further studies are needed to verify this and identify the underlying mechanisms. My study differed from these approaches by examining the interface of two habitats to investigate the mechanisms underlying subsidies. Like Ricketts et al. (2004), who studied pollinator visitation in tropical coffee plants in relation to distance from forest fragments and from narrow riparian forest strips, I investigated wetland subsidies by creating a transect radiating from a wetland, and observing pollination patterns along the distance gradient ranging from wetland through neighboring dry meadow into far dry meadow habitat. However, this study looks at different system than Ricketts et al. (2004), a wild wetland system vs. an agricultural system, respectively, and a smaller spatial scale, and evaluates the necessary prerequisites for a subsidy to potentially occur.

To address the hypothesis that wetland habitats subsidized pollinators and pollination services to dry meadow habitats, I addressed the following questions, many of which are assumptions that are necessary to support the overarching hypothesis. To determine the floral reward structure of wetland and dry meadow habitat types, I asked:

- (1) Do wetlands and dry meadows differ on average or at any point during the flowering

season in plant and flower density? To understand pollinator visitation rate as a function of habitat type, I asked: (2) Do pollinator visitation rates per site, per plant, or per flower differ in wetland and dry meadow habitats? (3) Do wetlands and dry meadows share pollinators? And (4) Does pollen movement between habitat types have directionality and do different distances from the wetland experience different levels of pollen movement?

Wetlands provide a vast array of ecosystem services, such as flood control, nutrient retention, and natural filtration, as well as support high biodiversity and provide a fresh water supply (Postel and Carpenter 1997), but little is known about pollination services that wetlands may provide. Since the 1780's, many States have lost over 50% of their wetlands, including the State of Colorado (Dahl 1990). Exploring the potential for pollination subsidies that some wetlands may provide to neighboring pollinators and flowers may inform wetland conservation initiatives.

METHODS

Study system

This study was conducted in the East River Valley in the Elk Mountains of Colorado near the Rocky Mountain Biological Laboratory (Gothic, Gunnison County, Colorado, USA, elev: 2900 m). In the East River Valley, a series of wetlands surround the main river, interdigitated with dry meadow habitat. A variety of nectar-rich plant species grow in wetland and dry meadow systems and have a diversity of pollinators (Table 1). Wetlands also contain pollen rich species, such as *Pedicularis groenlandica* (Scrophulariaceae), that don't produce any nectar (Macior 1968). Many common species, such as *Chamerion angustifolium* (Onagraceae), *Erigeron speciosus* (Asteraceae), and

Helianthella quinquenervis (Asteraceae), experience water limitation of flower production (e.g. Carroll et al. 2001, de Valpine and Harte 2001), and some, including *Delphinium nuttallianum* (Ranunculaceae) and *C. angustifolium*, experience water limitation of nectar production (e.g. Zimmerman 1983, Carroll et al. 2001). Several species, such as *Ipomopsis aggregata* (Polemoniaceae) and *Castilleja linariaefolia* (Scrophulariaceae), experience pollen limitation of seed production (e.g., Hainsworth et al. 1985, Zimmerman and Pyke 1988, Juenger and Bergelson 1997, Cariveau et al. 2004).

Study sites

Three sites, the Avery beaver pond area on the 401 trail (elev: 3000 m), the beaver pond under Gothic Mountain (elev: 2900 m), and Rustler's Gulch stream (elev: 3100 m), were used to determine if wetlands subsidize pollination in dry meadows. Each site had three 10 x 30 m plots at varying distances from a wetland: a plot in the wetland, a close dry plot centered 15 m away, and a far dry plot centered 25 m away (Figure 1). The plots are hereafter referred to as distance plots, but distance is used in a categorical sense rather than a numerical sense. As far as it was possible, the distance plots were set up in non-obstructed transects (i.e., without significant willow habitat) extending from a stream or a pond and approximately 10 m apart to maximize the opportunity for pollinator sharing. Each site was separated from all other sites by at least 2 km. The wetland at the Avery site consisted of the shoreline along a beaver pond, the wetland at the site under Gothic Mountain surrounded a small stream that drained from a beaver pond into the East River, and the Rustler's Gulch wetland consisted of a riparian zone along the Rustler's Gulch stream. The Avery and Rustler's Gulch sites contained slightly sloping dry

meadows that spread straight out from the wetlands. The Gothic site contained patches of steep dry meadows spreading out from the wetland.

Field methods

To ensure that the distance plots in each site were correctly characterized as wetland or dry meadow, I collected soil samples twice during the summer in all plots to measure soil moisture. Five 10 cm soil cores, collected from each corner and the middle of each distance plot, were combined, weighed wet, and reweighed dry after at least 48 hours at 60° C. I used these data to calculate water percentage by weight. To test whether the wetland and dry meadow plots differed in soil moisture, I compared overall distance plot means using a one-way ANOVA with distance (wetland, near dry, and far dry) as a fixed effect and Tukey's honestly significant difference (HSD) test. Site was removed from the model because it was not statistically significant ($F_{2,2} = 2.06$, $P = 0.17$)

Plant and flower density

Floral reward structure was characterized at each distance using floral abundance. Ideally, I would have also measured nectar and pollen volume and quality to estimate floral rewards at different distances. However, measuring nectar and pollen quantity in the field is inherently difficult due to the small quantities of reward produced relative to measurement error (Kearns and Inouye 1993), and nectar and pollen values are not available in the literature for most species. Because Tepedino and Stanton (1982) argue that floral abundance is often positively correlated with floral rewards, I compared floral abundances at difference distances as an indicator of relative floral rewards. Flowering

