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## ORIGINAL RESEARCH ARTICLE

### Remarkable long-distance returns to a forage patch by artificially displaced wild bumble bees (Hymenoptera: Apidae)

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Bumble bees are believed to minimize travel distance and time while seeking foraging resources, and to memorize landmarks and return to forage patches visited earlier. Given these abilities, if a worker is displaced, will it switch to a new forage resource close by or will it navigate back to the original forage patch? To address this question we collected 210 *Bombus vosnesenskii* workers from an ornamental *Spirea* patch, marked them with numbered tags, transported them in a cooler, and released them at seven distances, from 1.5 km to 16 km, in each of two directions. Each worker that returned to the *Spirea* patch was recaptured, and re-released at its first release location. Over 8 observation days, 54 workers from 11 release locations returned to the *Spirea* patch. Of these, 16 were recaptured twice, 13 three times, 5 four times and 1 five times. Nine workers returned from release distances  $\geq 10$  km, including one from 16 km, despite the presence of multiple rewarding resources between the release location and the *Spirea* patch. Returns were rapid—three workers released up to 5 km away were recaptured within 4 h, while a worker from 13 km returned within 30 h of release. Wind direction, wind speed, and release direction had significant ( $P < 0.05$ ) impacts on release-to-recapture-times. Also, workers returned significantly ( $P < 0.001$ ) more quickly during subsequent trips compared to their first return. These findings highlight the ability of displaced bumble bee workers to travel long distances, and to navigate back to familiar forage patches.

**Keywords:** bumble bee; artificial displacement; long distance travel; mark-recapture; colored numbered tags; *Bombus vosnesenskii*; forage resource

## Introduction

Bumble bees, *Bombus* spp. (Hymenoptera: Apidae), provide valuable pollination services for native plants and agricultural crops (Corbet, Williams, & Osborne, 1991; Free, 1993). Declines in their populations worldwide (Goulson, Lye, & Darvill, 2008; Grixti, Wong, Cameron, & Favret, 2009; Jacobson, Tucker, Mathiasson, & Rehan, 2018; Ogilvie et al., 2017; Senapathi et al., 2015) have led to conservation programs focused on the provision of appropriate foraging resources. Bumble bees are social insects that require continuous food resources for colony survival and growth (Alford, 1975). When environmental conditions are suitable, workers leave the nest to seek appropriate foraging resources, and return with pollen and nectar collected from flowers. Bumble bees are generally polylectic (generalist feeders) and forage on a wide range of plant species. However, workers have been shown to exhibit flower constancy, and to revisit the same type of flower even when resources that are equally or more rewarding are available close by (Chittka, Thomson, & Waser, 1999; Free, 1970; Gegear & Thomson, 2004; Heinrich, Mudge, & Deringis, 1977). Flower constancy in bumble bee workers is believed to be due to their limited ability to simultaneously store, process and recall multiple flower

colors or flower-handling techniques (Chittka & Thomson, 1997; Gegear & Laverty, 2005; Goulson, 2000; Manning, 1957; Waser, 1986; Wilson & Stine, 1996).

Bumble bees also return to flower patches visited earlier. The same flower type may be present in isolated patches at multiple locations within the foraging range, but workers tend to trapline (make repeated sequential visits to a series of foraging resources) and thereby return to the same patch day after day (Dramstad, 1996; Heinrich, 1976; Manning, 1957; Thomson, Slatkin, & Thomson, 1997). As in the case of flower constancy, workers can memorize landmarks, and save time and energy by returning to rewarding patches visited earlier (Osborne & Williams, 2001).

The distance from which bumble bee workers return to rewarding floral resource patches is not known. It is currently not possible to follow individual wild workers over long distances, and hence determining the outer limit from which workers will return to the same patch is a challenge. Bumble bees exhibit remarkable navigational abilities, and they are strong fliers, which enable them to cover long distances (Goulson & Stout, 2001; Heinrich, 1979; Osborne et al., 1999). However, beyond a particular distance, landmarks and cues associated

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Figure 1. A section of the flowering *Spirea* patch from which 210 *B. vosnesenskii* workers were collected, and re-observation of a marked worker that returned.

with the original foraging site and foraging route/trapline will no longer be visible, and workers may get lost while attempting to return to the same site (Osborne & Williams, 2001).

