

Bee foraging ranges and their relationship to body size

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Abstract Bees are the most important pollinator taxon; therefore, understanding the scale at which they forage has important ecological implications and conservation applications. The foraging ranges for most bee species are unknown. Foraging distance information is critical for understanding the scale at which bee populations respond to the landscape, assessing the role of bee pollinators in affecting plant population structure, planning conservation strategies for plants, and designing bee habitat refugia that maintain pollination function for wild and crop plants. We used data from 96 records of 62 bee species to determine whether body size predicts foraging distance. We regressed maximum and typical foraging distances on body size and found highly significant and explanatory nonlinear relationships. We used a second data set to: (1) compare observed reports of foraging distance to the distances predicted by our regression equations and (2) assess the biases inherent

to the different techniques that have been used to assess foraging distance. The equations we present can be used to predict foraging distances for many bee species, based on a simple measurement of body size.

Keywords Body size · Foraging distance · Apoidea · Bee · Pollination

Introduction

The distance over which animals forage can strongly affect their population dynamics, genetic structure, and life history; it can also affect these same traits in organisms with which they interact. As such, foraging distance is a critical component for understanding the persistence of populations and species interactions. Foraging distance also influences the spatial characteristics of many community interactions that have ecosystem-level consequences, such as predation, parasitism, nutrient transfer, seed dispersal, and pollination (Holling 1992; Ritchie and Olff 1999; Roland and Taylor 1997).

Bees are the primary pollinators for most ecological regions of the world (Axelrod 1960; Bawa 1990). Their foraging distance strongly influences the sexual reproduction of most flowering plants and can determine the genetic structure of plant populations (Campbell 1985; Waser et al. 1996). For example, pollinators may not visit small or isolated plant populations, leading to plant reproductive failure (Cunningham 2000; Lennartsson 2002). Conversely, long-distance foraging, even by introduced species, may rescue mating in otherwise doomed plants within habitat fragments (Dick 2001).

Bee foraging distance also affects agricultural production. Animal pollination is required to produce 15–30% of

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the US human food supply (McGregor 1976), while 75% of 107 fruit, nut, and vegetable crops that collectively make up 40% of the global plant-food supply benefit from animal pollination (Klein et al. 2006). Crop pollination is enhanced by bees that depend on natural habitats (Greenleaf and Kremen 2006a, 2006b; Klein et al. 2003a, 2003b; Kremen et al. 2004, 2002; Ricketts 2004). Many wild bees that pollinate crops nest in natural habitats and forage on crops within their daily travel distance (Ricketts 2004). Foraging distance therefore determines the spatial scale at which wild bees can provide pollination services to crops (Kremen 2005).

Foraging distance has been shown to increase with body size for various taxa. For example, for some vertebrate groups, body size is predictive of home range, a metric that is closely related to foraging distance. For many vertebrates, body size and home range area scale according to the function: $\text{range} = Y_0 M^b$, where Y_0 is a constant, M is body mass, and b is a scaling exponent (Haskell et al. 2002). The form of this relationship varies among studies and taxa, and it may be linear or either an increasing or decreasing nonlinear function (e.g., Harestad and Bunnell 1979; McNab 1963; Milton and May 1976; Schoener 1968; Turner et al. 1969). Theoretical explanations for the relationship between body size and foraging distance continue to be debated (e.g., Haskell et al. 2002; Jetz et al. 2004; Kelt and Van Vuren 2001; Makarieva et al. 2005). Evidence suggests that foraging range may increase with body size for four insect parasitoid species (Roland and Taylor 1997), but the relationship between body size and home range or foraging distance remains largely undescribed for most invertebrate taxa.

Three published studies have described relationships between bee body size and foraging distance. First, Van Nieuwstadt and Iraheta (1996) described a linear relationship between head width and foraging distance for four species of stingless bees (Tribe: Meliponini). Head width, however, may not vary predictably with body size across genera, and families (Cane 1987); thus, these results cannot be generalized to other bee taxa. Second, Gathmann and Tschamntke (2002) analyzed data from 11 records of 21 solitary bee species and found a linear relationship between body length, and foraging distance ($r^2 = 0.47$). The relatively low predictive power of this relationship may have been due to the choice of body length as a measure of bee size and the lack of consistency in field and statistical techniques between datasets. A third study observed that among four *Bombus* species, those with larger wingspans were estimated to have larger foraging ranges, but the relationship between body size and foraging range was not investigated mathematically (Westphal et al. 2006).

