

COMPARING LEVELS OF GEITONOGAMOUS VISITATION BY HONEY BEES AND OTHER POLLINATORS

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Journal of Pollination Ecology,
35(10), 2023, 170-179
DOI: [10.26786/1920-7603\(2023\)741](https://doi.org/10.26786/1920-7603(2023)741)

Received 13 February 2023,
accepted 2 June 2023

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Abstract—Geitonogamy, the transfer of pollen from one flower to another on the same plant, is often the primary means of self-pollination in flowering plants. For self-compatible plants, self-fertilization may lead to greatly reduced offspring fitness via inbreeding depression. For self-incompatible plants, geitonogamous pollen transfer can result in low seed set, even when stigmatic pollen loads are substantial. For multiple self-compatible, native Southern California plants, we found that honey bees visited more flowers per plant than native insects, and that offspring resulting from pollination by honey bees had reduced fitness relative to those resulting from native insect pollination. Here we investigate whether honey bees generally make more geitonogamous visits than other pollinators using data from a global survey of 41 manuscripts that report the number of flowers visited per plant by different floral visitors. Compared to the average of all non-honey bee visitors in a plant’s pollinator assemblage, honey bees visit significantly more flowers per plant, though they do not differ from the non-honey bee visitor with the highest rate of geitonogamous visitation. However, the disparity between rates of geitonogamous visitation by honey bees and non-honey bee visitors is a function of the frequency of honey bees relative to non-honey bee visitors. As honey bees become increasingly numerically dominant, there is a trend for their rates of geitonogamous visitation to increase, accompanied by a significant decline in flowers visited per plant by non-honey bee visitors. While we found that honey bees visited more flowers per plant compared to the average of other visitors, large or eusocial pollinators were as likely as honey bees to be the most geitonogamous visitor.

Keywords—Honey bees, *Apis mellifera*, native bees, geitonogamy, self-fertilization, self-pollination

INTRODUCTION

The western honey bee (*Apis mellifera* L.) is now found on all continents except Antarctica. In addition to being the most common crop pollinator, honey bees are also the most common single pollinating species in unmanaged habitats worldwide, accounting for approximately 13% of all flower visits (Hung et al. 2018). Though the terms used vary among authors, the “effectiveness” of each pollinator species has been predominantly evaluated as number of pollen grains deposited, or seeds or fruits set, following a single visit to a flower, and the “importance” of each pollinator usually evaluated as the product of its relative effectiveness and its relative frequency

of visitation (reviewed in Ne’eman et al. 2010). Across a wide range of both crop and natural plant species in both its native and introduced range, two recent meta-analyses have shown that the per-visit effectiveness of honey bees does not differ from the average non-honey bee floral visitor (Hung et al. 2019, Page et al. 2021).

While measures of per-visit effectiveness are certainly useful, such measures fail to account for differences in the quality of pollen deposited by different pollinators. The quality of pollen delivered might often be a function of the number of floral visits a pollinator makes per plant (geitonogamous visitation) before moving on to another plant. Geitonogamous visitation is often

the primary means of self-fertilization in plants with large floral displays (Snow et al. 1996; Eckert 2000) and the selfing rate has been shown to increase with successive visits to flowers on the same self-compatible plant (Karron et al. 2009). When reproduction is pollen limited or inbreeding depression is low, geitonogamous pollen transfer might be beneficial, but in many cases, it may reduce reproductive success. In self-incompatible plants, geitonogamous pollen transfer can result in low seed or fruit set even when the amount of pollen delivered is large relative to other floral visitors, as has been documented in both crop and non-crop plants (Diller et al. 2022; Eeraerts et al. 2020). Perhaps more importantly, self-fertilization in self-compatible plants can lead to greatly reduced fitness of offspring compared to cross-fertilization (reviewed in Winn et al. 2011). Reduced offspring fitness due to inbreeding depression can manifest in the proportion of zygotes that become seeds, and in traits after seed set such as germination rate, survival, growth, and reproduction. If honey bees or other pollinators regularly exercise high rates of geitonogamous visitation, their importance as pollinators may be regularly overestimated because resulting zygotes may have greatly reduced fitness.

For example, single visits by introduced honey bees to two self-compatible plant species in California (Travis & Kohn 2023) resulted in similar amounts of pollen deposition as did single visits from the suite of native pollinating insects. However, offspring fitness measured across life stages was 2-to-5-fold higher following single visits by native insects than by honey bees. These large fitness differences between seeds resulting from honey bee versus native insect pollination paralleled those measured following hand self-versus cross-pollination, and likely resulted from the fact that the number of flowers visited per plant by honey bees was approximately twice that of native pollinators for both plant species. In one of the few other studies of the effects of different pollinators on offspring fitness, Herrera (2000) measured the fitness of seeds of *Lavandula latifolia* that resulted from exposure to pollinators at different times of day. Seeds from flowers exposed to pollinators only during the early morning and late evening were significantly less likely to germinate and survive than seeds which resulted from flowers exposed to pollinators only during

the middle of the day. Large bees, the majority of which were honey bees, visit this plant throughout the day, but Lepidoptera and small bees, which made up a minority of pollinators, were more common in the middle of the day than when cooler temperatures prevailed. Herrera (2000) attributed the observed fitness differences to the fact that small bees and, particularly, Lepidoptera, visit fewer flowers per plant than do large bees. The fact that both Herrera's (2000) study and ours (Travis & Kohn 2023) implicate rates of geitonogamous visitation as causing large differences in the quality of pollen delivered, and the fitness offspring produced, motivated this analysis of whether high rates of geitonogamous visitation are a common feature of honey bee foraging in comparison to other floral visitors.