For studies on foraging distances of bumble bee workers, researchers have used captive colonies and diverse tracking techniques. By marking workers with colored paints and numbered tags, researchers have tracked foraging behaviors of diverse European bumble bee species in the range of 100 m to 1.75 km (Dramstad, 1996; Walther-Hellwig & Frankl, 2000). Harmonic radar used by Osborne et al. (1999) tracked individual workers of *Bombus terrestris* L. up to 631 m, while in recent studies by Woodgate, Makinson, Lim, Reynolds, and Chittka (2016, 2017), the same technique tracked individual bees within a radius of 800 m. A few studies have tracked bumble bee worker movement over longer distances. In a study by Goulson and Stout (2001), marked workers from captive colonies of *B. terrestris* L. were observed to return to their nest after artificial displacement from a distance of 9.8 km. More recently, Rao and Strange (2012) estimated that workers of the USA species, *Bombus vosnesenskii* Radoszkowski, could travel 11.6 km. This estimate was inferred with genetic markers, and represented half the distance between the most remote fields visited by wild workers from the same colony. In the current study, we used number tags to determine the distance from which displaced wild bumble bee workers will navigate back to a known rewarding resource. Workers that returned to the capture location were re-released at the same location of the first release. Release-to-recapture times were recorded and impacts of relocation direction and distance, prevailing wind speed, wind direction, and the return trip number, were

determined. The study was conducted with workers of *B. vosnesenskii*, the same species used in the study by Rao and Strange (2012). This medium tongue-length, ground-nesting species is distributed along coastal regions of the states of California, Oregon, and Washington on the west coast of USA, where it is common and increasing in abundance (Jha & Kremen, 2013; Koch, Strange, & Williams, 2012; Rao & Stephen, 2009).

## Materials and methods

### Study site

The study was conducted in June–July 2015 in Corvallis, Oregon, on the west coast of the USA. The foraging site consisted of two ornamental cultivated *Spirea japonica albiflora* hedges ( $53 \times 1.3 \text{ m}^2$ ;  $43 \times 1.3 \text{ m}^2$ ) (henceforth called the *Spirea* patch) on either side of a street on the Oregon State University campus ( $44.564617^\circ \text{ N}$ ,  $123.274339^\circ \text{ W}$ ). No other similar *Spirea* patches were present in the area. *Spirea japonica albiflora* is a deciduous shrub with numerous small white flowers clustered in dense panicles against which bumble bee workers are conspicuous (Figure 1). The *Spirea* patch drew honey bees (*Apis mellifera* L.) and other bees but the bumble bee species *B. vosnesenskii* was the dominant bee species observed during the study period.

### Bumble bee worker releases

Two hundred and ten wild *B. vosnesenskii* workers were collected from the *Spirea* patch and placed in a cooler. A unique colored numbered tag (Betterbee, Greenwich, NY; Figure 1) was attached dorsally to the thorax of each worker. After transportation in the cooler, 15 marked workers each were released at 14 sites located 1.5 km, 3 km, 5 km, 7.5 km, 10 km, 13 km, and 16 km, east and west of the *Spirea* patch. Release locations at the select distances from the *Spirea* patch were determined with Google Maps and Google Earth GPS software (Figure 2; Supplementary Material 1). Release locations east and west of the *Spirea* patch were selected for the study as landscapes in these directions differed considerably while those to the north and south were similar. On both sides, release locations closer to the *Spirea* patch consisted of residential areas. Farther away, the landscape was largely natural and undeveloped on the west side while large agricultural fields dominated the landscape on the east.

### Bumble bee worker returns

Observations on returns of tagged bumble bee workers were made by two investigators walking back and forth along the *Spirea* patch for 6 h per day, 3 h in the morning, and 3 h in the afternoon. Tagged workers that were recaptured from the *Spirea* patch were recorded, and once again artificially displaced and released from the same locations as their original releases. The study was





Figure 2. Landscape where the study was conducted showing the differences in terrain on east and west sides of the flowering *Spirea* patch from which *B. vosnesenskii* workers were collected and released at distances up to 16 km.

commenced on June 30 and ended on July 9 when bloom in the *Spirea* patch had declined. In all, observations were made for 96 h over 8 observation days.

