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Conserving All the Pollinators: Variation in Probability of Pollen Transport among Insect Taxa

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ABSTRACT: As concern about declining pollinator populations mounts, it is important to understand the range of insect taxa that provide pollination services. We use pollen transport information acquired over three years in two habitats at Badlands National Park, South Dakota, USA, to compare probabilities of pollen transport among insect taxa and between sexes of bees. Sampling was conducted on 1-ha plots, eight in sparse vegetation (May–October samples; \( N = 74 \) surveys) and 12 in wheatgrass prairie vegetation (June–July samples; \( N = 87 \) surveys). Insects contacting reproductive parts of flowers were netted, placed individually into tubes charged with ethyl acetate, then transferred to individual labeled glassine envelopes for transport to the lab. Pollen was removed from insect bodies with fuchsin jelly cubes which were then mounted on microscope slides for identification. The probability of taxa transporting only conspecific pollen (with respect to the plant species upon which it was collected), mixed pollen, only non-conspecific, or no pollen was estimated with multinomial logistic regression. Bees were the most commonly captured flower visitor and carried by far the most pollen (females >10× as much as males), but they were most likely to carry mixed pollen loads. Flies, beetles, and wasps were also common flower visitors and beetles were most likely to carry only conspecific pollen. Ants and diurnal lepidopterans were unlikely to carry any pollen. Bees, beetles, flies, and wasps varied in the timing and habitat in which they were most likely to transport pollen, suggesting that all played a role in providing robust pollination services.

Index terms: flower-visitors, Great Plains, Hymenoptera, non-Hymenoptera insects, pollination

INTRODUCTION

The first step in the act of pollination is to remove pollen from one flower and transfer it to another conspecific flower. From the plant’s point of view there are a variety of ways in which this first step can go wrong. A flower visitor may not subsequently visit a conspecific plant, may consume the pollen, or may use it to provision a nest, all of which result in pollen wastage from the plant’s perspective. The visitor may avoid touching the reproductive parts of the flower, instead gaining nectar without moving pollen at all. Finally, the visitor may be carrying non-conspecific pollen that attaches to the stigma, potentially clogging the stigma and preventing access by conspecific pollen grains.

Bees are considered quintessential pollinators due to their adaptations (e.g., barbed hairs on their bodies, to purposefully collect and transport pollen to their nests; Thorp 2000; Stavert et al. 2016). Despite lacking pollen-carrying adaptations, many other insects regularly visit flowers to consume the energy-rich nectar or pollen (Wardhaugh 2015), and have been shown to move pollen (Clinebell et al. 2004) and to be valuable contributors to crop pollination (Rader et al. 2016). As concern mounts for declining pollinators, most pollinator research and media attention have focused on bees. The contribution of non-bee flower visitors to pollen transport, especially in natural areas, has received scant attention, and the conservation status of the flies, beetles, wasps, and other potential pollinators is rarely addressed in discussions of conservation, management, and preservation of healthy plant-pollinator communities.

In this study we use pollen transport information acquired over three years in two habitats at Badlands National Park, South Dakota, USA, to compare over space and time probabilities of pollen transport among all flower-visiting insect taxa. We also contrast the relative differences between the pollen-carrying female bees and the males, which exploit floral nectar but do not purposefully transport pollen. The study is motivated by two overarching issues. First, most concern over declining pollinator populations involves their utility in crop production—the widely quoted “every third bite of food”—that largely is concerned with domestic bees or the extent to which wild bees can add to crop pollination. While crop pollination is important from a food security perspective, the greater landscape (both natural and anthropogenic) is richly populated with thousands of other plant species that require animal-mediated pollination to effectively reproduce. These pollination networks are crucial not only for plant reproduction, but arguably more so for sustaining nectar- and pollen-feeding insect populations, which are often more restricted in their pollen diets than plants are in their pollen transport requirements.
(e.g., Muller 1996; Larkin et al. 2008). Second, the strong focus on bees in the majority of studies begs the question of how important the contributions of other taxa are for pollen transport, especially in non-anthropogenic landscapes.

