

Chemical Ecology

Bumblebees Exposed to a Neonicotinoid Pesticide Make Suboptimal Foraging Decisions

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Abstract

Bumblebees are important pollinators of agricultural crops and wildflowers, but many species are in decline. Neonicotinoid insecticides are the most commonly used insecticide globally and can have negative sublethal effects on bumblebee colony growth and reproduction. Individual bumblebees can visit hundreds to thousands of flowers a day to forage for their colony. As such, they are a model species for studying optimal foraging, and small impairments to an individual's foraging decisions may have compounding effects on the colony's nutritional intake. We exposed bumblebees (*Bombus impatiens*) to an acute, field-realistic dose of the neonicotinoid insecticide imidacloprid, before allowing them to forage on an artificial floral array. We found that neonicotinoid-exposed bumblebees made suboptimal foraging decisions, as they were more likely to visit flowers located further apart than control bees. This indicates that for a given flower patch, individual bees exposed to a neonicotinoid will likely use more energy and forage less efficiently than unexposed bees, although further studies that directly measure energetic cost are required to confirm this. Given the robust and growing body of evidence demonstrating negative sublethal effects of neonicotinoids on bees, sublethal assessments on non-*Apis* bees should be made mandatory within the regulatory process.

Key words: *Bombus*, insecticide, learning, optimal foraging, imidacloprid, bee behaviour.

Insect pollinators, such as wild bees, are declining globally (Powney et al. 2019, Soroye et al. 2020, Zattara and Aizen 2021). These declines are driven in part by intensive agriculture, which reduces available floral resources and is heavily reliant on insecticides for controlling insect pests (Goulson et al. 2015, Siviter et al. 2021). Neonicotinoid pesticides are the most commonly-used insecticide group in the world (Simon-Delso et al. 2015). As water-soluble insecticides that are transported throughout plant tissue, neonicotinoids can reach the pollen and nectar of both target and nontarget plants, where bees and other pollinators can be exposed (Simon-Delso et al. 2015). Several studies have demonstrated that neonicotinoids can have significant sublethal effects on bees, which has resulted in a ban on the use of certain neonicotinoids (imidacloprid, thiamethoxam, clothianidin) in the European Union (Gill et al. 2012, Feltham et al. 2014, Rundlöf et al. 2015, Stanley et al. 2016, Woodcock et al. 2016, Pisa et al. 2017, Siviter et al. 2018b). However, neonicotinoid use is still common outside the EU, particularly in the United States (Bass et al. 2015).

An individual bumblebee can visit hundreds to thousands of flowers a day to collect nectar and pollen for its colony, and, as such, bumblebees have been used as a model species for studying optimal foraging for several decades (Heinrich 1983). When visiting a patch of flowers, bumblebees quickly learn floral traits that indicate rewarding flowers before following a number of rules to optimize their foraging efficiency between flowers (Heinrich 1983). Previous research has shown that neonicotinoids impair the olfactory learning of bumblebees (Stanley et al. 2015b, Siviter et al. 2018b, Muth and Leonard 2019, Muth et al. 2019, Smith et al. 2020), which can influence the type of flower visited, but how neonicotinoid exposure influences the optimal foraging rules bees have when moving between flowers is unknown. One such rule is that bumblebees will preferentially visit the closest available rewarding flower (Pyke 1979). Neonicotinoid exposure can impair bumblebee flight, motor skills, foraging motivation, and spatial cognition, and so it is often assumed that bumblebees exposed to neonicotinoids will forage less optimally between flowers when foraging on a small patch of flowers

(Williamson et al. 2014, Samuelson et al. 2016, Tosi et al. 2017, Lämäsä et al. 2018, Kenna et al. 2019, Muth et al. 2020, Phelps et al. 2020). For example, bumblebees acutely exposed to the neonicotinoid thiamethoxam fly quicker and show hyperactivity, which could result in bees flying further than necessary to visit equally rewarding flowers (Kenna et al. 2019). However, despite bumblebees being a model species for optimal foraging, the potential impact of neonicotinoid exposure on optimal movement between flowers and foraging efficiency has not been addressed.