Here, we re-examine the relationship between body size and foraging distance, using data from six families of bee.

We measure body size using intertegular span, which is a robust estimator of body mass (Cane 1987). Rather than constraining the body size–foraging distance relationship to a linear form, as was done in previous studies, we use a power function, and determine not only the strength of the relationship but also its shape. We develop a predictive relationship between body size and foraging distance. We then use a second data set to compare observed foraging distances to the distances predicted from body size and to test biases in field methods that have been used to measure bee foraging distance.

Methods

We reviewed 96 published records of foraging distances for 62 bee species from six families (Andrenidae, Apidae, Colletidae, Halictidae, Megachilidae, and Melittidae). We divided these data into two categories: (1) records that allow for an estimate of maximum foraging distance and (2) records reporting an observed foraging distance with no information on how it relates to maximum foraging distance. We considered only those records in the first category for inclusion in the regression analyses of foraging distance on body size. Records that were not used in regression analysis were included in our comparison of observed and predicted foraging distances and in comparing the biases in various methods.

Records of estimated maximum foraging distance

Records that estimated maximum foraging distance used three different methodologies: homing, feeder training, and bee dance interpretation. In homing research, bees are captured at the nest and released at various distances from the nest to determine how many bees return from various distances (e.g., Fabre 1914; see Table S1). In order to produce a standardized measure among records, we performed logistic regressions on the raw data from 15 species to generate the predicted distance for return of 90% of individuals (hereafter “maximum homing distance”) and 50% of individuals (hereafter “typical homing distance”). Records that did not provide data on the number of bees released and proportion returned at various distances were excluded from regression analyses but were included in our other analyses.

In the feeder training technique (e.g., Van Nieuwstadt and Iraheta 1996; see Table S2), artificial feeders are set out near the nest. After a learning period, the feeders are moved to successively larger distances from the nest until bees no longer forage at them. The maximum distance at which bees forage at artificial feeders reflects the maximum distance at which it is energetically profitable to

forage at an artificial feeder and will depend on the availability of alternative resources. For feeder training results we were unable to obtain the original data; therefore, we used the maximum foraging distance estimate reported in the original studies (hereafter maximum feeder training distance), rather than a maximum predicted foraging distance from logistic regression, as above. Some researchers also reported the distance at which bees stopped recruiting foragers to the artificial feeder (hereafter maximum communication distance).

The bee dance interpretation technique (e.g., Beekman and Ratnieks 2000) determines the distance of actual foraging trips under natural conditions and can therefore be used to measure both typical and maximum foraging distance. It is limited to bees having a dance language and has been used to study foraging distance for only four *Apis* species (Dyer and Seeley 1991). We did not analyze data from these four species because the sample size would have been too small for meaningful statistical analysis. Additionally, we did not review the extensive data on *Apis mellifera* foraging distance that has been collected using the bee dance interpretation technique, because our focus is on interspecific, not intraspecific, variation.

Records of observed foraging distance but not maximum foraging distance

Records that reported observed foraging distance but not maximum foraging distance were those using a variety of techniques: mark–recapture, genetic analysis, pollen mapping, nest–forager association, nest–plant association, harmonic radar, and nest site addition. In the mark–recapture technique, bees are marked at the nest and located while foraging (e.g., Kapyla 1978; see Table S3). This method has the advantage of directly observing the distance of actual foraging trips. However, search area expands as the square of the distance from the nest, so the number of marked bees in the landscape is quickly diluted. Most of the data we found were not obtained with equal sample effort per unit area and the number of recaptured bees was too small to rarify the data to correct for unequal sample effort (e.g., Walther-Hellwig and Frankl 2000). Without sufficient sample effort near the outer edge of the foraging range, it is not possible to determine maximum foraging distance, and unequal search effort at different distances precludes the determination of typical foraging distance.