METHODS

Sampling was conducted on 1-ha plots (133 m × 75 m). Twelve plots were in sparse (sp) vegetation (May–October 2010 and 2011; N = 74 surveys) and 12 in wheatgrass prairie (wg) vegetation (June–July 2012; N = 87 surveys). Badlands sparse vegetation is characterized by highly erodible clay soils with patchy vegetative cover. Wheatgrass prairie, in contrast, is composed of mainly silty, well-drained soils with nearly 100% vegetative cover.

Surveys were centered on flowering periods of plant species of interest: four plots on Astragalus barrii Barneby (May–June; early), four on Eriogonum visherii A. Nelson (July–August; mid; Larson et al. 2014), and four on Chrysothamnus parryi (Eriogonum parryi var. parryi [A. Gray] G.L. Nesom & Baird; September–October; late) in sparse and 12 on Cirsium arvense (L.) Scop.–infested or noninfested (Larson et al. 2016) wheatgrass prairie (2012; mid) (Figure 1). Individual studies will be referred to by the habitat type and timing of surveys: sp-early 2010 or 2011, sp-mid 2010 or 2011, sp-late 2010 or 2011, and wg-mid 2012, respectively. We sampled insects on warm days with low winds and mostly clear skies between 0900 and 1700 hours. Ten 2 m × 75 m parallel belt transects, 13 m apart at their midpoints, traversed the 1-ha plots and were used for insect sampling, with 20 min spent on each transect (200 min total per plot per visit).

No more than five insects were captured on any individual plant on a transect to avoid oversampling plant species with large flowering displays. Insects in contact with reproductive parts of flowers were netted, placed individually into tubes charged with ethyl acetate, then transferred to individual, labeled glassine envelopes within a larger ethyl acetate-charged jar for transport to the lab. We recorded date, time of day, plant species upon which it was captured, and study site for each individual insect. Vials were cleaned with a tissue after removal of each insect to reduce pollen transfer from one insect to another.

Insects were pinned and identified to the lowest taxonomic category possible. Most bees and butterflies were identified to species, but many other taxa were separated only into morphospecies within insect families or genera (Table S1 – Refer to BioOne to view online). Pollen was removed from insect bodies, including corbicula when present, with fuchsin jelly cubes which were then mounted on microscope slides for identification and counting (Kearns and Inouye 1993). Even though pollen present in corbicula is not available for pollination, it does indicate visitation to that species and the potential that pollen could have been transferred among flowers prior to grooming. We identified pollen under a light microscope at 10–100x with the aid of a reference collection made in and around the study plots. Fewer than 10 pollen grains of a plant species was considered contamination (Bosch et al. 2009). Ten or more pollen grains were considered evidence of a visit to that flower species; estimates >10 grains were placed in categories (10–100, 101–1000, 1001–10,000, and >10,000 per species) because counts were less precise at higher densities of pollen. We searched slides systematically and exhaustively for pollen species and all were recorded; it was not until data analysis that species represented by <10 grains were removed from the data set.

Analysis Methods

The probabilities of insect taxa transporting only conspecific pollen (with respect to the species upon which the insect was captured), mixed conspecific and non-conspecific pollen, only non-conspecific pollen, and no pollen were estimated with multinominal logistic regression (Hosmer et al. 2013). We estimated probabilities of pollen transport by different taxonomic groups (ants, bees, beetles, flies, diurnal lepidopterans, wasps, and “other” flower visitors; see Table 1 for identities of “other” visitors) for all studies pooled to observe overall trends. To examine variation in pollen transport for taxonomic groups among habitat and timing of survey, we performed similar multinominal logistic regressions individually for bees, beetles, flies, and wasps, the most abundant flower visitors in these study sites. Despite being reasonably abundant, ants were not included in the analysis of variation among habitats and timing due to their overall very low probability of carrying pollen.

We also estimated probabilities of pollen transport by families of bees, flies, and wasps. Ninety-nine percent of bees and 92% of flies were identified to family. Taxonomic resolution of the other taxa was not sufficient for family-level analyses. Breaking the data into the smaller units resulted in some families not being represented in one or more pollen-carrying categories (logistic regression requires representation in each category to avoid quasi-complete separation problems), so these families were omitted from the analysis, but are included in summaries of pollen grains carried. Finally, we estimated probability of pollen transport by male vs. female bees.

