

AGGRESSION BETWEEN FLORAL SPECIALIST BEES ENHANCES POLLINATION OF *HIBISCUS* (SECTION *TRIONUM*: MALVACEAE)

B. J. Sampson¹, C. T. Pounders, C. T. Werle, T. R. Mallette, D. Larsen, L. Chatelain and K. C. Lee

USDA-ARS Thad Cochran Southern Horticultural Laboratory, Poplarville, MS 39470 USA

Abstract—Specialist oligoleges are bees with narrow dietary niche breadths often touted to have foraging specializations that enhance their pollination efficiency above that of co-foraging generalists (polyleges) such as honeybees *Apis mellifera* L. This study and many comparative pollinator efficacy studies in crops show that oligoleges on a per bee basis are not always the most efficient pollinators. Percentage of stigmatic contact visits by populations of oligolectic *Ptilothrix bombiformis* (Cresson) in Maryland and Mississippi show that adult bees contact stigmas and transfer 70+ pollen grains during 2% - 3% of floral visits. As low as these percentages seem, pollination efficiency of this bee varies from negative values due to the removal of stigmatic pollen during some visits to increases of 30% as *Hibiscus* petals close and spikes of 300% - 1000% as *Ptilothrix* adults display aggression inside flowers. Aggressive *P. bombiformis* tussle with each other, often grappling with, lunging at, and biting conspecifics. Opponents will often lose their balance, tumble around inside flowers and, in the process, more efficiently pollinate host blooms. Such aggressive interactions constituted 5% of visitation bouts to *Hibiscus* flowers, yet accounted for ~20% of contact visits that transferred 10 or more pollen grains per stigma. Tussles therefore represent brief agonistic entanglements that can enhance the pollination efficiency of solitary bees at host plants with large herkogamous blooms. More complex behavioural interactions between different sexes and species of foraging bees may explain the importance of greater bee diversity to overall pollinator effectiveness.

Keywords: aggression, courtship, effectiveness, mutualism, pollinators, seed set

INTRODUCTION

Pollen flow in most flowering plant taxa depends on numerous pollinator species as well as on male and female bees to varying degrees. Bee species that are specialists (oligoleges) gather pollen and nectar from a narrow range of related floral hosts, others are generalists (polyleges) visiting upwards of 100 - 200 plant species for food. Presumably among these, oligoleges are the most efficient pollinators due to close evolutionary relationships with their preferred floral hosts and associated foraging specializations. However, in some bee-plant mutualisms of economic importance, individual adult bees appear equitably efficient at pollinating their respective floral hosts despite difference in gender and level of sociality. For instance, male bees are often considered trivial pollinators because they gather no pollen and do not care for their offspring and so tend to be rare floral visitors. Male bees of some oligolectic species may be passive yet effective pollinators due to their hairiness and sheer abundance. In fields of summer squash, for instance, males and females of the oligolege *Peponapis pruinosa* (Say) are both efficient pollinators, their visits producing seeded *Cucurbita pepo* fruits of similar size. A 9:1 male-biased foraging density of *Peponapis pruinosa*, perhaps due to the males' permanent residence in a field, seemingly render male *Peponapis* as effective as or more effective than females (Cane et al. 2011). Polyleges such as honeybees can be

efficient pollinators too, even those species that resort to flower robbery to obtain nectar. At rabbiteye blueberry blooms, *Vaccinium virgatum* Aiton, legitimate floral visits by oligolectic *Habropoda laboriosa* Fab., *Osmia ribifloris* (Cockerell), and polylectic honeybees *Apis mellifera* L. set similar fruit sets of ~40% (Sampson & Cane, 2000). Polylectic male carpenter bees (*Xylocopa* spp.) and honeybees were believed to circumvent pollination by robbing blueberry flowers of nectar through holes cut into the bases of corollas. Yet, floral robbers turned out to be efficient pollinators of blueberry. Two robber visits transferred as much compatible pollen as did single legitimate visits by oligolectic *H. laboriosa* (Sampson et al. 2004). Even exotic bees are effective pollinators of plants with which they share little or no evolutionary history. For example, an exotic generalist from Mexico, the orchid bee *Euglossa dilemma* Friese, is now naturalised in Florida and can outperform indigenous bee species as pollinators of invasive *Solanum* (Liu & Pemberton 2009). In the mutualism studied here, polylectic bumblebees (*Bombus* spp.) are ~5 time more efficient at contacting *Hibiscus* stigmas than are the plant's own oligoleges, mallow bees *Ptilothrix bombiformis* (Cresson) (Apidae: Emphorini), a difference likely due to the larger body size of *Bombus* workers (Willmer & Finlayson 2014).