In the genetic analysis approach (Darvill et al. 2004; Knight et al. 2005; see Table S3), foraging social bees are collected along a transect across a landscape, and tested to determine which bees are sisters (i.e., are foraging from the same nest). One-half of the distance between the locations where a pair of sisters was collected is the minimum

estimated maximum foraging distance. The maximum foraging distance may be greater than the observed distance because the nest may not be located midway between where the sisters were collected.

In the pollen mapping technique (e.g., Packer 1970; see Table S3), pollen taken from the nest is identified, a floral resources map is made, and distance is estimated between the nest and the flowers from which pollen was collected. This method assumes bees travel to the nearest patch of a given pollen resource; thus, as reported in the literature, pollen mapping measures the minimum foraging distance for a particular floral resource.

In the nest–forager association technique (e.g., Robertson 1966; see Table S3), nest sites and foraging bees of a particular species are located and the distance between them is measured. This technique has the potential to measure actual foraging distance and could therefore be used to estimate maximum and typical distances. However, the research we reviewed did not use marked individuals, and it was not clear that all nests in the area had been located. Thus, the observed foragers may have been from an undiscovered nest.

The nest–plant association technique (e.g., Westrich 1996; see Table S3) is only suited for oligolectic bees. Like the pollen-mapping method, this technique identifies the distance between the nest site and the nearest flowers on which the bees are observed. It shows that the bees forage at least that distance but does not measure maximum or typical foraging distance.

Harmonic radar has been used to track bumble bee foraging trips (Osborne et al. 1999). This technique had the advantage of recording actual foraging trips and therefore had the potential for determining maximum and typical foraging distances. However, many of the bees that were observed flew beyond the radar's range of 600 m and/or were lost as they flew behind physical barriers such as hedges.

In the nest site addition method (Gathmann and Tscharnke 2002), nest boxes are placed at different distances from flowers. If bees nest successfully in boxes located some distance from the nearest flowers, then one can conclude that bees forage at least that far.

Measuring body size

For all species for which we found foraging distance data, we assessed body size by measuring the distance between the wing bases, intertegular (IT) span, on a sample of 5–10 individuals, using a dissecting microscope and calibrated ocular micrometer (Tables S1–S3). IT span measures the thorax, which contains the flight muscles, and is empirically related to dry body mass: $IT\ span = 0.77(\text{mass})^{0.405}$ ($R^2 = 0.96$; mass in mg and IT in mm; Cane 1987).

Analyses

To test the relation between IT span and foraging distance, we fit a power function (Haskell et al. 2002). Within the subset of records that determined maximum or typical foraging distance, we partitioned biases inherent to each data collection technique and reduced variation in our analyses by performing a separate analysis for data produced from each technique. Of the three techniques that have been used to determine maximum foraging distance, only the homing and feeder training techniques have been used on sufficient species to allow for regression analyses. For our analyses of the homing and feeder training datasets, we first log-transformed the data to obtain a linear relationship and then used least squares linear regression to parameterize the relationship between IT span and foraging distance. We examined the influence of potential outliers using Cook's D (Quinn and Keough 2002). Log transformation improved homogeneity of residuals across the range of the independent variable. This is the statistically correct approach, but it tended to produce smaller foraging distance estimates for bees with the largest body sizes. We therefore included an alternative nonlinear regression fit (using SAS Proc NLIN, SAS v 8.2). To compare our results for the relationship between bee IT span and foraging distance to those for the relationship between vertebrate body mass and home range area, we converted our log-transformed parameters to the power-function form, then converted our units of IT span to body mass (Cane 1987), and finally linear foraging distance to home range area (assuming home range to be a circle with foraging distance as its radius).

Predictive value of body size and foraging distance

We tested the predictive value of the linear regression equations by comparing predicted and known foraging distances for a second dataset; namely, those 64 records from our literature review that did not meet our criteria for inclusion in the regression (summarized in Table S3). For each species, we measured IT span as described above and compared the reported foraging distance to the maximum foraging distance predicted by the regression. To look for systematic differences among techniques for measuring foraging distance, we subtracted the foraging distance observed in each of these additional records from the foraging distance predicted by the regression equation. A negative value of the resulting metric shows that, according to our model, the observed value was an overestimate while a positive value indicates an underestimate. For each type of technique, we used a one-sample t -test to determine if the

differences deviated significantly from zero (Sokal and Rohlf 1997). Because pollen mapping and nest-plant association techniques measure the minimum distance between the nest and floral resources, for data collected with those techniques, we expected observed distances to be less than predicted distances. We expected a similar pattern for the bee tracking study because the technology was unable to record longer flights and for the mark-recapture research because sample effort often decreased at greater distances from the nest. We expected that maximum foraging distances for homing records that were not used in the regression analyses would be similar to distances predicted from the regression equations but that they would be variable; these measurements were not standardized by logistic regression to obtain the ninetieth percentile maximum foraging distance.