All multinominal logistic regression models were conducted using the logistic procedure with a generalized logit link function (link = glogit) in SAS version 9.4 (SAS Institute Inc. 2015). Within each analysis, each insect captured was treated as an independent experimental unit. Overall model tests were conducted to test the hypothesis that all probabilities were the same for all levels of the predictors (e.g., taxa, habitat/timing, family, or sex of bees). We computed confidence intervals for each probability and created plots of the probabilities with confidence intervals.

RESULTS

All insect specimens, their taxonomic identifications, and category of pollen carried by site and timing are in Table S1 (Refer to BioOne to view Table S1 online). The full data set used in these analyses is available in Larson et al. (2018).

Bees were by far the most frequent flower-visitor group (1841 individual bees
Figure 1. Map of study locations at Badlands National Park, South Dakota, USA.
versus 1970 individuals of all other taxa combined) and 87% of bees carried pollen (Table 1). Most taxa had roughly similar proportions of members carrying pollen between years in sparse habitat; wasps were a notable exception (Table 1). Bees carried more pollen than did other taxa (Table S2 - Refer to BioOne to view online), but male bees carried more than an order of magnitude less pollen than did females (Table S3 - Refer to BioOne to view online). Male bees still carried more pollen than other insect taxa (cf. Tables S2 and S3 - Refer to BioOne to view online). Probabilities of carrying conspecific, mixed, non-conspecific, and no pollen varied among taxa (chi-square = 645.77, df = 18, \( P < 0.0001 \)). Beetles and bees had the highest probabilities of carrying only conspecific pollen, followed by flies and wasps (Figure 2). In contrast, ants, diurnal lepidopterans, and “other” flower visitors (acridids [grasshoppers], arachnids [spiders], cicadellids [leafhoppers], cixiids [planthoppers], Ephemeroptera [mayflies], Hemiptera [true bugs], Nematocera [midges], Symphyta [sawflies], tettigoniids [katydids], Zygoptera [damselflies]) were very likely to carry no pollen. Wasps and bees had a higher probability of carrying mixed than conspecific-only pollen loads (Figure 2).

Of the four taxon groups that were both abundant and likely to carry pollen (bees, beetles, flies, and wasps), each had a unique profile with respect to habitat and season (Figure 3; bees: chi-square = 150.1705, df = 9, \( P < 0.0001 \); beetles: chi-square = 40.2081, df = 9, \( P < 0.0001 \); flies: chi-square = 99.9355, df = 9, \( P < 0.0001 \); wasps: chi-square = 62.2049, df = 9, \( P < 0.0001 \)). All of the taxa had probabilities between 0.20 and 0.30 of carrying only conspecific pollen in sp-early. Flies and beetles had high probabilities of pure conspecific pollen loads in sp-mid, but although beetles had a similarly high probability of carrying conspecific pollen in wg-mid, flies were highly unlikely to carry any pollen in that habitat (Figure 3b, 3c). Bees were the least variable among habitat and season, but their pollen loads were often most likely to be mixed (Figure 3a).

Bee families varied in their likelihood of
carrying conspecific, mixed, non-conspecific, or no pollen (chi-square = 108.8143, df = 12, \( P < 0.0001 \)). With the exception of the halictids (sweatbees), bee families were uniformly very unlikely to carry no pollen (Figure S1a - Refer to BioOne to view online). All had higher probabilities of carrying mixed or conspecific pollen than only non-conspecific pollen, with *Bombus* (bumblebees) having the highest probability of carrying mixed pollen loads; *Bombus*, along with other apids, also had the lowest probabilities among bee groups of carrying only conspecific pollen. Although they differed in pollen transport probabilities overall (chi-square = 90.38, df = 3, \( P < 0.0001 \)), male and female bees were similarly likely to carry only conspecific pollen (probability [95% confidence interval] = 0.296 [0.256, 0.337] and 0.307 [0.282, 0.332] for males and females, respectively). Females were more likely to carry mixed loads (probability [95% confidence interval] = 0.428 [0.402, 0.455] and 0.264 [0.225, 0.303] for females and males, respectively) and less likely to carry no pollen than males (probability [95% confidence interval] = 0.086 [0.071, 0.101] and 0.246 [0.208, 0.284] for females and males, respectively).