To our knowledge there is no quantitative synthesis comparing levels of geitonogamous visitation by honey bees to those of other pollinators. Here we make use of published studies that record the number of flowers visited per plant before a pollinator leaves that plant for another, or to return to its nest. Due to their current worldwide range, super-generalist foraging habits, high abundances in both agricultural and at least some natural habitats (Hung et al. 2018), and our observations from California, that honey bees visited approximately twice as many flowers per plant before moving on than did the suite of other, native, visitors (Travis & Kohn 2023), we embarked on an analysis of geitonogamous visitation rates comparing honey bees to the other pollinators visiting particular plants.

Here we analyse rates of within-plant visitation by honey bees and other pollinators found in published literature to answer three questions. First, do honey bees visit more flowers per plant before moving on compared to other pollinators? We predicted that honey bees would make more geitonogamous visits than the average among non-honey bee pollinators. Second, compared to the non-honey bee pollinator that makes the most geitonogamous visits, do honey bees consistently visit more flowers per plant? We hypothesized that honey bees would most often exhibit the highest level of geitonogamous visitation among all floral visitors to plants studied. Third, does the difference between honey bees and non-honey bees in flowers visited per plant increase as honey

bee numerical dominance increases? It has been shown previously (Hung et al. 2019) that the proportion of visits from honey bees (their degree of numerical dominance) increases with the abundance of a floral resource. We hypothesized that as honey bee dominance of visitation to a particular plant species increases, so might the disparity in flower visits per plant between honey bees and non-honey bee pollinators. This is because when honey bees focus their foraging on a productive floral resource (Hung et al. 2019), their rates of geitonogamous visitation may increase. Conversely, when honey bees are removing a large amount of the available pollen and nectar from a particular floral resource, other pollinators might reduce their foraging effort on this resource, and their rate of geitonogamous visitation might decline.

MATERIALS AND METHODS

LITERATURE SCREENING

We used three methods to compile data comparing floral visits by honey bees to other flower visitors. First, we conducted a “Web of Science” (WoS) literature search to collect relevant manuscripts. Due to the extremely variable language used to describe insect visitation to flowers, we constructed the following WoS query (modified from Page et al. 2021): “A* mellifera” AND “pollinat* effectiveness” OR “pollinat* efficacy” OR “pollinat* efficiency” OR “pollinat* intensity” OR “pollinat* importance” OR “pollinat* level” OR “flower visits per plant” OR “visits per plant*”. We then employed a similar query in Google Scholar. In July 2022, these searches yielded 609 results. After removing duplicates and erroneous results, we had 522 published manuscripts. Lastly, an additional 30 papers were added after examining literature that was collected and analysed in two previous meta-analyses likely to include pertinent visitation data (Herrera 2020; Page et al. 2021).

For our analysis, we were interested in data quantifying the number of flowers visited per individual plant before moving on (geitonogamous visitation) by honey bees and other flower visitors, which left us with 41 relevant manuscripts which comprised 50 unique plant-pollinator surveys (Appendix 1). For plant species with large inflorescences with hundreds of small

flowers or plants that occurred in extremely high densities, documenting the number of flowers visited per plant was not feasible. Instead, researchers documented the number of umbels or inflorescences visited per plant (e.g. *Asphodelus albus*, Obeso et al. 1992; *Polemonium caeruleum*, Zych et al. 2013), or the number of flowers visited per quadrat (*Seseli farenyi*, Rovira et al. 2004). These studies were also included in our analysis. The proportion of visitors that were honey bees was also of interest and was reported in 35 of these manuscripts. We extracted flower visitation data directly from texts, or occasionally ($N = 8$) from graphs using ImageJ (Schneider et al. 2012). Each manuscript had visitation data for honey bees and at least one other pollinator taxon or group. If there was more than one non-honey bee visitor documented, we calculated the mean number of flower visits per plant for all non-honey bee visitors. We also extracted information such as the names of the plant species, whether it is a crop, flower visitor taxon or group (birds, Coleoptera, Diptera, etc.), if the study was conducted in the honey bee’s native range, and the proportion of visitors that were honey bees, where reported.

The flowers visited per plant by honey bee and non-honey bee visitors were documented for 44 different plant species. Nine of these species were crops, and the remaining were native species found in intact habitats at the study location. Visitation data for some plant species (*Asclepias incarnata* [$N = 2$], *Asclepias syrica* [$N = 2$], *Linaria lialacina* [$N = 2$], and *Vicia faba* [$N = 3$]) were described in multiple manuscripts and included as unique occurrences in our analysis, as study location, flower visits per plant, pollinator assemblages, and relative honey bee abundance were variable between studies.

STATISTICAL ANALYSIS

Paired T-tests, mixed effect linear models, and Fisher’s exact tests were constructed and analysed in R (v. 3.5.0, 2021), using packages lme4 (Bates et al. 2015), nlme (Pinheiro et al. 2019), lmerTest (Kuznetsova et al. 2017), lsmeans (Lenth 2016), ggplot2 (Wickham 2016), and plyr (Wickham 2011). Logistic regressions were conducted using JMP (version 16).