From these examples, we posit similarly sized bees at least on an individual basis deposit similar amounts of pollen and set similar fruit and seed sets despite differences in gender, level of sociality, degree of floral host specialization, and geographic origin (Greenleaf & Kremen 2006; Matsuki

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*Corresponding author: blair.sampson@ars.usda.gov

et al. 2008). However, the pollination effectiveness of any bee species is determined by a bee's average pollination efficiency, and more importantly, by overall foraging abundance (Winfree et al. 2014). Oligoleges in fact are often the most effective pollinators due to high foraging abundances maintained by a strong innate fidelity for host blooms. Males are often less fidelic than females are; however, they remain close to host blooms with the expectation of finding mates. At host blooms, male bees behave quite differently than females do. Therefore, their foraging movements, amorous approaches to females, and aggressive displays could have unintended consequences for pollination efficiency and rates of host plant outcrossing: negative or positive (Spira et al. 1992; Nagamitsu & Inouye 1997; Santa Anna-Aguayo et al. 2014).

The large herkogamous blooms of *Hibiscus* have a wide gap between their anthers and stigmas that large, hairy, and fast moving bees such as *P. bombiformis* periodically cross (Baker & Hurd 1968). Higher bee abundance could increase pollination of herkogamous flowers in two fundamental ways: first, through the simultaneous increase in floral traffic and stigmatic contact and second, and more intriguingly, by aggressive intrafloral interactions, which may stir greater pollinator movement. In effect, abundance and efficiency, the two factors of a pollinator's effectiveness, are not mutually exclusive. Pollinator abundance could enhance the pollination efficiencies of bee species by increasing incidences of agonistic interactions inside host flowers (Cane et al. 2011; Santa Anna-Aguayo et al. 2014). Therefore, we observed tussles between aggressive bees of a solitary oligolege *Ptilothrix bombiformis* and given the enormous amount of pollen they discharge, we posit that such pollinator aggression increases pollen transfer and seed set of their *Hibiscus* hosts.

MATERIALS AND METHODS

We studied the *Ptilothrix-Hibiscus* mutualism because *P. bombiformis* are large abundant solitary bees (13 - 17 mm) and oligoleges that vector pure loads of pollen gathered from related species of Malvaceae, principally from wild and cultivated *Hibiscus* (Rust 1980). In the field, *Ptilothrix* males (Fig. 1A) are identifiable by distinctive patrol flights above flowers, which often involve darting in and out of blooms in search of receptive females. *Ptilothrix* females were identified by more methodical flight paths between *Hibiscus* flowers and by dense and often pollen-laden pollen brushes (scopae) on their hind legs (Fig. 1B). *Ptilothrix* at Mississippi *Hibiscus* came from natural nesting populations at two semi-urban/rural sites: Poplarville in 2009 and McNeill in 2014.

Hibiscus is an excellent species to study bee-plant interactions because plants produce daily 1 to 5 large, short-lived (1-day-old), herkogamous flowers that present bees with enormous spiny pollen grains (~150 - 200 μm) that are easily counted on stigmas with a low-power magnifying lens. Since counts of stigmatic pollen can be performed on intact pistils, we can draw a direct relationship between bee pollination efficiency (stigmatic pollen loads) and host reproductive success (seed set). Chosen for these studies were

