Movement of nest-searching bumblebee queens reflects nesting habitat quality

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Abstract

1. Movement of foraging animals can be used as an indirect index of habitat quality because movement patterns are expected to shift in association with resources resulting in increased time spent in high-quality habitat. Here, we observed movement of bumblebee (Bombus impatiens) queens as an indirect metric of nesting habitat quality.

2. At a farm in Massachusetts, we recorded flight paths by visual observation of nest-searching B. impatiens queens in three land cover types (hay fields, meadows and forests). According to previous research at this field site, these land cover types represent both high-quality (meadows, forests) and low-quality habitat (hay fields) for nesting bumblebees. Using flight path data, we estimated diffusion coefficients of nest-searching queens (i.e., the rate at which queens explore habitat during nest-searching), as an integrative measure of movement.

3. We found that nest-searching queens explored meadows and forests more slowly than hay fields; we calculated diffusion coefficients of 0.198, 0.272, and 0.762 m² s⁻¹ for bees searching for nests in meadows, forests, and hay fields, respectively. In hay fields, nest-searching queens had smaller step lengths and straighter flightpaths than in other land cover types.

4. Nesting ecology of bumblebees is a key knowledge gap. We showed that nest-searching queens search more thoroughly in areas associated with previously reported high nest densities. Therefore, our research suggests that behaviour of nest-searching queens can also be a proxy for nesting habitat quality. Extending these methods to other Bombus species in other landscapes would be a valuable direction for future research.

KEYWORDS
area-restricted search, Bombus impatiens, bumblebee, habitat, movement, nest-searching

INTRODUCTION

Ecological theory predicts that in heterogeneous environments foraging animals should spend more time in areas where resources are abundant than in areas where resources are sparse (Turchin, 1998).

 altering movement behaviour is one way to alter time spent in different areas. This foraging tactic, also known as area-restricted search, is characterised by slower movement and/or more frequent turns in high-quality habitat. Researchers have used this principle to evaluate habitat preferences of marine vertebrates, relying upon remote...
tracking methods to identify regions where animals engage in area-restricted search (Freitas et al., 2008). Furthermore, as area-restricted search can be induced by the presence of prey (Kareiva & Odell, 1987), animal movement has also been used to evaluate prey abundance indirectly (Chimienti et al., 2017). Although area-restricted search is primarily regarded as a foraging strategy, animal movement has also been used to evaluate behavioural responses of Lepidoptera (butterflies and moths) to non-foraging resources (e.g., adults responding to larval host plant availability; Brown et al., 2017; Crone et al., 2019; Evans et al., 2020; Schultz et al., 2012). In this study, we leverage similar methods to quantify the nest-searching strategy of bumblebee queens (Bombus impatiens) as an indirect metric of nesting habitat quality.

Quantifying movement behaviour can offer advantages over habitat-quality assessments based on counting the number of animals in an area. Although it is often assumed animals are most abundant in high-quality habitat, abundance can be mismatched with quality if quality is defined in terms of demographic metrics such as higher survival or reproduction (Van Horne, 1983). Movement behaviours can be more reliable indicators of habitat quality than estimates of abundance (Winker et al., 1995). For example, in a study of stream salmonids, immigration rates (a movement-based measure of habitat selection) were less temporarily variable than estimates of abundance (Bélanger & Rodríguez, 2002). In addition, quantifying movement behaviours (flight speeds, turning angles) may be an advantageous way to measure habitat quality in study systems where focal species are encountered infrequently. Because movement is tracked continuously, more information is generated per individual via assays of movement than via abundance surveys (in which each individual leads to only a single data point) (Fauchoad & Tveraa, 2003; Lode, 2000).

