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# Inferring the foraging ranges of social bees from sibling genotypes sampled across discrete locations

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**Abstract** A knowledge of the distances regularly travelled by foraging bees is essential to understanding the movement of pollen across landscapes, and has implications for the conservation of both pollinators and plants. Unfortunately, the movements of bees are difficult to measure directly at ecologically relevant scales. A common strategy for quantifying the foraging ranges of social bees is to sample the genotypes of foragers across a landscape. Individual foragers can be assigned to colonies with polymorphic genetic markers, and the dispersion of siblings in space can be used to make inference about colony locations and foraging movements. Several previous studies have sampled sibling genotypes at discrete locations (for example, at regular points along a transect), rather than in continuous space. Restricting the collection of bees to discrete locations presents a number of considerations for sampling design and data analysis. In this paper, we develop a spatially-explicit, model-based framework for the simulation and estimation of foraging ranges. Using these tools, we simulated experiments to characterise the efficacy of different sampling strategies, and provide an example with actual data that demonstrates the advantages of our method over an approach based on regression.

**Keywords** social bees · foraging range estimation · sibship reconstruction · sampling design · spatial analysis

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## 1 Introduction

Social bees are among the most iconic groups of study in the field of foraging biology. Like other bees, they require pollen and nectar resources to feed themselves and produce reproductive offspring. However, unlike solitary species, social bees forage collectively and are believed to have much higher individual foraging demands due to the high and prolonged demands of brood care (Heinrich 2004). This high level of foraging activity is one potential reason why social bees, such as honey bees, bumble bees, and stingless bees, are managed alongside crops within many agricultural systems, and are also often highly effective crop pollinators (Bohart 1972). While landscape-level foraging is important for both natural and agricultural systems, past work on social bee foraging has largely focused on small spatial scales (Osborne et al 1999) and little is known about the drivers of foraging across landscape scales.

The spatial scale at which colonies forage – the area within which foragers travel to find food, and disperse pollen among plants – is intimately related to the survival and growth of individual colonies (Williams et al 2012; Osborne et al 2008) and the plants they pollinate (Bond 1994). The spatial frequency distribution of foragers from a given colony (*foraging kernels*) is key to predicting the movement of pollen between individual plants and the spatial distribution of floral resources required by bee populations (Goulson et al 2010; Lonsdorf et al 2009). However, the foraging distances of small insects such as bees are extremely difficult to measure directly. Past studies examining foraging ability have largely used feeder or colony member displacement experiments to determine maximum foraging distances (reviewed in Greenleaf et al 2007); while these studies allow for species-comparisons in feeder/displacement response, they do not measure foraging in response to the distribution of floral resources. More recent methods use radio or radar tracking

(Osborne et al 1999; Lihoreau et al 2012), and these provide much more detailed information about finer scale foraging movements, response to local resources, and changes in foraging movements across a foraging bout. However, these studies are often costly and labour intensive, and do not scale to populations and landscapes. Technologies which can measure movements across a wide radius (such as harmonic radar) are often only suitable for open, unobstructed habitats and require colonies to be either located (a non-trivial task) or to be reared and placed at selected locations, limiting use for wild colonies.

For social bees, genetic tools provide a cost-effective means to estimate foraging range in wild populations, without prior identification of the colony locations (Darvill et al 2004). The essential idea is that sibling foragers can be associated with the same colony using polymorphic genetic markers, and the dispersion of siblings in space carries information about both foraging distance and the colony location. Since Chapman et al (2003) and Darvill et al (2004) first proposed using the spatially-referenced genotypes of foraging bumble bee siblings to make inferences about foraging patterns, many studies have employed this technique to address questions about the spatial ecology of bumble bees. Initial efforts used sibling-genotype derived distances to compare the foraging ranges of different bumble bee species (Knight et al 2005), whereas more recent applications have examined how foraging range is influenced by the floral community (Jha and Kremen 2013), land use (Dreier et al 2014), and plant phenology (Jha and Pope, *in review*). Foraging siblings that are captured in continuous space bring the most information about colony locations. However, sampling in continuous space involves humans searching for bees across the entire foraging kernel (often multiple km) with insect nets, and so requires a considerable effort to cover moderate spatial and temporal scales. A less laborious alternative is to catch bees and sample their DNA at discrete locations (see for example Darvill et al 2004; Jha and Kremen 2013). Discrete sampling can be performed in a systematic way across large spatial areas, either by active trapping (with insect nets), or with passive trapping (such as with blue vane traps). Passive traps can be left for several days, providing genetic material with relatively little monetary and logistic cost, although all passive traps which provide genetic material from bees are lethal. However, the accuracy and efficacy of these schemes has not been examined critically, and often the methods used to analyse these data falsely assume that data was collected in continuous space (Darvill et al 2004; Knight et al 2005; Jha and Kremen 2013).

The literature on trapping methodology for the estimation of population densities and space use is vast and encompasses both design (e.g. Foster and Harmsen 2012; Sun et al 2014; Royle et al 2013b) and analysis (e.g. Worton 1987; Efford 2004; Royle et al 2013a). In our opinion, this applied literature provides valuable insights into methodological approaches for inferring foraging movements from sibling genotypes. There are three main facets to trapping social bees that deserve close consideration, given their relevance to predicting nesting and foraging dynamics. First, the spatial distribution of forage and colony densities can range from clumped to homogeneous and should be considered in any generative model that aims to describe nesting and foraging behaviour. Specifically, we posit that relative visitation rate to a spatial location must consider forage quality, as this affects bee patch visitation (Robertson et al 1999). Past studies on social bee colonies have shown that foraging kernels are not always symmetric (e.g. Visscher and Seeley 1982), and thus models should not automatically assume symmetry. Instead, we expect that when averaged over individuals, foraging patterns will reflect the distribution of forage in the landscape, relative to the colony location. The traps may non-randomly vary in attractiveness, as a function of the forage quality near the traps; and unobserved (but attractive) areas of the landscape may 'compete' with traps for bees.

Second, average foraging distance can be estimated at different levels of organisation, and it is important to distinguish among them. For example, past studies have estimated the foraging distance of individuals (Zurbuchen et al 2010); the average foraging distance of colonies (Jha and Kremen 2013); and the average foraging distance across landscapes and species (Knight et al 2005). The estimation of individual foraging distances can be rephrased as the estimation of colony locations, and is a necessary step in estimating the average foraging range at higher levels of organisation. In the past, the colony location has typically been estimated by the centroid of forager locations (Knight et al 2005; Jha and Kremen 2013). When bees are sampled at discrete locations, the centroid will clearly be a function of the distance between traps and the trapping arrangement, and so is a biased estimate of the colony location. Whether or not bees are captured in discrete or continuous space, the reality is that the locations of colonies are unknown but can be estimated along with the foraging kernel. To accommodate these considerations, we advocate a model-based approach which explicitly incorporates the method of data collection and the spatial locations of collections.