The probabilities of carrying conspecific, mixed, non-conspecific, and no pollen varied among fly families (chi-square = 67.1026, df = 18, \( P < 0.0001 \)). Anthomyiids (dung flies), asilids (robber flies), and bombyliids (bee flies) were more likely to carry no pollen than conspecific, non-conspecific, or mixed pollen. Calliphorids (blow flies) and empidids (dance flies) were most likely to carry purely conspecific pollen; syrphids (hoverflies), as well as being the most frequently collected of the flies, were more likely to carry pure and mixed conspecific/non-conspecific pollen loads than purely non-conspecific or no pollen (Figure S1b - Refer to BioOne to view online). Like flies, wasp families were highly variable in pollen transport (chi-square = 75.3816, df = 18, \( P < 0.0001 \)). Braconids (largely comprising parasitoid wasps) and pompilids (spider wasps) were likely to carry no pollen; only vespids (yellowjackets, hornets, paper and potter wasps, among others) were clearly more likely to carry mixed and conspecific than non-conspecific or no pollen loads (Figure S1c - Refer to BioOne to view online). Several families of both flies and wasps had small numbers, resulting in large confidence intervals.

**DISCUSSION**

Sheer numbers of pollen transporting bees and the huge numbers of pollen grains found on their bodies attest to their overall value in pollination, especially in the sparse habitats at Badlands National Park. Nonetheless, the variety and number of other insect taxa that carried pollen suggest they create robust capacity for pollination under a variety of environmental conditions that may not always favor bee visitation and pollen transport (Kuehsel and Bluethgen 2015; Rader et al. 2016). For example, Kuehsel and Bluethgen (2015) documented increased community-level thermal tolerance when more insect taxa were present. Taxa were functionally redundant, yet increased the range of temperatures at which flowers could be pollinated. Clearly, not all insects that simply carry pollen are effective pollinators (Wardhaugh 2015) and our study was not designed to evaluate pollinator effectiveness. What we have shown, however, is that taxa other than bees have the potential to move nontrivial amounts of pollen and their varied patterns of floral visitation in time and space could help plants buffer temporary losses of bee visitors during unfavorable environmental conditions. Despite the capacity of plants to use chemical and physical means to restrict pollinator visitations by some insects and favor the evolution of specialized insect pollinators, outside of the orchid family they rarely do so. Permitting and encouraging visitation by a range of pollinators would seem to be an appropriate bet-hedging approach given that non-bees can and do regularly carry significant amounts of pollen.

Ants are generally considered to be poor pollinators, despite the affinity of some species for flowers. Pollen does not readily adhere to their relatively hairless bodies and others have noted that chemicals released by the metapleural glands (secretory glands that produce chemicals with antibiotic properties; Yek and Mueller 2011) of some
ants can be toxic to pollen (e.g., Beattie et al. 1984; Gómez and Zamora 1992). Ants also are less likely than flying insects to visit flowers on plants separated by any distance, resulting in a high likelihood for within-plant pollination if ants do carry pollen from one flower to another (summarized in Domingos-Melo et al. 2017). This is likely reflected in our observation that those ants that did carry pollen were most likely to carry only conspecific pollen and very unlikely to carry mixed pollen loads. Nonetheless, ants are at times the dominant flower visitors in herbaceous habitats (Bosch et al. 1997) and can be key pollinators in a variety of habitats, including, for example, for milkweed species in mountainous and arid Mediterranean sites (Gómez et al. 1996) and for the rare Trinia glauca at various locations in England (Carvalheiro et al. 2008).