Bumblebees (Bombus spp.) illustrate the need to understand habitat quality with relatively little data. In spite of extensive past research about bumblebee habitat selection during foraging, we know very little about habitat selection during nesting (Liczner & Colla, 2019). In large part, this knowledge gap has been attributed to the difficulty of finding bumblebee nests. A handful of researchers have conducted formal surveys of bumblebee nest densities (Harder, 1986; Iles et al., 2019; O’Connor et al., 2017; Pugesek & Crone, 2021); however, these studies can be incredibly time intensive and, in some cases, have only limited success. Other studies have used counts of nest-searching queens along transects as an indirect metric of nesting habitat quality (Lanberman et al., 2019; Lye et al., 2009; O’Connor et al., 2017; Svensson et al., 2000). Abundances of nest-searching queens are positively, albeit weakly, correlated with nest densities (O’Connor et al., 2017). There is some concern, however, that queen abundance may be an unreliable indicator of habitat quality if the presence of nest-searching queens is more indicative of an inability to locate a suitable nest site than preference for a habitat type (O’Connor et al., 2017). Identifying alternative, easy-to-implement methods for assessing bumblebee nesting habitat is necessary to better understand bumblebees throughout their life cycles.

Bumblebees are also an interesting model system for studying habitat preferences because they are central place foragers once nests are established, and different habitat features may define nesting and foraging habitat. Bumblebees require flowers as food resources through most of their life cycle, but, because of floral phenology, the location of these resources could differ between colony establishment in spring and peak colony size later in the year (Pope & Jha, 2018). Furthermore, most bumblebee species nest in cavities on the ground surface or below ground, and the most suitable cavities may not be located in the habitat types with the most floral resources (Pugesek & Crone, 2021).

In general, studies of bumblebee habitat have focussed on flowers during summer, when most colonies are largest. However, ecologists have recently noted that areas which are poor sources of floral resources during summer, like forests, provide key resources for bumblebees at other times in their life cycle (Mola, Hemberger, et al., 2021). For example, forests are important sources of early-spring forage (Bertrand et al., 2019; Mola et al. 2021b) and may be preferred as nesting and overwintering habitat (Lanberman et al., 2019; Williams et al., 2019).

In this study, we quantify the movement of nest-searching queens of the common eastern bumblebee (B. impatiens) in three land cover types: forests, meadows and hay fields. We know from past research in this study system (Pugesek & Crone, 2021) that these land cover types differ in nesting habitat quality. Our past study showed that B. impatiens nests were equally abundant in forests and meadows but were absent from hay fields (Pugesek & Crone, 2021). Nests also produced nearly three times as many new queens in forests than meadows (Pugesek & Crone, 2021). Here, we leverage this information to evaluate whether movement behaviour of queens during nest-searching reflects these differences in habitat quality. We quantified movement behaviour of nest-searching queens by visually tracking individuals in the field and discretising flight paths into steps characterised by their length, time and turning angle (i.e., change in direction; Turchin, 1998). Following standard methods (Turchin, 1998), we combined these three measures into a single diffusion coefficient. The diffusion coefficient increases with longer steps, shorter times and straighter movement and thus integrates the three measures of movement into a single metric of how long animals spend in a particular habitat type. For other animal taxa, estimates of diffusion coefficients have been used to predict long-term rates of movement through the landscape (Schultz, 1998). However, as we are targeting focal individuals during one specific behavioural mode, our estimates of diffusion coefficients instead represent the rate at which a given land cover type was explored during nest searching; lower diffusion coefficients mean animals spend more time in an area and search it more thoroughly. As an additional measure of search behaviour, we monitored the amount of time queens spent inspecting potential nest sites from the ground during bouts of nest searching. This metric separates two aspects of the ‘time’ component of movement; speed during flight vs. the proportion of time spent flying.

If movement behaviour is a good indicator of nesting resources, we expect that nest-searching queens would have lower diffusion coefficients (shorter steps, slower flight and/or sharper turns) and spend more time inspecting nest sites in meadows and forests (higher-quality nesting habitat) than through hay fields (low/no-quality nesting habitat). If movement behaviour responds to nesting habitat
quality in terms of end-of-season reproductive output, we would also expect that nest-searching queens would have lower diffusion coefficients and spend more time searching for nest sites in forests than in meadows. Because we defined points in our paths by locations where queens stopped flying to inspect the ground for nest sites, differences in step lengths might directly reflect the rates at which queens encounter potential nest sites. In contrast, differences in turning angle are less obviously related to resource density per se. Thus, these predictions reflect a range from passive responses to higher resource density (e.g., shorter steps and more time searching on the ground in forests and meadows than hay fields) to behaviours that imply innate preferences that would lead queens to spend more time in areas with more resources or higher quality habitat (e.g., more tortuous movement, preference for forests over meadows).