plant densities were measured at each distance once per week starting a few weeks into the flowering season and continuing for eight weeks, using 15 different randomly chosen 0.56 m² square quadrats for each sampling. Flower densities were estimated by counting flowers on up to 10 plants per species. To assess the relationship between distance from wetland and plant and flower density, I used separate nested, repeated measures (rm) ANOVAs with distance (wetland, near dry site, and far dry) as a fixed effect, site[distance] as a random effect, and week as the repeated term. Distance was tested over the nested term, and all other factors were tested over the error term. Site was used as a random effect to test the null hypothesis that distance has an effect in each site, but averaged over the whole population of wetland-dry meadow systems from which my three sites were sampled, it has no effect (Newman et al. 1997). I did not include interactions with week in the models because none were statistically significant (here and below). Densities were normalized using a square-root transformation. I then broke the analyses down by flower morphology (asters, complex, open, small, and umbel) and main pollinator type (bumble bees and flies/solitary bees) to assess whether there were trends for particular functional groups. Flower morphology affects what type of pollinators can visit, or choose to visit, a flower (Harder 1985) and pollinator type is important because bumble bees respond differently to habitat scale than solitary bees and flies (Thomson 1981). I defined asters as flowers in the Asteraceae family, complex flowers as flowers with non-simple structure (e.g., tubular or nectar spurs), open flowers as non-asters and non-small flowers that contained exposed anthers and stigma, small flowers as flowers no greater than 1 cm in diameter, and umbels as umbel and corymb shaped flowers. I also

looked at patterns in floral density in different weeks (in particular, weeks in which all nine distance plots were sampled) during the flowering season using one-way ANOVAs.

Pollinator visitation

Pollinator visitation rates within and among distance plots were used to estimate pollination levels. Pollinator observations were conducted at each distance plot for up to 90 minutes once per week. The time of day for observations was varied from week to week to control for temperature and time-of-day bias. Not all visitors to flowers are effective pollinators (Inouye 1980); therefore, I used a method similar to Momose et al. (1998) and only recorded visitors that came into contact with floral sexual organs. When possible, pollinators in the distance plots were identified on the wing and followed from one plant and flower visit to the next until they left the plot. I recorded their time spent on each plant and flower, as well as their total time in the plot. Pollinators that could not be identified on the wing were collected for identification in the lab.

Visitation rate was calculated as number of pollinator visits observed per distance plot per minute. In calculating visitation rate, I excluded the time spent following visitors from the total observation time. Pollinator visitation rate was also standardized by flower density and flowering plant density to assess whether wetlands supported more pollinators on a per resource basis. To compare visitation rates by pollinators at difference distances, I used nested, rm-ANOVAs, as described above, with visitation rate, visitation rate per plant, and visitation rate per flower as response variables. Visitation rates were normalized using a square-root transformation. ANOVAs were also performed separately on bee (and other members of the order Hymenoptera) and fly

(order: Diptera) visitation to assess whether visitation varied by pollinator types. Flies and bees have been shown to have different pollination efficiencies and different visitation rates (Herrera 1987).

Pollinator identity was used to determine the degree of pollinator sharing between distance plots. Bees were identified to genera using Michener et al. (1994). Flies were identified to the family. Only the bee data were used for calculating the similarity between distance plots due to more complete identification of the bee collection, and in general, bees have been shown to be more effective pollinators than flies (Herrera 1987). Similarity between wetland and near dry distance plots as well as wetland and far dry distance plots was assessed using Morisita's Percent Similarity Index (Krebs 1989). Square root-transformed percent similarities were compared using a two-sided, two-sample t-test.

Pollen flow

Pollen movement in the wet and nearby dry distances plots was examined twice during the summer, once at the Avery site and once at the Gothic site, using powdered fluorescent dye particles (Radiant Dye Corp., Richmond, CA) that act as pollen analogues (Waser and Price 1982). The dye was applied to the dehiscing anthers of flowers during the morning using a toothpick and a haphazard sampling of non-dyed flowers were inspected at dusk for pollen receipt using an ultraviolet flashlight (Kearns and Inouye 1993). A different dye color was used in each distance plot to assess the magnitude and directionality of pollen transfer within and among distances. To standardize dyeing effort, one hour was spent haphazardly dyeing flowers within each

distance plot. The number and species of flowers dyed and inspected for dye were recorded. The ratio of percentage dye on inspected flowers to percentage of flowers dyed was used to estimate pollen movement within and among the distance plots.

RESULTS

Soil Moisture

Soil moisture varied among distances, with wetlands having almost three times higher soil moisture by mass than the near and far dry meadow plots ($F_{2,2} = 14.93$, $P = 0.0004$; Fig 2). The wetlands had significantly higher soil moisture than the dry meadows (Tukey's HSD, $P < 0.002$ for each wet-dry distance plot comparison) and the two types of dry meadow plots, near and far, had similar moisture levels (Tukey's HSD, $P = 0.95$).

Plant and floral densities

(1) Do wetlands and dry meadows differ on average or at any point during the flowering season in plant and flower density? I found no difference in overall flower density with respect to distance ($F_{2,6} = 0.52$, $P = 0.62$; Fig. 3) or in flowering plant density with respect to distance ($F_{2,6} = 2.40$, $P = 0.17$; Fig. 4). Average flower density in the transect was 33.1 ± 3.4 flowers per m^2 (mean $\pm$ 1 standard error) and average flowering plant density was 9.8 ± 2.2 plants per m^2 . However, flower and plant density varied significantly throughout the flowering season, with peak flower and plant density early-summer (flower density, $F_{7,46} = 6.42$, $P = 0.0001$, Fig 5.; plant density $F_{7,46} = 4.63$, $P = 0.0005$). In addition, I found significant differences in flower and plant density among

the sites (flower density, $F_{6,46} = 3.98$, $P = 0.0027$; plant density, $F_{6,46} = 4.58$, $P = 0.0001$). The Rustlers site had about 30% more flowers than either of the other sites, and slightly more flowering plants.

When floral density was broken down by flower morphological group, I found significant differences with respect to distance only for plants in the Asteraceae (Table 2). Asters had their lowest densities in wetlands (Fig. 6). Site effects were significant in all groups except for the umbels. Rustlers contained 75% more Asteraceae flowers and slightly more open and small flowers than the other sites, while Avery had a slightly higher number of complex flowers. Week effects were significant in all groups except for small flowers. Asteraceae flower density peaked late summer, while other groups had early summer peaks (Fig. 7).