Third, estimates of foraging will depend on the spatial distribution of traps (Sun et al 2014), and the design of the trapping scheme should be carefully considered with reference to the size of the landscape and the question under investigation. For example, if the question revolves around the relative differences in average foraging range across landscapes, biased but consistent estimates may accurately answer the question. Studies which have used discrete trapping to sample bee genotypes have typically done so by collecting along a transect (Darvill et al 2004; Knight et al 2005;

Goulson et al 2010; Jha and Kremen 2013). Traps arranged in grids are commonly used when estimating movement and density of mammals (but see Parmenter et al 2003; Pearson and Ruggiero 2003). A compromise between a single transect and a grid is two perpendicular transects (a 'cross'), and another option is to place traps at random throughout the landscape. In general, the efficacy of a trapping scheme depends upon the extent and density of the grid, in relation to the spatial scale at which animals are moving (Sun et al 2014) and the overlap between the animals' range and the traps (Bondrup-Nielsen 1983). By trap density, we mean the number of traps within a fixed area and given trap arrangement, such that increasing the density will decrease the space between traps.

In this paper, we provide four main contributions: **(1.)** A simple simulation scheme that generates foraging kernels for various colonies, and incorporates the spatial location of the colony and the spatial arrangement of forage. From these foraging kernels, simulation of samples within a trapping array follows easily. **(2.)** A Poisson-process based approach to estimating foraging range from trapping data, that integrates over uncertainty in colony location and incorporates differential attractiveness of traps. **(3.)** A set of simulated experiments to assess the efficacy of different trapping schemes for estimating average foraging range at varying levels of sampling effort and organisation (i.e. colony, landscape). **(4.)** A comparison of our model to a previously used regression method, when applied to a dataset of bumble bee collections across a heterogeneous floral landscape. Our results illustrate how a combination of the genetic identification of sibships and passive trapping can be adapted to specific goals, such as identifying colony locations, or testing hypotheses about differences in foraging distance across landscapes.

## 2 Methods and models

### 2.1 Simulation of data

To make simulation more tractable, we discretise continuous space into a raster by dividing the landscape into a grid of equal sized cells: let $\mathscr{J}$ be the set of all cells. Assume that some number of colonies nest in the landscape: let $\mathscr{C}$ be the set of all colonies. Let $\eta(j)$ be the rate at which colonies occur in cell $j \in \mathscr{J}$; then colonies are independently located according to an inhomogeneous Poisson process, with a given colony occurring in cell $j$ with probability $\frac{\eta(j)}{\sum_{i\in J}\eta(i)}$.

We generate foraging kernels for colonies via a simple Poisson process model. Let $\lambda_i(j)$ be the rate of visitation for colony $i \in \mathscr{C}$ at cell $j \in \mathscr{J}$. Let $\{s,c\}$ be indices which denote the cell and colony for a random 'visitation' event in the Poisson process (an event where a bee of a given colony visits a given cell). For a given event, the probability that a bee from colony $i$ visits site $l$ is:

$$\Pr(s = l|c = i) = \frac{\lambda_i(l)}{\sum_{j\in\mathscr{J}}\lambda_i(j)} \tag{1}$$

Equation 1 gives the foraging kernel for colony $i$: the frequency of bees from that colony across the landscape. Using the foraging kernels of all colonies in the landscape, we can calculate the frequency with which different colonies will be represented in traps. Let $\kappa$ be some subset of cells where traps are located. The probability that a given bee from colony $i$ visits one of the cells (traps) in $\kappa$ is:

$$\Pr(s \in \kappa|c = i) = \sum_{k\in\kappa}\Pr(s = k|c = i) = \frac{\sum_{k\in\kappa}\lambda_i(k)}{\sum_{j\in\mathscr{J}}\lambda_i(j)}$$

The total number of foragers in the landscape is $N$, and the number of foragers in colony $i$ is $n_i$. The probability that a bee selected at random from the population belongs to colony $i$ is $\Pr(c = i) = \frac{n_i}{N}$. From the definition of conditional probability, the probability that a bee from a given site $j$ belongs to colony $i$ is:

$$\Pr(c = i|s = j) = \frac{\Pr(s = j|c = i)\Pr(c = i)}{\Pr(s = j)} \tag{2}$$

Where the denominator is the probability that a bee (from any colony) visits cell $j$, and is calculated as

$$\Pr(s = j) = \sum_{i\in\mathscr{C}}\Pr(s = j|c = i)\Pr(c = i)$$

Therefore, the probability that a bee (from any colony) visits any of a set of cells $\kappa$ with traps is:

$$\Pr(s \in \kappa) = \sum_{i\in\mathscr{C}}\Pr(s \in k|c = i)\Pr(c = i)$$

Given that a bee visits any of a set of cells $\kappa$, the probability that a bee from any colony visits a *particular* trap $k \in \kappa$ is:

$$\Pr(s = k|s \in \kappa) = \frac{\Pr(s = k)}{\Pr(s \in \kappa)} \tag{3}$$

To simulate from the joint distribution $\Pr(s,c|s \in \kappa)$, draw $k \in \kappa$ from $\Pr(s = k|s \in \kappa)$ (Equation 3), draw a value of $c$ from $\Pr(c = i|s = k)$ (Equation 2), and update $N$ and $n_i$ accordingly. Repeat this process until a stopping rule is reached, such as the acquisition of a certain number of samples per trap. Because a bee is removed from the population with each trapping event, the conditional probability in Equation 2 changes during the trapping process. Effectively, the more bees from a colony that are captured, the less likely is a subsequent capture from that colony.

Given this model, the expected foraging distance can be calculated at various levels of organisation. Define $d_{ij}$ as the Euclidean distance between the centroids of the cell $j$ and and the cell where colony $i$ is located, i.e. as $d_{ij} \equiv \|x_j -$

$\delta_i\|$ where $x_j$ and $\delta_i$ are vectors, respectively containing the Cartesian coordinates of centroids for cell $j$ and the cell containing colony $i$. The expected foraging distance for a colony can be calculated from the foraging kernel $\Pr(s|c=i)$ as $\mathbb{E}[d_{ij}] = \sum_{j\in\mathscr{J}} \|x_j - \delta_i\| \Pr(s=j|c=i)$. The expected foraging distance for a landscape can be calculated by averaging over colonies as $\mathbb{E}[d] = \sum_{i\in\mathscr{C}} \Pr(c=i)\mathbb{E}[d_{ij}] = \sum_{i\in\mathscr{C}} \frac{n_i}{N}\mathbb{E}[d_{ij}]$.

The distribution of colonies in space and the foraging kernel of a select colony are determined by the functions $\eta(j)$ and $\lambda(j)$. For succinctness, we define both as simple log-linear functions. Let the quality of nesting resources within cell $j$ be $v_j$; then the rate with which colonies occupy the cell is $\eta(j) = \exp\{\phi v_j\}$. The parameter $\phi \in [0,\infty)$ controls the degree to which colonies are clustered in cells with high-quality nesting resources. Let $f_j$ represent the quality of floral resources in cell $j$, and let $d_{ij}$ be the geographic distance from the cell to colony $i$ (as defined in the previous paragraph). The visitation rate to a cell from the colony is $\lambda_i(j) = \exp\{-\beta d_{ij} + \theta f_j\}$. The parameters $\beta, \theta \in [0,\infty)$ control the degree to which bees are concentrated close to the colony and in cells with a high forage quality. The overall effect is to generate asymmetric foraging kernels which reflect to a greater or lesser extent the distribution of floral resources across the landscape (Figure 1A). We note that these foraging kernels are marginal with respect to individuals: we do not seek to replicate patterns of individual behaviour, but instead to represent the long-run frequency of foragers across the landscape, for the colony as a whole.