**MATERIALS AND METHODS**

**Study site**

Appleton Farms (42°38′52.09″N, 70°51′1.01″W) is a 266-hectare working farm located in Essex County, Massachusetts. The surrounding landscape is a mixture of farmland, residential areas and forest preserve. Crops are produced on the eastern side of the farm; the western side of the farm, where our study area was located, was dominated by semi-natural grassland (hay fields, pastures) with fragmented natural areas (wet meadows, pine stands, etc.). At the time of this study, larger hay fields were hayed frequently (>3 times per year), whereas meadows were mowed once annually to prevent succession. Although many of the forested areas on the farm were not intensively managed, the understory of these fragments tended to be relatively open.

We searched for queens mainly within a 16-ha area on the farm, which included portions of a 40-ha hay field, 0.75-ha dry meadow, as well as pine plantings and stands of hardwood deciduous trees (see Figure 1). The hay field was seeded with a mixture of pasture grasses (e.g., Phleum pratense, Dactylis glomerata) and legumes (e.g., Medicago sativa, Trifolium spp.). The soil in the hay field was somewhat compacted, and the ground below new spring growth was bare. In the meadow, dominant vegetation included native grasses (e.g., Schizachyrium scoparium), herbaceous native perennials and woody plant species (e.g., Vaccinium angustifolium). Little was in bloom in meadows at the time of our study, and thatch was present on ground below new growth. In forests, leaf litter covered the ground in most areas; decaying stumps, which *B. impatiens* queens are known to use as nesting substrate (Plath, 1922), were also present. Although some weedy flowering plants were in bloom at our study site at the time of our study (e.g., Taraxacum spp.), queens seemed to rely primarily on flowering trees for forage.

**Flight paths surveys**

We collected flight path data by observing wild *B. impatiens* queens over a 3-week span in 2018 (April 26th–May 16th). Nest-searching queens move in a highly stereotyped, zig-zag flight pattern that makes them easy to discriminate from foraging queens (Svensson et al., 2000). We only followed individuals that were engaging in this behaviour. Focal individuals (N = 95) were encountered opportunistically. To distribute sampling across land cover types, we generally monitored 2–3 individuals in a land cover type before moving to a different area of the farm (Table 1), although land management activities prevented us from working in some areas on some survey days. We monitored 1–13 individuals each day we surveyed (N = 13). Surveys were conducted from 9:00 AM to 3:30 PM, when the weather was clear or overcast (but not rainy).

We collected flight path data (Figure 1) using methods modified from Cresswell et al. (1995) and Schultz (1998). Specifically, we mapped flight paths by following focal queens on foot from a distance (>1 m) and dropping a numbered flag at locations where the queens landed on the ground to inspect an area as a potential nest site (on-the-ground surveys were possible due to the fact that nest-searching queens fly slowly). As we watched queens, we took note of the time queens began each inspection from the ground and at which the

**TABLE 1** Number of flight paths collected in each land cover type

| Land cover | Total # of flight paths collected | Total # of flight paths (greater than two steps) |
|------------|----------------------------------|-----------------------------------------------|
| Hay field  | 21                               | 16                                            |
| Meadow     | 41                               | 21<sup>b</sup>                                |
| Forest     | 29                               | 22                                            |
| Total      | 95<sup>a</sup>                   | 59<sup>b</sup>                                |

<sup>a</sup>Four flight paths were started in field margins, but these were later excluded from our analysis due to low sample size.

<sup>b</sup>One flight path started in the hay field and two flight paths started in the meadow crossed a habitat boundary.

![Figure 1](image_url) Example flight paths of queen *Bombus impatiens* searching for nest sites in (a) hay fields, (b) forests, and (c) meadows, and (d) an aerial view of our field site overlaid with flight paths of queen *B. impatiens*. Fifty-three flight paths are represented, as flight paths for six queens were collected outside the boundaries of the image. Flight paths in hay fields, meadows, and forests are represented in goldenrod, light green and dark green, respectively.
A bumblebee flight path with two steps. Points A, B, and C represent locations where the focal individual inspected a potential nest site from the ground. The turning angle between the two steps is represented by the letter theta (θ).