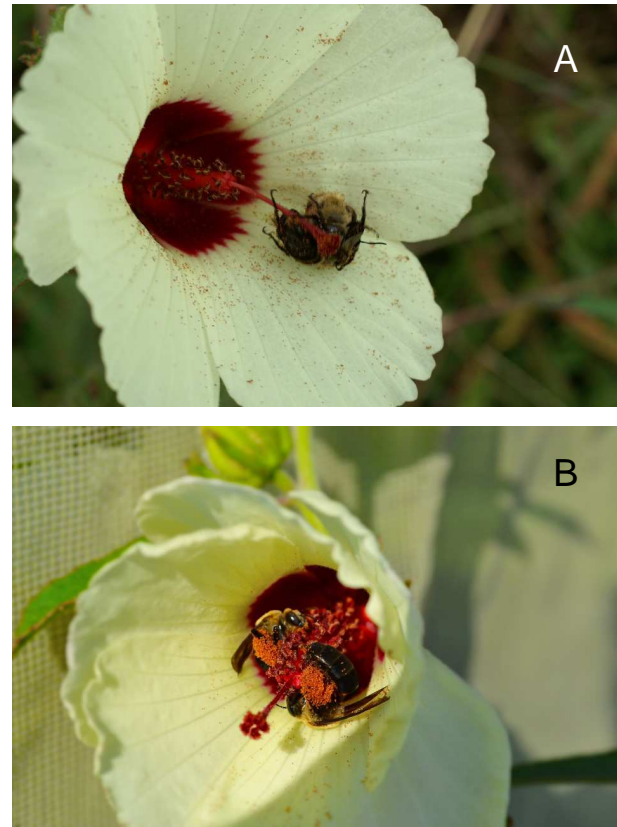


FIGURE 1. Intrafloral movements of *Ptilothrix bombiformis*. (A) A tussle between two male bees. Audible buzzes and grappling quite pronounced. Note the field of scattered pollen grains on the petals left by the two squabbling males and the bees close proximity to the stigma. (B) Co-visitation by two *P. bombiformis* females without significant interaction.

three *Hibiscus* species, each grown from wild-collected seed: *H. laevis* All., *H. coccineus* (Mendik.) Walter, and *H. moscheutos* sbsp. *incanus* (J.C. Wendl.) Ahles. Plants of the first two species, *Hibiscus laevis* and *H. coccineus*, were irrigated daily in 12 L pots at the Poplarville site in 2009. Seeds of *Hibiscus moscheutos incanus* were sown along 75-m of unirrigated row at the McNeill site in 2014. Diploid *H. laevis* and *H. coccineus* ($2n = 38$ chromosomes, Group II *Hibiscus* sect. *Trionum*) were grown together on the same container pad because both species freely intercross and should not affect seed set of the other. Although, diploid *H. moscheutos incanus* (Group I, *Hibiscus* sect. *Trionum*, $2n = 38$) has the same number of chromosomes as *H. laevis* and *H. coccineus*, the former's putative genetic incompatibility with Group II species required us to plant *H. moscheutos* elsewhere, so as to ensure optimal seed set in open pollination controls (Wise & Menzel 1971).

Lumite® mesh cages (1.5 m^3) excluded bees from flowers on four plants of each *Hibiscus* species. Cages were removed for 15 - 60 min between 0800 and 1015 h to expose newly open flowers to *P. bombiformis*, a species responsible for 98 - 99% of floral visits at both the Poplarville and McNeill study sites. Observations of floral visitors lasted 10 d in 2009 (21 - 31 Aug) and 1 month in 2014 (16 July - 14 August). Eleven levels of floral visitation were recognized in *Ptilothrix*: (1) no visits, (2) single male