Given that the locations of both colonies and bees are modelled as a function of an underlying resource landscape, how is this resource landscape determined? We simulate the spatial distributions of nesting and floral resources as independent Gaussian random fields under a Brownian variogram (Schlather et al 2015). Each variogram model has a single parameter that controls the spatial clustering of resources: parameter values close to zero generate landscapes where resources of varying quality are more or less evenly scattered through space (white noise), while parameter values close to two generate landscapes where resource quality follows a gradient.

## 2.2 A model for discrete trapping

The simulation procedure described in section 2.1 uses a spatially explicit model of forage and nesting resources across the landscape. In contrast, when estimating foraging ranges from trapping data we assume that the investigator has no knowledge of colony sizes or the distribution of nesting and foraging resources, but can assess forage quality at the exact location of the trap. In other words, the investigator has a limited understanding of the landscape and would like to estimate foraging ranges from collections at traps. To estimate colony locations and foraging distances, a simple model considers a set of traps $\kappa$ in continuous two-dimensional space, with spatial coordinates $x_k = \{x_1^k, x_2^k\}$ and quality of forage $f_k$ for trap $k \in \kappa$. The occurrence of bees from colony $i$ in the traps follows a Poisson process with rate $\lambda_i(k)$. A simple form for $\lambda_i(k)$ allows the visitation rate to decay with the distance between trap and colony, to increase with forage quality, and also incorporates random trap-specific and colony-specific variation. For example,

$$\begin{aligned} \ln\lambda_i(k) &= -\beta\|x_k - \delta_i\| + \theta f_k + \zeta_i + \varepsilon_k, \\ \varepsilon_k &\sim \mathscr{N}(0, \sigma^2\Sigma(\rho)),\ \zeta_i \sim \mathscr{N}(\mu, \tau^2) \end{aligned} \tag{4}$$

In this model, the set of unknown parameters which must be estimated is $\Theta = \{\delta_i, \beta, \theta, \zeta, \varepsilon, \mu, \sigma^2, \rho, \tau^2\}$: where $\delta_i = \{\delta_1^i, \delta_2^i\}$ are the spatial coordinates of the colony, $\beta$ controls the distance-decay of the rate with distance between colony and trap, $\theta$ controls the attractiveness of forage quality at traps, $\zeta_i$ is a colony-specific random intercept centered around a global intercept $\mu$ with standard deviation $\tau$, and $\varepsilon_k$ is a trap-specific random effect with standard deviation $\sigma$ and spatial correlation matrix $\Sigma$ with parameters $\rho$. Assume that some set of colonies $\mathscr{C}$ is observed during the course of the study: given a set $y = \{y_{ik} : k \in \kappa, i \in \mathscr{C}\}$ of trapped bees which have been associated with the $i$th colony through genetic markers, the likelihood can be written as

$$\mathscr{L}(\Theta|y) = \prod_{i\in\mathscr{C}} \left( \frac{\exp\{-\Lambda_i(\Theta)\}}{Y_i!} \prod_{k\in\kappa} \lambda_i(k;\Theta)^{y_{ik}} \right)$$

where $\Lambda_i(\Theta) = \sum_{k\in\kappa} \lambda_i(k;\Theta)$ and $Y_i = \sum_{k\in\kappa} y_{ik}$.

The intuition underlying the model is that traps which are located further away from a colony receive fewer bees from that colony, and traps which are located in resource-rich areas will receive more bees. Depending on the colony location, and on the relative attractiveness of traps, different frequencies of bees are expected to occur at traps. By finding values of parameters which maximise the similarity between expected and observed frequencies, we can estimate the geographic locations of colonies, the parameters underlying the foraging kernel, and the attractiveness of traps.

An important point is that the model described here treats colony locations as unknown quantities which must be estimated *simultaneously* with the parameters governing visitation rates. In practice, this is an important consideration as there is dependence in the joint distribution of colony locations and the parameters which determine visitation rates to traps. For example, consider a scenario where three traps have captured equal amounts of bees (Figure 1B). The traps have different levels of forage quality, indicated in Figure 1B by colour (darker shades indicate higher quality). The shape of the conditional probability distribution of the colony location depends on the attractiveness of forage quality to foraging bees (parameter $\theta$ in Equation 4), and how averse the