Statistical analyses

Using flight path data, we estimated parameters to calculate a diffusion coefficient, D, for each queen using the correlated random walk approach (see Brown & Crone, 2016; Turchin, 1998).

\[
D = \frac{M_2 + (2M_1^2 + (\cos\theta - 1)\cos\theta)}{4t},
\]

where \((M_1)\) is the average step length, \((M_2)\) is the average squared step length, \((t)\) is the average step time (including time spent in flight and on the ground), and \((\cos\theta)\) is the average cosine of the turning angle (Figure 2).

We estimated movement parameters for each bee from raw tracking data using linear mixed effects models with random effects of focal bee ID and survey date, implemented using the lme4 package in R (Bates et al., 2015). Response variables (move length, squared move length, step time and cosine of turning angle) did not always meet the assumptions of normality, but we did not transform the data prior to fitting models because, according to Jensen’s inequality, transformation would alter coefficient values (Crone, 2013; see Appendix S1 for analyses with transformed data and similar statistical conclusions). We used the predict function to extract coefficients for each individual bee, estimated at a new date to remove effects of date (for further explanation, see lme4 documentation for predict[ ] with ‘allow.new.levels = T’). We used estimates of average step length, squared step length, step time and cosine of turning angle extracted from these mixed effects models to calculate a diffusion coefficient for each queen (Turchin, 1998). We analysed diffusion coefficients for queens searching for nests in different land cover types using a generalised linear model with a fixed effect of land cover type. Estimates of the diffusion coefficient for each queen were natural-log transformed to better meet assumptions of normality. This model included no random effects because we had one estimate of the diffusion coefficient for each queen and because we had already removed effects of date.

Slower movement during nest searching could reflect slower flight or more time spent searching for nests on the ground. To separate these behaviours, we compared the proportion of time each queen spent inspecting potential nest sites from the ground in different land cover types. We analysed these proportions using linear mixed effects models with land cover type as a categorical predictor variable. Using a Gaussian model was appropriate in this case because data were approximately normal (i.e., residuals were unimodal and approximately symmetric, estimated means were not close to zero or one and estimated confidence intervals did not include impossible values), and because these proportions were from continuous measures of time, and thus were not appropriate for analysis as count data.

The significance of predictor variables for linear and linear mixed effects models was determined using F-tests and Wald \(\chi^2\) tests, respectively, implemented using the \texttt{anova} function (package \texttt{car}, Fox & Weisberg, 2019). Post-hoc comparisons of estimated marginal means were made using \texttt{emmeans} function (package \texttt{emmeans}, Lenth, 2020).

RESULTS

We recorded the flight paths of 95 queen bumblebees (\textit{B. impatiens}) searching for nests sites at Appleton Farms (Table 1). Of these, 59 individuals inspected at least 3 potential nest sites from the ground (Table 1). Three individuals searched for nest sites in more than one land cover type during a single flight path (Table 1).

We calculated a diffusion coefficient of 0.762 (95% CI: 0.591–0.980) m² s⁻¹ for queens searching for nests in hay fields, 0.198 (95% CI: 0.160–0.245) m² s⁻¹ for queens in meadows, and 0.272 (95% CI: 0.224–0.331) m² s⁻¹ for queens in forests (Figure 3; comparison across habitats: \(F = 35.1, df = 2, p < 0.0001\)). High diffusion in hay fields is primarily attributable to differences in step length across land cover types: \(N = 3\) out of 59 individuals; steps which crossed habitat boundaries were removed from our data set.

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To avoid repeated sampling of the same individual, we attempted to capture and mark the focal individual with a coloured paint marker (Sharpie paint, oil-based marker; 19/95 individuals followed were successfully marked). We resighted only one of these 19 marked individuals, which suggests ~5% of paths in our data were individuals who we followed more than once. In other study systems, resight rates of tagged bumblebee queens tend to be very low, for example, 16% of tagged queens resighted by Stenström and Bergman (1998).