Here we assessed whether acute exposure to the neonicotinoid imidacloprid influenced bumblebee (*Bombus impatiens*) foraging decisions between flowers at a small spatial scale. We used existing behavioral data, recorded as part of a previous experiment (Muth et al. 2019), which demonstrated that acute neonicotinoid exposure impaired bumblebee olfactory learning. We (i) tested whether imidacloprid exposure affected the distance between chosen flowers and (ii) addressed whether this neonicotinoid affected the time that bumblebees spent moving between flowers. Based on previous research showing negative effects on bee cognition, motor abilities, and flight (Samuelson et al. 2016, Siviter et al. 2018b, Kenna et al. 2019, Muth et al. 2019), we predicted that bumblebees exposed to imidacloprid would be less optimal foragers, choosing flowers further apart and taking longer to fly between flowers than unexposed bees.

Materials and Methods

The experiment was originally designed to determine the potential impact of the neonicotinoid imidacloprid on bumblebee olfactory and color learning (Muth et al. 2019). We purchased commercially-reared bumblebees (Koppert Biological Systems), and sequentially connected them to a flight arena (L × W × H: 122 × 59 × 59 cm) that contained 48 artificial flowers (Fig. 1). Individual bumblebees were either fed a single acute dose of 0.45ng of imidacloprid in 20µl of 30% (w/w) sucrose (experimental treatment) or 20 µl of untreated 30% (w/w) sucrose (control treatment), 1 hour before being given access to the flight arena. The imidacloprid dose falls within the range found in the nectar and pollen of treated crops (see Table S2 in Siviter et al. 2018b). Half of the flowers in the arena were colored purple and scented with linalool, and half were blue and scented with geraniol (Fig. 1). Bumblebees were trained over two training trials where one type of flower was rewarded, containing 4 µl of 50% (w/w) sucrose (i.e. a positively reinforcing conditioned stimulus; CS+). The other flower type was not rewarding, containing only 4 µl of water (i.e. a neutral or negatively reinforcing conditioned stimulus; CS-). We tested 36 bees from 3 colonies. All bees completed at least one trial and all but two bees (both from the experimental treatment) completed both trials (Trial 1 sample sizes: blue/geraniol as the CS+, purple/linalool as the CS-: control $n = 9$, treatment $n = 9$; purple/linalool as the CS+, blue/geraniol as the CS-: control $n = 9$, treatment $n = 9$). The results of the study demonstrated that neonicotinoid-exposed bumblebees made fewer correct visits in the training phase than control bees. Treated bees also displayed impaired olfactory, but not color learning in an unrewarded test trial (for full details see Muth et al. 2019). The time that bees spent, and distance traveled between visited flowers was not recorded or analyzed as part of the previous work.

To address whether imidacloprid also affected bumblebee optimal foraging choices within a small flower patch, we used the existing videos to assign each flower a spatial location on a grid (Fig. 1). For each flower visit by a bee, we recorded: (i) the spatial location of the flower (see Fig. 1) which allowed us to calculate the minimum

distance that bees needed to fly between visiting flowers. We also calculated (ii) the proportion of rewarding flowers immediately surrounding the flower that the bee had just visited to determine the percentage chance that the bee would visit a rewarding flower. The proportion of the four rewarding flowers immediately surrounding a given flower could be 0%, 25%, 50%, 75% or 100%; (Fig. 1) and was consistent across the control and treatment groups (mean % of rewarding flowers ± SD: control = 48.8 ± 27.47 ; treatment = 47.5 ± 27.7). As such, even if olfactory learning is impaired (Muth et al. 2019), we would expect the average distance between flowers not to differ between treatment groups. We also recorded (iii) the color of the flower, (iv) the time of the visit, and (v) whether the flower was rewarding or unrewarding. Measures iii–v had already been recorded for the analysis used in Muth et al. (2019), but measures i–ii were added to the existing data.