### Analyses of impacts of factors on duration of return

The period between release and return to the *Spirea* patch of each marked worker was calculated, and impacts of worker release direction, prevailing wind direction, and wind speed, on the duration of return were determined using regression analysis (SAS/STAT, 2011). Only daylight hours between 600h and 2100h were included. Based on selection of independent variables with a linear or quadratic relationship with the dependent variable (Return-Time), the initial model included Release Distance, Release Distance<sup>2</sup>, Release Distance<sup>3</sup>, Release Direction (east coded as 1 and west coded as 0), Wind Speed, and Wind Direction during daylight hours. The dependent variable Return Time was square root transformed in all models to improve the equality of residues.

To determine if wind speed had a differential impact on workers released east and west of the *Spirea* patch, the speed of the dominant, daytime, mid-summer wind direction in the study region (NNW) was included in the analysis. Wind directly from the north or south was assumed to be neutral. Wind direction and prevailing wind speed, taken three times per hour, were obtained from “<https://www.timeanddate/weather/usa/corvallis>.” The average wind speed and direction during daylight hours during each individual worker flight return time (release to recapture) was extracted from this data set

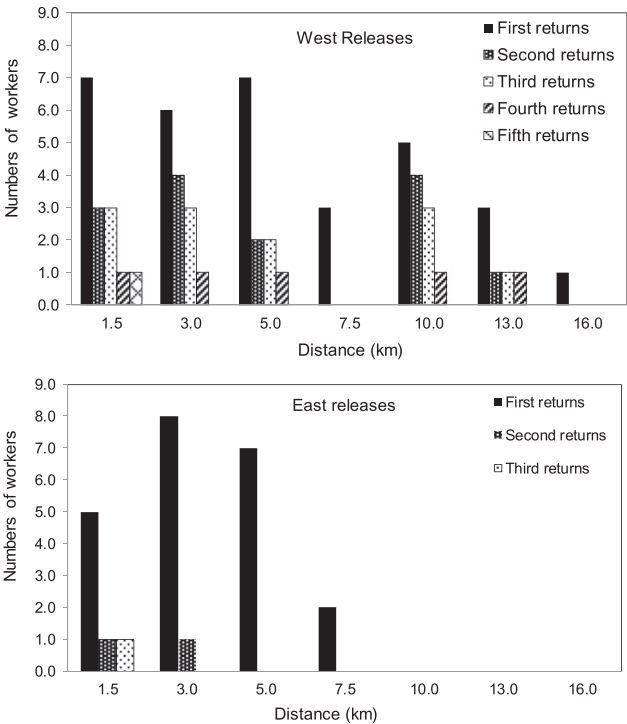


Figure 3. First and subsequent observed returns of *B. vosnesenskii* workers released from seven distances east and west of the *Spirea* patch from which they were collected.

using vector trigonometry embedded in an Excel file (Supplementary Material 2). A modified wind direction variable was generated to adjust for the transition between 359° NNW and 1° NNE (Supplementary Material 3).

Once the best-fit regression model was obtained from the above environmental variables (Supplementary

Table 1. Summary of the analyses of impacts of factors on *B. vosnesenskii* worker returns to the *Spirea* patch.

Variable Entered	Model Entry			Model Parameters	
	Partial R-Square <sup>a</sup>	F	P	Variable Coefficient	SE
Intercept		133.52	<0.0001	9.735	0.842
Release Distance	0.0190	3.27	0.0757	0.070	0.039
Release Direction	0.0412	6.78	0.0117	0.683	0.262
Wind Speed	0.3435	39.79	<0.0001	-0.620	0.098
Wind Direction	0.0871	36.32	<0.0001	-0.052	0.009
Categorical Variable Return Trip Number <sup>b</sup>					
Return 2	0.0468	30.23	<0.0001	-2.306	0.419
Return 3	0.0872	16.15	0.0002	-2.242	0.558
Return 4	0.0321	18.41	<0.0001	-2.823	0.658