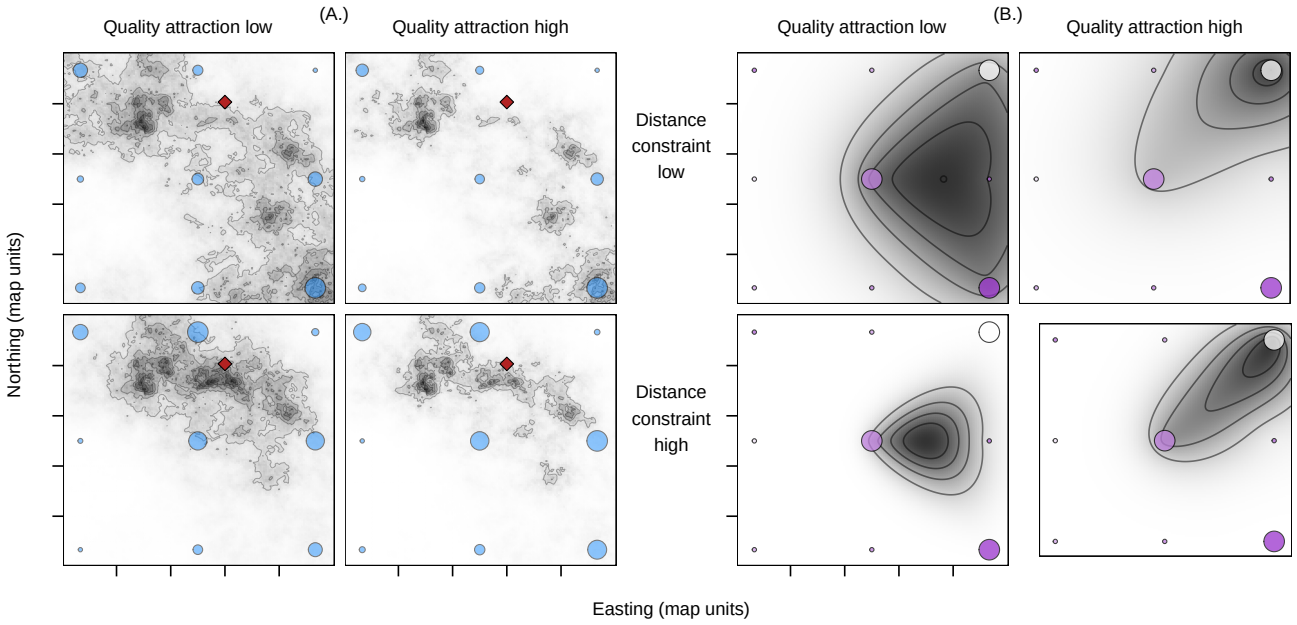


**Fig. 1** **(A)** The foraging kernel of bees (darker areas represent higher visitation) as a function of two parameters, which control the distance that bees travel (rows) and their affinity for quality forage (columns). The effect of increasing 'attractiveness' of forage quality is to focus bee activity on high-quality regions. The effect of the distance constraint is to focus bee activity on nearby regions. The diamond indicates the colony location. The points represent a trapping grid; the size of points reflects the relative probability that a bee will show up in that trap. This illustrates how the model can create asymmetric foraging kernels which depend both on the colony location and the configuration of the landscape. **(B)** The likelihood surface for the unknown location of a colony (darker areas represent a higher probability), where bees from the colony have been caught in equal number at three traps. The trapping grid is shown as coloured points: the size of the points reflects the number of bees captured at the trap, and the shade of the points represents the forage quality at the trap (low is light, high is dark). The colony is expected to lie close to the low-quality trap when affinity for forage quality is high. As the distance constraint increases, the expected colony location becomes equidistant to the three traps. The posterior distribution of the colony location is dependent on the parameters controlling the foraging kernel, and all must be estimated simultaneously.

bees are to travelling long distances from the colony (parameter $\beta$ in Equation 4). In particular, if bees are attracted to high quality forage and not averse to travelling far, then the most probable location for the colony is proximal to the unattractive occupied trap. If bees are averse to travelling far, then the most probable location for the colony is between the three occupied traps. An estimation scheme which assumes that the colony location is the centroid of observed foragers–or sequentially estimates the colony location/foraging distances then the parameters governing visitation rates–could easily be biased if traps differ in attractiveness. In contrast, the simultaneous estimation of colony locations and trap attractiveness will appropriately account for dependencies between these parameters.

We are intentionally vague about the definition of 'forage quality' in this model. In reality, forage quality can be decomposed into many constituent factors (i.e. floral display size and species richness), all of which can be included in the definition of the visitation rate $\lambda(k)$. Finally, note that the form of $\lambda_i(k)$ in Equation 4 can easily be extended to include behavioural effects such as trap avoidance, varying exposures (variation in trapping times across traps), *etcetera*. We refer the reader to the extensive literature of modelling of trapping processes (for a good reference see Royle et al 2013b).

## 2.3 Estimation of average foraging range

We fit the model in section 2.2 by Markov chain Monte Carlo (see Appendix A for implementation details). Assume that the Markov chains converge and we end up a total of $T$ samples from the joint posterior distribution of the parameters $\Theta$. We use the generic notation $\Theta^{(t)}$ to indicate the value of the parameters in sample $t \leq T$ of the Markov chain. An estimator of the location of colony $i$ is the expectation of $\delta_i$ w.r.t. the joint posterior distribution,

$$\hat{\delta}_i = T^{-1} \sum_{t=1}^{T} \delta_i^{(t)} \approx \mathbb{E}[\delta_i | \Theta_{-\delta_i}, y] = \int \delta_i d[\Pr(\delta_i, \Theta_{-\delta_i} | y)]$$

For a given Monte Carlo iteration, the expected foraging distance of the colony can be estimated as the weighted average of the distance between the colony location and trap locations, where the weights are the estimated probability of

a trap being visited by a bee from that colony:

$$d_i^{(t)} = \sum_{k \in \kappa} \|\delta_i^{(t)} - x_k\| \frac{\lambda_i(k;\Theta^{(t)})}{\Lambda_i(\Theta^{(t)})}$$

And then the expectation of $d_i$ w.r.t. the joint posterior is approximated as $\mathbb{E}[d_i] \approx T^{-1} \sum_{t=1}^{T} d_i^{(t)}$. Intuitively, $\lambda_i(k)$ is an model-based estimate of the visitation rate of colony $i$ to location $k$: $\lambda_i(k)$ is estimated from the data, and is in turn used to estimate the average foraging distance. Clearly, this estimate will be sensitive to the form of the model; but will be accurate if the model is approximately correct. A more 'naive' estimate weights the distance between colony and trap by the proportion of bees found at that trap; i.e. by replacing the weights $\frac{\lambda_i(k;\Theta^{(t)})}{\Lambda_i(\Theta^{(t)})}$ with $\frac{y_{ik}}{Y_i}$.

The estimated average foraging distance for a landscape is calculated in a similar fashion, but sums visitation rates across colonies:

$$l^{(t)} = \sum_{i \in \mathscr{C}} \sum_{k \in \kappa} \|\delta_i^{(t)} - x_k\| \frac{\lambda_i(k;\Theta^{(t)})}{\sum_i \Lambda_i(\Theta^{(t)})}$$

and as before is a model-based estimator which can be averaged over Monte Carlo samples to get an approximate expectation. A naive estimator would use the proportion of bees (out of the entire collection of bees) as a weight; i.e. would replace $\frac{\lambda_i(k;\Theta^{(t)})}{\sum_i \Lambda_i(\Theta^{(t)})}$ with $\frac{y_{ik}}{\sum_i Y_i}$.

To estimate the relative difference in foraging distance between two landscapes where the same trapping scheme was employed, we estimate the posterior probability that the first landscape has a greater expected foraging distance than the second landscape as:

$$\begin{aligned} \Pr(l_1 > l_2) &= \int \int \mathbb{I}[l_1 > l_2] d\Pr(l_2|\Theta_2) d\Pr(l_1|\Theta_1) \\ &\approx \frac{1}{T} \sum_{t=1}^{T} \mathbb{I}[l_1^{(t)} > l_2^{(t)}] \end{aligned}$$

where $l^{(t)}$ is defined as above with a subscript that indicates the landscape, and $\mathbb{I}$ is the indicator function (which evaluates to 1 if the inner inequality is true, and 0 otherwise).

### 2.4 Simulated experiments

We run a number of simulated experiments where we randomly (uniformly) select values of the parameters controlling both the locations of colonies and foragers; and the configuration of traps in the landscape. The simulation process is: (1) simulate parameters for the foraging and nesting landscape; (2) simulate a nesting and foraging landscape; (3) simulate colony locations and parameters controlling forager behaviour; (4) randomly select a trapping setup from a set of predefined options; (5) simulate the trapping process; (6) fit the model and obtain estimates. We simulate nearly 7,500 simulated experiments and 1 million simulated colonies. The trapping schemes considered include grid, transect, cross, and random placement of traps. For each of these topologies, we vary the density of traps (the number of traps in a fixed area). The spacing of traps is a function of both the spatial arrangement and the density, as described in the introduction. We use the same spatial resolution in all simulated experiments: a landscape raster which is 1000 by 1000 map units, within which is nested a 500 by 500 'study area' where traps are located.

## 3 Results

*Colony locations* The accuracy with which a colony location is estimated using the methods described above depends primarily on the true location of the colony in reference to the trapping grid (Figure 2). Colonies which are proximal to traps will be located with greater accuracy.