Results

Foraging distance increased with body size (IT span) nonlinearly; larger bees had disproportionately larger foraging distances than smaller bees (Fig. 1; Table 1). This result was consistent for regressions with all four dependent variables: maximum homing distance, typical homing distance, maximum communication distance, and maximum feeder training distance. The nonlinear regression produced larger estimates of foraging distance for bees with larger IT span than did the log-transformed linear regression approach. The difference was due to data for *Eufresia surinamensis*. After log transformation the influence of this datum was modest and met criterion for inclusion in our analysis (Cook's $D = 0.6$, Quinn and Keough 2002). In the raw form it strongly affected the power parameter (b), thus analyses with and without this species are included for completeness (Table S4). When we converted our parameters (log distance = $\log Y_0 + b \log IT$) to those associated with home range (Range $Y_0 M^b$) with units of area and body mass, the exponent (b) was 2.7 for maximum homing, 1.9 for maximum feeder training, and 2.3 for maximum communication.

Techniques that have been used to assess foraging distance varied in whether they produced observed distances that were generally higher or lower than the distances predicted by our regressions. The predicted maximum based on homing data exceeded the observed distance in 45 of 63 records. For the feeder training data, the predicted maximum exceeded the observed distance in 51 of 63 records (Fig. 2). On average, the observed foraging distances obtained from each technique were less than predicted based on body size for all techniques except nest forager association (Fig. 2).

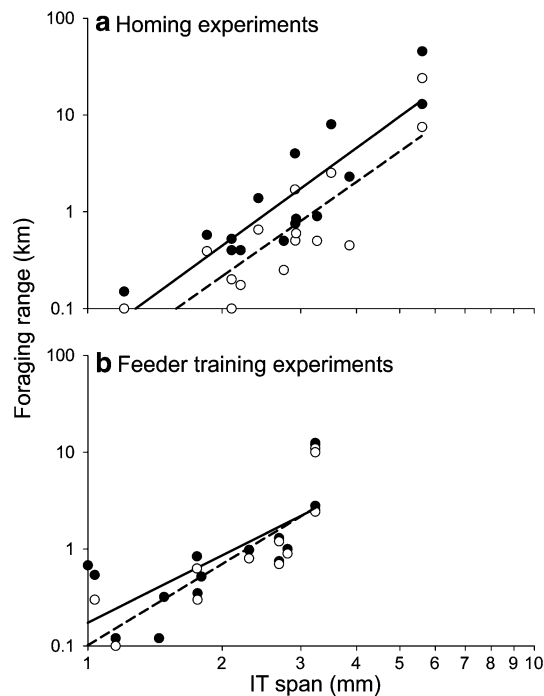


Fig. 1a–b The relationship between bee foraging range and body size [as intertegular (*IT*) span] from literature review of **a** homing experiments or **b** feeder training experiments. All variables were log-transformed; data were analyzed with least squares linear regression. Homing distances are defined as the predicted distance for return of 90% (“maximum,” *filled circles*) or 50% (“typical,” *unfilled circles*) of individuals. Data from feeder training experiments show estimate of maximum foraging distance (“maximum feeder training distance,” *filled circles*) and the distance at which bees stopped recruiting foragers (“maximum communication distance,” *unfilled circles*)

Discussion

Across diverse bee taxa, we found highly significant and explanatory positive, nonlinear relationships between *IT* span and four different estimates of foraging distance: maximum homing distance, typical homing distance, maximum feeder training distance, and maximum communication distance. Our regression equations provide ecologists and land managers with a powerful tool to predict bee foraging distances based on a simple measurement of body size.