When floral density was broken down into primary pollinator groups, there were no distance effects (Table 3). Bumble bees and flies/solitary bees visited all distances equally. However, I did find significant site effects for both bumblebee and fly/solitary bee groups, and a significant week effect for the flies and solitary bees group. Fly/solitary bee-pollinated flowers had flowering peaks early in the summer, while bumble bee-pollinated flowers peaked mid-season (Fig. 8).

I also tested whether flower density varied among wetland and dry meadow habitats at any point during the season. However, I found no significant differences with respect to distance for any of the weeks I tested (Table 4; Fig. 9).

Pollinator visitation rates

(2) *Do pollinator visitation rates per site, per plant, or per flower differ in wetland and dry meadow habitats?* I found no difference in pollinator visitation rates with respect to distance ($F_{2,6} = 0.32$, $P = 0.74$), visitation rate standardized by flower density ($F_{2,6} = 0.13$, $P = 0.88$, Fig. 10), or visitation rate standardized by plant density ($F_{2,6} = 0.73$, $P = 0.52$). Average visitation rate was 1.15 ± 0.06 visits per minute (mean $\pm$ 1 standard error), average visitation rate standardized by flower density was 0.055 ± 0.004 visits per minute per flower per m^2 , and average visitation rate standardized by flowering plant was 0.20 ± 0.03 visits per minute per plant per m^2 . As with density, I found significant effects of week (visitation rate, $F_{7,47} = 4.34$, $P = 0.0009$; visitation rate per flower, $F_{7,47} = 2.58$, $P = 0.0244$; visitation rate per plant, $F_{7,47} = 3.75$, $P = 0.0026$) and of site (visitation rate, $F_{6,47} = 2.68$, $P = 0.0254$; visitation rate per flower, $F_{6,47} = 2.33$, $P = 0.047$; visitation rate per plant, $F_{6,47} = 3.24$, $P = 0.0096$). Visitation rate was highest in late summer, peaking at 1.69 pollinators per minute during week 6, visitation rate standardized by flower density peaked in week 7 with 0.086 visits per minute per flower per m^2 , and average visitation rate standardized by flowering plant peaked in week 7 with 0.306 visits per minute per plant per m^2 . Averaged across the summer, the Rustlers site had about 50% more visitors than either of the other sites, although standardized by flower and plant density, Avery had slightly higher rates than the other sites. Analysis of hymenoptera and diptera visitation also showed no significant distance affects, but significant site and week affects (Table 5). Hymenoptera averaged 0.18 ± 0.01 visits per minute and Diptera averaged 0.85 ± 0.06 visits per minute. Standardizing by flower or plant density also yielded non-significant results (data not shown).

(3) *Do wetlands and dry meadows share pollinators?* Wetlands have very similar, although not identical, bee pollinators as surrounding dry meadows. The wetland-near meadow similarity, $78.8\% \pm 3.0\%$ (mean $\pm$ 1 SE), was slightly higher than the wetland-far meadow similarity, $71.5\% \pm 9.7\%$, although the difference was not statistically significant ($t_2 = 0.60$, $P = 0.61$).

(4) *Does pollen movement between habitat types have directionality and do different distances experience different levels of pollen movement?* In the pollen (dye) flow experiment, I calculated a movement ratio (percentage of inspected flowers containing dye / percentage flowers dyed) to measure pollen movement. A higher movement ratio indicates higher pollen movement, and ratios above one indicate that dye from one flower is transferred on average to more than one other flower. The dye movement ratios in the dry meadows were higher (12.0 at Gothic and 19.7 at Avery) than the wetlands (9.3 at Gothic and 4.3 at Avery). Most of the dye movement took place within distance plots; I only found one instance of dye transfer between distance plots.

DISCUSSION

Subsidies are common across natural habitats (Polis et al. 1997). I investigated the hypothesis that wetlands subsidize pollination to dry meadows. However, I found little support for this hypothesis. I found no difference in plant or flower density between wetlands and dry meadows. Despite finding evidence for pollinator sharing between habitat types, I found no significant pollinator spillover into dry meadows. Moreover, I found no difference in pollinator visitation rate between distance plots, and little pollen transfer among distance plots (and higher pollen transfer within plots).

I had expected to see pollinators traplining to high resources in the wetland (Ackerman et al. 1982) and diffusing outward to pollinate nearby flowers in dry meadows, resulting in a spillover of pollen and pollinators from the wetlands to the near dry meadows. I had initially predicted that wetlands would provide higher floral rewards, indicated by higher floral abundance, and that those rewards would support higher pollinator abundance, especially if pollinators are food-limited. If such a subsidy were present, I should have found higher visitation rates and more pollen movement within the wetlands. A spillover of pollination services from the wetland to the dry meadow would have resulted in better pollination in the near dry meadow than the far dry meadow, if pollinators are shared between habitat types. Near dry meadow flowers would have more pollen transfer due to higher numbers of visitors or more pollen deposited per visitor. In the case of a subsidy, I would have expected to see higher visitation rates in the near dry meadows than in the far dry meadows.

Although my study found little evidence of pollination subsidies in subalpine wetlands, other studies have found evidence supporting subsidies in multi-habitat systems. Many recent studies have examined pollinator spillover from agricultural systems to nearby wild habitat (e.g., Kremen et al. 2007, Rand et al. 2006), in which high crop pollinator abundances spillover into neighboring wild habitat. Additionally, feral pollinators can subsidize cropland. For example, forest fragments in Costa Rica increase pollination service to nearby coffee plants (Ricketts 2004). Evidence of inter-habitat pollination subsidies has also been found in wetland systems. For example, vernal pools containing showy floral displays and upland habitats where pollinators nest are linked through pollination (Thorp and Leong 1998). Kremen et al. (2004) found that mean

pollen deposition per flower by native bees had a significant, positive correlation to the proportion of riparian habitat in an area. However, not all wetland pollination studies support the existence of wetland subsidies, and the relationship between floral density and pollinator abundance is not always predictable (e.g., Totland 1994, Schmitt 1983). For example, pollinator visitation rates to coffee plants in Costa Rica did not increase with the presence of neighboring riparian forest strips, despite high numbers of flowering tree species in the forest (Ricketts 2004). Even though evidence for pollination subsidies has been highlighted in other systems, pollination subsidies may not be operating between wetland and dry meadow habitats in the system I studied. Unlike the vernal pool systems, I found little evidence that floral displays were showier in wetlands.