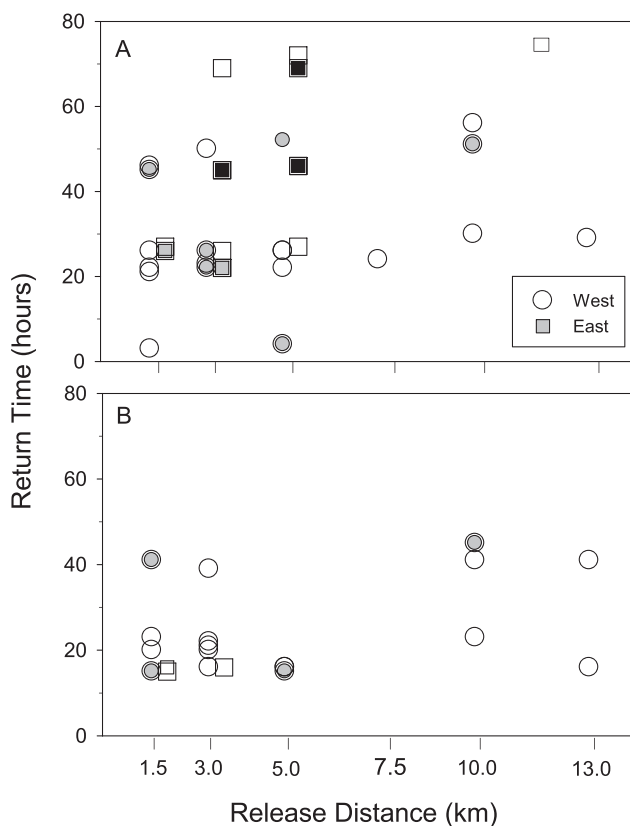
<sup>a</sup>Partial R-squares after all significant variables entered, df = 1, 59.<sup>b</sup>Compared against Return Trip 1.

Figure 4. The relationship between Return Time and Release Distance of *B. vosnesenskii* workers. (a) Returns of workers after the first release (Trip 1). (b) Returns of workers after recapture and re-release (Trips 2–5). Circles = workers released on the west side; Squares = workers released on the east side; ○, □ = returns of one worker, ●, ■ = returns of two workers; ◐, ◑ = returns of three workers.

Material 4), the Return Trip Number associated with each worker that returned was added as a categorical variable (with associated dummy variables) to determine if worker return times to the *Spirea* patch were shorter with repeated releases. The relationship between Return Time and Release Distance as influenced by Return Trip Number was further examined by comparing first return trips with those of subsequent return trips (2 through 5) using proc GLM.

## Results

### Bumble bee worker first returns

Of the 210 *B. vosnesenskii* workers released, 54 (25.7%) were recaptured on the *Spirea* patch. Across all observation periods, 32 of 105 (30.5%) workers were recaptured from all seven west release locations while 22 of 105 (21%) workers were recaptured from four of the seven east release locations (Figure 3). The observations indicated that, from some release locations, ~50% of workers returned. Eight workers were re-observed from the 3 km location east of the *Spirea* patch, while seven workers were re-observed from the 5 km east and the 1.5 km and 5 km west locations. Of the 45 workers released  $\geq 10$  km or further from the *Spirea* patch on the west, 9 (20%) were re-observed (Figure 3). The farthest release location from which a worker returned was 16 km on the west.

### Multiple returns of bumble bee workers

Of the 54 workers that were recaptured on the *Spirea* patch, all but one (stolen with the cooler in which it was stored) were released a second time. Of these, 16 were recaptured a second time, 13 a third time, 5 a fourth time, and 1 a fifth time (Figure 3). Thus, in all, 35 bumble bees returned more than once to the *Spirea* patch.

The pattern of multiple returns differed across the two directions of release. Only three of the 35 that re-returned were from eastern release sites; one re-returned twice from the 1.5 km location, and one re-returned once from 3 km (Figure 3). The remaining 32 re-returns included recaptures from five release locations on the west (Figure 3). Of these, 11 (34%) recaptures were made of workers released 10 km or 13 km from the *Spirea* patch. One worker each from 1.5 km, 3 km, 5 km, 10 km, and 13 km were recaptured four times. The worker that returned 5 times was released at the 1.5 km location.