The diurnal lepidopterans we observed were even less likely to carry pollen than were ants. Systems in which lepidopterans, especially moths, are known to be effective pollinators are often quite specialized, with
moths laying eggs on pollinated flowers so that larvae can consume the subsequently produced seeds (Cuautle and Thompson 2010; Hahn and Brühl 2016). Orchids also have well-known specialized relationships with moths (e.g., Travers et al. 2011). Hahn and Brühl (2016) found only seven studies of moth pollination carried out in natural areas of Europe and North America, however, suggesting that the importance of moths in the temperate zone is understudied outside of agricultural settings. Our methods did not target nocturnal lepidopterans, which likely are more important for night-flowering species in the Caryophyllaceae (pinks) and Onagraceae (evening primroses) than the diurnal generalists captured in this study. The most often-captured butterfly in our study, *Plebejus melissa* (Melissa blue), carried a negligible amount of pollen and its larvae are seed predators (Green and Bohart 1975). This contrasts with Wist and Davis (2013), who considered *Phoebis sennae* (cloudless sulfur) to be a good pollinator of *Echinacea angustifolia* (narrow-leaved purple coneflower) in Saskatchewan.

Flies are increasingly being recognized as important pollinators (Larson et al. 2001; Inouye et al. 2015; Orford et al. 2015). Elberling and Olesen (1999) described increasing importance of dipteran pollination with latitude; in our South Dakota study sites, flies were the second-most common group captured on flowers, but bees, beetles, and wasps all had pollen on their bodies more frequently. It has been shown that flies may be important contributors to resilience in pollination systems as land use intensifies and climate changes, especially in that they function well at temperatures outside the range preferred by other taxa (Kudo et al. 2004; Kuehnel and Bluthgen 2015). In contrast to Kudo et al. (2004), flies at our sparsely vegetated study sites were unlikely to carry pollen early in the season, but were more likely to carry conspecific pollen at mid-season sparse sites than were bees, beetles, or wasps. Habitat mattered, however; flies were unlikely to carry pollen at wheatgrass prairie sites, which were also surveyed at mid-season. Although syrphids have received the most attention as pollinators (e.g., Lucas et al. 2018), other families of flies are also able to transport pollen and effectively pollinate flowers (Kearns and Inouye 1994; Tepedino et al. 2011; Orford et al. 2015). Calliphorids and syrphids were both relatively abundant and likely to carry conspecific and mixed pollen loads at Badlands study sites; bombyliids, which hover in front of flowers and use their long tongues to extract nectar, and the often tiny anthomyiids were also common flower visitors, but were less likely to carry pollen.

Wasp, other than the special case of fig wasps, often are reported to make up a rather small proportion of flower visitors (Harmon et al. 2011; Willmer et al. 2017); this was not the case at the Badlands sites, where wasps and flies were nearly equally captured at flowers, the two groups being surpassed in number only by bees. Wasps in the present study were overall as likely as bees to carry some pollen on their bodies (0.85 vs. 0.87 for wasps and bees, respectively), and even more likely to do so than bees in wheatgrass prairie (0.87 vs. 0.75 for wasps and bees, respectively). Likely owing to their use of nectar rather than pollen as a resource, wasps were less likely than bees to carry only conspecific pollen. As Mello et al. (2011) pointed out, the ecology of wasp predation is better studied than that of wasp pollination; network studies supported the generalized nature of wasp–flower interactions. Similarly, in the Badlands study sites, wasps were most likely to carry mixed pollen loads. Sphecid (thread-waisted) wasps have been found to be effective at moving pollinia among conspecifics of some *Asclepias* species in the Midwestern United States (Thiess et al. 2007), and a guild of flowering plant species has been described that is pollinated by *Hemipepsis* (Pompilidae) wasps in South African grasslands (Shuttleworth and Johnson 2012). These families, along with the braconids and chrysidids (cuckoo wasps), were uncommonly encountered at the Badlands study sites. The two common wasp families, crabronids (cidacekillers and mud daubers, among others) and vespid (paper wasps), displayed the expected generalist habits as indicated by their likelihood of carrying mixed pollen loads.

