Pesticide-altered foraging behaviour as a pathway to ecological traps in pollinators: An individual-based modelling approach

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Abstract

Understanding the risks of pesticide exposure in agricultural environments is crucial for maintaining essential agroecosystem services. Pollinators' behaviour can influence exposure routes, but their role in the formation of pesticide-induced ecological traps has received little attention. Using an individual-based modelling framework (BEE-STEWARD), I examined how three behavioural processes – preference for mass-flowering crops, inadvertent social information (ISI) use, and pesticide-induced foraging bias – affect nectar and pollen visitation rates of buff-tailed bumblebees (*Bombus terrestris*) to pesticide-treated crop patches located near or far from the colony. All behavioural processes increased visitation to treated patches, though their magnitude and context differed. Crop preference consistently elevated visitation rates, ISI use amplified nectar foraging on nearby crops when combined with preference, and pesticide-induced bias in foraging behaviour strongly increased pollen visits across distances. These results suggest that pesticides capable of altering patch quality assessment can create ecological traps for pollinators, even when untreated patches are available. Incorporating behavioural pathways into pesticide risk assessments could improve mitigation strategies in pesticide-treated agricultural landscapes.

Keywords: bumblebees; foraging; pesticide exposure; sub-lethal effects; individual-based modelling

1. Introduction

Pesticide use is an integrated element of intensive agriculture aiming for global food security. However, its environmental impact can threaten human health (Smagghe et al. 2023), biodiversity (Sánchez-Bayo and Wyckhuys 2019) and various ecosystem services (Rumschlag et al. 2020). Even though environmentally friendly agricultural approaches have been advocated by both governing and conservation organisations in the last decades, the majority of plant health programs are still based on chemical control (Deguine et al. 2021), so pollinators and natural predators of pests are often at risk due to their frequent exposure to agrochemicals. As exposure risk can negatively impact population stability and species interactions at the ecosystem level (Richman et al. 2022; Nicholson et al. 2024), a better understanding of pesticides' adverse effects on non-target organisms and the way these effects are mitigated is essential to maintain key agroecosystem services and achieve sustainable food production.

The amount of pesticides found in agricultural landscapes is highly inconsistent, and it is not well understood if pollinators can influence their exposure risk when pesticide contamination varies spatially and temporally (Olaya□Arenas et al. 2020). Evidence suggests that some pollinating insects, such as honeybees and bumblebees, cannot detect even the lethal concentrations of pesticides in nectar (Kessler et al. 2015; Parkinson et al. 2023), so foraging individuals cannot behaviourally mitigate their pesticide exposure level by avoiding contaminated food sources (but see Olaya□Arenas et al. (2020) for a lepidopteran counterexample). If so, exposure patterns are most likely determined by how pesticide-treated food patches are distributed within pollinators' foraging range. However, intrinsic and induced preference for specific food sources can modify such distribution-based exposure levels. Natural preference for certain types of flowers (e.g., Lanterman Novotny et al. 2023; Huang et al. 2024) may enhance exposure risk if those plant species are more often treated with pesticides than alternative food sources. Besides, mass-flowering crops can attract pollinators disproportionally to their patches during seasonal blooms (Riggi et al. 2024). Pesticide-induced preference may also emerge through physiological dependence, due to the addictive nature of some active ingredients or co-formulants. For instance, experimental findings proved that pollinators can develop a preference for food treated with neonicotinoid pesticides (Kessler et al. 2015; Arce et al. 2018), and similarly induced preferences were also observed for other substances like alcohol and caffeine (Arnold et al. 2021; Ostap-Chec et al. 2021). Finally, pesticide exposure may alter some specific aspects of foraging behaviour that

lead to a shift in optimal food preferences. For instance, prolonged exposure to pesticides may hinder locating the floral scent source (Kárpáti et al. 2024), or induce biases that result in visiting food sources located further apart (Siviter et al. 2021a) or foraging less persistently (Ohlinger et al. 2022). Pesticide exposure may also reduce activity (Baines et al. 2017) or motivation to forage (Lämsä et al. 2018; Muth and Leonard 2019), or directly alter pollinators' natural preference for the flower types they usually exploit (Gill and Raine 2014; Phelps et al. 2018). Such behavioural changes can also result in higher pesticide exposure if the more frequently visited food patches are more likely to receive – directly or indirectly (Ward et al. 2022) – regular pesticide treatments. Natural and pesticide-induced preferences are not mutually exclusive and may dynamically shape actual exposure patterns together.

The ecological significance of inadvertent social information ('ISI' henceforward) use lies in the possibility of inducing strong correlations in the behaviours and space use of many individuals (Gil et al. 2018). ISI use is a well-known phenomenon in pollinating insects (Grüter and Leadbeater 2014), but its contribution to exposure risk during foraging has remained unexplored. Bees often rely on social cues when they do not have personal information about surrounding food sources or finding them would be more costly (Dawson et al. 2013; Jones et al. 2015), and so ISI use facilitates the localisation and exploitation of new food sources (Worden and Papaj 2005; Avarguès-Weber and Chittka 2014) and helps to avoid predators (Dawson and Chittka 2014). The presence of conspecifics can also provide a cue about the quantity of resources in the visited flowers (Leadbeater and Chittka 2009). However, relying on social information may also limit the time spent searching for alternative food sources and making independent foraging decisions, resulting in sub-optimal foraging (Avarguès-Weber et al. 2018). For instance, attracting conspecifics to the same foraging patches could facilitate the spread of foraging biases or induce preference among colony members.

Ecological traps are maladaptive consequences of naturally adaptive behaviour in human-altered environments (Robertson and Hutto 2006), and ISI use has previously been shown to be responsible for the emergence of such traps in group-living mammals (e.g., Donaldson et al. 2012; Sigaud et al. 2017). In pesticide-treated agricultural landscapes, the interaction between preference for pesticide-treated food patches and ISI use could lead to elevated exposure patterns. Visiting pesticide-treated food patches represents a sub-optimal foraging choice if the associated sub-lethal effects negatively affect individual behaviour, physiology

or colony growth. These adverse effects can be further amplified if ISI use facilitates the exploitation of such patches and thus copying the patch choice of conspecifics increases colony exposure to the pesticide's sub-lethal effects, ultimately leading to severe reductions in fitness (e.g., Baron et al. 2017; Crall et al. 2019).