### Time between release and returns

Three workers were observed returning to the *Spirea* patch the same day that they were released. One worker released 1.5 km on the west returned within 3.5 h while 2 workers released 5 km away returned within 4 h. From the east side, no workers were observed returning the same day. The day after release, 38 returns (including first and subsequent releases) were recorded, including 27 from the west and 11 from the east. One worker each from 10 km and 13 km were observed to return within 30 h of the initial release (including night hours). On the second day after release, 21 returns were observed, 15 from the west and 6 from the east. In all, of the 89 returns (54 first returns and 35 re-returns) observed, 62 (70%) were observed within 2 days. Five workers were recorded returning on 3 consecutive days. The worker from the farthest release location on the west (16 km away) was recaptured 5 days after initial release.

### Factors affecting return time

The model output of the initial 4-variable model with F statistics and P-values are presented in [Supplementary Material 4](#). The partial R-squares and associated F-statistics and P-values of the significant variables with the subsequent addition of Return Trip Number are presented in [Table 1](#). Of the four continuous variables in the model, Wind Speed had the greatest correlation with Return Time, followed by Wind Direction, Release Direction, and Release Distance. With the addition of Return Trip Number (2–4), the adjusted R-squared of the model improved from 0.4278 ([Supplementary Material 4](#)) to 0.6161.

In the regression model, the main effect of Release Distance on Return Time was significant at  $P = 0.0757$  due to its interaction with Return Trip Number. When Return Trips 2–5 were compared against Return Trip 1, Return Trips 2, 3, and 4 were significantly different from Return Trip 1 ([Table 1](#)), indicating that the relationship between Return Time and Return Trip differed for Return Trip 1 compared to these trips. When Return Trip 1 was separated from Return Trips 2–5, there was no relationship with Release Direction for Return Trip 1 ([Figure 4a](#);  $F = 0.38$ , d.f. = 1,38,  $P = 0.5442$ ), but there was for workers on Return Trips 2–5 ([Figure 4b](#);  $F = 6.71$ , d.f. = 1,16,  $P = 0.0197$ ).

The model coefficients presented here describe the quantitative relationship between the explanatory variables and the square root of Return Time. Back-transforming regression coefficients so that they apply directly to the dependent variable is problematic. This is particularly true when the transformation is non-linear (such as square root), and results in substantial interpretation difficulties. Accordingly, we present the original variable coefficients from the regression model.

The five explanatory variables—Release Direction, Release Distance, Wind Direction, Wind Speed, and Return Trip Number—differed in the magnitude of their impacts on Return Time. The absolute value of the four continuous variable coefficients ranged from 0.683 to 0.052, a factor of 13.1 ([Table 1](#)). Release Direction had the largest coefficient (positive), and indicated that workers released to the east took substantially longer to return than those released to the west. Wind Speed had the next highest coefficient (negative), indicating that as wind speed increased return time decreased. The opposite signs of the coefficients for Release Direction and Wind Speed suggest that there was an interaction between the two, with higher winds reducing return time more for workers released to the west than those released to the east.

The negative coefficients of Return Trips 2–4 indicated that bees returning a second, third, and fourth time were re-observed sooner at the *Spirea* patch ([Table 1](#)). This variable and its coefficient were strongly influenced by workers released at shorter distances ( $\leq 5.0$  km) as they made the most repeat trips.

The positive coefficient for Release Distance indicated that, as Release Distance increased so did Return Time, but its effect (coefficient) was small ([Table 1](#)). As mentioned above, this overall relationship is due to the Return Trips 2–5. We followed up with two separate GLM analyses (Return Trip 1 alone, and Return Trips 2–5) to explore the precise impact of Return Trip on the Return Time and Release Distance relationship. The coefficient for Return Trip 1,  $-0.037$ , was not significantly different from zero (GLM,  $P = 0.5422$ ). The coefficient for Return Trips 2–5 was 0.128 (GLM,  $P = 0.0197$ ). Investigating further, the separate coefficients for the individual Return Trips 2, 3, and 4 were not significantly different from each other (GLM,  $P > 0.30$ ), so there was no additional significant decrease in the relationship between Return Time and Release Distance beyond the second return trip. There was only one Return Trip 5 so it could not be statistically compared to Return Trips 2, 3, and 4.