visits (3) single female visits, (4) two non-interacting males, (5) two non-interacting females, (6) a non-interacting male and female, (7) two interacting males, (8) two interacting females, (9) an interacting male and female, (10) near simultaneous visits by 3-5 (3+) bees without interaction, and (11) open pollination. Aggressive bees that come into physical contact often grappled, bit, and buzzed one another, behaviours hereafter referred to as “tussles”. Non-interacting bees generally avoided each other in blooms and never made physical contact or acted in a belligerent fashion. After each *Ptilothrix* floral visit or visitation bout, a hands-free jeweller’s loupe aided in counting pollen grains that accrued on each of *Hibiscus*’ five or six stigmatic lobes. In an attempt to increase sample size, grass stems were tied around flaring petals of select *H. moscheutos incanus* flowers (petal angle: $\theta' = 17^\circ - 23^\circ$) to shape blooms into a narrower tube (petal angle: $\theta' = 0^\circ - 10^\circ$) that might bring *Ptilothrix* bees into closer contact with stigmas and incite agonistic intrafloral behaviour. Petal angle in degrees (θ') was calculated for radially symmetrical flowers of *Hibiscus* using the equation:

$$\theta' = \tan^{-1}\left(\frac{Dc - Db}{2h}\right) \quad 0^\circ \leq \theta' \leq 90^\circ$$

Where Dc is flower diameter at its aperture, Db is calyx diameter, and h is floral depth. θ' is derived from an imaginary right triangle with $x = h$ where x extends perpendicular from the outer edge of the calyx to the flower aperture, and $y = \frac{1}{2}(Dc - Db)$ is the distance between the petal’s outer edge and the point where x intersects y at a right angle.

After a single visit by a bee to a *H. laevis* or a *H. coccineus* bloom, or after 10 to 20 visits to each *H. moscheutos incanus* flower, paper price tags were tied to ovaries to flag seed capsules for harvest 7 - 30 days later. Cages were then replaced. A high proportion of seedless capsules in our *H. coccineus* population required the manual cross-pollination of additional flowers to determine full seed set in to rule out sterility in this species. Optimal seed set in the field for the other two species was considered to be analogous to sets acquired by open pollination whereby flowers during their entire life were freely accessible to pollinators. Likewise, optimal seed set in *H. moscheutos* could be estimated from a plot of cumulative seed set versus successive bee visitation. Field experiments were completely randomized (CRD) with bee visitation bouts and seed capsules serving as replicates. To deal with skewed data distributions containing a high proportion of zeros, non-parametric Kruskal-Wallis ANOVAs and multiple Wilcoxon two-sample exact tests were used to identify treatment differences among mean single-visit stigmatic loads in all three *Hibiscus* species and seed set in the type II *Hibiscus* species. Chi-square test identified any non-random patterns in the frequency of contact visits resulting from intrafloral tussles between *P. bombiformis*. Non-linear regression (PROC NLIN in SAS) estimated both *Ptilothrix* pollination efficiency and the least amount of stigmatic pollen needed for full seed set in *H. moscheutos incanus*.

RESULTS AND DISCUSSION

Floral oligoleges are often touted as being highly efficient pollinators. Their numerous foraging specializations often favour rapid synchronous flight, copious pollen harvest, and strong host fidelity (Strickler 1979; Liu & Pemberton 2009). Synchronous flight enables bees to vector viable pollen to host stigmas during peak receptivity. Efficient pollen harvests result in the delivery of pure loads of compatible pollen. Strong host fidelities displayed by male and female oligoleges often increase bee foraging abundance, interfloral traffic, and thus pollination rates. Although these three fundamental adaptations of oligoleges theoretically favour high rates of host outcrossing, plants themselves have very different genetic interests than those of their pollinators. Therefore, if reproductively advantageous to do so, plants limit floral access to very specific and highly efficient pollinators by means of such floral adaptations as small stigmas, narrow corollas, long pistils, and changes in floral phenology (Harder and Aizen 2010; Sletvold et al. 2010).