In this study, I conducted a theoretical investigation about how ISI use, preference for the crop, and a recently demonstrated pesticide-induced foraging bias can influence the pesticide exposure risk of pollinators on an agricultural landscape. I used the buff-tailed bumblebee (*Bombus terrestris*) as the model species, an important pollinator of both crops and wildflowers in temperate regions (Hutchinson et al. 2021), and a common visitor of the used mass-flowering crop, oilseed rape (*Brassica napus*; 'OSR' henceforward), the dominant oil crop in Europe (Perrot et al. 2024). I included the above behavioural processes in the individual-based model implemented in BEE-STEWARD, a research and decision-supporting simulation tool that enables researchers, policymakers and practitioners to predict the impact of land-use characteristics and interventions on colony and population dynamics in various bumblebee species (Twiston Davies et al. 2021). I examined how patch visitation – and thereby the level of exposure – change with the presence of ISI use and different parameter values of preference for OSR in a landscape consisting of a grassland (i.e., natural nesting and foraging habitat) and eight OSR (i.e., foraging habitat during the crop's flowering period) patches. Moreover, a recent study showed that chronic exposure to a formulation containing a neonicotinoid insecticide frequently applied in OSR cultivations (Kathage et al. 2018; Dworzańska et al. 2020) reduced buff-tailed bumblebees' ability to orient toward the floral blend-containing scent source (Kárpáti et al. 2024). By incorporating a similar effect into the model, I also explored how a pesticide-induced behavioural alteration may further modulate foragers' pesticide exposure on this simulated landscape. I assessed the magnitude of the effect of these three parameters on the visit rate of OSR patches at two different distances (i.e., in close or far OSR patches) during nectar and pollen foraging (i.e., proportion of nectar visits and proportion of pollen visits, respectively). In addition, I evaluated the relationship between these visit rates and proxies for pollination capacity and colony fitness under the default model settings.

2. Materials and methods

2.1. Description of the applied model

Simulations were run in BEE-STEWARD (www.beesteward.co.uk; Twiston Davies et al. 2021), a software into which the landscape exploration module of BEESCOUT (Becher et al. 2016) and the individual-based model of Bumble-BEEHAVE (Becher et al. 2018) has been integrated. Pollinator behaviour is determined by stimuli and thresholds that scale up to colony-level processes, enabling the simulation of population survival and performance on the landscape level over multiple years. The underlying parts of the software are parameterised with empirical data from the UK, describing colony dynamics of six bumblebee species and plant species characteristics, including details on flower shape, resource production, and flowering period. The model also incorporates energy budgets and depletion of resources to facilitate the emergence of competition both within and between pollinator species. With sensitivity analysis and validation, the Bumble-BEEHAVE model has been demonstrated to make realistic predictions for buff-tailed bumblebee colonies within the boundaries of independent empirical observations (Becher et al. 2018). For a detailed description of the underlying models and procedures, see Becher et al.'s (2016, 2018) supplementary materials (Appendices S02 and S05, respectively).

In short, the simulated landscape is 2-dimensional, consisting of 300 × 210 grid cells and comprises patches that provide foraging and/or nesting opportunities. Patches are spatially explicit and implemented as one or more food sources, each representing a single plant species. If a patch contains multiple food sources, these can be layered, i.e. placed at the same location and linked with each other. The simulations start at the beginning of the year with an initial number of hibernating queens that, after emerging from hibernation, search for suitable nest sites in semi-natural habitats (exact dates drawn from a characteristic distribution). Queens that survived the searching process and successfully founded a colony must collect resources to lay the first batch of eggs, then forage and care for the brood simultaneously until the first adult workers emerge. After that, the queen's activity is limited to egg laying, while the workers are responsible for nursing and foraging. Foragers' choices on which patch to exploit are based on maximising the foraging rate for pollen and the energetic efficiency for nectar, primarily determined by the distance from the colony, handling time, and the amount of the given resource available in the patch (Knapp et al. 2019). Colony growth depends on resource collection, whereas population dynamics result from the number of mated queens that leave the colony and enter into hibernation until the following spring (Becher et al. 2018).

2.2. Model extensions

I modified the original code by incorporating the parameters ‘ISI use’, ‘preference for OSR’ and ‘foraging bias’ into the model (Table 1). I also included additional functions in the extended version to obtain patch-specific nectar and pollen visitation data. To reduce the computational time of the simulations, the code of the original model was converted from NetLogo 5.3.1 to 6.4.0 (Wilensky 1999).

In the original foraging module, the model sorts the list of known foraging patches by their distances to the bee’s colony. In the presence of ‘ISI use’, foragers’ choice of where to collect nectar or pollen is influenced by the presence of conspecifics. Individuals’ known patches are first divided into two types: one type is where others are currently foraging, and the other type is the unoccupied patches. Then, both lists are sorted by the distances of patches and the bee’s colony, and the lists are compiled so the occupied patches appear first in the compiled list (see the ‘Foraging_SortKnownPatchesListREP’ function in the extended code). The modified function is later called during both nectar and pollen foraging.

When foragers’ activity is set to ‘searching’, inexperienced foragers and those unsatisfied with their previous patch search for a new flower patch. In the original model, foragers’ chance of finding a patch is determined by a default detection probability function based on the distance between a given food source and the colony’s location (‘DetectionProbREP’; Becher et al. 2016). If ‘preference for OSR’ is set to a non-zero value, the ‘foraging_searchingProc’ procedure (which utilises the detection probability function) is modified in a way that a given proportion of bees (represented by the provided non-zero value) search for a patch from the list of available OSR patches during the OSR flowering period, while others bees’ patch-finding process is unaffected by the type of flower present in the patch.

The foraging bias included in the extended model is based on a recent finding of Kárpáti et al. (2024). This study examined the peripheral olfactory detection of a floral blend and foraging behaviour of buff-tailed bumblebee workers exposed to acetamiprid, a neonicotinoid insecticide. One of the main results was that treated bumblebees had a decreased likelihood of finding the floral blend source (that was associated with the presence of syrup during the chronic pesticide treatment), resulting in a random choice between the control and blend scent sources in the behavioural trials. This finding suggests that exposed individuals could not correctly assess which presented scent source was rewarding. As scent is generally associated

with the presence of resources in flowers (Wright and Schiestl 2009), I mimicked a similar effect by modifying the 'Foraging_bestLayerREP' function that reports the most profitable layer within the currently used flower patch based on minimal handling time. In the original model, handling time ('handlingTimePerFlower_s' function) for nectar foraging is determined by the time needed to travel to the next flower plus the time to test whether it contains nectar, divided by the filling level of the flower, plus the time needed to collect the nectar once a filled flower is found. During pollen foraging, handling time is calculated from the time needed to travel to the next flower multiplied by the number of flowers needed to be visited, divided by the filling level of the flower, plus the time needed to collect the pollen once a flower with pollen is found. In the presence of 'foraging bias', filling levels are set to 1, so handling times are not dependent on actual filling levels when bumblebees are exposed to a pesticide. Still, only those patches are considered where the filling level > 0. For simplicity, I assumed that all bees are affected by the pesticide application on OSR patches irrespective of the patch individuals exploit (as the resources stored within the colonies can also be contaminated), but only during the OSR flowering period (i.e., from day 114 to day 136).