A direct consequence is that the arrangement of traps influences how much improvement in the accuracy of colony location can be achieved by increasing the density of traps within a fixed area. This is a trivial consequence of the fact that in the limit of trap density, a grid becomes continuous on a rectangle, a transect becomes continuous on a line, and so on. In other words, traps arranged in a grid cover the trapping area to a nearly uniform degree and so an increase in the density of the grid improves accuracy nearly uniformly over the trapping area. In contrast, increasing density along the transect increases the accuracy nearly uniformly along the transect (but little benefits estimation for colonies lying outside the transect). The probability that a colony is detected also depends greatly on its spatial location. However, increasing the density of traps, regardless of the trap arrangement, will increase the spatial scale at which colonies are detected (albeit at different rates, Supplementary Figure 1).

*Average colony foraging distance* The average foraging distance of the colony can only be estimated up to limit determined by the size of the trapping area. The size of the trapping area in our simulations is 500 map units, and this asymptote occurs between 400 and 500 map units (Figure 3). Below this asymptote, the direction and magnitude of error is a function of the true average foraging distance: the shape of this relationship is influenced by the arrangement of traps, the density of traps, and the number of captured bees (Figure 3). For all trap arrangements, there is a positive bias in the estimated foraging range of the colony, when the number of captured bees per colony is low. In general, this bias is inconsistent across values of the true average foraging distance; but the inconsistency is most extreme for transects with a low density of traps.

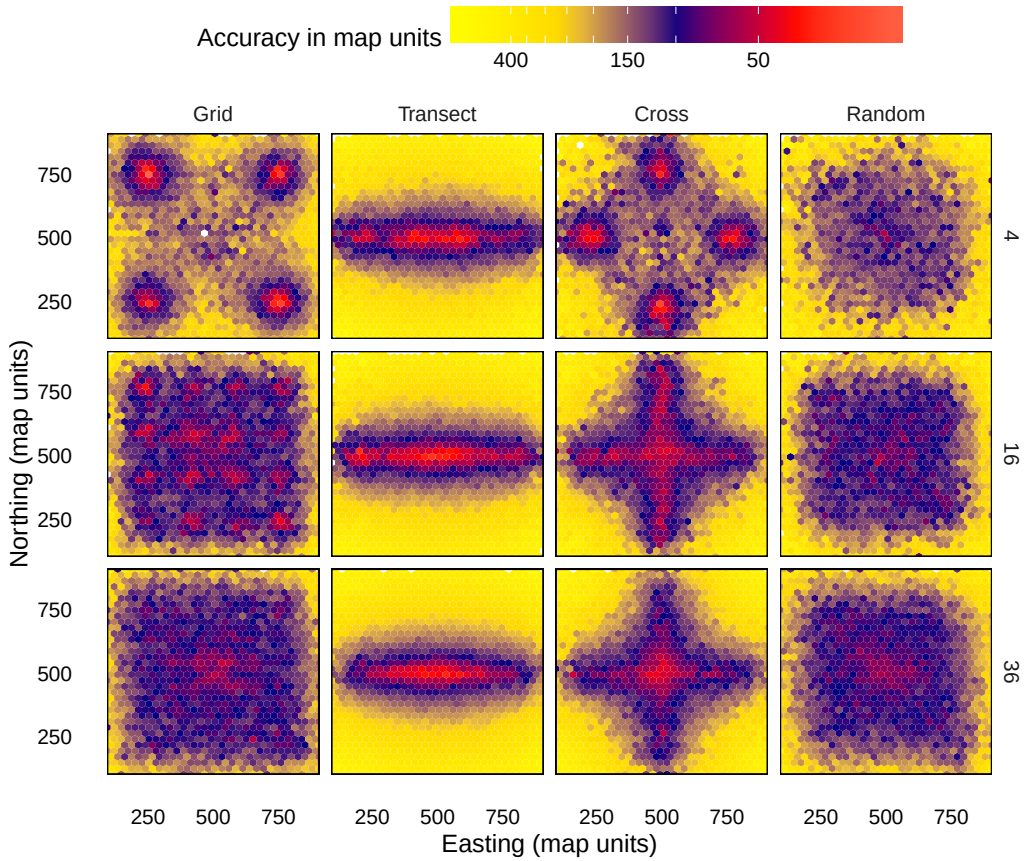


**Fig. 2** The accuracy with which a colony location is estimated, as a function of the spatial location of the colony. Colour at a given coordinate corresponds to the (average) accuracy with which a colony location at that coordinate was estimated. Shown for four trapping schemes (columns) across trap densities (rows; 4, 16, and 36 traps).

*Average landscape foraging distance* Like the estimated average foraging distances for colonies, estimates for the average foraging distance for landscapes are constrained by the size of the trapping grid. In general, an increase in the number of bees caught in the landscape improves the accuracy of estimation (Figure 4). When low numbers of bees were captured, estimates were positively biased. However, the arrangement of traps and density of traps influences whether this bias is consistent, and also how quickly accuracy increases with number of captured bees. By consistent bias, we mean that although estimates may be biased upwards, the amount of bias does not vary across the true values of foraging range.

*Relative foraging distance* All trapping arrangements and densities were able to distinguish between the average foraging ranges of landscapes, given that the relative magnitude of the difference was extreme enough. However, the arrangement and density of traps has a strong influence on the power to accurately detect the direction of the relative difference in the average foraging range (Figure 5). In general, the grid arrangement was slightly more accurate than other methods at high trap densities. However, all trapping schemes showed an increase in power with increasing trap density, and at the highest density all arrangements performed similarly.

## 4 Application to *Bombus* data

In this section, we illustrate how the model developed in section 2.2 can be used to infer an influence of the environment on foraging movement, using data from Jha and Kremen (2013). These data consist of *Bombus vosnenskii* foragers collected along eight 1-km transects in the California chaparral. Each transect consisted of five sites, and at each site the floral community was censused: the average density of floral resources, the variation in the density of floral resources, and the species richness of flowering plants were measured (see Jha and Kremen 2013, for details regarding data collection) for details about data collection). Individual bees were genotyped at polymorphic microsatellite markers and assigned to sibships using COLONY (Wang 2004). The goal of the analysis is to determine whether individual