In particular, floral density and flowering plant density did not differ significantly with respect to distance. I assumed that because many plants in the East River Valley are water limited for floral and nectar production (e.g., Carroll et al. 2001, de Valpine and Harte 2001, Zimmerman 1983), wetlands would have higher floral reward levels than nearby dry meadows. However, I did not find significant differences between flower or flowering plant numbers in the different types of habitat, with the exception of flowers in the Asteraceae family, which were found at *lower* density in wetlands than in dry meadows. Asters have been found to photosynthetically compete well under water stress (Peterson and Bazzaz 1978), which may explain this pattern. The Asteraceae floral density curve differed in shape from other flower morphologies. Waser and Real (1979) suggest that such sequential flowering peaks allow habitats to maintain higher levels of pollinators by providing a food source throughout the summer. I found no evidence of significant differences with respect to distance of floral densities at different weeks

throughout the summer and no sequential flowering peaks between distance plots.

However, my study missed the first weeks of the flowering season, so I cannot rule out if any interesting patterns occurred then. The importance of sequential flowering between dry meadows and wetlands in this system remains to be tested. In some agricultural systems, wetlands predominately support pollinator populations during early spring, while farm fields tend to support pollinators more in the late summer (Kremen et al. 2002).

In this study, I only measured flower and plant density and did not estimate per flower nectar and pollen production. Although the wetlands did not have a notably different number of flowers or flowering plants, different species compositions in the two habitats could also indicate differential nectar production rates (Raine and Chittka 2007). Although I didn't compute statistics on floral species diversity, based on observations, I expect there was a notable difference in floral species structure between wetland and the two dry meadow plots (S. Dunklee, personal observation.) Wetlands contain many nectar and pollen rich species (Table1). Factors besides water could be governing floral and nectar quantity. Higher amounts of shade in wetlands could affect herbivory levels (Louda and Rodman 1996) and flower production (Jiang and Egli 1993), nutrient levels could be influencing percent flower cover (John and Turkington 1995) and flowering heads (Campbell and Halama 1993), and dry meadow flowers may have adapted to produce floral rewards more efficiently (Galen 1999). Floral reward quality, such as nectar concentration (Irwin et al. 2004), and pollinator preference (Chittka et al. 1999) are also important in characterizing floral reward structure. Our use of floral density to

characterize floral reward structure did not take into account overall nectar production rates, nectar concentration, or pollinator preference.

I found no significant differences in pollinator visitation rates, visitation rates per flower, or visitation rates per plant with respect to distance. I had originally hypothesized that if many wetland pollinators live in neighboring habitats but come to wetlands to feed, the wetlands could be providing them with a resource subsidy. Many of the solitary bees found pollinating wetlands nest in dry meadows, either in the ground or in dry wood vegetation (O'Toole and Raw 1991). As long as pollinators didn't avoid the wetland habitat due to willow tree obstruction (Rathcke and Jules 1993) or become eaten by predators (Knight et al. 2005), the wetland could support a higher pollinator population. However, because I did not find higher floral resources in wetlands or higher visitation rates to wetlands, these results suggest that wetlands do not subsidize rewards for pollinators in dry meadows. I found no evidence for a resource subsidy from the pollinator's perspective, although completely removing the wetland resources would provide a stronger additional test of this result. From the plant's perspective, if a pollination subsidy was operating, I would predict that the near dry meadow site would have a higher visitation rate than the far dry meadow site. However, I found no significant differences in pollination rate per resource across distance. It is likely that pollinators acted as optimal foragers (Zimmerman 1983).

I found evidence of pollinator sharing between distance plots but no indication of inter-plot pollen movement. The results of my bee similarity test suggest high pollinator similarity (and maybe sharing) between distance plots, and therefore support a key assumption which underlies my subsidy hypothesis. However, since the wet-near

meadow similarity was not significantly larger than the wet-far meadow similarity, I found no evidence of a spillover effect from the wetlands. The strong pollinator similarity in spite of the notable differences in floral species structure between habitats suggests that the bee pollinators may be generalists that often switch between flower species (Chittka et al. 1999). Moreover, I didn't detect pollen dye movement between distance plots, either because the distance between the plots was too far or there simply wasn't inter-plot movement. Intra-plot pollen transfer indicated a higher pollen movement ratio in the near meadows than in the wetlands. This suggests that pollinators as a group are more effective at moving pollen in the dry meadows than in the wetlands, given that visitation rate didn't vary with respect to distance. Perhaps pollinators in the dry meadows visit more flowers on average, or spend more time on each flower, than pollinators in the wetlands. High pollinator similarity and no indication of pollen movement between sites suggest that pollinator populations visit both habitat types, but individual pollinators do not switch habitat types during a foraging bout. An experimental study of pollinator movement with comparable floral densities to this study found that pollinators averaged fewer than 30 cm between floral visits, and often switched direction, resulting in flower revisitation (Carter and Real 1997). Under these conditions, it would take many visits for a pollinator to travel the 10 m between my distance plots, and the chance of any dye being transferred that far may be slim.

For flowers and plants, results from this study indicated greater differences among sites than within sites, despite a significant percent soil moisture difference between distance plots. These results suggest that something besides water governs floral density and pollinator levels. Perhaps site-specific environmental factors, such as temperature

(Martinez del Rio and Burquez 1986, Totland 1994), soil nutrients (Burkle 2008), pollinator habitat availability (Schiller et al. 2000), predator presence (Knight et al. 2005) or habitat patchiness (Debinski and Holt 2000), are more important than soil moisture at the plant-pollinator levels. The East River Valley experiences inter-annual and intra-annual variation in climatic and pollinator composition. For example, Burkle (2008) observed fewer bees in the East River Valley in 2007 compared with 2005 and 2006, and suggests that factors such as climate, predation, or nest site availability may play an important role in pollinator abundance and species structure. Additionally, rainfall varies greatly from year to year and over the course of the summer (S. Dunklee, personal observation), which creates variation in floral abundance and floral rewards. The degree to which inter-annual, inter-site, and intra-site variation in floral resources drives plant-pollinator interactions warrants further study (Waser and Ollerton 2006).