2.3. Simulated agricultural landscape with foraging patches

The landscape consisted of one grassland and eight oilseed rape (*Brassica napus*) patches (Fig. 1). The central grassland patch can provide nectar and pollen for the bumblebees year-around and also serves as a nesting habitat where queens can establish new colonies after emerging from winter hibernation. This patch is a good-quality habitat for bumblebees containing 22 different flowering plant species (Becher et al. 2018). The OSR patches represent habitats that are unsuitable for nesting and solely consist of oilseed rape crop that flowers from day 114 until day 136 in each simulation year. All patches had a 200 m radius, resulting in a 125 663.7 m^2 patch area. Due to the spatial distribution of OSR patches around the grassland patch, four OSR patches were closer to the central patch (distance between patch edges: 15 m) than the diagonally located OSR patches (186.9 m). The former patches were termed 'close OSR patches', whereas the latter 'far OSR patches'. The exploitation of close and far OSR patches was examined separately.

2.4. Characteristics of the simulation runs

Simulations were run over 50 years in 50 iterations to determine if the default number of total hibernating queens (set to 500) is appropriate for the model and from which year the population can be assumed to be in equilibrium (Hui 2006; Fig. S1A). Based on the results, I

took year 10 as the year when the bumblebee population was likely to reach equilibrium in the simulated landscape and thus subsequently analysed the data obtained in the 10th year. The initial number of hibernating queens was also 500 in all iterations. I ran the simulations 50 times in all combinations of 'ISI use' (absent or present), preference for OSR (ranging from 0 to 1 by 0.1) and foraging bias (present or absent), totalling 2200 simulations. Models were run individual-based under the 'intermediate foraging mortality' scenario. I also used the setting where males were not unlimited.

I evaluated the model by its ability to reproduce the following patterns. First, as semi-natural habitats support pollinators by providing nectar, pollen and nesting resources over the whole season (Williams et al. 2012; Rundlöf et al. 2014), the simulated bumblebee population reaches equilibrium if only the grassland patch is present (Fig. S1B). Second, preference for OSR and ISI use do not substantially affect the number of pollen and nectar visits, i.e., these parameters have little impact on bees' general foraging activity (Fig. S2). Third, preference for OSR and ISI use do not considerably alter the bumblebee population's pollination capacity and fitness either (Fig. S3).

2.5. Analysis of model outputs

All simulations and calculations were performed using R 4.3.2 (R Core Team 2023) and RStudio v2024.04.2.764 (Posit Team 2024). Instead of applying frequentist hypothesis testing during the analysis, I evaluated the magnitude of differences between simulation runs with different parameter settings and reported parameter estimates with corresponding uncertainty following the recommendations of White et al. (2014). From the simulation outputs, I assembled the following data from the 10th simulation year for subsequent analysis: the number of visits associated with nectar foraging on each patch between day 114 and day 136 (i.e., during the OSR flowering period), the number of visits related to pollen foraging on each patch between day 114 and day 136, total number of adult workers and number of colonies on day 149, and total number of hibernating queens on day 365. I calculated the proportions of nectar and pollen visits from the patch visits data for the close and far OSR patches. Then, I used these variables to characterise the magnitude of exploitation and, with it, the exposure level to the pesticide on these two types of OSR patches. The sum of the proportions determined for the close and far OSR patches represented the total exposure in the simulated landscape during nectar and pollen foraging. The total number of adult workers and the number of colonies variables were used as proxies for the pollination capacity of the

simulated bumblebee population, and the total number of hibernating queens was considered a proxy for fitness (as in Knapp et al. 2019).

I fitted linear polynomial models on the proportion of nectar and pollen visits on the close and far OSR patches with the preference for OSR as a predictor in four scenarios. In the 'baseline' scenario, bumblebees' foraging decisions followed the original model settings (i.e., no ISI use or foraging bias). In the 'only ISI use' scenario, conspecifics' presence in the patches could affect bees' foraging decision on where to collect resources. In the 'only foraging bias' scenario, bees suffered a foraging-related behavioural alteration due to the simulated exposure to acetamiprid on the OSR patches. In the 'both ISI use and foraging bias' scenario, ISI use and foraging bias was present and could influence bees' foraging behaviour. In one iteration, the bumblebee population died out before day 136 of the 10th year (in the 'only foraging bias' scenario), and in an additional one, it went extinct before the end of the 10th year (in the 'baseline' scenario); simulation results from these iterations were excluded from the corresponding analyses. To better illustrate the role of ISI use, I also fitted linear polynomial models on the contribution of ISI use to the proportion of nectar and pollen visits calculated as mean differences between the two scenarios with the absence and presence of ISI use at each preference value in far and close OSR patches. To obtain differences for these calculations, I randomly paired corresponding iterations from the two scenarios. For all models, the optimal number of degrees was determined by calculating the AICc value for each candidate model (with *k* ranging from 1 to 3) using the 'AICcmodavg' R package (Mazerolle 2023). Model assumptions were checked by plot diagnosis using the 'DHARMa' R package (Hartig 2022). The final models were the most parsimonious from the candidate model set with appropriate diagnostics and a good fit (i.e., ΔAICc<2). From these models, I evaluated the magnitude of differences between simulation runs with different parameter settings and calculated parameter estimates with 95% CI to characterise the effect of predictors on specific dependent variables. In the case of second-order polynomial regressions, critical values were computed with the help of the 'mosaic' R package (Pruim et al. 2017). Inverse estimations from the fitted models were calculated using the 'investr' R package (Greenwell and Kabban 2014).

3. Results

3.1. Nectar visits on close OSR patches

Both OSR preference and ISI use influenced which patches bees exploited during the OSR flowering period, but in different ways. OSR preference strongly increased the proportion of nectar visits to nearby OSR patches (Fig. 2a). In the 'baseline' scenario (i.e., using the original model setting), as well as the 'only ISI use' and 'only foraging bias' scenarios, this relationship followed a quadratic trend, whereas in the combined (i.e., 'both ISI use and foraging bias') scenario it was linear (Table S1).