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cover types ($\chi^2 = 13.8, df = 2, p = 0.001$); queen *B. impatiens* had longer step lengths when searching for nest sites in hay fields (6.5 m, 95% CI: 5.0–8.0 m) than in meadows (3.4 m, 95% CI: 2.1–4.6 m) and forests (3.4 m, 95% CI: 2.2–4.7 m, Figure 4a). Turning angles differed significantly among land cover types ($\chi^2 = 7.6, df = 2, p = 0.023$): sharper turns were made by queens searching for nests in forests (82.0°, 95% CI: 78.9–85.0°) when compared to queens searching for nests in hay fields (75.3°, 95% CI: 70.9–79.7°, Figure 4b) but not in meadows (78.0°, 95% CI: 74.8–81.2°, Figure 4b). Step times were shorter for queens searching for nests in forests (29.1 s, CI: 19.3–39.0 s) relative to meadows (49.0 s, 95% CI: 38.1–59.9 s) and hay fields (57.3 s, 95% CI: 44.5–70.2 s) (Figure 4c; $\chi^2 = 13.3, df = 2, p = 0.001$).

Two movement parameters (step length and time) differed moderately among individuals surveyed, as indicated by random effect standard deviations of 2.06 (step length) and 19.45 (step time), whereas turning angles did not differ much among individuals surveyed (random effect SD = 0.06; Table 2). Movement parameters did not differ much among survey dates (Table 2); however, given the structure of our data (i.e., only a few flight paths were collected each day), it is difficult to disentangle variation attributed to bee ID and variation attributed to date. In addition, the model that used step time as a dependent variable was a singular fit (Table 2; similar results were obtained with this model and a model that did not include a random effect of date).

The amount of time queens spent inspecting potential nest sites by crawling on the ground ranged considerably (4%–96% of total time

**Figure 3** The diffusion coefficient, $D$, for queen bumblebees searching for nests within hay fields, forests and meadows calculated using the correlated random walk approach. Boxplots depict values for each individual, calculated from coefficients for each queen from mixed models (random effects of queen; see Methods). Asterisks indicate significant pairwise comparisons, with + representing $p$-values between 0.1 and 0.05, * representing $p$-values between 0.01 and 0.05, ** representing $p$-values between 0.001 and 0.01, and *** representing $p$-values less than 0.001.

**Figure 4** (a) Average step distance, (b) Average turning angle and (c) Average step time for queen *Bombus impatiens* searching for nests in three land cover types. Error bars are 95% confidence intervals for fixed-effect coefficients, not the random effect values for each individual used in Figure 3 (see Methods). Asterisks indicate significant pairwise comparisons, with + representing $p$-values between 0.1 and 0.05, * representing $p$-values between 0.01 and 0.05, ** representing $p$-values between 0.001 and 0.01 and *** representing $p$-values less than 0.001.
spent nest-searching, and differed significantly across land cover types \((F = 3.8, df = 2, p = 0.028)\). Queens spent more of their time on the ground in forests (49.6%, 95% CI: 39.8%–58.8%) than they spent on the ground in hay fields (35.1%, 95% CI: 24.1%–45.9%) or meadows (36.1%, 95% CI: 26.4%–45.6%, Figure 5). There was no much variation in this behaviour across survey dates (random effect SD = 0.09, residual SD = 0.19).

**DISCUSSION**

Our results support the theoretical prediction that animals move in ways that increase the time spent in higher-quality land cover types. Nest-searching *Bombus impatiens* had lower diffusion coefficients in land cover types associated with high nest densities (forests and meadows) than low-quality habitat (hay fields) (c.f. Pugesek & Crone, 2021). Although such a result could be perceived as confirmatory, it is exciting that general rules developed from taxa like foraging seabirds (Chimienti et al., 2017) or habitat-searching butterflies (Evans et al., 2020; Schultz et al., 2012) can apply in a new context. This finding is especially relevant for bumblebees, since nesting habitat quality is poorly understood (Liczner & Colla, 2019), and nest-searching queens are easier to observe than nests themselves. Indeed, nests are challenging to find in many ground-nesting species, e.g., ground-nesting birds (Shewring & Vafidis, 2021). To the extent that other taxa have a conspicuous nest-searching life stage, it would be interesting to explore movement behaviour as a surrogate for habitat quality in other taxa.