Body size explained substantial variation in foraging distance whether based on homing or feeder training data, despite the different assumptions underlying the two techniques. Homing experiments (e.g., Rau 1929) do not directly measure foraging distance. Instead, they integrate across flight/ foraging range capacity, familiarity with the landscape, physiology, quality of navigation cues available, flying conditions on a particular day, navigation strategy, and memory capability. Thus, results from homing experiments may be affected by availability of suitable landmarks (Collett 1996) or physiographic features (Southwick and Buchmann 1995), cloud cover (Schone and Kuhme 2001; Rossel 1993), and wind conditions (Judd and Borden 1989; Murlis et al. 1992) and should therefore be considered as a proxy measurement for foraging range. In contrast, feeder-training experiments (e.g., Van Nieuwstadt and Iraheta 1996) directly measure bee foraging distance, although they too are influenced by environmental factors. The similar parameters generated from the homing and feeder training data help to validate results from homing experiments. Body size explained more variation in homing distance than in feeder training distance. Greater residual variation in the analysis based on feeder training is not surprising. Original feeder training data were unavailable, so the maximum training distances could not be standardized among records by logistic regression as was done for the homing data set. Furthermore, bees will use or not use feeders depending in part on the quality of the surrounding resources. The resulting highly variable estimates among landscapes may have caused the greater residual variation in our analyses.

For bees, the relationship between body size and foraging distance fits a power function with $b > 1$: larger bees forage disproportionately farther than smaller bees. Similar studies conducted for vertebrates have found the power relationship to be linear, accelerating, or decelerating, depending on the taxa and the study (e.g., Harestad and Bunnell 1979; McNab 1963; Milton and May 1976; Schoener 1968; Turner et al. 1969). In this study, when we converted our regression equations to the same units and functional form used in past research on vertebrates, we found that the scaling exponent in the equation relating

Table 1 Parameters (mean ± 95% confidence levels) describing relationship between the log of intertegular (*IT*) span (*X*) and the log of foraging distance (*Y*) according to the function $\log Y = \log a + b \log X$

Dependent variable	<i>n</i>	$\log a$	<i>b</i>	<i>R</i> ²	<i>F</i>
Maximum homing distance (km)	16	−1.363 ± 0.517	3.366 ± 1.084	0.776	45.02
Typical homing distance (km)	16	−1.643 ± 0.582	3.242 ± 1.218	0.718	33.05
Maximum feeder training distance (km)	17	−0.760 ± 0.412	2.313 ± 1.155	0.548	18.20
Maximum communication distance (km)	13	−0.993 ± 0.521	2.788 ± 1.314	0.665	21.80