With no OSR preference, the proportion of nectar visits (predicted value [95% CI]) ranged from 0.271 [0.26; 0.282] to 0.376 [0.363; 0.388] across scenarios, lowest in the baseline. At 100% OSR preference, this proportion increased to 0.497 [0.486; 0.508]–0.633 [0.62; 0.646]. ISI use also promoted visitation to nearby patches, with its effect scaling linearly with preference. This pattern held both with (*intercept* = 0.07 [0.05; 0.08]; β = 0.0003 [0.0001; 0.0006]) and without foraging bias (*intercept* = 0.11 [0.1; 0.12]; β = 0.0003 [0.0001; 0.0005]; Fig. 1a inset).

In the absence of OSR preference and ISI use, foraging bias alone increased the proportion of nectar visits to the level expected if 27.5% of bees preferentially foraged on close OSR patches, increasing visits modestly (from 0.271 [0.26; 0.282] to 0.311 [0.299; 0.322]). However, when ISI use was present, foraging bias no longer affected visitation rates.

3.2. Nectar visits on far OSR patches

On far OSR patches, nectar visits increased linearly with OSR preference (Fig. 2b; Table S1). The smallest increase occurred in the 'baseline' scenario (0.064 [0.06; 0.067] to 0.116 [0.112; 0.121]), while the largest was in the combined scenario (0.082 [0.078; 0.086] to 0.137 [0.132; 0.142]).

ISI use had little influence overall. Without foraging bias, its effect did not change with preference (*intercept* = 0.02 [0.01; 0.03]; β = 0.0001 [-0.01; 0.01]). With foraging bias, the contribution was marginal, showing only a weak trend with preference (*intercept* = 0.007 [0.0007; 0.0129]; β = 0.0088 [-0.0015; 0.019]; Fig. 2b inset).

In the absence of OSR preference and ISI use, foraging bias slightly increased nectar visits (0.064 [0.06; 0.067] vs. 0.075 [0.072; 0.077]), equivalent to 23.8% of bees preferentially

visiting far OSR patches. When ISI use was present, however, foraging bias had no additional effect.

3.3. Pollen visits on close OSR patches

OSR preference strongly increased the proportions of pollen visits to close OSR patches (Fig. 3a). In the 'baseline' scenario, the proportion nearly quadrupled (0.111 [0.091; 0.131] to 0.392 [0.372; 0.412]), and with both ISI use and foraging bias, they nearly doubled (0.341 [0.327; 0.355] to 0.579 [0.564; 0.593]).

ISI use alone had little effect (Fig. 3a inset). Without foraging bias, its contribution was highest at 0% (0.036 [0.008; 0.066]) and 100% preference (0.043 [0.014; 0.071]), with a minimum at 47.3% preference. With foraging bias, ISI contributions did not vary with preference (*intercept* = 0.03 [0.01; 0.05]; β = 0.006 [-0.03; 0.04]).

Foraging bias itself had a pronounced effect, raising pollen visits to levels equivalent to 78.1–79.8% OSR preference. The proportion of pollen visits increased from 0.111 [0.091; 0.131] to 0.311 [0.297; 0.325] without ISI use, and from 0.148 [0.127; 0.168] to 0.341 [0.327; 0.355] with ISI use.

3.4. Pollen visits on far OSR patches

A positive effect of OSR preference was also observed on far OSR patches (Fig. 3b). Across all scenarios, visits increased linearly (Table S1), from 0.023 [0.02; 0.027] to 0.104 [0.097; 0.112] in the 'baseline' and from 0.09 [0.083; 0.097] to 0.148 [0.139; 0.157] in the combined scenario.

ISI use had negligible influence regardless of foraging bias. Without bias, its maximum contribution was 0.006 [-0.006; 0.018] at 0% preference; with bias, its effect remained minimal (*intercept* = 0.001 [-0.011; 0.013]; β = 0.002 [-0.018; 0.022]; Fig. 3b inset).

By contrast, foraging bias alone strongly increased the proportion of pollen visits even when OSR preference was absent. This effect matched scenarios with 83.5–85.7% OSR preference, increasing visits from 0.023 [0.02; 0.027] to 0.089 [0.084; 0.095] without ISI use, and from 0.027 [0.024; 0.031] to 0.09 [0.083; 0.097] with ISI use.

3.3. Relationship between the proportions of visits and the proxies for pollination capacity and fitness

In the 'baseline' scenario, the proportion of pollen visits across all OSR patches was positively related to the total number of adult workers (β=469.37 [79.35; 859.4]) and the number of colonies (β=55.63 [16.77; 94.5]), but did not increase the total number of hibernating queens (β=352.4 [-57.92; 762.7]; Fig. 4, Fig. S4). The proportion of nectar visits across all OSR patches had no similar effect on either measure (total number of adult workers: β= 448.9 [-199.1; 1096.93]; number of colonies: β= 27.98 [-37.4; 93.36]; total number of hibernating queens: β= 561.5 [-124.99; 1247.99]).

4. Discussion

The extent to which ecological traits can modify foragers' pesticide exposure and its subsequent impacts is less known in non-*Apis* bees (Raine and Rundlöf 2024). Simulation results indicated that all investigated behavioural processes increased foragers' visit rate on OSR patches in the simulated landscape where the buff-tailed bumblebee population existed in equilibrium. Still, their effect differed substantially in magnitude and context. The original model predicted that, on average, 33.9% of nectar and 14.2% of pollen visits occurred on the close and far OSR patches. As expected, preference for the crop notably increased both visit rates, so when all bees preferred collecting resources from OSR during its flowering period, 61.8% of nectar and 49.8% of pollen visits occurred on these patches. The maximum exposure, however, was observed when ISI use and the modelled foraging bias was also present, increasing the visit rates further to 76% in nectar and 73.3% in pollen foraging, respectively. A decisive result is that the foraging bias alone significantly increased the rate of pollen visits (from 13.4-17.4% to 40-43.1%) on the crop patches, potentially amplifying this exposure pathway to the pesticide's additional adverse effects. Under the original model settings, the proportion of pollen visits on all OSR patches was positively associated with colony growth measures representing the population's capacity for pollination but not with reproductive performance. This observation corroborates with the findings of previous field studies that the presence of a mass flowering crop within the colonies' foraging range does not necessarily translate into a higher production of sexual offspring (Westphal et al. 2009; Williams et al. 2012). Because of that, a preference for mass-flowering OSR crops is unlikely to be strongly favoured by natural selection. However, if the pesticide applied to the crop induces a foraging bias – among other effects – that impairs bees' ability to accurately assess patch depletion, an ecological trap may emerge in pesticide-treated foraging patches, leading

to more pronounced sub-lethal effects on colony growth. This finding implies that even in the presence of alternative food sources during crop bloom (Rundlöf et al. 2022; Carturan et al. 2023), bumblebees may collect resources disproportionally from contaminated resource patches and the resulting risk of exposure can be prolonged if crops with different pesticide application schedules (e.g., consecutive in time) are present within their foraging range.