The magnitude of differences between honey bee and non-honey bee flower visits per plant is likely influenced by the total number of flowers

available on a particular plant. To account for this, we calculated Z-scores using raw flower visits per plant data for both honey bees and the average, non-honey bee visitor, then employed a paired T-test. To compare the number of flower visits per plant by honey bees to the non-honey bee visitor that made the most visits per plant, we again constructed a paired T-test with Z-scores from honey bees and the non-honey bee pollinator with the most visits per plant from each study.

The effect of honey bee numerical dominance (i.e. the percent of all foraging bouts that were completed by honey bees, or the proportion of all observed visitors that were honey bees) on Z-scores calculated from visits per plant was assessed with a linear mixed effects model, with visitor identity (honey bee or non-honey bee), honey bee dominance, and their interaction as fixed effects. Because this interaction was significant (see results) we made separate models to assess the effect of honey bee dominance on the Z-scores of honey bees and on non-honey bee flower visitors. Whether or not the study was conducted in the honey bee's native range was included as a random effect and significance was evaluated using likelihood ratio tests.

Pollinators were categorized into 9 groups: honey bees, birds, bumble bees, solitary bees, wasps (hymenopterans in the sub order Apocrita which are neither ants nor bees), Diptera, Lepidoptera, Coleoptera, and ants). We then tested the association of pollinator group with the outcome (being the most geitonogamous visitor or not) after tabulating the number of times each pollinator group was included in a study and the number of times it made the most visits per plant. In two studies, honey bees and a member of another pollinator group were tied for the most visits per plant. In those studies, no pollinator was recorded as the most geitonogamous visitor. We first used the logistic regression platform in JMP to test for overall heterogeneity among groups and then inspected the odds ratios produced to determine which groups differed significantly from one another (Table S1). Because logistic regression statistics can be unreliable when expected values for some cells are small, we then used Fisher's exact test to verify the major findings from logistic regression (Table S1). P-values for pairwise post-hoc tests to assess which groups

differed significantly were adjusted using sequential modified Bonferroni corrections for multiple hypothesis testing.

RESULTS

GEITONOGAMOUS VISITATION BY HONEY BEES AND NON-HONEY BEE FLOWER VISITORS

We found flowers visited per plant data of honey bees and at least one other floral visitor for 44 different plant species representing 27 families. Overall, honey bees made more visits per plant compared to the average of non-honey bee pollinators ($t = 3.236$, $P = 0.002$). However, when honey bee visits per plant were compared to the most geitonogamous non-honey bee flower visitor, there was no significant difference in Z-scores of visits per plant. ($t = -1.367$, $P = 0.178$, Fig. 1).

GEITONOGAMOUS VISITATION AND HONEY BEE NUMERICAL DOMINANCE

Thirty-five of the 41 manuscripts contained frequency data for the floral visitors studied, allowing for the assessment of the relative proportion of observed visitors that were honey bees. Honey bee numerical dominance was extremely variable, as honey bees comprised between 0.5% to 95% of all foraging bouts to particular plants, with an average of 41% (S.E.= 4.65). Neither visitor identity (honey bee or non-honey bee, $P = 0.7749$) or honey bee dominance ($P = 0.8789$) significantly influenced geitonogamous visitation, but the interaction of honey bee dominance and visitor identity was significant ($P = 0.0007$, Table 1). When analysed separately, as honey bees became more dominant in the dataset, Z-scores for visits per plant by honey bees tended to increase but this was not statistically significant ($P = 0.1037$, Table 1). On the other hand, Z-scores for visits per plant by non-honey bee flower visitors decreased significantly as honey bees became more dominant ($P < 0.0001$, Table 1, Fig. 2).

COMPARING DIFFERENT GROUPS OF POLLINATORS

A non-honey bee visitor made the most visits per plant in 25 of the 50 studies in the dataset (Fig. 3). Logistic regression indicated significant heterogeneity among the nine groups in the likelihood of being the most geitonogamous visitor (Table 2, $\chi^2_1 = 30.9$, $P = 0.0001$). Odds ratios suggested that while honey bees, birds, and bumble bee species did not differ from one