All *P* values <0.001

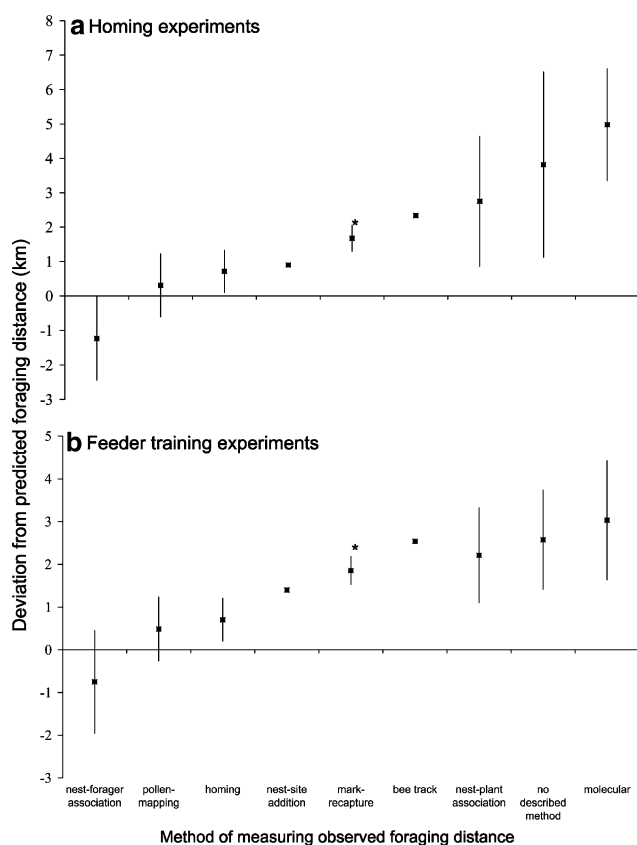


Fig. 2a–b Differences between predicted and observed measures of bee foraging distance (mean \pm SE). Predicted foraging distances were based on the regression of **a** homing distance and **b** feeder training distance on IT span. Observed foraging distances were obtained by various methods [see Table S3 for original data; nest–forager association ($n = 8$), pollen-mapping ($n = 11$), homing ($n = 7$), nest-site addition ($n = 1$), mark–recapture ($n = 14$), bee track ($n = 1$), nest–plant association ($n = 7$), no described method ($n = 15$), and molecular ($n = 5$)]. Positive values suggest that the given observational method underestimates maximum foraging distances. Significant differences from zero, as determined by one-sample t -test, are denoted by asterisks (indicating $P < 0.01$). Standard error bars are not given for methods with a sample size of 1

body mass to foraging area (Y_0M^b , where Y_0 is a constant, M is body mass, and b is a scaling exponent) ranged from 1.9 for maximum feeder training distance to 2.3 for maximum communication distance to 2.7 for maximum homing distance. These values are higher than previously found for vertebrates (0.51–1.39, reviewed in Jenkins 1981). One explanation for this is that bees typically do not have exclusive home ranges. In contrast, the organisms examined by most vertebrate studies partially or completely exclude conspecifics from their home ranges. All else being equal, when home ranges are not exclusive, they must be larger because resources are shared among individuals or groups. Alternatively, for animals that fly, home range may increase disproportionately with body size because flight tends to be more efficient in larger animals (Harrison and Roberts 2000).

We had hypothesized that records produced with the pollen mapping, mark–recapture, nest site addition, nest–plant association, and bee tracking techniques would produce smaller foraging distance estimates than the maximum distances predicted by our regression equations. While the deviation was statistically significant only for mark–recapture records, the differences between observed and predicted were in the direction expected for all five of these techniques. This pattern supports the relationship we described between body size and foraging distance and suggests that our regression equations do not underestimate foraging distance.

In addition to body size, maximum and typical foraging distances may be influenced by life-history characteristics, such as sociality or trophic specialization. All of the species tested using feeder training were eusocial. The homing method was used for many solitary species and also for two eusocial species, *L. Dialictus umbripenne* and *Bombus terrestris*. Observed distances for both eusocial species fall above the model prediction in the homing data set; however, so do data for four solitary species (Fig. 1; Table S1). We could not determine whether trophic specialization affects foraging distance because the regression analyses included only one species that is a confirmed specialist, feeding on only one or a few pollen species. All species tested with feeder training were trophic generalists. The homing data set encompasses species from different families with diverse life histories and includes social, solitary, generalist, and specialist bees, while the feeder training data included only bees in family Apidae; thus, we suggest restricting the application of the model from feeder training data to family Apidae.

Foraging distances will vary with environmental conditions, such as the density and distribution of floral resources and the general physical resistance of the different habitats to flight (e.g., Ricketts 2001). Theoretical (Cresswell et al. 2000) and empirical work provide evidence that the quantity and quality of available floral resources also affect foraging distance. For example, both honey bees (*A. mellifera*) and *Megachile rotundata* have been observed to increase their foraging distances as the distance to high-reward resources increased (Beekman and Ratnieks 2000; Bacon et al. 1965) and with resource scarcity (Steffan-Dewenter and Kuhn 2003). Honey bees will fly farther to get some resources than to acquire other resources (Gary et al. 1972), and their foraging distance varies as a function of landscape context (Steffan-Dewenter and Kuhn 2003). Data in our analysis on *A. mellifera* from habitats differing in resources (Michener 1974) illustrates such variation.

Nonetheless, body size alone explains substantial variation in bee foraging distance. Measuring body size (IT span) in bees is a quick and efficient method that can now be used to estimate foraging distance based on the equations we

present. This practical and robust approach for estimating bee foraging distances will be valuable for understanding the scale at which bee populations respond to the landscape, for understanding the role of bee pollinators in affecting plant population structure, for planning conservation strategies for rare plants, and for designing refugia that help to maintain pollinator communities and pollination function for natural plant communities and agricultural crops.

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