Chronic pesticide exposure often leads to multiple sub-lethal effects (Siviter et al. 2021a; Desneux et al. 2007; Tosi et al. 2022). Previous studies showed that exposure to field-realistic concentrations of acetamiprid following application (>3360 ppb; see in Tóth and Kovács 2024) can result in various colony- and individual-level symptoms in bumblebees including significant reductions in drone count (Camp et al. 2020a; Weitekamp et al. 2022), drone weight (Weitekamp et al. 2022; Camp et al. 2020b), number of pupae (Weitekamp et al. 2022), number of interactions in the colony, immune response, worker body size (dependent also on food quality; Straub et al. 2023), and biased foraging-related parameters (some dependent also on weight; Kárpáti et al. 2024; Tóth and Kovács 2024). The conducted simulations indicate that even a single pesticide-induced foraging bias can change the patch exploitation pattern of bumblebees in a way that makes other sub-lethal effects more likely to appear. There are various forms of pesticide-induced biases in cognition or foraging behaviour, such as the impairment of spatial memory (Samuelson et al. 2016), disruption of odour coding and discrimination ability (Andrione et al. 2016), foraging less persistently (Ohlinger et al. 2022) or visiting food sources located further apart than unexposed individuals (Siviter et al. 2021b), which might have similar exposure-enhancing effects in bumblebees. This finding strongly suggests that induced foraging biases may have far-reaching consequences in pollinating insects, not necessarily on overall consumption but on the level of pesticide exposure and the likelihood of developing multiple sub-lethal effects.

Exposure to pesticides is known to disrupt within-nest social networks and social interactions in bumblebees (Crall et al. 2018, 2019; Straub et al. 2023), but the extent to which social information use modulates patch visitation patterns represents a crucial gap in knowledge (unlike in honeybees; Hasenjager et al. 2024). These simulations provide the first evidence that ISI use increases visitation rates on specific resource patches (predicted values ranging between 0.007 [0.001; 0.013] and 0.144 [0.132; 0.156]). In accordance with initial expectations and previous findings, ISI use enhanced the impact of natural preference for the crop during nectar foraging, but its effect was mitigated by the pesticide-induced foraging

bias. In this study, ISI use was modelled as simply as possible to obtain conservative estimates of its impact, i.e., patches visited by others were preferred to unoccupied patches irrespective of the number, condition or foraging success of those conspecifics. However, insects can follow various strategies regarding when to use social information and whom they should copy (Grüter and Leadbeater 2014), so incorporating more complex decision rules in the model, if characteristic of buff-tailed bumblebees, could refine the obtained predictions. Second, a few but large patches in the simulated landscape represented a coarse-scale resolution of resources for the foraging bees. While such spatial distribution of crop patches is not unrealistic in modern agricultural environments, the contribution of ISI use to exploitation patterns could be considerably higher than the observed one at a fine-scale resolution of small resource patches.

Simulations showed a substantial discrepancy in how the modelled foraging bias and ISI use affected the visit rates on OSR patches during nectar and pollen foraging. Patch choice decisions related to these two resources differ in the Bumble-BEEHAVE model incorporated in BEE-STEWARD: the calculation of handling time for nectar foragers follows the model of Harder (1983) and the energetic efficiency of exploiting a patch (i.e., energy gained compared to the energy needed to exploit given layer) plays a crucial role in determining the most profitable food source, whereas pollen foraging, in the lack of detailed data and existing models, is modelled to maximise foraging rate. In addition, the priority of nectar and pollen foraging is also different in the model, and individuals always search for nectar if the stimulus for this task in the bee's colony is higher than the bee's associated threshold, regardless of the stimulus-threshold relationship of the other tasks (including pollen foraging). Since these differences do not necessarily explain the observed asymmetry in the effect of the investigated parameters, the possible mechanisms behind the pattern should be explored further, especially as exposure routes via syrup and pollen may lead to distinct sub-lethal effects. For instance, in a study where both routes of exposure to acetamiprid were examined within the same experimental setup (Weitekamp et al. 2022), exposure via nectar resulted in fewer drones in the examined bumblebee colonies, while the pollen exposure route significantly reduced drone weight. Besides, although bees may consume more syrup than pollen, pesticide intakes via the two routes will depend on the pesticide concentrations in these two resources, thus their capacity to exert sub-lethal effects may vary (Azpiazu et al. 2019). Nevertheless, Lonsdorf et al. (2024) recently proved that pesticide exposure via pollen foraging in bumblebees can be satisfyingly predicted by a spatially explicit model characterised only by

the pesticide level and a distance-based foraging process from the colony locations. This finding implies that this exposure pathway could be robustly estimated across heterogeneous agricultural landscapes, even if the available information is limited.

This study provides *in silico* evidence that previously overlooked aspects of pollinator behaviour do not mitigate but increase pesticide exposure risk and corroborates with field observations that mass-flowering crops can competitively dilute pollinator densities in agricultural landscapes (Riggi et al. 2024; Holzschuh et al. 2011). In particular, simulation results imply that a pesticide-induced foraging bias may lead to greater exploitation of crop patches, increasing bumblebees' exposure level to the pesticide in pollen without changing overall pollen consumption. Through positive feedback, such shifts in preference may facilitate the accumulation of sub-lethal effects of pesticides in real-world scenarios. Future efforts should extend the BEE-STEWARD model to more behavioural aspects of pollinator foraging that could potentially influence visitation patterns to differently treated resource patches. In addition, if more sub-lethal effects could be included in the model, it would allow an evaluation of the conditions under which their accumulation is likely to occur and the magnitude of their overall impact on colonies. In that way, we could have an even more powerful tool for predicting the impact of pesticide exposure on bumblebee population dynamics and exploring intervention options to mitigate the pesticide-associated risks for pollinators in agricultural landscapes.