Two caveats are important in the interpretation of this study. First, I only had three replicates of each distance transect. It was not possible to gain detailed information on floral density, pollinator visitation, and pollen flow within distance plots within a large number of replicates. Thus, on the one hand, one could argue that I simply did not have enough power to detect a significant effect of distance on pollination subsidy. However, that is unlikely the case. Power analyses suggested that in some cases, I would have needed at least 750 replicates to find a statistically significant effect of distance on flower densities and visitation rates at $\alpha = 0.05$, suggesting that my results may indeed indicate a lack of an effect rather than simply low statistical power. Nonetheless, the best test of this hypothesis would involve a manipulative study that removed all floral resources from wetlands and assessed subsequent pollinator visitation and pollen movement in dry

meadow habitats. Second, future studies need to consider the scale of study sites and distance plots in order to better isolate pollinator abundances at each distance. For example, given that solitary bees have a foraging range of 150 m to 600 m (Gathmann and Tscharntke 2002), bee abundances may not change much among distance plots separated by only 10 m. Thomson (1981) found that bumble bees respond to habitat patches that are about 1000 m², while flies and solitary bees respond to habitats patches of 500 m². For less mobile pollinators, the special scale may be much smaller. The distance plot sizes in this study were about 300 m², so they may not have been large enough to optimally detect foraging decisions.

Although I detected no evidence of pollination subsidies operating in this study, pollination subsidies may affect ecosystem dynamics in other types of habitat edges (Kremen et al. 2007, Rand et al. 2006). Habitat fragmentation is common as human impacts on natural systems increase (Ashworth et al. 2004), and edge effects are having inconsistent impacts on different ecosystems (Debinski and Holt 2000). Increased fragmentation and land use intensification has been shown to alter pollinator abundance and richness (Brosi et al. 2008, Steffan-Dewenter and Westphal 2008). The framework in this study could be expanded to investigate pollination subsidies in habitat edge systems other than subalpine wetlands and meadows.

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Table 1. Nectar- and pollen-rich flower species in the East River Valley, Colorado and their primary habitat and pollinators. Common pollinators determined by this study (S. Dunklee, personal observation) and by Pyke (1982).

Flower (Genus and species)	Family	Common Habitat	Common Pollinators
<i>Cardamine cordifolia</i>	Brassicaceae	Wetland	Flies, butterfiles, solitary bees
<i>Ipomopsis aggregata</i>	Polemoniaceae	Dry meadow	Hummingbirds
<i>Aconitum columbianum</i>	Ranunculaceae	Wetland	Bombus, flies
<i>Delphinium barbeyi</i>	Ranunculaceae	Wetland and dry meadow	Bombus, flies
<i>Potentilla pulcherrima</i>	Rosaceae	Dry meadow	Flies, solitary bees
<i>Castilleja linariaefolia</i>	Scrophulariaceae	Wetland and dry meadow	Bombus, hummingbirds
<i>Castilleja sulphurea</i>	Scrophulariaceae	Wetland and dry meadow	Bombus, hummingbirds
<i>Pedicularis groenlandica</i>	Scrophulariaceae	Wetland	Bombus, flies

Table 2. Nested rm-ANOVAs for the effects of distance, site, and week on flower density broken down by different flower morphological groups. See methods section for a description of morphology classification.

Flower Morphology	df	F	P
Aster			
Distance	2,6	7.06	0.027
Site(distance)	6,46	2.49	0.036
Week	7,46	7.12	<0.001
Complex			
Distance	2,6	1.16	0.38
Site(distance)	6,38	9.31	<0.001
Week	7,38	7.06	<0.001
Open			
Distance	2,6	0.13	0.88
Site(distance)	6,46	6.63	<0.001
Week	7,46	20.54	<0.001
Small			
Distance	2,6	0.88	0.46
Site(distance)	6,42	6.66	<0.001
Week	7,42	1.87	0.099
Umbel			
Distance	2,6	3.51	0.088
Site(distance)	6,33	2.23	0.064
Week	7,33	3.78	0.004

Table 3. Nested rm-ANOVA results for the effects of distance, site and week on flower density classified by primary pollinator.

Type of Primary Pollinator	df	F	P
Bumble bee			
Distance	2,6	0.95	0.44
Site(distance)	6,45	2.44	0.040
Week	7,45	1.09	0.38
Fly/solitary bee			
Distance	2,6	1.06	0.40
Site(distance)	6,47	7.31	< 0.001
Week	7,47	7.43	< 0.001

Table 4. One-way ANOVA for the effects of distance on flower density at particular weeks during the study.

Week	df	F	P
2	2,6	0.61	0.58
3	2,6	0.55	0.6
4	2,6	0.2	0.83
8	2,6	1.37	0.32

Table 5. Nested rm-ANOVAs for the effects of distance, site, and week on pollinator visitation rates broken down by pollinator type

Pollinator Type	df	F	P
Hymenoptera			
Distance	2,6	0.22	0.81
Site(distance)	6,42	4.29	<0.002
Week	7,42	6.55	<0.001
Diptera			
Distance	2,6	0.33	0.73
Site(distance)	6,47	2.45	0.04
Week	7,47	9.01	<0.001

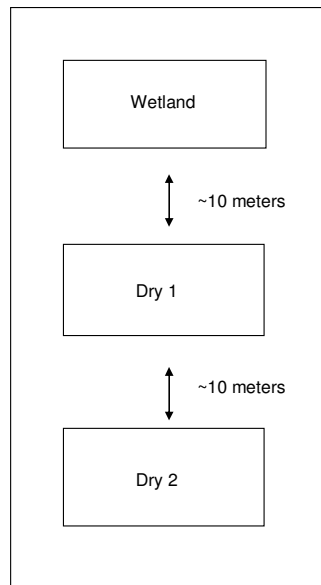


Figure 1. Sites consisted of three, 10 x 30 m distance plots centered at 0 m, 15 m, and 25 m from a wetland. Each site was separated by all other sites by at least 2 km.