Our studies as well as those reviewed by Larsson (2005) suggest that floral hosts for genetic reasons will evolve floral architectures that limit or promote pollinator efficiency, even the efficiencies of specialized floral oligoleges. As a result, many bees of similar size may be more equally efficient depending on how well they “fit” host floral morphology. For instance, unrelated bee taxa on a per bee basis appear to pollinate diverse plant taxa (e.g., *Vaccinium*, *Cucurbita*, *Solanum*, and *Hibiscus*) equally or nearly so (Spira et al. 1992; Sampson et al. 2000; 2004; Liu & Pemberton 2009; Cane et al. 2011). Efficiencies in fact may be lower for highly specialized bees that are capable of rapidly harvesting host pollen while minimizing pollen load loss by avoiding female parts of host flowers. This seems true of *Ptilothrix bombiformis*, a bee species that manages to contact host stigmas 2% - 3% of the time (Spira et al. 1992), hardly a proficiency one expects from such large, pilose, and specialised pollinators (Fig. 1). Clearly, the mating system of *Hibiscus* shares with blueberry a wide separation between stamens and pistils, which reduces the likelihood of geitonogamous mating (i.e., self-pollination, Sampson et al. 2013). *Hibiscus*’ large 7 - 8 cm wide flowers increases the number of paths a bee can take to exit a flower without ever contacting a stigma. In such a case, a pollinator’s size importantly affects pollination efficiency more than its degree of pollen specialisation. Similarly, at other floral hosts, the size of a bumblebee or a syrphid fly determines the ability of each insect to load plant stigmas with pollen. For each millimetre of intergular span, a worker bumblebee loads periwinkle (*Vinca minor*) stigmas with 10 additional pollen grains. Larger bumblebees and hoverflies were 4 to 5 times more efficient pollinators of blueweed (*Echium vulgare*) than were their smallest counterparts (Willmer & Finlayson 2014). In the bee-plant mutualism studied here, larger and more rotund bumblebees, though resembling *Ptilothrix*, transfer ~5 times more *Hibiscus* pollen (Spira et al. 1992). Bumblebees are not as effective as *P. bombiformis*, since they rarely visit *Hibiscus* flowers and then only for nectar.

Hibiscus plants throughout their range seem to limit the individual pollination efficiency of their principal pollinator, *P. bombiformis*. Using the pollination threshold provided by Spira et al. (1992), Mississippi and Maryland *Ptilothrix* deposit about 70 pollen grains with each successful contact with *Hibiscus* stigmas, which occurs only ~3% of the time. In Mississippi, 21% of contact visits by *P. bombiformis* each transferred ≥ 10 pollen grains, on average, a satisfactory quantity to accrue enough pollen for seed set and offset any pollen knocked off stigmas by visiting bees. The latter was a surprising finding; we had not expected that 7% of *Ptilothrix* visits each resulted in the removal of 1 - 10 stigmatic pollen grains. We chose to lower our pollination threshold by a factor of seven from that reported by Spira et al. (1992), as 75 - 100 grains per flower were sufficient for full seed set in two of our three floral host species (*H. moscheutos incanus* and *H. laevis*, (Figs 2 - 4). In contrast, optimal seed set in more northern populations of *H. moscheutos* reportedly require many more pollen grains for full seed set, 360 - 700 grains per stigma (Spira et al. 1992). This higher threshold could very well reflect a different phenotypic response to a colder climate, which may affect pollen availability, pollen viability, or ovule fertility (García et al., 2000). Accordingly, our revised pollination threshold for a contact visit at our Mississippi plantings is the transfer of 10+ pollen grains. Since full seed in *Hibiscus* requires multiple visitation, we estimate that *H. laevis* and *H. moscheutos* requires a minimum of 8 to 10 contact visits by *Ptilothrix* (Figs. 3 and 4). Estimating a similar pollination threshold for *Hibiscus coccineus* was difficult because of high degree of sterility in this population. Our *H. coccineus* plants produced very small capsules (~0.35 g) containing ~75% - 80% fewer seeds than the other two species despite our best efforts to manually pollinate stigmas (Fig. 3). Single visits by *Ptilothrix* females did produce seed sets equal to the optimal seed set for *H. coccineus* (i.e., 5 seeds, Fig. 3), confirming the higher pollination efficiencies of pollen-gathering female bees when compared with the efficiencies of male bees. However, possible sterility resulted in very poor seed set in *H. coccineus* and only manual pollination (saturated stigmatic pollen loads) produced capsules with a few small seeds (Fig. 3).