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6. Author contribution statement

The author confirms sole responsibility for the following: conceptualisation, methodology, data curation, formal analysis, investigation, validation, visualisation, and writing.

7. Data availability statement

The extended model is available from the corresponding author on reasonable request. The R script for the analysis of model outputs and data supporting the results are archived and available at Figshare (https://figshare.com/s/acee9613adfc7757267b).

8. Declaration of competing interests

The author has no conflict of interest to declare.

9. Ethics approval

Not applicable.

10. Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work, the author used the GPT-4o and GPT-5 models (OpenAI Inc., USA) to assist writing and improve the readability and language of the manuscript. After using this product, the author reviewed and edited the content as needed and take full responsibility for the content of the published article.

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Table 1. Additional parameters in the extended BEE-STEWARD model.

Parameter	**Description**	**Range (unit)**
Preference for OSR	When this parameter is set above zero, a corresponding proportion of bees search for a patch from the list of available OSR patches during the OSR flowering period.	0-1 (0.1)
ISI use	When using ISI, foragers collect nectar or pollen from patches where conspecifics are present, provided such foraging sites are known.	0 or 1 (1)*
Foraging bias	With foraging bias, filling levels (if >0) are set to 1, making handling times independent of actual filling levels when bumblebees are exposed to a pesticide during the OSR flowering period.	0 or 1 (1)*

*either absent (0) or present (1)

Figure captions

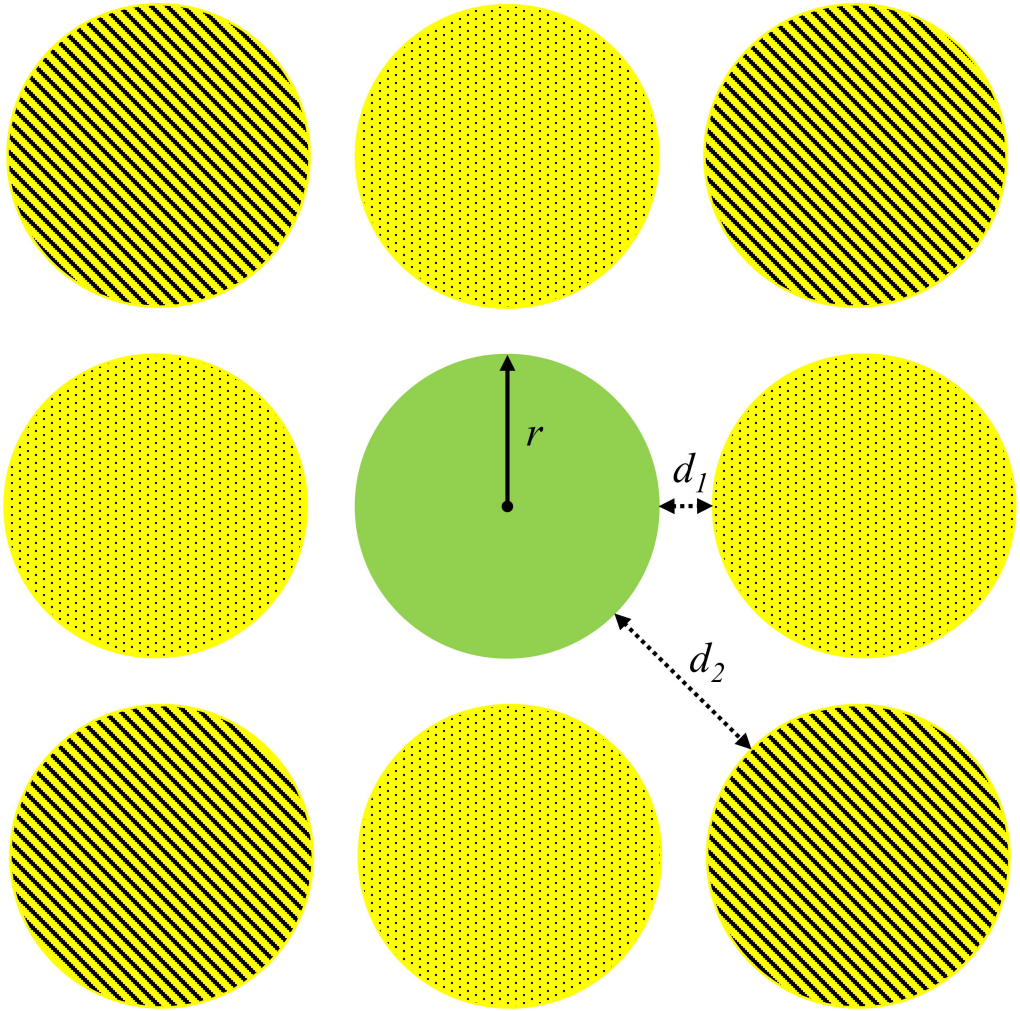
Figure 1. Schematic diagram of the simulated landscape consisting of a grassland (green) and multiple oilseed rape (OSR) patches (yellow). All patches had a 200 m radius (*r*), resulting in a 1256.64 m^2 patch area. Due to the spatial distribution of OSR patches around the grassland patch, four OSR patches were closer to the central patch (d_1: 15 m) than the diagonally located OSR patches (d_2: 186.9 m). The former patches were termed 'close OSR patches' (with dotted pattern), whereas the latter 'far OSR patches' (with diagonal pattern). Distances on the diagram are not on scale.