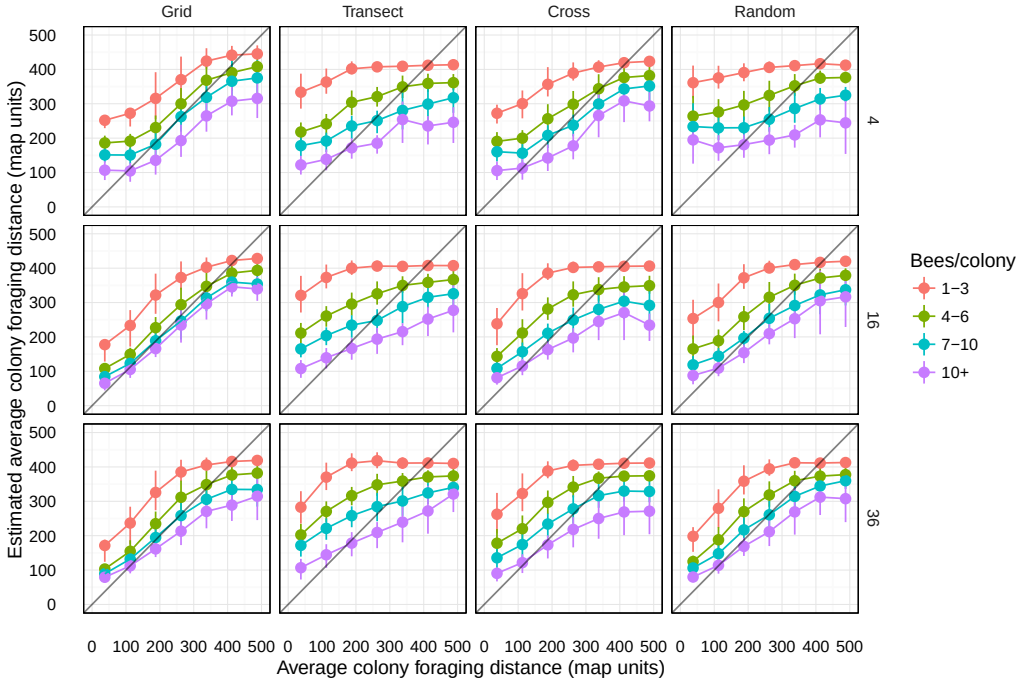


**Fig. 3** The true average foraging range for colonies, plotted against estimates of average foraging range (point: mean over all simulations; vertical lines: 50% quantiles). The black line shows a one-to-one relationship between estimated and true values. Shown for four trapping schemes (columns) across increasing trap densities (rows; 4, 16, 36 traps), at four different levels of sampling intensity (shade of lines/points).

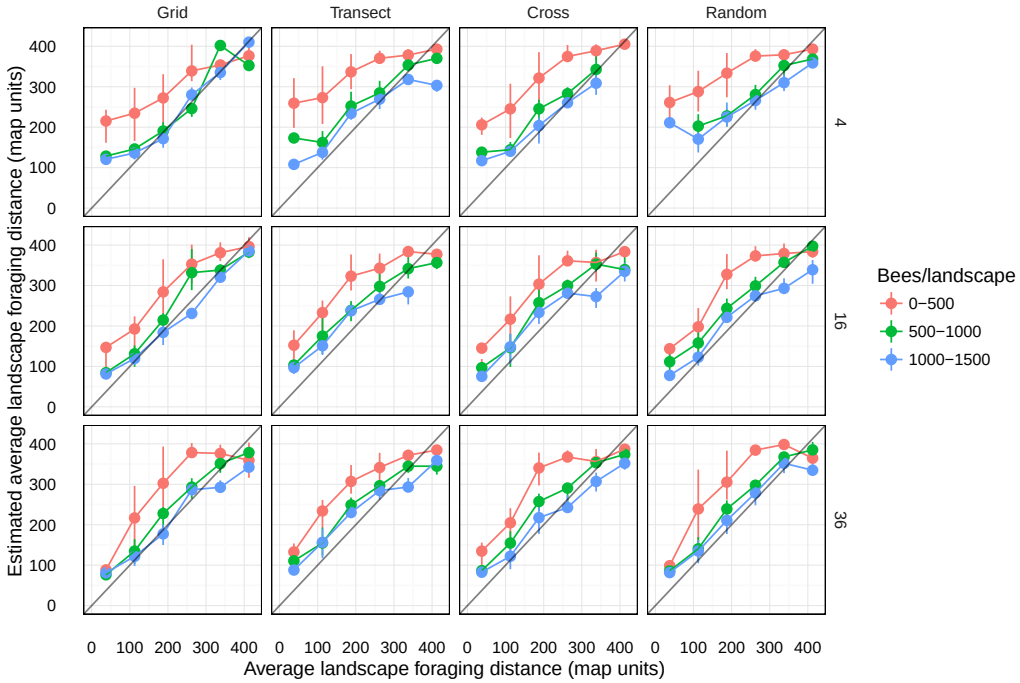


**Fig. 4** The true average foraging range of landscapes, plotted against estimates of average foraging range across simulated experiments. The points shown the average estimate over simulations, and the vertical lines give 50% quantiles. The black line shows a one-to-one relationship between estimated and true values. Shown for four trapping schemes (columns) across increasing trap densities (rows; 4, 16, 36 traps), at four different levels of sampling intensity (shade of lines/points).

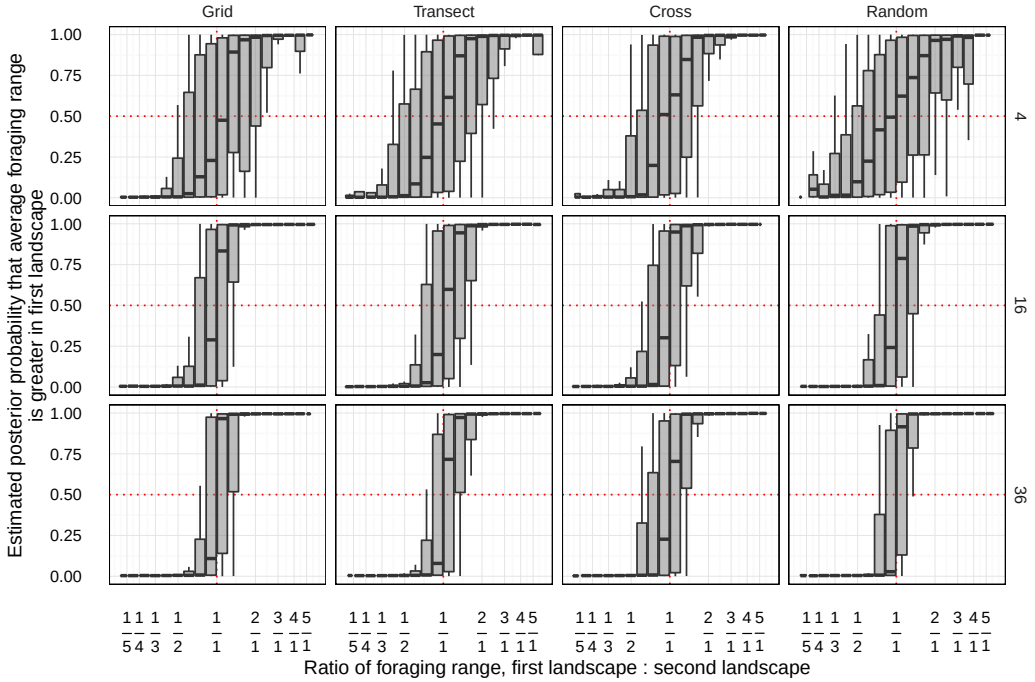


**Fig. 5** The estimated posterior probability that the first landscape (of a pair of landscapes) has a higher average foraging range; as a function of the true ratio of foraging ranges. The spacing on the x-axis is scaled as the log-ratio. Results from simulated experiments are binned into boxplots. Shown for four trapping schemes (columns) across increasing trap densities (rows; 4, 16, 36 traps).

foragers will travel longer distances to reach certain types of floral communities. To facilitate comparison between different methods of analysis, we include only the 70 colonies with at least two siblings.