In addition to informing nesting ecology, altered movement behaviour in relation to nesting habitat is interesting because some aspects of nesting habitat quality could be passive responses to encountering resources, but others seem unlikely to be so. Nest-searching queen step distances and step times were both longer in hay fields than in other land cover types. Because steps were defined by stops to inspect potential nest sites, these behaviours indicate that nest-searching queens stopped infrequently to inspect potential nest sites in low-quality (hay fields). Similarly, other animals stop more frequently when they encounter resources more often. For example, cabbage white butterflies (*Pieris rapae*) tend to fly in straight lines regardless of host plant density, but make shorter steps in dense stands of hostplants because they stop frequently to oviposit (Root & Kareiva, 1984). In bumblebees, the tortuosity of movement (as measured by changes in turning angles in relation to habitat quality), also differed between hay fields and forests. Moving in straight lines decreases the amount of time individuals spend in a land cover type, relative to its area (Turchin, 1998), but is not directly related to resource encounter rates. Therefore, area-restricted search of queen bumblebees during nest searching seems to reflect a combination of direct effects of resource density (encountering more possible nest sites) and more thorough searching (via more tortuous movement) in land cover types with fewer resources.

It is less obvious whether the movement of nest-searching queens reflects longer-term quality in terms of reproductive output later in summer. Queens in forests (the higher quality habitat type for new queen production) spent more time nest-searching from ground, compared to both meadows and hay fields. This behaviour could reflect more interest in finding nest sites in forests (due to higher future habitat quality) or could simply reflect greater difficulty locating nest sites in forests. Furthermore, diffusion coefficients were slightly higher in forests than in meadows, rather than lower, as would be expected due to higher new queen production in forests (Pugesek & Crone, 2021; see also Lanterman et al., 2019). In other taxa, area-restricted search is triggered by indirect cues like the presence of foraging conspecifics (in bats; Roeleke et al., 2020) or landscape features.
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(e.g., responses to ocean shelf edge in seabirds; Weimerskirch et al., 2007). However, our results indicate broadly that bumblebees may not change their movement in relation to indirect cues for habitat quality, in terms of future reproduction. Nonetheless, it could be interesting to further explore the mechanisms behind increased search time on the ground. In addition to differences in habitat quality, movement could also be affected by habitat structure. Baltimore checkerspot butterflies (Euphydryas phaeton), for example, tend to disperse more slowly through forested matrix than grassland matrix, likely because lower temperatures in forests inhibit butterfly movement (Brown et al., 2017; Crone et al., 2019). For foraging birds in forests, habitat structure can play an important role in the search tactics used to locate resources. Birds searching in dense vegetation may need to perform more thorough searches, and thus move at slower rates, to locate cryptic resources (Holmes & Recher, 1986; Robinson & Holmes, 1982). Unlike butterflies, bumblebees are robust fliers that can forage even in inclement weather (Corbet et al., 1993), and thus are unlikely to be greatly affected by cooler temperatures in shaded areas. However, it might be harder for queens to manoeuvre through forests, or to find nest sites in areas where the ground cover is dense. Potential nest sites, including entrances of rodent burrows and fallen logs (Lanterman et al., 2019), could be easily obscured by leaf litter or other vegetation. The effects of habitat structure and preference on animal movement are not mutually exclusive. Given that other authors have raised concerns that the abundance of nest-searching queens is more indicative of inability to locate a suitable nest site than preference (O’Connor et al., 2017), it would be valuable to further explore the cues bumblebees rely upon to find nest sites in order to disentangle the factors which could impact movement behaviour.

Although bumblebees changed their movement in response to nesting resource density, the magnitude of behavioural differences between land cover types was smaller than in many published studies of insect movement. For example, Schultz (1998) found that the average diffusion coefficient of female fender’s blue butterflies was 14 times larger in non-habitat than in areas where host plants were abundant, and Crone et al. (2019) found that the average diffusion coefficient of Baltimore checkerspot butterflies was 15 times larger in open matrix than in high-quality habitat. In contrast, the average diffusion coefficient of nest-searching queen bumblebees was approximately 3.5 times larger in hay fields than in meadows and forests. Many butterfly species are habitat specialists and cannot oviposit in areas where there are no host plants available. In contrast, B. impatiens may be able to occasionally nest in hay fields. Although no nests of B. impatiens were found in hay fields by Pugesek and Crone (2021) in 2018 or 2019, we encountered one B. impatiens nest in a hay field during other field work in 2020 at our study site (Pugesek, unpublished data). We also observed subterranean nests of other Bombus species in hay fields (Pugesek & Crone, 2021). In other areas in the United States, bumblebee nests of other species have been found in croplands and semi-natural grasslands (Rao & Skyrn, 2013; Webb, 1961). Therefore, the smaller differences in movement among land cover types in this study may reflect smaller differences in habitat quality.