Wind Direction, while significant in the regression analysis, had the lowest quantitative impact on Return Time. This probably is due to the limited variation in average wind direction during the period of the releases. The coefficient of Wind Direction was negative, which indicates that the impact of Wind Direction on Return Time applied to workers released to the east but not from the west.

### Discussion

The mark-recapture study reported here underscores the ability of bumble bee workers to travel long distances after artificial displacement, and to navigate back to the site of capture. While the observations reported here are, in themselves, noteworthy, it is important to note that they only represent *minimum* estimates in



terms of numbers of returns and the return times, as workers could have missed detection by the investigators or they could have returned outside of the observation periods included in the study, which covered a fraction of summer daylight hours.

In the current study, the tagged workers were artificially displaced and thus the returns do not represent a natural phenomenon. Still, the return of 54 wild *B. vosnesenskii* workers to the same foraging *Spirea* patch from which they were collected, from two directions, and from distances up to 16 km, is remarkable. *Spirea* is not native, and is not listed as a flowering species for drawing native bees in conservation programs. Alternative multiple foraging resources that are known to be attractive to bumble bees (examples: lavender, linden) were abundant and blooming at multiple locations between the capture and release points during the period of the study. Thus, while nutritional quality and quantity can shape bumble bee foraging strategies (Vaudo, Patch, Mortensen, Tooker, & Grozinger, 2016), workers may be driven to return to known foraging resources that they have visited earlier. Research is needed to determine whether workers of other species exhibit similar long distance flight abilities for returning to familiar foraging resources. Such foraging patterns across species need to be considered when developing programs for promotion of bumble bees (Rao & Strange, 2012).

The multiple returns to the same *Spirea* patch of individual workers after artificial displacement is also noteworthy. Of the 53 workers that were re-released, 30% were re-observed a second time, 25% a third time, 9% a fourth time, and 2% a fifth time. This included five workers that were re-observed on three consecutive days. No similar study with multiple releases has been reported. In a two-year mark-recapture study by Osborne and Williams (2001), 28% of marked workers were re-observed in one year and 21% in the second. However, re-observations were not made from locations at various distances as in the current study, but represented worker returns a week later to multiple patches ( $9 \times 9 \text{ m}^2$ ) on which they were released. Also, out of 28% marked workers re-observed in the first year, only 4.5% were re-observed twice and <1% thrice. Re-observations in the second year were lower. No bee was observed more than three times in either year.

The current study provides strong and direct evidence that bumble bee workers can cover distances  $\geq 10$  km. We recorded five workers that returned from 10 km, three from 13 km, and one from 16 km during the 10-day study period. Additionally, a marked worker from the 16 km west location was spotted on another ornamental bush (*Abelia* sp.) ~600 m NW of the *Spirea*. These observations support the estimate (derived with genetic markers) of 11.6 km travelled by *B. vosnesenskii* workers in the study by Rao and Strange (2012). A side

note unrelated to the focus of the study is that the marked worker on the *Abelia* was observed 23 days after its initial capture and release, which indicates that foraging workers can live for at least three weeks. Earlier studies (Goldblatt & Fell, 1987; Rodd, Plowright, & Owen, 1980; da Silva-Matos & Garófalo, 2000) have examined longevity of bumble bee workers that remain in colonies but little is known of foraging worker longevity due to the challenges of tracking workers in flight. The expectation is that foragers will not live as long as workers that remain in the nest due to exposure to diverse risks. Specialist foragers of the tropical *B. morio* were estimated to live 36.4 days (Garófalo, 1978) but mark-recapture studies of the temperate *B. vagans* and *B. terricola* indicated that foragers rarely lived for more than a week or two (Morse, 1986).

We recorded twice as many (24) worker returns from distances  $\leq 5$  km than those (11) released farther away (7.5 km–16 km). This is not unexpected since memorization of landmarks and/or reconnecting with traplines will be more challenging as distance increases. Workers have limited ability to simultaneously memorize and recall features related to multiple types of flowers (Gegebar & Lavery, 1995, 1998, 2001, 2005; Lavery, 1994a, b; Woodward & Lavery, 1992), and would be similarly limited in recalling the greater numbers of landmarks encountered over longer distances. It is thus remarkable that one worker each from 10 km and 13 km on the west side were recaptured on the *Spirea* patch four times during the eight days of observation.