By modifying equation 4 to address the research question, we model the log capture rate of foragers at a site $j$ that is $d_{ij}$ km distant from colony $i$:

$$\ln \lambda_i(j) = d_{ij}(-\eta + \theta_1 r_j + \theta_2 f_j + \theta_3 v_j) + \zeta_i + \varepsilon_{ij} \qquad (5)$$

where for site $j$ the covariates $\{r_j, f_j, v_j\}$ are the centered and scaled floral species richness, average floral density, and coefficient of variation of floral density. In this model, $\zeta_i$ is the log capture rate at the colony location (i.e., when $d_{ij} = 0$). As the distance from the colony increases, the log capture rate decreases linearly with slope $\Delta_d(\ln \lambda)$. If the floral assemblage is homogeneous, so that the centered covariates $r_j, f_j, v_j = 0$ for all $j$, then $\Delta_d(\ln \lambda) = \eta$. The coefficients $\theta$ allow $\Delta_d(\ln \lambda)$ to vary continuously for different types of floral assemblages. The errors $\varepsilon_{ij}$ are Gaussian and are included to account for over-dispersion in the observed counts.

The biological interpretation of this model is that the number of foraging siblings decreases with the distance from the colony: the attractiveness of a site to foragers is effectively penalised by the travel distance. At the colony location, the capture rate is not influenced by the floral assemblage (because bees would be captured at the colony location regardless of the surrounding vegetation). As the distance from the colony increases, the capture rate decreases at different rates for different types of floral assemblages (Figure 6A). Thus, floral assemblages that are attractive to foraging bees are visited despite being far from the colony. The motivation underlying this model is to express the decline in forager abundance with distance as a function of characteristics of the floral community.

For the sake of comparison, we also analyse the data using a method similar to that used in (Jha and Kremen 2013): a hierarchical regression model which regresses the average pairwise distance between siblings ($\bar{d}_i$) onto the floral covariates averaged across sibling locations ($\bar{r}_i, \bar{f}_i, \bar{v}_i$). Random intercepts are included for each transect, so that

$$\mathbb{E}[\bar{d}_i] = \alpha_{s_i} + \beta_r \bar{r}_i + \beta_f \bar{f}_i + \beta_v \bar{v}_i$$

where $\{\beta_r, \beta_f, \beta_v\}$ are regression coefficients that model the change in average pairwise distance per unit increase in the pooled floral covariates. We use Bayesian methods for inference, but both models could be fit by penalised likelihood.

The two approaches to analysis lead to very different conclusions. The regression model predicts that bees will travel greater distances to forage at species-rich sites; and gives no evidence that the average or coefficient of variation of floral density have an influence on foraging distance (Figure 6B; black points are posterior means, black lines are 95% credibility intervals). In contrast, our model of capture rates predicts that bees will travel greater distances to sites with few flowering species, and a dense and homogeneous

distribution of floral resources (Figure 6C). An example of this type of floral assemblage is one dominated by a mass-flowering, evenly distributed shrub species.

The contradiction between these two sets of results is striking. To compare the accuracy of the methods while making few assumptions about the true biological process, we simulated data from a null model where bees were placed randomly (uniformly) across transect sites, while retaining the floral covariates and the numbers of bees per colony from the original data. On a dataset simulated from this null model, an accurate method of analysis should conclude that distance travelled does not depend on floral covariates. The rate of spurious conclusions (Type-I errors) can be assessed by trials across many datasets simulated from the null model. In almost all of the trials, the capture rate model gave the correct conclusion for all floral covariates, and on average gave parameter estimates close to 0. These results are shown in Figure 6C: the grey numbers are the proportion of 95% credibility intervals that contained 0; and the grey density is the distribution of posterior means from 1000 null simulations. For all parameters, the true rejection rates were above the expected 0.95.

In contrast, the regression model gave parameter estimates that were biased away from 0, on average. The estimated regression coefficient for richness from the original data–despite being positive and apparently 'significant'–fell well within the distribution of posterior means from the null simulation, indicating that the positive coefficient should not be taken as evidence for an effect of floral species richness on foraging distance. The true rejection rates for the regression model applied to the null simulations were well below the nominal 95% (Figure 6B).

Why does the regression model perform so poorly, and lead to apparently spurious conclusions? One possible reason is that bees are collected across a discrete sample space and there are a finite number of possible combinations between the response variable (average pairwise distance) and the covariates (average site characteristics). For example, a colony with two captured bees has only one possible spatial arrangement that gives the maximum possible pairwise distance of 1 km: the bees would have to be located at opposite ends of the transect. There are two arrangements that give the second largest possible pairwise distance of 0.75 km, and so on. If the sites near the ends of the transect have an above-average floral species richness, then large pairwise distances will always be associated with increasing species richness, regardless of how the foraging bees are actually behaving. In such a situation, an apparent effect of species richness from a regression would be an artefact of the spatial configuration of sampling locations with regard to the floral community. The model of capture rates developed in this section does not suffer from these artefacts, because the occurrence of bees is modelled directly across a discrete sample space.

## 5 Discussion

Bees are effective pollinators of many flowering plant species (Fenster et al 2004), and so are an indispensable component of terrestrial ecosystems that also provide pollination services to many crop plants (Kremen et al 2002). Social bees are generalist pollinators, and can travel long distances within a single foraging bout (Hagen et al 2011). Bees depend upon floral resources for carbohydrates and protein, and many plants depend upon bees for transmission of gametes; and thus the spatial scale at which foraging bees regularly move is extremely relevant to our understanding of how the landscape impacts the fitness of both parties (Jha and Dick 2010). From an applied perspective, a knowledge of the foraging range of pollinators such as bees is of great importance for the planning of habitat restoration and crop pollination (Keitt 2009; Lonsdorf et al 2009). The estimation of colony locations can also be used for estimating population densities, and evaluating nesting habitat for conservation planning.

Here, we have described a spatially explicit, model-based approach for simulating and estimating foraging range from siblings genotyped at discrete locations. Although most of the applications we describe are simple, such a model-based approach easily accommodates complex effects at both the landscape- and colony- level. For example, the foraging range of bees could be modelled as a function of the average forage quality of the landscape, such that foraging kernels expand or contract depending on the phenology of plants throughout the landscape (Jha and Pope, *in review*). Our approach accurately depicts the sampling process (repeated captures at discrete locations) rather than assuming that the trapping locations are located continuously across the landscape, and also treats the colony locations as a unknown parameter to be estimated along with the foraging kernel; rather than sequentially estimating the colony location and then the foraging kernel. In practice, this is important as the shape of the foraging kernel can cause traps to vary in attractiveness: failing to account for this while estimating colony locations can introduce substantial error.