Statistical Analysis

Our analysis was based on an information–theoretic model selection approach. For each analysis we carried out, we compared the full model (containing all factors and covariates), all subsets of the full model, and a null model containing just the random factors and the intercept. We used AICc values to determine which models best fit the data and in cases when $\Delta AICc < 2$, model averaging was used to determine parameter estimates and confidence intervals (see Supp Table S1 [online only] for a full list of models).

We tested whether acute exposure to imidacloprid affected bumblebee foraging in terms of the distance between flowers that bees visited, and the time bees spent flying between them. Both were analyzed using a general linear mixed-effects model (Bates et al. 2015). Treatment (control or imidacloprid-treated), percentage of surrounding rewarding flowers (0, 25, 50, 75, or 100%), flower type trained to (blue/ geraniol or purple/ linalool), reward type (rewarding or unrewarding), visit number (continuous variable), trial (1 or 2) were included within the full model. We also included 5 interactions (i) visit number and treatment (ii) visit number and

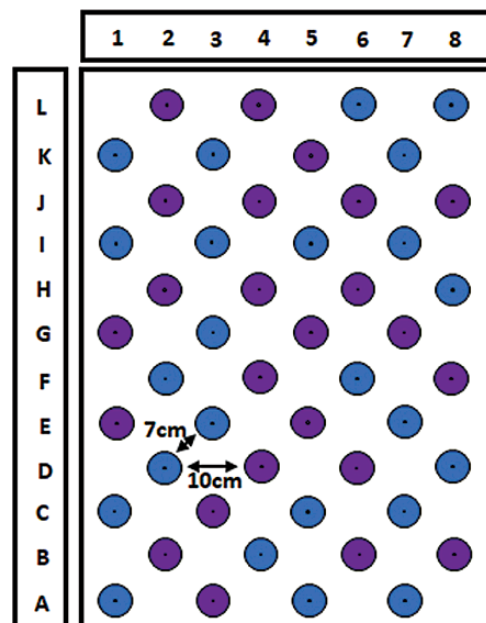


Fig. 1. Diagram of the floral array containing 48 artificial flowers. Grid positions were used to calculate the distance between flowers.

flower type trained to (iii) treatment and rewarding flower (iv) trial number and visit number and (v) a three-way interaction between trial, treatment, and visit number (see [Supp Table S1 \[online only\]](#)). Both the individual bee and colony identity were included as random factors in the analysis addressing the distance traveled, and bee was included as a random factor when analyzing the time spent between flowers. The model failed to converge when colony was also included within the model; note that the time spent between flowers was similar across colonies (see [Supp Fig. S3 \[online only\]](#)). See [Supp Table S1 \[online only\]](#) for a breakdown of all models.

We used R (version 3.5.2) and the packages *Hmisc*, *lme4*, and *MuMin* (Bates et al. 2015, Barton 2016, Harrell and Dupont 2018).

Results

Bumblebees exposed to an acute dose of imidacloprid foraged in a less optimal manner than control bees, visiting flowers that were located further apart ([Fig. 2A](#): treatment, parameter estimate (PE) = 0.79, 95% confidence intervals (CI) = 0.08 to 1.51). As expected, bees flew further when there were fewer rewarding flowers surrounding the flower they were on (percentage of surrounding rewarding flowers, PE = -0.02, CI = -0.03 to -0.01). The flower type to which bees were trained (blue + geraniol, purple + linalool) did not influence these results (see [Supp Tables S1 and S2 \[online only\]](#)).