The short duration of returns recorded in the current study is also remarkable. Within 4 h of the first release, two workers were observed to return from 5 km. Also, 38 returns (including first and second returns) were observed the day after the release, including a worker each from 10 km and 13 km on the west. Additionally, 70% of all 89 first (54) and subsequent (35) returns were recorded within two days of their respective releases. In contrast, in the homing study conducted with captive colonies of *B. terrestris* by Goulson and Stout (2001), the shortest return time recorded was 6 h from a release distance of 2 km, and workers from 10 km returned in two days.

A significant relationship was found between the duration of return and the release distance for return trips 2–5. As expected, workers re-released farther away from the *Spirea* patch took more time to return than those that were re-released closer to it. However, the relationship did not hold for the first returns, and this is noteworthy. Also, re-released workers returned more quickly compared to first returns. These results indicate that, on the first return trip, irrespective of the distance of the release location relative to the *Spirea* patch, workers spent time seeking cues that led to the traplines for returning to the foraging site. Once these were memorized, workers were able to return more quickly to the *Spirea* patch. With experience, flight

distance and duration are reduced as shown earlier in the study by Woodgate et al. (2017).

Landscape structure has been shown to affect bumble bee foraging distances (Jha & Kremen, 2013; Redhead et al., 2016). In the current study, foraging resources in urban areas on both sides were similar but the natural areas on the west likely included a greater abundance of bee foraging resources compared with the large fields of wind pollinated grasses (tall fescue, annual and perennial grass, orchardgrass/cocksfoot) raised for seed in the east. Thus, differences in terrain and spatial cues in each direction could be factors that led to more bees returning from the west than the east, and for workers returning from all seven release locations on the west but from only four locations to the east (up to 7.5 km). Bumble bee nest abundance could also have affected returns from the two directions but it was not possible to locate nests of the returning workers. In the study by Jha and Kremen (2013), *B. vosnesenskii* nests were estimated to be higher in natural areas compared to human altered landscapes. However, in a study by Rao and Skyrn, (2013), a high nest abundance of the ground-nesting species *B. nevadensis* Cresson was recovered from vole burrows in a grass seed field further north of the current study location. Thus, either side could have had a higher nest abundance or both sides could have had similar numbers of nests. However, if more workers initially collected from the *Spirea* patch originated from nests in the natural areas on the west, this could account for the higher returns of workers from west release points.

Another east-west difference noted was the duration of returns of workers from the two release directions due to prevailing wind direction and speed. Workers released on the east side took longer to return than those released to the west, and higher winds reduced return time to a greater extent for workers released to the west than those released to the east.

The underlying mechanisms and factors that led bumble bee workers to the same foraging patch after relocation to distances  $\geq 10$  km in the current study are unknown. Flying is energetically costly and workers are expected to minimize their travel distances and time to maximize energy gain (Heinrich, 1975). In the current study, the workers were artificially displaced and energy would have been expended only during returns, but the multiple returns from  $\geq 10$  km are still noteworthy. In the earlier study on artificial displacement by Goulson and Stout (2001), marked workers from *B. terrestris* colonies released at various locations returned from distances up to 9.8 km. Workers typically return to their nest multiple times each day and hence homing instincts would have enabled the workers to return from long distances. It is possible that homing instincts were the factor that influenced the return in the current study too; homing instincts could have enabled the workers to return to their nests, and during their next trip out

they could have recalled and detected cues associated with their traplines that led them to the *Spirea* patch. In the study by Goulson and Stout (2001), five large commercial bumble bee colonies were used for studying the returns of displaced workers to their nests while the current study examined the returns of wild bees. As indicated earlier, it was not possible to locate the nests of the returning workers. Hence, homing abilities could have been involved but other factors could also have led to workers returning to the same *Spirea* patch.

While 16 km is a long distance for a bumble bee worker to travel back to a foraging patch from which it was collected, it may not be the outer limit from which workers can return after displacement. Further research with new techniques that can track individual workers over long distances beyond 16 km are needed for insights into foraging abilities beyond those reported here.

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### Supplementary material

Supplementary material is available for this article at: <https://doi.org/10.1080/00218839.2019.1584962>

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