Using simulated data, we have illustrated that different schemes vary in their efficacy for estimating foraging range at various levels of organisation (individuals, colonies). In general, traps arranged in grids provide the most accurate estimates of foraging range across scales. However, our simulations suggest that discrete sampling methods will provide low accuracy in the estimates of individual foraging ranges, or the average foraging distances of colonies; with anything less than unrealistic densities of traps and captured siblings. On the other hand, as long as sufficient numbers of bees and colonies are captured within a landscape, the average foraging range across the landscape can be estimated with reasonable accuracy, or at least with consistent bias for all trapping

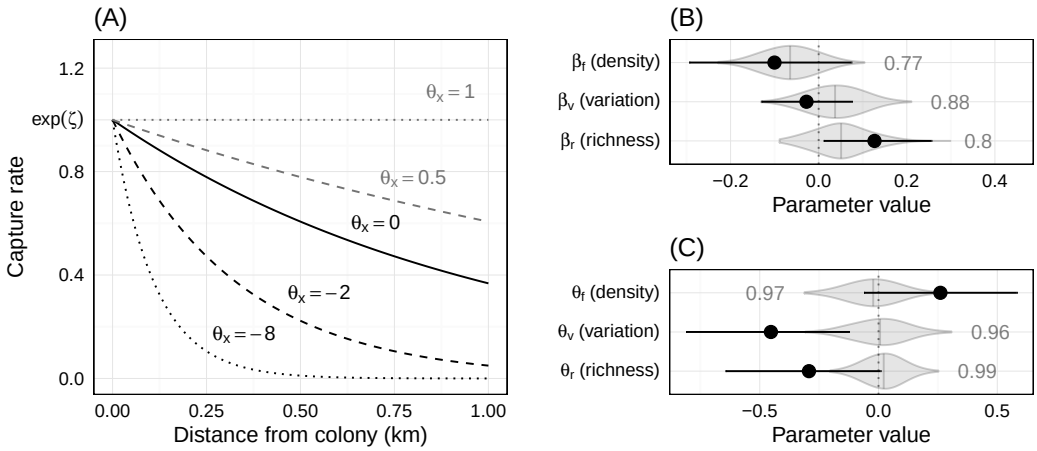


**Fig. 6** **(A)** An hypothetical illustration of how visitation can decline across distance at rates that depend on the floral community, following the model in equation 5. The parameter $\theta_x$ controls how a single floral covariate $x$ influences the decline in visitation with distance from the colony. In this example, $x = 1$, $\exp\{\zeta\} = 1$, and $\eta = -1$. Negative values of $\theta_x$ imply that floral communities with $x > 0$ will be visited relatively less frequently at far distances. **(B-C)** Summary of results from the regression model (panel **B**) and the capture rate model (panel **C**) described in section 4. For key parameters, posterior means and 95% credibility intervals are shown as black points/lines. Positive values imply that foragers will travel further for increasing values of the covariate. The grey shaded regions show the density of posterior means across 1000 simulations from a null model where bees are distributed uniformly at random. The grey numbers give the proportion of 95% credibility intervals that contain 0 across these null simulations.

methods. Even small numbers of traps can be effective at detecting differences in foraging range across landscapes, and our simulations suggest diminishing returns with increasing trap density with regard to estimation of foraging ranges at different scales. However, increasing the density of traps may substantially increase the probability of detecting distant colonies. If the goal of estimation is a measure of colony density within a landscape, even a transect may provide reasonable spatial coverage with a sufficient density of traps.

Using a dataset of wild bumble bee genotypes from the Californian chaparral (Jha and Kremen 2013), we gave an example of how a transect design with a low trap density can be used to infer foraging behaviour across a heterogeneous landscape. Our analysis of these data suggests that bumble bees travel further to forage on dense, less variable, less speciose floral communities. Areas dominated by an evenly distributed, mass-flowering species are relatively conspicuous, and may encourage return trips by foraging bees by consistently providing pollen and nectar resources. Previous work has suggested that in variable environments, foraging bumble bees act to increase consistency in rewards while reducing the time spent searching (Biernaskie et al 2009). The strongest effect in our analysis is a preference of bees for the sites with the least variability in floral density. Such sites would have a consistent spatial distribution of floral resources, and so would reduce the time spent by bees in intrasite movement. Most strikingly, our method of analysis gives very different results from a regression-based approach that found an increase in foraging distance to species-rich floral communities. By simulation, we show that the conclusion from the regression analysis could easily result from a null model where foragers are located uniformly at random across transect sites. In contrast, the model developed in this work consistently returns correct results. We speculate that the poor performance of the regression approach under the null model is due to a chance association between high floral species richness and relatively distant transect locations. Collections of bumble bee genotypes from the wild often contain few bees per colony, and we conclude that the choice of the method used to analyse these sparse data can have a large influence on subsequent biological inference. Care must be taken to employ a model that makes realistic assumptions about the sampling process.

In this work, we are influenced by the vast applied literature on the design and analysis of trapping experiments stretching back to the 1940s (see Worton 1987; Royle et al 2013b), especially recent work on spatially-explicit capture-recapture models (Royle et al 2013a). Our contribution is to develop a simulation framework for the particular case of trapping social bees, to develop inferential methods for data matching this framework, and to demonstrate that the general approach can be effective for answering certain questions and ineffective for others. The tools we present here will be useful to those planning to use these types of methods. In particular, the R and C++ programs used to simulate data are available online (*github.com/nspope/foraging*). These programs are implemented as classes and designed in an object-oriented fashion; the user can define novel methods that define the visitation rates of foragers, the spatial arrangement of traps, and the stopping rule. User-defined methods interface easily with the existing code, allowing a

great deal of flexibility in terms of the simulated study design.

We do not expect the results we present above to be relevant to every study; however, we suggest that scientists use simulation to investigate the efficacy of a study design before deploying it. Given that sampling genetic material across many colonies and landscapes involves a great deal of effort and also frequently results in substantial mortality of bees, it is essential to try to maximise the amount of information carried per bee. As an example, in our simulations we observe that a density of 16 traps provides equivalent results to trap densities twice as large. These results imply that savings in human effort and bee mortality can be achieved by optimising sampling design with regard to the research question, and our worked example with *B. vosnesenskii* illustrates that a small but efficient sampling scheme may be deployed effectively across multiple landscapes. Simulation tools, such as the ones we develop here, can provide rough estimates of the sampling effort that is optimal for these applications. Finally, we note that with any estimation method, it is important to characterise the error associated with specific assumptions. In the context of this work, we have presented a method which tries to generate estimates of foraging range by integrating over uncertainty in the location of the colony and the shape of the foraging kernel. A source of error which we have not explored here (but we believe to be extremely important) is the uncertainty associated with sibling assignment by probabilistic genetic methods. A second topic which we do not address in this paper, but we feel is deserving of attention, is the use of extant land classification maps in study design and analysis. We will address these topics in a future study.

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## A Appendix. Details of implementation

We fit the models described in Sections 2.2 and 4 by Markov chain Monte Carlo, using the Bayesian computational platform Stan (Carpenter et al 2015). Stan uses a variant of a technique known as Hamiltonian Monte Carlo to generate proposals that are relatively far apart in parameter space yet have a high acceptance probability, and so is quite efficient for fitting high-dimensional models with relatively short Markov chains. We use multiple Markov chains per model fit, and monitor mixing and convergence visually and with the scale-reduction factor of Gelman and Rubin (1992). Initial runs suggested that models converge quickly, within a few hundred iterations. For our simulation experiments, we automatically flagged model fits that showed signs of not converging (using a threshold for the scale reduction factor), and also visually inspected a random sample of fitted models. The STAN code implementing our model is given in the supplementary material. We use vague log-normal priors for parameters controlling the shape of the foraging kernel, half-normal priors for variance components, and uniform priors for colony locations (with support on the rectangular area of the landscape used for simulations).

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