Acute exposure to imidacloprid did not affect the time it took for bumblebees to fly between flowers ([Fig. 2B](#): treatment, PE = -4.14, CI = -15.17 to 6.88). Bumblebees moved faster between flowers in the second trial compared with the first ([Supp Figs. S1 and S2 \[online only\]](#)): trial, PE = -21.09, CI = -27.03 to -15.16; visit number, PE = -1.20, CI = -1.54 to -0.87; visit number \times trial, PE = 0.55, CI = 0.33 to 0.78) suggesting performance improved over time (for full results see [Supp Tables S1 and S2 \[online only\]](#)).

Discussion

Neonicotinoids can be expressed in the nectar and pollen of treated crops and nontarget wildflowers where bees may be acutely exposed ([Stewart et al. 2014](#), [Botias et al. 2015](#), [Long and Krupke 2016](#)). In the current experiment, we exposed bees foraging on a small spatial scale to a field-realistic dose of a neonicotinoid and found that treated bees flew to flowers spaced further apart than unexposed

bees. This finding suggests that neonicotinoid-exposed bumblebees will use more energy to obtain similar resources.

Flying is energetically demanding and so suboptimal foraging decisions, even on a small scale, will likely compound to negatively impact bee foraging efficiency ([Heinrich 1983](#)). We found that bees exposed to imidacloprid flew on average 11.4 cm between flowers compared with 10.6 cm for unexposed bees, a 7.8% increase. While this difference may seem trivial, bumblebees visit hundreds of flowers in a single foraging bout, and thousands daily, and so even a small fall in efficiency will be energetically costly. For example, in our experiment, bumblebees visited on average 74 flowers (\pm SD 12.5) in a foraging bout. Even when tested on this small spatial scale (L \times W \times H: 122 \times 59 \times 59 cm), bees exposed to imidacloprid flew on average an additional 59cm in a single foraging bout. Further studies that measure the energetic cost of these suboptimal foraging decisions are required to quantify their impact. Importantly, it is also possible that the observed impact on optimal foraging may not scale proportionally, but rather, increase if tested on a larger spatial scale. Furthermore, the bumblebees in our experiment were tested in optimal environmental conditions. Environmental factors such as wind speed ([Hennessy et al. 2020](#)), extreme temperatures and humidity ([Sanderson et al. 2015](#)), and biotic stressors such as parasites ([Gegear et al. 2006](#)) could all interact with pesticide exposure to exacerbate the effects on foraging decisions.

Neonicotinoid exposure can affect bumblebee flight velocity and endurance ([Kenna et al. 2019](#)), which could offer a potential mechanism for our observed results. Neonicotinoids act as agonists of nicotinic acetylcholine receptors (NACHRs) which disrupt cholinergic transmission and lead to neural inactivation in the mushroom bodies of the brain ([Palmer et al. 2013](#)). This can cause hyperactivity ([Williamson et al. 2014](#)), impair motor abilities ([Kenna et al. 2019](#), [Muth and Leonard 2019](#), [Muth et al. 2020](#), [Phelps et al. 2020](#)), and increase flight velocity (at the cost of flight endurance) ([Tosi et al. 2017](#), [Kenna et al. 2019](#)). Impaired motor abilities and hyperactivity could potentially explain the results in the present study; anecdotally, bees appeared to have difficulty flying and landing on flowers compared to controls and flew in a “frantic” manner (personal observation, F.M.). Since we found no effect of the time that bumblebees spent flying between flowers, this may suggest that bees were flying faster between flowers spaced further apart. Regardless of the underlying mechanism, our results suggest that acute exposure to imidacloprid could reduce bumblebee foraging efficiency, which could have cascading effects on colony nutrition, growth, and reproduction ([Gill et al. 2012](#), [Bryden et al. 2013](#)).