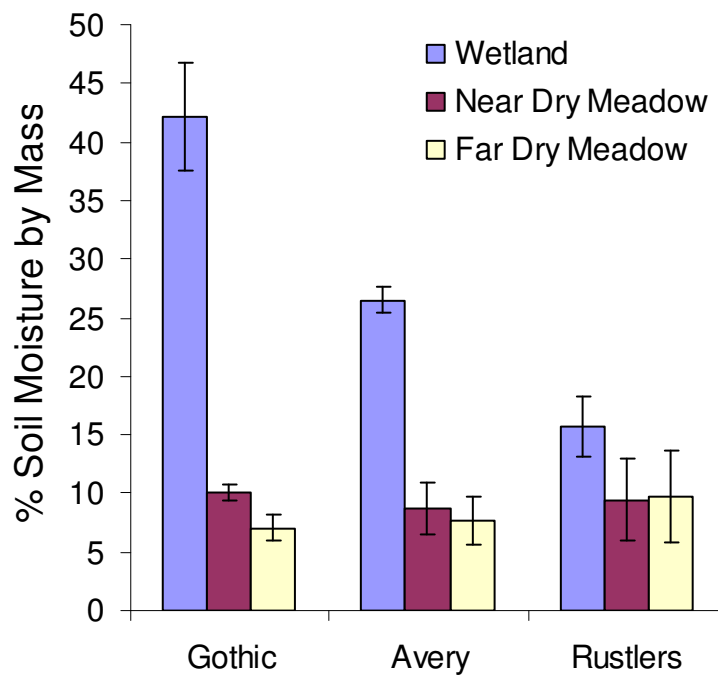


Figure 2. Percentage soil moisture in the sites during the summer. Error bars represent ± 1 SE.

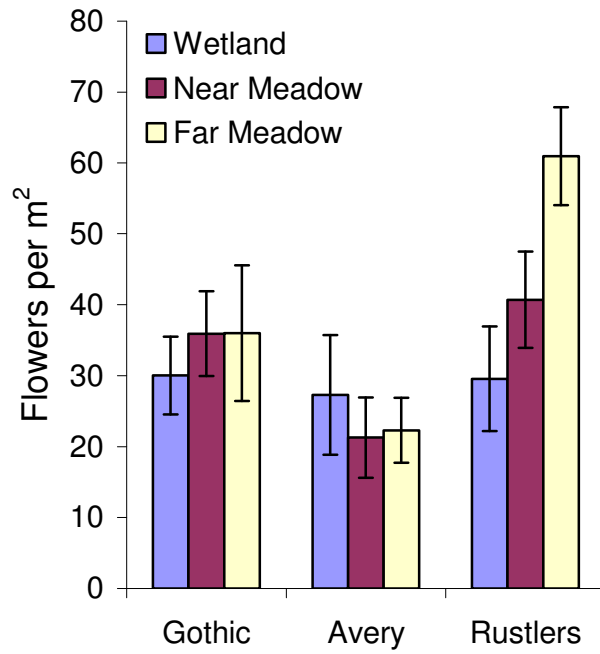


Figure 3. Flower density did not vary significantly with respect to distance. Error bars represent ± 1 SE.

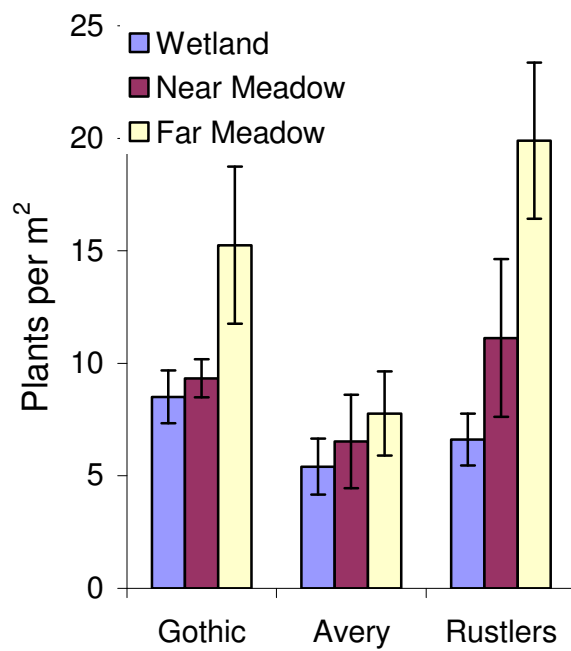


Figure 4. Flowering plant density did not vary significantly with respect to distance. Error bars represent ± 1 SE.