Monitoring queen movement on foot has strengths and limitations compared to remote telemetry methods. A few studies have used radio telemetry or harmonic radar to monitor the flight paths of large-bodied bees like Bombus and Exaerete frontalis, typically with the objective of exploring habitat use or estimating home-range sizes (Hagen et al., 2011; Makinson et al., 2019; Wikelski et al., 2010). For bumblebees, bouts of nest-searching are often punctuated by longer-distance flights, during which queens move too quickly to follow from the ground. Spring queens have also been observed to ‘mass migrate’ across large bodies of water (Fijen, 2020) and have been sighted over 50 km away from shore (Mikkola, 1984). Small radio trackers might allow researchers to evaluate bumblebee movement across multiple behavioural modes, though, with current technology, radio trackers weigh down bees considerably and can adversely affect fitness (Hagen et al., 2011). Although radio trackers do not seem to have a major impact on the amount of time queens spent at rest, at least early on in the spring (Makinson et al., 2019), they may impact other aspects of queen behaviour, including the ability of queens to explore cavities in the ground. In the future, it could be beneficial to use a combination of on-the-ground and remote tracking methods to collect flight path data on bumblebee queens, in order to capture a more realistic picture of spring movement (Makinson et al., 2019).

Our study also informs monitoring abundance of nest-searching queens to assess habitat associations. After emerging from hibernation, queen bumblebees can spend a considerable amount of their time on the ground, burrowing beneath leaves or vegetation (Makinson et al., 2019; Webb, 1961), where they are probably less conspicuous than bees in flight. We found that nest-searching queens spent a greater proportion of time searching for nests from the ground in forests than in other land cover types. Therefore, spring queens are probably less detectable in forests (in our system) and, more generally, in any land cover types where they spend more time on the ground. Although we do not estimate detection probabilities of nest-searching queens in this study, our results suggest that survey methods that account for imperfect detection (e.g., mark-recapture; Bowers, 1985) would be valuable in obtaining accurate estimates of queen abundance in different land cover types.

In conclusion, the relationship between habitat quality and movement has been studied extensively in other insect taxa (Crone et al., 2019), and most studies have found that animals move more slowly in high-resource land cover types. We show that this general relationship holds for nest-searching bumblebee queens. Our study is the first of its kind for nest-searching Hymenoptera (bees, ants and wasps). The basic result that bumblebees, like many insects, perform area-restricted search opens up at least two future lines of research. The first is the extent to which bumblebees modify their behaviour in relation to resource density and habitat structure. This line of research would be an interesting complement to our knowledge of bumblebee movement during foraging. The second is a methodological tool for identifying bumblebee nesting habitat. Although the species targeted in this study, B. impatiens, is a relatively common bumblebee species,
movement behaviour may be especially useful in identifying habitat for rare bumblebee species. We are hopeful that approaches presented in this paper will be useful in assessing habitat associations for species of conservation concern.

**AUTHOR CONTRIBUTIONS**

Genevieve Pugesek led field work, while both Genevieve Pugesek and Elizabeth E. Crone conceived ideas, designed methodology, conducted data analyses and contributed to writing this manuscript.

**ACKNOWLEDGEMENTS**

We would like to acknowledge Risa McNellis for her assistance in the field. Furthermore, we thank Russell Hopping for his help in locating field sites and the Trustees of Reservations for their support. Funding for this research was provided by and by the Tufts University College of Arts and Sciences. This work was conducted while Elizabeth E. Crone was funded by NSF DEB 13-54224.

**CONFLICT OF INTEREST**

The authors declare no conflict of interest.

**DATA AVAILABILITY STATEMENT**

To better ensure reproducibility of results, we have published all code and data associated with this manuscript to the Figshare Digital Repository. Our code and data can be found at the following link: https://figshare.com/articles/dataset/Data_and_code_from_Movement_of_nest-searching_bumblebee_queens_reflects_nesting_habitat_quality/16416849.

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SUPPORTING INFORMATION
Additional supporting information may be found in the online version of the article at the publisher’s website.

Data S1 Estimates of movement parameters (step length, step time and turning angle) using transformed data.