Much of the research on neonicotinoid exposure and bumblebee foraging has focused on chronic exposure. Chronic exposure to neonicotinoids can in some cases increase the number of active foragers within a colony as individual workers perform longer foraging bouts and return with less nectar and pollen ([Gill et al. 2012](#), [Feltham et al. 2014](#), [Gill and Raine 2014](#), [Stanley et al. 2016](#)). This can reduce the amount of time allocated to other colony functions such as thermoregulation and brood care ([Crall et al. 2018](#)). Less research has assessed the impact of acute neonicotinoid exposure on bumblebee foraging performance, but acute neonicotinoid exposure can impair foraging motivation, flight duration, and learning and/or memory ([Samuelson et al. 2016](#), [Siviter et al. 2018b](#), [Kenna et al. 2019](#), [Muth and Leonard 2019](#), [Muth et al. 2019](#)) which can have concurrent effects on bumblebee pollination performance ([Stanley et al. 2015a](#), [Stanley and Raine 2016](#)). Previous research would indicate that chronic neonicotinoid exposure has larger effects on pollen foraging than nectar foraging ([Feltham et al. 2014](#)), which may similarly

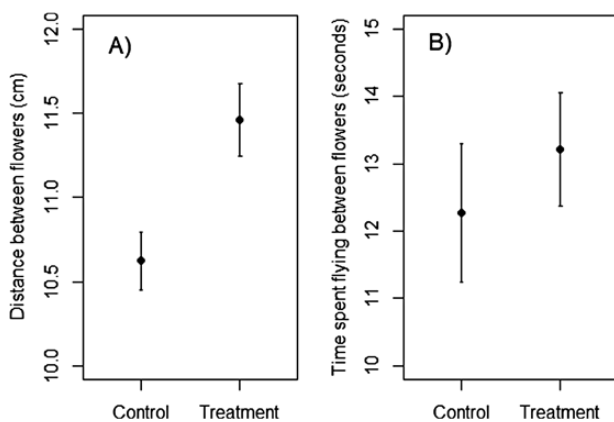


Fig. 2. For bumblebees fed either a control or neonicotinoid treated sucrose solution, (A) the mean distance (\pm SEM) between flowers visited and (B) the mean time spent (\pm SEM) between flowers, when foraging on an artificial floral array.

be explained by effects on cognition, motor coordination, and flight, since pollen collection is a complex motor skill that requires learning (Raine and Chittka 2007). However, our results show that the neonicotinoid insecticide imidacloprid can reduce foraging efficiency when foraging for nectar alone on relatively morphologically simple flowers.

There is now a wealth of data showing negative sublethal impacts of neonicotinoids on bumblebee behavior (Gill et al. 2012, Lämsä et al. 2018, Siviter, et al. 2018b, Muth and Leonard 2019, Muth et al. 2019, Smith et al. 2020). Even considering just a single component of behavior, i.e., learning, there are at least 50 studies on the effects of neonicotinoids (Siviter et al. 2018b, Muth and Leonard 2019). Beyond behavior, a number of studies demonstrate clear negative effects of neonicotinoids on bumblebee colony growth and reproduction (Bryden et al. 2013, Rundlöf et al. 2015, Pisa et al. 2017). This evidence, therefore, suggests that restrictions on the use of neonicotinoids will likely benefit bees (Woodcock et al. 2016). Similarly, novel insecticides, such as flupyradifurone and sulfoxaflor, that are chemically distinct from neonicotinoids, but share a similar mode of action, also have similar sublethal effects on bees (Tong et al. 2019; Siviter and Muth 2020; Siviter et al. 2020a, 2020b) (but see Siviter et al. 2019). The fact that neonicotinoid pesticides are still widely used, and that novel insecticides are similarly harmful, confirms that changes to the agrochemical regulatory process are required if we are to better protect bees and other pollinators from the unwanted consequences of insecticide use (Siviter et al. 2018a, Franklin and Raine 2019, Sgolastra et al. 2020, Siviter and Muth 2020).

Supplementary Data

Supplementary data are available at *Environmental Entomology* online.

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Data Availability

All data is available online (<https://osf.io/t8fgr/>).

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