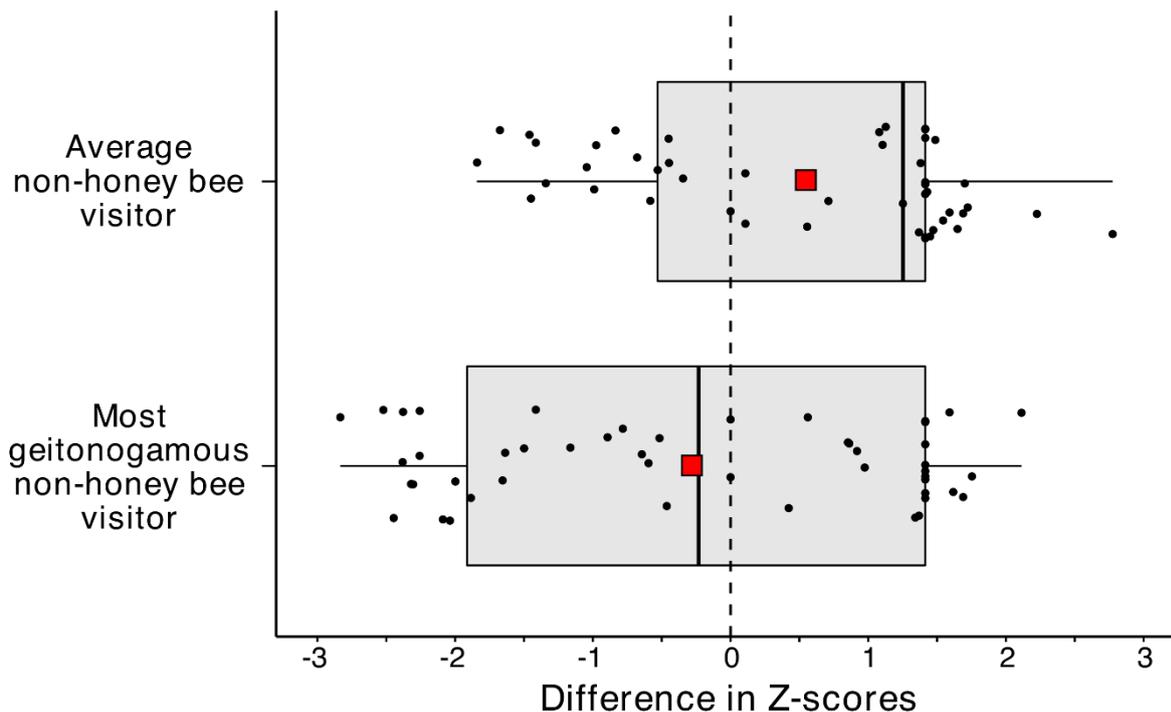


Figure 1. The difference in the Z-scores of the number of flowers visited per plant between honey bees and the average non-honey bee visitor (top bar) and most geitonogamous non-honey bee visitor (bottom bar). Bold lines show medians; red boxes means; grey boxes indicate the middle 50 percent and whiskers the full range of the data. Positive values indicate honey bees visit more flowers per plant compared to non-honey bee pollinators.

another, all three groups differed significantly from solitary bees and wasps in the likelihood of being the most geitonogamous visitor. In addition, odds ratios indicated birds were significantly different from wasps and Lepidoptera though the *P*-values were between 0.04 and 0.05 for these comparisons which involve small sample sizes making statistical inference by this method somewhat unreliable. Neither Coleoptera nor ants

were found to be significantly different from any other groups in this analysis, likely due to the small sample of studies that included them. To gain statistical precision but also avoid being overly penalized for multiple comparisons, we implemented Fisher’s exact test for five groups (honey bees, birds, bumble bees, solitary bees, and wasps). This test showed significant heterogeneity among the included groups (*P* = 0.001). Fisher’s

Table 1. A) Analysis of Z-scores of flower visits per plant by honey bees compared to the average among non-honey bee pollinators (Visitor ID) as a function of honey bee numerical dominance. After discovery of the significant interaction term, separate regressions of the Z-scores for visits per plant of honey bees (B) and non-honey bees (C) were run against honey bee numerical dominance. Honey bee native status (yes or no) was a random effect in all models.

Variable	Test Statistic	P-value
A) Visitor ID	$F_{(1,81)} = 0.082$	0.775
Honey bee Dominance	$F_{(1,81.1)} = 0.023$	0.879
Visitor ID * Honey bee Dominance	$F_{(1,81)} = 12.420$	0.001
Honey bee native status	$\chi^2_1 = 0.301$	0.583
B) Honey bee Dominance	$F_{(1,39.6)} = 2.774$	0.104
Honey bee native status	$\chi^2_1 = 0.261$	0.610
C) Honey bee Dominance	$F_{(1,41)} = 22.611$	>0.001
Honey bee native status	$\chi^2_1 = 0.000$	1