Although floral hosts sometimes limit bee pollination efficiency in order to prevent autogamous pollen transfer, there may be sufficient variability in a bee's pollination efficiency to result in pollen surpluses on stigmas (Spira et al. 1992). At our fields, *Ptilothrix* bees constituted 98 - 99% of floral visitors and were amply abundant to transfer stigmatic pollen loads at or above the 100-grain threshold for full seed set (Figs 2 - 4). Most *P. bombiformis* visits led to zero pollen deposition rates or, what was noteworthy, to the removal of stigmatic pollen grains 7% of the time. Although pollination efficiencies of single visits by both male and female *Ptilothrix* were low and sometimes negative, efficiency was quite a dynamic pollinator trait. For instance, *P. bombiformis* behaviours such as foraging and courtship and to a lesser extent, floral traits such as petal closure and stigmatic area, increased rates of host pollen deposition by 30% - 1000%. In solid stands of our *H. laevis* and *H. coccineus* for instance, 23% - 29% of visits transfer 10+

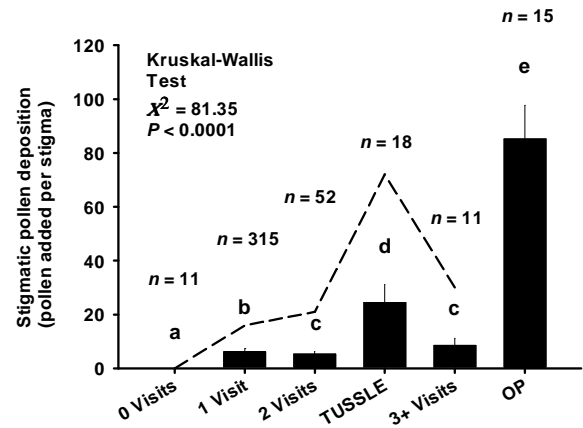


FIGURE 2. Net stigmatic pollen loads transferred to three species of *Hibiscus*. Flowers after tussles between 2 bees, no visits, single visits, double visits, triple, or near-simultaneous visits, and open pollination (OP) by *Ptilothrix bombiformis*. Black bars represent mean stigmatic pollen deposition including $1 \pm SE$. Sample sizes are shown above bars and mean differences denoted by different letters according to multiple Wilcoxon 2-sample exact tests. The dashed line above the first 4 bars indicates the percentage of visits that transferred 10+ pollen grains onto *Hibiscus* stigmas (“contact visits”).

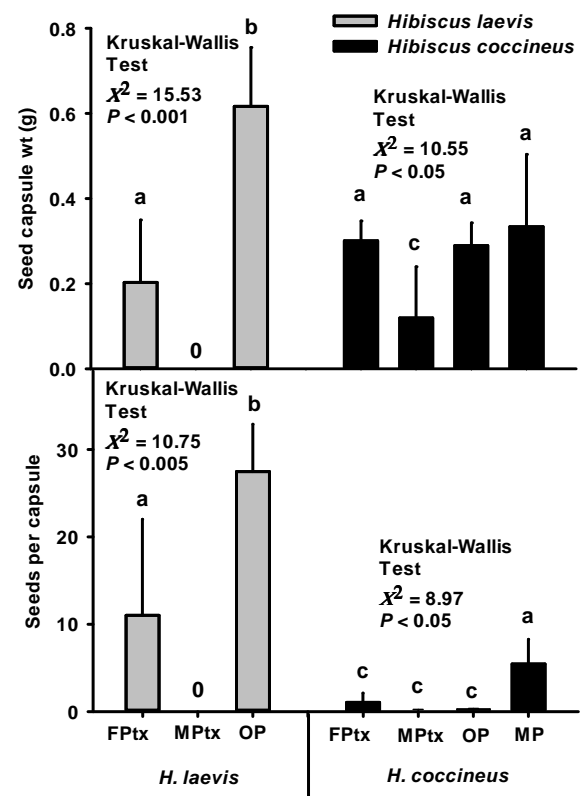


FIGURE 3. Comparative pollination efficiencies of single contact visits by male *Ptilothrix bombiformis* (MPtx) and females (FPtx) in the 2009 study based on seed capsule weight and seed set (seeds per capsule) of *Hibiscus laevis* and *H. coccineus*. For comparison, some flowers were openly pollinated (OP) and manually pollinated (MP) with stigmas saturated with compatible pollen (*H. coccineus* only). Bars (+SE) denote mean stigmatic pollen loading per visit. Different letters above the bars indicate means that were different according to multiple comparisons of rank scores using Wilcoxon two-sample exact tests across the two Type II species of *Hibiscus*: *H. laevis* and *H. coccineus*.