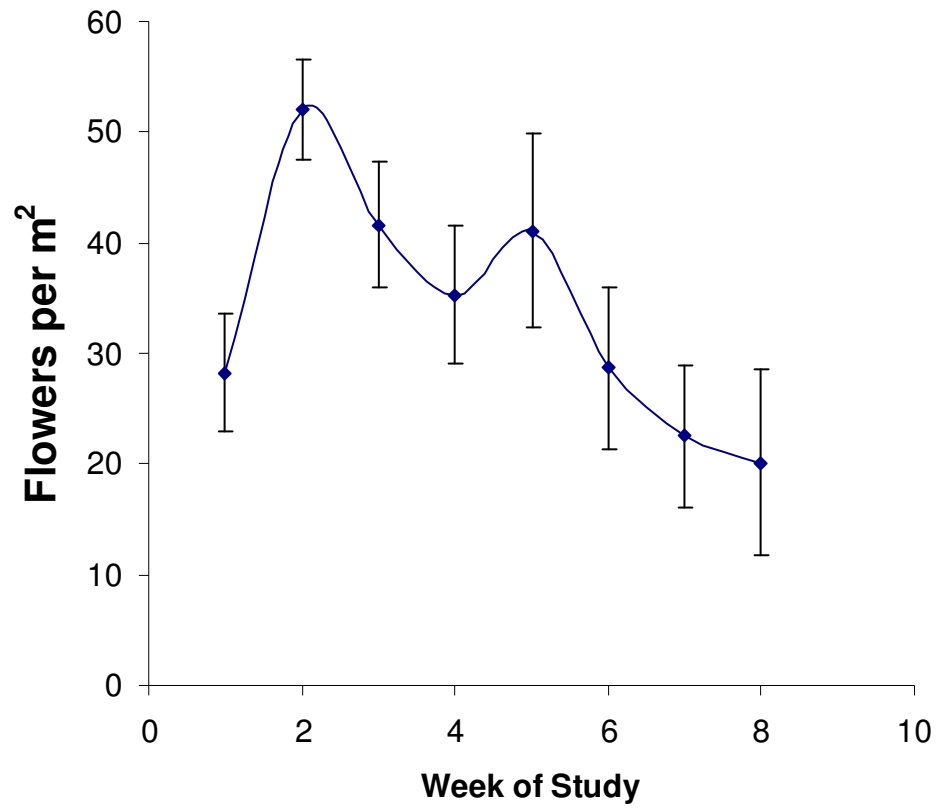


Figure 5. Average floral density for all distance plots during the flowering season. Error bars represent ± 1 SE.

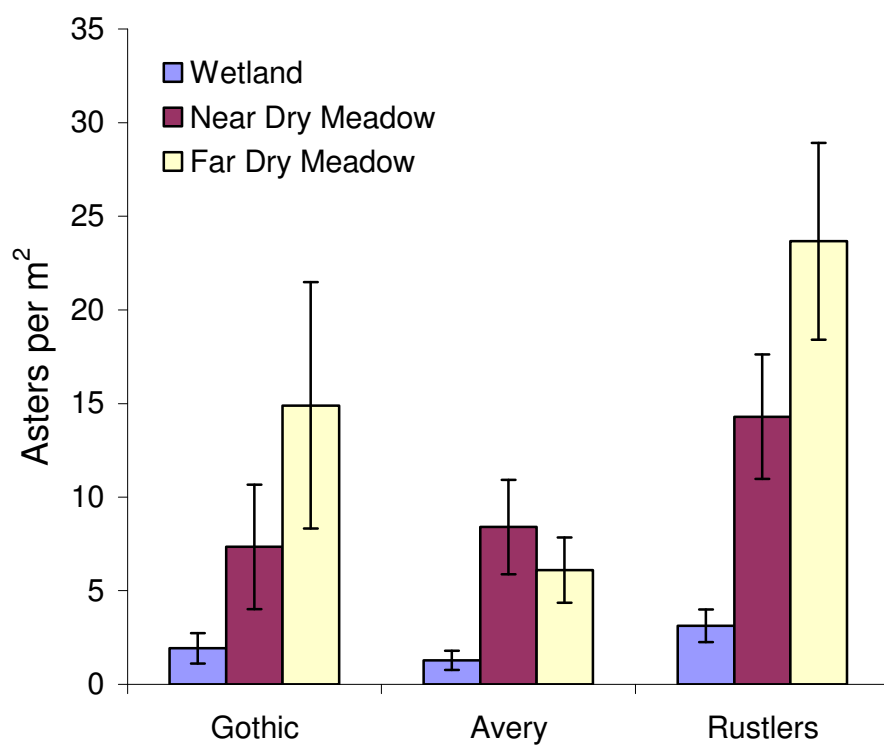


Figure 6. Aster flower density varied significantly with respect to distance. Error bars represent ± 1 SE.

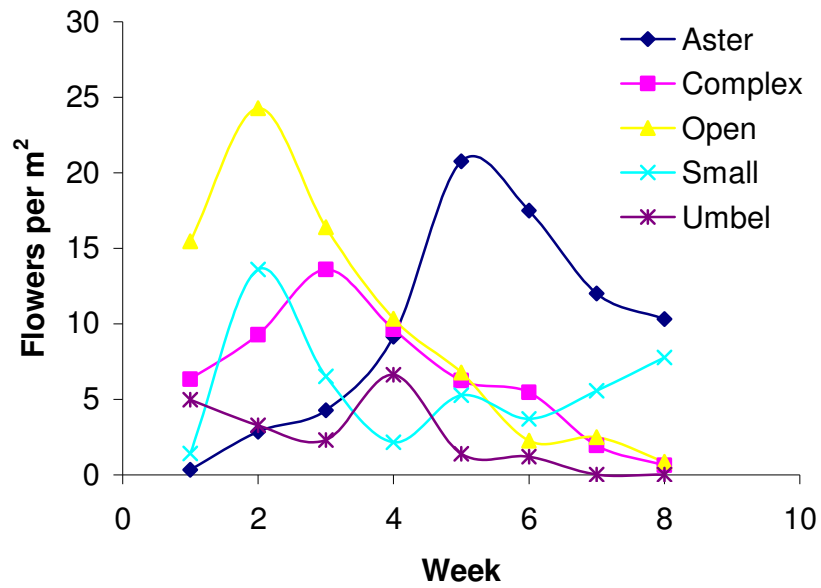


Figure 7. Flower density by floral morphology type over the summer, averaged across sites and distance plots.

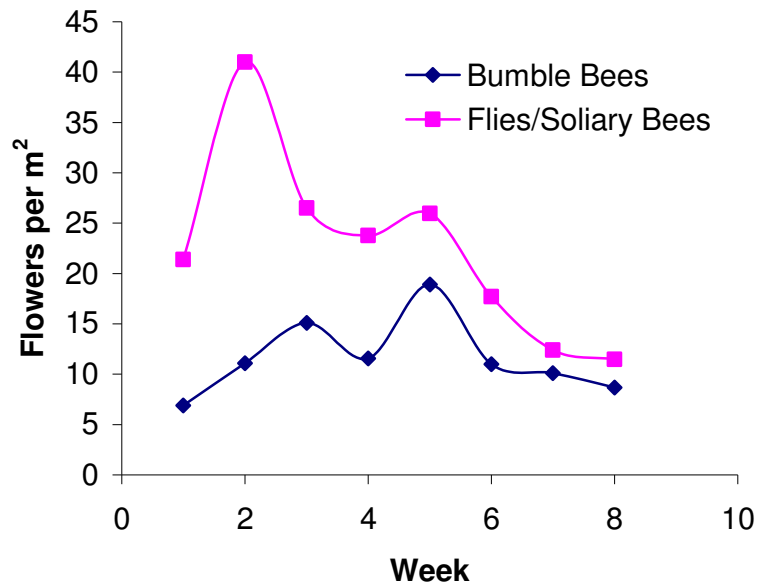


Figure 8. Flower density by functional pollinator type over the summer, averaged across sites and distance plots.