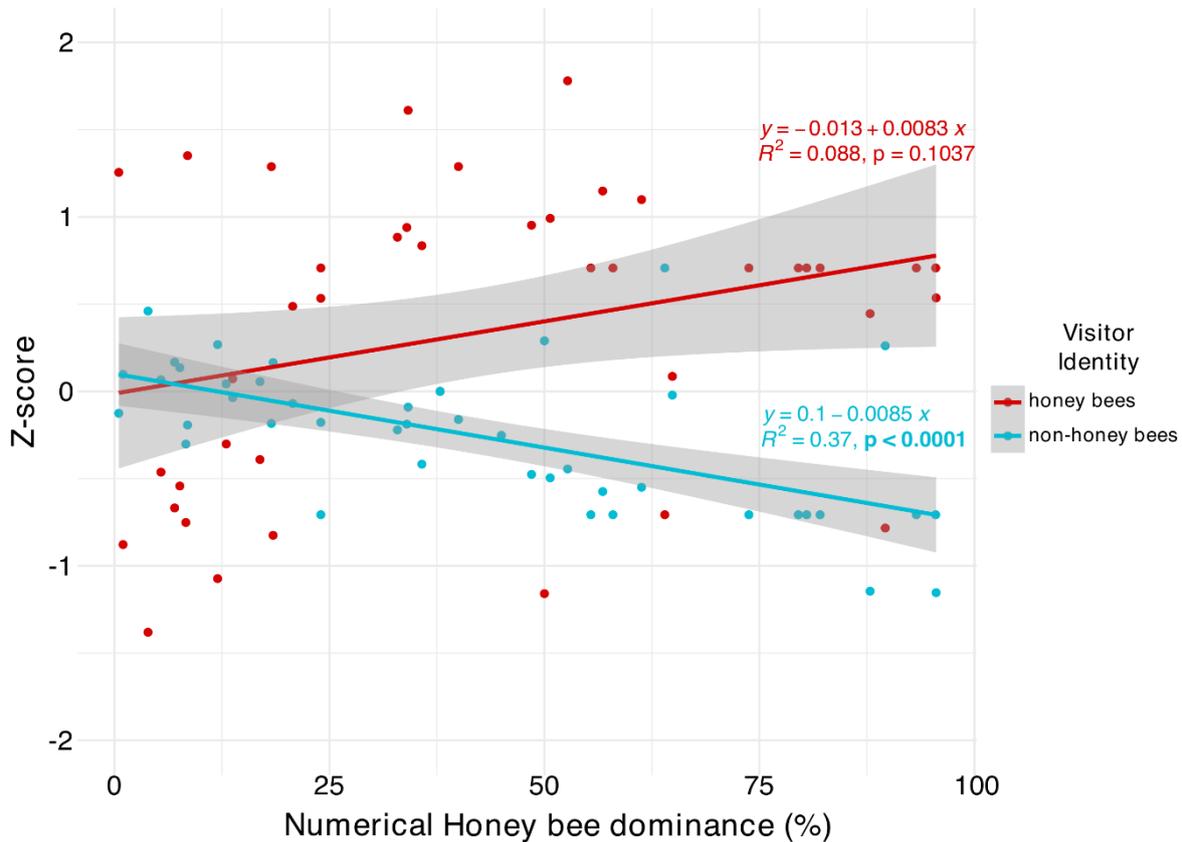


Figure 2. The Z-scores of the number of flower visits per plant for honey bees (red) and non-honey bees (blue) visitors as a function of honey bee numerical dominance. Points represent Z-scores for either visitor type. Regression lines and corresponding 95% confidence intervals are presented for each visitor type.

exact pairwise post-hoc tests confirmed results from the logistic regression analysis. There were no significant differences among honey bees, birds, and bumble bees, but all three groups differed significantly from solitary bees and wasps in the probability of being the most geitonogamous visitor in the pollinator assemblage (Table 2).

DISCUSSION

We found partial support for our predictions regarding geitonogamous visitation by honey bees relative to other pollinators and the effect of honey bee dominance on these relative levels. Though there was considerable variation among plant species studied, overall, our analysis found that honey bees made more flower visits per plant than the average among other pollinators visiting particular species. Contrary to our hypothesis, however, rates of geitonogamous visitation by honey bees did not consistently exceed those of the non-honey bee pollinator with the highest average

number of visits per plant. As honey bee numerical dominance among visitors to particular plant species increased, we found that the difference between levels of geitonogamous visitation by honey bees and the average of other pollinators also increased. As honey bee visitation became more common, they tended to make more visits per plant, but this trend was not statistically significant. However, non-honey bee flower visitors made significantly fewer flower visits per plant as honey bee numerical dominance increased, possibly due to resource removal by honey bees. Conversely, geitonogamous visitation by honey bees was often quite low when they made up only a small percentage (< 25%, Fig. 2) of floral visitors. This may reflect that honey bees found at least some of these species unprofitable and moved on after sampling only a few flowers. Interestingly, since the slopes for changes in levels of visits per plant by honey bee and non-honey bee pollinators were similar, but of opposite sign (Fig. 2), the level of geitonogamous visitation a plant

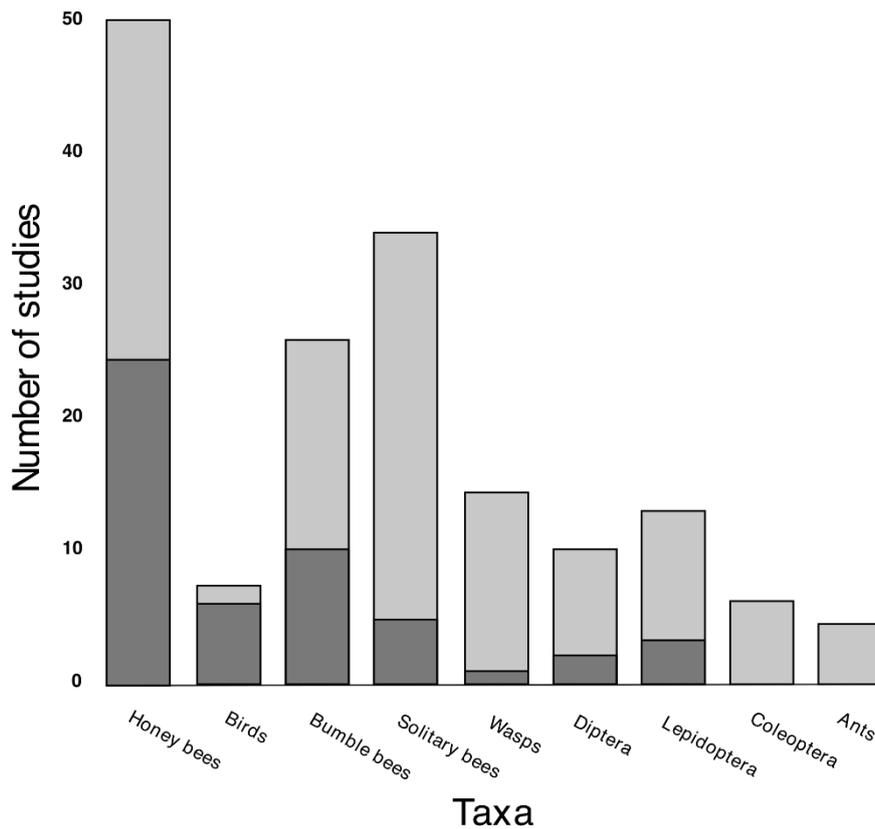


Figure 3. Light shaded bars represent the number of studies a particular floral visitor or group were present in the visitor assemblages. Dark shaded bars represent the number of studies where that visitor or group made the most visits per plant.