Beetles are often characterized as inefficient pollinators due to their propensity for remaining on a single flower for long periods as they consume petals and other flower parts, actions that also make it difficult to discern if pollination is actually occurring (Bernhardt 2000). Nonetheless, beetles are strong fliers and in open grasslands with high winds, beetles may be important for cross-pollination. Overall, beetles at Badlands study sites were the taxa most likely to carry only conspecific pollen on their bodies. In fact, they were more likely to carry no pollen than mixed pollen loads, which, similar to results of Bosch (1992), suggests either long periods on a single flower or a strong fidelity to one species (or both). Only in late-season sparse habitats were beetles most likely to carry mixed pollen loads, perhaps due to the high diversity of late-blooming *Asclepias* species (daisy family), flowers of which are easily accessible to generalist foragers. Pollination by beetles is better known in tropical environments (Wardhaugh 2015); our data suggest the value of increased understanding of their role as pollinators in grassland ecosystems.

As expected, bees were the most abundant and most likely to carry pollen of the flower visitors collected at our Badlands sites. Halictids far outnumbered other bee families and were the only family at all likely to not carry pollen on their bodies, which may contribute to their reputation as poor pollinators (e.g., Lau and Galloway 2004; McIntosh 2005). Nevertheless, halictids have been found to carry out effective pollination (Horsburgh et al. 2011) and their numbers alone further suggest their importance at these Badlands sites. In particular, Larson et al. (2014) found the halictid *Lasioglossum packeri* to be the most faithful visitor to the rare Great Plains endemic *Eriogonum visheri*. A. Nelson (Visher’s buckwheat).

Because male bees do not provision nests and, therefore, only use pollen and nectar for immediate energy needs, the amount of pollen on their bodies is less than that of females. However, much of the pollen carried by females can be unavailable to flowers (Thorp 2000), so this difference may be less consequential than the numbers imply. Perhaps of greater importance is the likelihood of male bees having mixed pollen loads, especially true among apids...
Many different kinds of insects visit flowers for reasons unrelated and often unhelpful to pollination (Wardhaugh 2015). One hundred twenty-one insects not typically thought of as pollinators were captured on flowers at Badlands study sites; collectively, they were more likely to carry pollen than diurnal lepidopterans or ants. The likelihood that that pollen would reach a receptive stigma is a separate and here unanswered question.

CONCLUSION

We have documented the wide variety of insects that carry pollen in two habitats in the North American Great Plains. No single taxonomic group was the most likely to carry conspecific pollen over all sample periods or in each habitat. For this reason, we echo others (Orford et al. 2015; Wardhaugh 2015) in calling for increased efforts to understand the role of non-bee insects in pollination. As concern mounts for declining bee populations, there is much to be gained both in terms of causal understanding and identification of alternative pollinating insects, by increasing our understanding of the breadth of pollination services. Likewise, as climate change results in greater instability in environmental conditions, conservation of a variety of insect pollinators that thrive in different conditions will provide the greatest probability for continued maintenance of these key mutualisms over time.

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LITERATURE CITED


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Figure S1. (Refer to BioOne to view online) Probability (plotted as points) and 95% confidence intervals (plotted as error bars) that (a) bee families (and the genus Bombus), (b) fly families, and (c) wasp families carried conspecific pollen only, mixed conspecific and non-conspecific pollen, non-conspecific pollen only, or no pollen. Families that did not occur in all four pollen transport classes (see methods) were excluded, as were specimens that we could not identify to the family level. Data were pooled across all studies. Number of individuals is in parentheses after family name.

Table S1. (Refer to BioOne to view online) Insect species or morphspecies by pollen-transport category and habitat-season. Sp = Badlands sparse; Wg = Wheatgrass prairie. BADL followed by a number refers to the morphspecies identifier by which reference specimens can be located.

Table S2. (Refer to BioOne to view online) Estimates of conspecific (with respect to the plant species on which the insect was captured) pollen grains carried by insect taxa in each habitat-timing of survey and year. Estimates given as a range and represent the average number of conspecific pollen grains per individual. See Methods for procedures used to estimate pollen abundance. Sp=spars; Wg=wheatgrass prairie.

Table S3. (Refer to BioOne to view online) Estimates of pollen grains counted on slides made from pollen removed from male (n = 496) or female (n = 1345) bees. Estimates given as a range and represent the average number of pollen grains per individual. 99.7% of bees were identified to family.