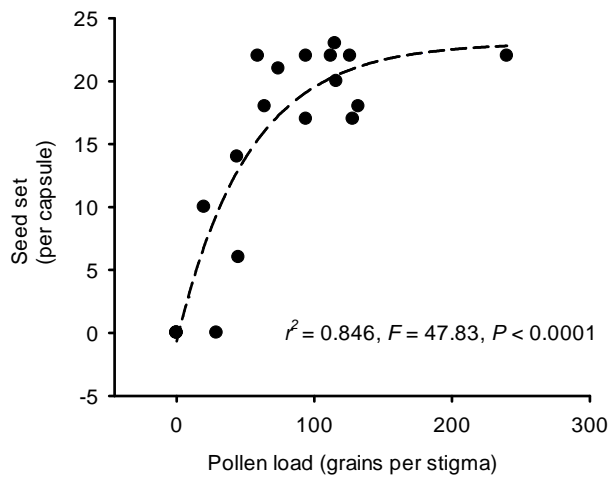


FIGURE 4. Effect of *Ptilothrix bombiformis* pollination efficiency on *H. moscheutos incanus* seed set in the 2014 study. Line shows a strong curvilinear response of host reproductive output to stigmatic pollen loading by visiting *P. bombiformis*.

pollen grains to host stigmas. These two species also have flowers bearing larger upturned stigmas. In contrast, 19% of visits effect significant pollen transfer (10+ grains) in a floral host such as *Hibiscus moscheutos incanus* that has comparatively straighter pistils and smaller stigmatic lobes (Fig. 1). Aging *Hibiscus* flowers also furl petals, which bring bees into greater contact with stigmas. A reduction in petal angle ($\Delta\theta' = -13^\circ$ to -17°) enhanced *P. bombiformis* efficiency 30% from 5.39 ± 0.75 grains per visit ($N = 253$ bee visits) to 7.75 ± 1.68 grains per visit ($N = 47$ bee visits, $\chi^2 = 5.24$, $df = 1$, $P < 0.05$). Such a link between host floral morphology, pollination efficiency, and large pollen loads might be advantageous to plants such as *Hibiscus* whose vigorous offspring are products of intense pollen-tube competition (Spira et al. 1992). Thus, selection favouring dynamic floral traits may have encouraged rarer bee visits

that efficiently and simultaneously transfer substantial quantities of multiple pollen genotypes.

Although, single floral visits by *Ptilothrix* appear rather inefficient, when two bees enter flowers and interact physically, the scenario changes entirely. Two *P. bombiformis* by interacting inside blooms mutually increase their pollination efficiency by an astonishing 300% – 1000%. Hence, bee intrafloral behaviour shaped by host floral morphology exerted the greatest influence on this bee’s pollination efficiency. As expected, single visits by pollen-laden females loaded stigmas with twice as much pollen as male visits had (Table 1); a sufficient quantity to initiate seed set in fertile *H. laevis* and largely infertile *H. coccineus* (Fig. 3). However, sequential visitation by *Ptilothrix* bees does not guarantee the accrual of stigmatic pollen. Field observations in Mississippi concur with those of Spira et al (1992) in Maryland, 1 to 5 sequential visits by *P. bombiformis* to *H. moscheutos* flowers were not additive in their ability to accrue pollen onto stigmas (Fig. 2). Bees must strike the stigma to effect pollination, a rather rare event. Unexpectedly however, 7 in 10 floral visits involving two tussling *P. bombiformis* contacted stigmas and transferred compatible pollen loads. Tussles between *Ptilothrix* bees of either gender involve bumping, lunging, biting, grappling, and tumbling around in host flowers (Fig. 1A), agonistic behaviours that increased rates of stigmatic contact from 20% – 30% to 70% (Fig. 2) and transfer rates 11-fold from 3 to 34 pollen grains per bee visit (Table 1). Aggressive male bees often tussle with rival males in flowers or struggle with unreceptive pollen-foraging females during copulation attempts (Santa Anna-Aguayo et al. 2014). Females accosted by males in this way often emit audible distress buzzes from inside flowers. Such tussles while quite rare (5% of floral visits) accounted for 18% of contact visits ($\chi^2 = 94.72$, $df = 2$, $P < 0.0001$, Table 1). Copulation attempts by bees inside flowers resulted in a doubling of stigmatic pollen transfer. In