Table 2. Fisher's Exact Test and post hoc pairwise comparisons used to assess variation in the probability of a pollinator group being the most geitonogamous visitor (outcome: yes or no).

	P-value
Fisher's Exact Test	0.001
Pairwise Fisher's Post Hoc	Adjusted P-value
Honey bees vs. Birds	0.316
Honey bees vs. Bumble bees	0.894
Honey bees vs. Solitary bees	0.009
Honey bees vs. Wasps	0.014
Birds vs. Bumble bees	0.314
Birds vs. Solitary bees	0.014
Birds vs. Wasps	0.014
Bumble bees vs. Solitary bees	0.026
Bumble bees vs. Wasps	0.046
Solitary bees vs. Wasps	1

receives may not be affected by the frequency of honey bee visitation, and their rate of self-pollination and self-fertilization may likewise be unaffected. This conclusion is supported by the fact that when the interaction of pollinator type

and honey bee dominance was included in the model, there was no main effect of pollinator type or honey bee dominance on the level of geitonogamous visitation a plant received.

It should be noted that, despite the large number of pollination studies screened, relatively few ($N = 35$) met the criteria for use in Figure 2. Therefore, this analysis should most profitably be used to generate hypotheses open to experimental test. To investigate whether levels of geitonogamous self-pollination remain constant across the range of visitation frequency by honey bees to a particular plant, one needs to measure the rate of self-pollination, or self-fertilization of a self-compatible plant, when it is rarely versus frequently visited by honey bees. Increased frequency of honey bee visitation on particular plants is often accompanied by large changes in the frequency and composition of its non-honey bee pollinators (Dupont et al. 2003; Magrath et al. 2017; Prendergrast et al. 2021). For instance, Magrath et al. (2017) showed that the non-honey bee pollinating fauna of *Cistus crispus* is largely displaced by honey bees when they spill over from adjacent agricultural crops that have ceased to

bloom. Interestingly, the reproductive success of this self-incompatible plant declined when honey bees became the dominant floral visitor, possibly due to the transfer of high levels of self-pollen. In another example, introduction of managed honey bees to wildlands in a national park on the island of Tenerife resulted in major losses of pollinator diversity to several plant species (Dupont et al. 2003), again exemplifying the ease with which the honey bee abundance can be manipulated and the effects it may have on reproduction of particular plants could be measured. Such studies would be far more persuasive than the conclusions drawn from a meta-analysis such as ours which involved comparing results across a wide variety of plants using studies not designed to rigorously test hypotheses concerning the behaviours of different pollinators and their effects on plant reproduction.

Honey bees, birds, and bumble bees shared similar likelihoods of being the most geitonogamous visitor, and each of these groups was significantly more likely to visit more flowers per plant compared to solitary bees or wasps. Both body size and sociality are likely involved in differences in behaviour of these types of pollinators. Honey bees have a relatively large body size, large colonies, and must collect a surplus of pollen and nectar to feed their nestmates during periods of resource dearth (Doeke 2015). For birds, heightened levels of geitonogamous visitation are likely due to their large energy requirements compared to endothermic insects (Brown et al. 1978). Bumble bees also may have greater energy requirements compared to most non-honey bee insect pollinators due to their large body sizes and the eusocial nature, likely causing them to forage more methodically compared to solitary insects. Solitary bees were present in many studies ($N = 34$) but were recorded as the most geitonogamous visitor in only four. Two of these four most geitonogamous solitary bees were *Habropoda tarsata* and *Xylocopa virginica* which are similar or larger in size compared to honey bees and much larger than average among solitary bees, again suggesting body size plays a role in determining how many flowers a pollinator visits per plant. Wasps were observed foraging on flowers in fourteen studies but were only the most geitonogamous visitor in one. That wasps also had a significantly lower probability of being the most geitonogamous visitor despite their relatively

large size and sometimes social natures may have to do with the fact that thirteen of the studies included predatory Vespids (*Polistes* and *Vespula*), whose diets often include significant harvesting of non-floral resources. These wasps likely visit flowers for only part of their energy requirements.

The number of flowers visited per plant, though important, may not be the only determinant of the proportion of self-pollen deposited on a plant's stigma by a particular floral visitor. For instance, Diller et al. (2022) showed that birds, on average, visited more flowers per plant than did honey bees on the self-incompatible, mass flowering, *Aloe ferox*. While cumulative pollen deposition by birds and bees was similar, seed set following bee pollination was much reduced in comparison to bird pollination, apparently due to deposition of higher amounts of self-pollen by honey bees. Lower quality pollen delivered by honey bees to *Aloe ferox* may be due to other behaviours such as the fact that a single bee may visit only one plant before returning to the nest and then return to the same large *Aloe ferox* individual on its next foraging bout. Nevertheless, while the number of flowers visited per plant is not the sole determinant of geitonogamous self-pollination, it varies widely among floral visitors and may often contribute to variation in plant reproductive success resulting from visits by different pollinator species.