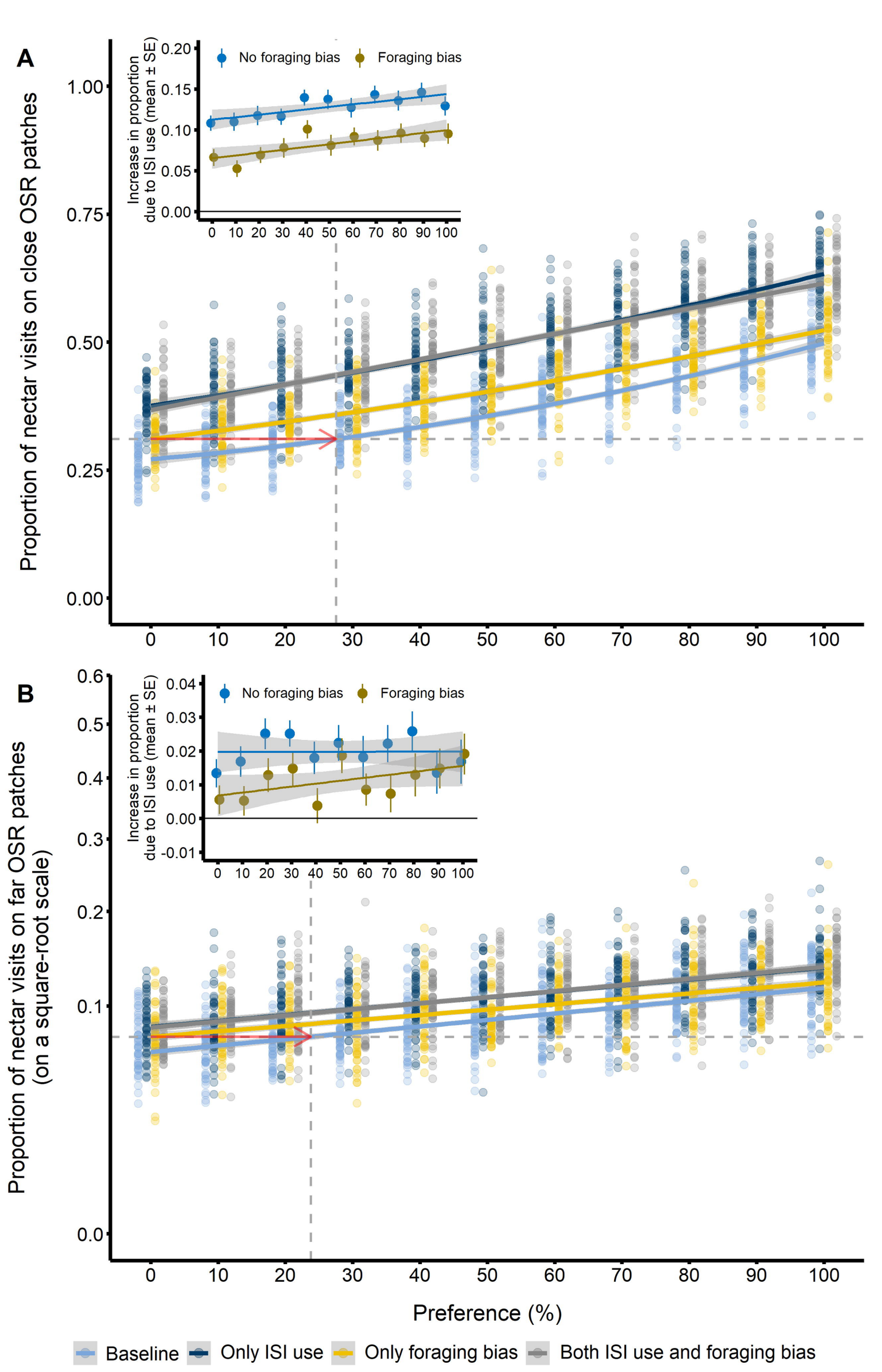
Figure 2. Relationship between the preference for OSR and the proportion of nectar visits on the close (A) and far (B) OSR patches in the examined four scenarios ('Baseline': light blue; 'Only ISI use': dark blue; 'Only foraging bias': yellow; 'Both ISI use and foraging bias': dark grey). Insets indicate the contributions of ISI use to this measure fitted against preference in the absence (blue) and presence of foraging bias (brown). Symbols in the insets represent mean differences (i.e., the mean difference in the proportion of nectar visits between the two scenarios with the absence and presence of ISI use at each preference value), and vertical lines show the corresponding SEs. All trend lines were fitted using polynomial approximations with the degree of the corresponding final models. In the main panels, light red arrows show at which preference value the predicted proportion of nectar visits in the 'baseline' scenario matches the value predicted in the 'only foraging bias' scenario at zero preference (in the presence of ISI use, foraging bias did not increase the proportion of nectar visits on either close or far OSR patches; Table S2). In panel b, the y-axis is on the square-root scale because models were fitted to square-root transformed data.

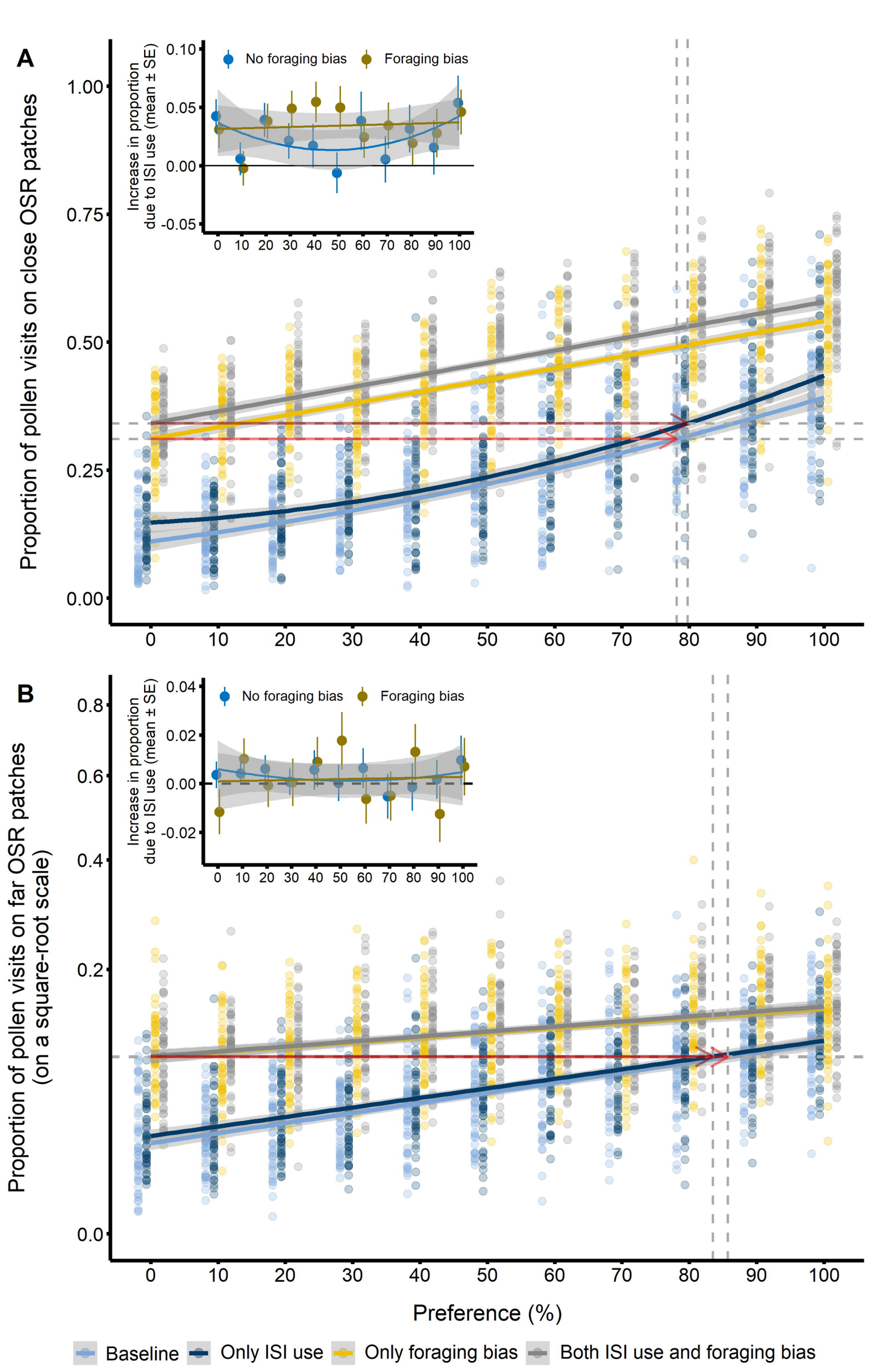
Figure 3. Relationship between the preference for OSR and the proportion of pollen visits on the close (A) and far (B) OSR patches in the examined four scenarios ('Baseline': light blue; 'Only ISI use': dark blue; 'Only foraging bias': yellow; 'Both ISI use and foraging bias': dark grey). Insets indicate the contributions of ISI use to this measure fitted against preference in the absence (blue) and presence of foraging bias (brown). Symbols in the insets represent mean differences (i.e., the mean difference in the proportion of pollen visits between the two scenarios with the absence and presence of ISI use at each preference value), and vertical lines show the corresponding SEs. All trend lines were fitted using polynomial approximations with the degree of the corresponding final models. In the main panels, red