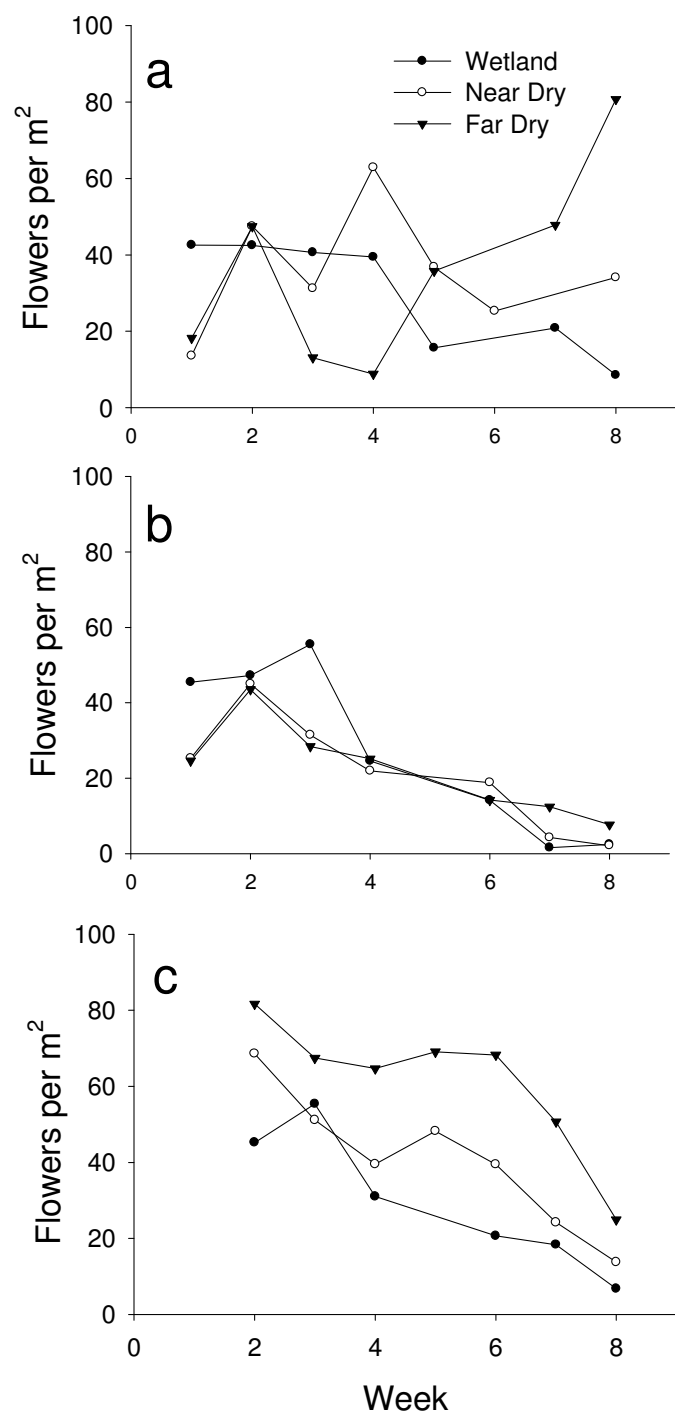


Figure 9. Flower density across the flowering season for (a) Gothic, (b) Avery, and (c) Rustlers sites.

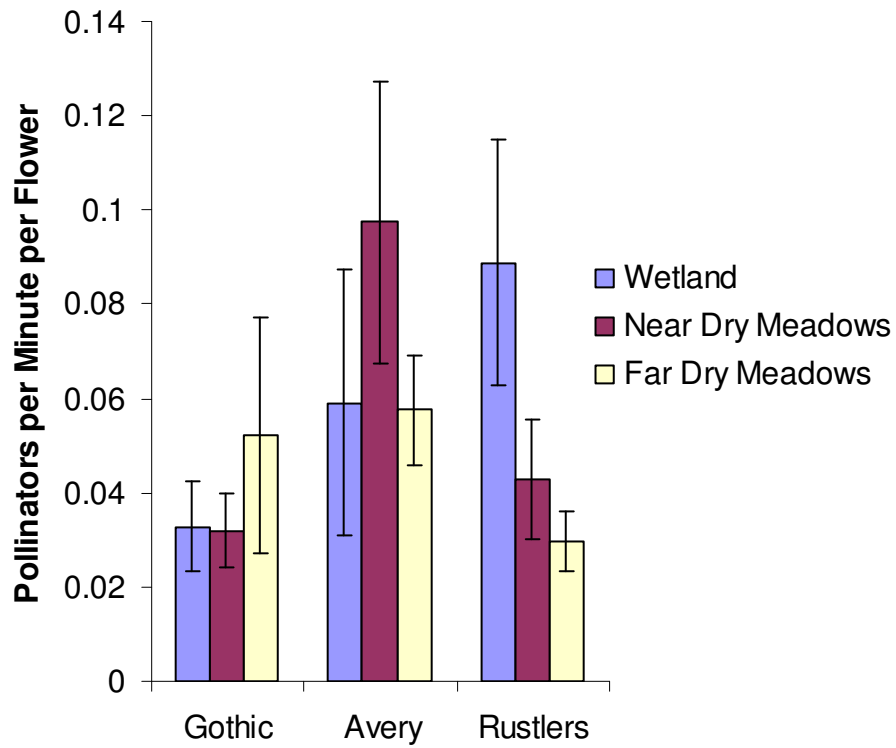


Figure 10. Pollinator visitation rate per flower in the sites. Error bars represent ± 1 SE.