In this study we showed that, on average, honey bees exhibit higher levels of geitonogamous visitation than the average among other pollinators that visit the same plant. In addition, the disparity in the degree of geitonogamous visitation by honey bees versus non-honey bee visitors increased as honey bees become more numerically dominant among floral visitors. Because honey bees tend to display high levels of geitonogamous visitation, their visits may often deposit high levels of self-pollen. In self-incompatible plants, low seed or fruit set may result. In self-compatible plants, offspring may be more likely to result from self-fertilization and suffer the negative consequences of inbreeding depression. Where true, the importance of a pollinator to a plant's reproductive success will be inaccurately estimated if only the amount of pollen delivered, and the frequency of visitation are considered, as is common for the assessment of a

pollinator's importance. Strong differences in plant reproductive success due to differences in the frequency and amount of self-pollen delivered are quite probable, given the prevalence of self-incompatibility (Igc & Kohn 2006) as well as the high frequency of strong inbreeding depression in self-compatible species (Winn et al. 2011).

ACKNOWLEDGEMENTS

D.J.T. was supported by grants from Sea and Sage Audubon Society, the Messier Family Fund and by a UC MRPI grant to J.R.K. We thank D. Holway and two anonymous reviewers for helpful suggestions on the manuscript.

AUTHOR CONTRIBUTIONS

D.J.T and J.R.K. conceived this work. D.J.T. carried out all data collection. Statistical analysis was performed by D.J.T and J.R.K. The manuscript was prepared by D.J.T and J.R.K.

DISCLOSURE STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

The data used to write this article are available as supplementary data in the online version of this article, see below. Please contact the corresponding author for data requests.

APPENDICES

Additional supporting information may be found in the online version of this article:

Appendix 1. Manuscripts reviewed for pollinator visitation analysis

Appendix 2. Table A1. Logistic regression and odds ratios to determine if a particular pollinator taxon is more likely to be the most geitonogamous flower visitor compared to other taxa.

REFERENCES

- Aizen MA, Harder LD (2009) The global stock of domesticated honey bees is growing slower than agricultural demand for pollination. *Current biology* 19: 915-918. <https://doi.org/10.1016/j.cub.2009.03.071>
- Armbruster P, Reed DH (2005) Inbreeding depression in benign and stressful environments. *Heredity* 95: 235-242. <https://doi.org/10.1038/sj.hdy.6800721>
- Brown CR, Jain SK (1979) Reproductive system and pattern of genetic variation in two *Limnanthes* species. *Theoretical and Applied Genetics* 54: 181-190. <https://doi.org/10.1007/BF00263049>
- Brown JH, Calder III WA, Kodric-Brown A (1978). Correlates and consequences of body size in nectar-feeding birds. *American Zoologist* 18: 687-738. <https://doi.org/10.1093/icb/18.4.687>
- Carneiro LT, Martins CF (2012) Africanized honey bees pollinate and preempt the pollen of *Spondias mombin* (Anacardiaceae) flowers. *Apidologie* 43: 474-486. <https://doi.org/10.1007/s13592-011-0116-7>
- Diller C, Castañeda-Zárata M, Johnson SD (2022) Why honeybees are poor pollinators of a mass-flowering plant: Experimental support for the low pollen quality hypothesis. *American Journal of Botany* 109: 1305-1312. <https://doi.org/10.1002/ajb2.16036>
- Doeke MA, Frazier M, Grozinger CM (2015) Overwintering honey bees: biology and management. *Current opinion in insect science* 10: 185-193. <https://doi.org/10.1016/j.cois.2015.05.014>
- Dupont YL, Hansen DM, Valido A, Olesen JM (2004) Impact of introduced honey bees on native pollination interactions of the endemic *Echium wildpretii* (Boraginaceae) on Tenerife, Canary Islands. *Biological Conservation* 118: 301-311. <https://doi.org/10.1016/j.biocon.2003.09.010>
- Dupont YL, Hansen DM, Olesen JM (2003) Structure of a plant-flower-visitor network in the high-altitude sub-alpine desert of Tenerife, Canary Islands. *Ecography* 26: 301-310. <https://doi.org/10.1034/j.1600-0587.2003.03443.x>
- Eckert CG (2000) Contributions of autogamy and geitonogamy to self-fertilization in a mass-flowering, clonal plant. *Ecology* 81: 532-542. [https://doi.org/10.1890/0012-9658\(2000\)081\[0532:COAGT\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2000)081[0532:COAGT]2.0.CO;2)
- Eeraerts M, Vanderhaegen R, Smagghe G, Meeus I (2020) Pollination efficiency and foraging behaviour of honey bees and non-*Apis* bees to sweet cherry. *Agricultural and Forest Entomology* 22: 75-82. <https://doi.org/10.1111/afe.12363>
- González-Varo JP, Vilà M (2017) Spillover of managed honeybees from mass-flowering crops into natural habitats. *Biological Conservation* 212: 376-382. <https://doi.org/10.1016/j.biocon.2017.06.018>
- Goulson D (2003) Effects of introduced bees on native ecosystems. *Annual Review of Ecology, Evolution, and Systematics* 1-26. <https://doi.org/10.1146/annurev.ecolsys.34.011802.132355>
- Hung KLJ, Kingston JM, Lee A, Holway DA, Kohn JR (2019) Non-native honey bees disproportionately dominate the most abundant floral resources in a biodiversity hotspot. *Proceedings of the Royal Society B: Biological Sciences* 286: 20182901. <https://doi.org/10.1098/rspb.2018.2901>
- Hung KLJ, Kingston JM, Albrecht M, Holway DA, Kohn JR (2018) The worldwide importance of honey bees as pollinators in natural habitats. *Proceedings of the*