TABLE 1. Mean amount of pollen transferred per visit (Mean \pm SE) to *Hibiscus* stigmas by *Ptilothrix bombiformis* that interact (contact) or do not (no contact). Recognized visitation interactions include 1) no visits, virgin flowers, 2) single visits by male bees, 3) single visits by female bees, 4) almost simultaneous visits by two males, male and female, or two females, and 5) almost simultaneous visits by two males, two females, or a male and a female that led to a tussle inside a flower. Different letters indicate significantly different means according to multiple Wilcoxon 2-sample exact tests.

Co-visitor	Mean \pm SE stigmatic pollen loads per bout	% all visits or bouts (% all contact visits, \geq 10 pollen grains per bout)	Co-visitor		
			None	Male	Female
None		81% (67%)	0 \pm 0a (n = 11)	3.23 \pm 0.91b (n = 90)	7.37 \pm 1.59c (n = 225)
Male (no contact)		14% (15%)		3.00 \pm 1.24b (n = 10)	5.93 \pm 2.24b (n = 15)
Female (no contact)					5.89 \pm 1.52b (n = 27)
Male (contact, tussle)		5% (18%)		34.5 \pm 18.50* (n = 2)	13.3 \pm 3.10d (n = 8)
Female (contact, tussle)					33.3 \pm 13.6d (n = 8)

fact, *Ptilothrix* females on average transfer 5 times more pollen after tussling with males and other females. Tussling bees improve pollen loading in three ways. First, a withdrawing bee, once disturbed, will often take a rather chaotic spiral flight path out of a flower, which guides it closer to the stigma (Boyadzhiev 1999). Second, two grappling bees often lose traction and become a tumbling ball, which effectively doubles pollinator size and hence the probability of stigmatic contact. Third, pollen grains ejected from the bodies of tussling bees will settle onto host stigmas (Fig. 1A). These three outcomes together may lead to huge surpluses of stigmatic pollen, which in non-pollen-limiting species of *Hibiscus*, intensifies pollen-tube competition, leads to non-random mating, and thereby enhances paternal reproductive success (Spira et al. 1992).

Higher abundances of both male and female oligoleges enhance pollination efficiencies in unexpected ways. Aggressive bees interacting with one another inside flowers during foraging trips and courtship can transfer more host pollen to stigmas. While *Ptilothrix* males pollinate *Hibiscus* less efficiently than females do, they make up for a low individual efficiency with a greater collective efficiency. Male antagonism toward rival males and attempted copula with females can incite enough chaos inside flowers to triple stigmatic pollen transfer and contribute enough pollen grains to sire one-fifth of a host plant's seeds. Moreover, the furling petals of aging *Hibiscus* blooms may further enhance pollination efficiency by coaxing *Ptilothrix* to fly into stigmas. Greater bee abundance and higher species diversity may collectively enhance host pollination through higher incidences of aggression between floral visitors. Therefore, the gestalt concept of "the whole is greater than the sum of its parts" also seems applicable to bee pollination. Pollination is not simply the gradual linear accrual of pollen, but is punctuated with intense pollen loading wrought by pollinators interacting inside flowers, sometimes violently.

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