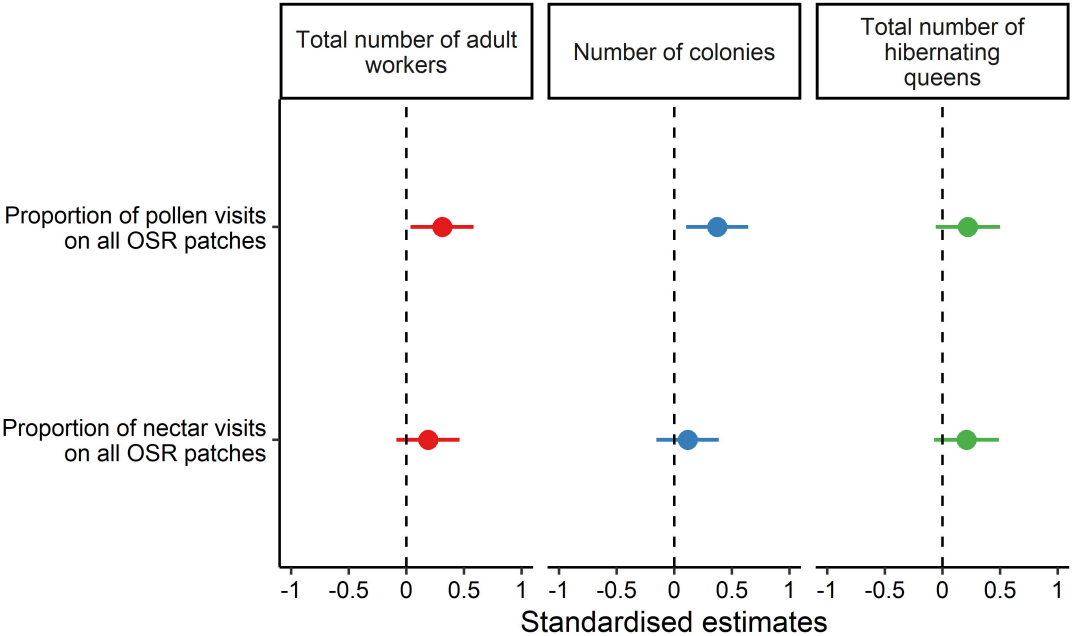
arrows show at which preference value the predicted proportion of nectar visits in the 'baseline' scenario matches the value predicted in the 'only foraging bias' scenario at zero preference (in the absence of ISI use: light red; in the presence of ISI use: dark red; Table S2). In panel b, the y-axis is on the square-root scale because models were fitted to square-root transformed data.

Figure 4. Forest plot for the standardised parameter estimates (with corresponding 95% CI) of the proportion of nectar visits and the proportion of pollen visits on all OSR patches calculated from the linear regressions fitted on the proxies for pollination capacity and fitness. The total number of adult workers and the number of colonies were measured on day 149, whereas the total number of hibernating queens was measured on day 365 of the 10th simulation year.


r
d1
d2


A
Proportion of nectar visits on close OSR patches
1.00
0.75
0.50
0.25
0.00
0 10 20 30 40 50 60 70 80 90 100
Increase in proportion due to ISI use (mean ± SE)
0.20
0.15
0.10
0.05
0.00
No foraging bias
Foraging bias
B
Proportion of nectar visits on far OSR patches (on a square-root scale)
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Increase in proportion due to ISI use (mean ± SE)
0.04
0.03
0.02
0.01
0.00
-0.01
Preference (%)
Baseline
Only ISI use
Only foraging bias
Both ISI use and foraging bias


A
Proportion of pollen visits on close OSR patches
1.00
0.75
0.50
0.25
0.00
0
10
20
30
40
50
60
70
80
90
100
Increase in proportion due to ISI use (mean ± SE)
0.10
0.05
0.00
-0.05
No foraging bias
Foraging bias
B
Proportion of pollen visits on far OSR patches (on a square-root scale)
0.8
0.6
0.4
0.2
0.0
Increase in proportion due to ISI use (mean ± SE)
0.04
0.02
0.00
-0.02
No foraging bias
Foraging bias
Preference (%)
Baseline
Only ISI use
Only foraging bias
Both ISI use and foraging bias


Total number of adult workers
Number of colonies
Total number of hibernating queens
Proportion of pollen visits on all OSR patches
Proportion of nectar visits on all OSR patches
-1
-0.5
0
0.5
1
Standardised estimates