- Royal Society B: Biological Sciences 285: 20172140. <https://doi.org/10.1098/rspb.2017.2140>
- Igic B, Kohn JR (2006) The distribution of plant mating systems: study bias against obligately outcrossing species. *Evolution*, 60: 1098-1103. <https://doi.org/10.1111/j.0014-3820.2006.tb01186.x>
- Karron JD, Holmquist KG, Flanagan RJ, Mitchell RJ (2009) Pollinator visitation patterns strongly influence among-flower variation in selfing rate. *Annals of Botany* 103: 1379-1383. <https://doi.org/10.1093/aob/mcp030>
- Kennedy CM, Lonsdorf E, Neel MC, Williams NM, Ricketts TH, Winfree R, Kremen C (2013) A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. *Ecology letters* 16: 584-599. <https://doi.org/10.1111/ele.12082>
- Knight, SE, Waller DM (1987) Genetic consequences of outcrossing in the cleistogamous annual, *Impatiens capensis*. I. Population-genetic structure. *Evolution* 41: 969-978. <https://doi.org/10.1111/j.1558-5646.1987.tb05870.x>
- JMP®, Version 16 (2022) SAS Institute Inc., Cary, NC 1989-2021.
- Magrath A, González-Varo JP, Boiffier M, Vilà M, Bartomeus I. (2017) Honeybee spillover reshuffles pollinator diets and affects plant reproductive success. *Nature Ecology, Evolution* 1: 1299-1307. <https://doi.org/10.1038/s41559-017-0249-9>
- Ne'eman G, Jürgens A, Newstrom-Lloyd L, Potts SG, Dafni A (2010) A framework for comparing pollinator performance: effectiveness and efficiency. *Biological Reviews* 85: 435-451. <https://doi.org/10.1111/j.1469-185X.2009.00108.x>
- Page ML, Nicholson CC, Brennan RM, Britzman AT, Greer J, Hemberger J, Williams NM (2021) A meta-analysis of single visit pollination effectiveness comparing honeybees and other floral visitors. *American Journal of Botany* 108: 2196-2207. <https://doi.org/10.1002/ajb2.1764>
- Prendergast KS, Dixon KW, Bateman PW (2021) Interactions between the introduced European honey bee and native bees in urban areas varies by year, habitat type and native bee guild. *Biological Journal of the Linnean Society* 133: 725-743. <https://doi.org/10.1093/biolinnean/blab024>
- Price MV, Waser NM (1979) Pollen dispersal and optimal outcrossing in *Delphinium nelsoni*. *Nature* 277: 294-297. <https://doi.org/10.1038/277294a0>
- Roubik DW (1978) Competitive interactions between neotropical pollinators and Africanized honey bees. *Science* 201: 1030-1032. <https://doi.org/10.1126/science.201.4360.1030>
- Sáez A, Morales CL, Ramos LY, Aizen MA (2014) Extremely frequent bee visits increase pollen deposition but reduce drupelet set in raspberry. *Journal of Applied Ecology* 51: 1603-1612. <https://doi.org/10.1111/1365-2664.12325>
- Schemske DW, Pautler LP (1984). The effects of pollen composition on fitness components in a neotropical herb. *Oecologia* 62: 31-36. <https://doi.org/10.1007/BF00377369>
- Schemske DW (1983) Breeding system and habitat effects on fitness components in three neotropical *Costus* (Zingiberaceae). *Evolution* 523-539. <https://doi.org/10.2307/2408265>
- Schneider CA, Rasband WS, Eliceiri KW (2012) NIH Image to ImageJ: 25 years of image analysis. *Nature Methods* 9: 671-675. <https://doi.org/10.1038/nmeth.2089>
- Sheridan PM, Karowe DN (2000) Inbreeding, outbreeding, and heterosis in the yellow pitcher plant, *Sarracenia flava* (Sarraceniaceae), in Virginia. *American Journal of Botany* 87: 1628-1633. <https://doi.org/10.2307/2656739>
- Snow AA, Spira TP, Simpson R, Klips RA (1996) The ecology of geitonogamous pollination. *Floral biology*. Springer, Boston Massachusetts, pp 191-216. https://doi.org/10.1007/978-1-4613-1165-2_7
- Thomson DM (2016) Local bumble bee decline linked to recovery of honey bees, drought effects on floral resources. *Ecology Letters* 19: 1247-1255. <https://doi.org/10.1111/ele.12659>
- Travis DJ, Kohn JR (2023) Honey bees (*Apis mellifera*) decrease the fitness of the plants they pollinate. *Biorxiv* 538464 [Preprint] doi: <https://doi.org/10.1101/2023.04.26.538464>
- Waller DM (1984) Differences in fitness between seedlings derived from cleistogamous and chasmogamous flowers in *Impatiens capensis*. *Evolution*: 427-440. <https://doi.org/10.2307/2408501>
- Winn AA, Elle E, Kalisz S, Cheptou PO, Eckert CG, Goodwillie C, Vallejo-Marín M (2011) Analysis of inbreeding depression in mixed-mating plants provides evidence for selective interference and stable mixed mating. *Evolution: International Journal of Organic Evolution* 65: 3339-3359. <https://doi.org/10.1111/j.1558-5646.2011.01462.x>
- Wright S (1984) *Evolution and the genetics of populations, volume 1: genetic and biometric foundations*. University of Chicago press, Illinois.
- Zych M, Stpicyńska M, Roguz K (2013) Reproductive biology of the Red List species *Polemonium caeruleum* (Polemoniaceae). *Botanical Journal of the Linnean Society* 173: 92-107. <https://doi.org/10.1111/boj.12071>