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Distance models as a tool for modelling detection probability and density of native bumblebees

Darin J. McNeil[1,2] | **Clint R. V. Otto**[3] | **Erin L. Moser**[4] | **Katherine R. Urban-Mead**[5] | **David E. King**[6] | **Amanda D. Rodewald**[1,2] | **Jeffery L. Larkin**[4]

[1]Department of Natural Resources, Cornell University, Ithaca, New York

[2]Cornell Laboratory of Ornithology, Ithaca, New York

[3]U.S. Geological Survey, Northern Prairie Wildlife Research Center, Jamestown, New York

[4]Department of Biology, Indiana University of Pennsylvania, Indiana, Pennsylvania

[5]Department of Entomology, Cornell University, Ithaca, New York

[6]Department of Environmental Conservation, University of Massachusetts, Amherst, Massachusetts

Correspondence
Darin J. McNeil, Department of Natural Resources, Cornell University, Ithaca, NY.
Email: djm462@cornell.edu

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Abstract

Effective monitoring of native bee populations requires accurate estimates of population size and relative abundance among habitats. Current bee survey methods, such as netting or pan trapping, may be adequate for a variety of study objectives but are limited by a failure to account for imperfect detection. Biases due to imperfect detection could result in inaccurate abundance estimates or erroneous insights about the response of bees to different environments. To gauge the potential biases of currently employed survey methods, we compared abundance estimates of bumblebees (*Bombus* spp.) derived from hierarchical distance sampling models (HDS) to bumblebee counts collected from fixed-area net surveys ("net counts") and fixed-width transect counts ("transect counts") at 47 early-successional forest patches in Pennsylvania. Our HDS models indicated that detection probabilities of *Bombus* spp. were imperfect and varied with survey- and site-covariates. Despite being conspicuous, *Bombus* spp. were not reliably detected beyond 5 m. Habitat associations of *Bombus* spp. density were similar across methods, but the strength of association with shrub cover differed between HDS and net counts. Additionally, net counts suggested sites with more grass hosted higher *Bombus* spp. densities whereas HDS suggested that grass cover was associated with higher detection probability but not *Bombus* spp. density. Density estimates generated from net counts and transect counts were 80%–89% lower than estimates generated from distance sampling. Our findings suggest that distance modelling provides a reliable method to assess *Bombus* spp. density and habitat associations, while accounting for imperfect detection caused by distance from observer, vegetation structure, and survey covariates. However, detection/non-detection data collected via point-counts, line-transects and distance sampling for *Bombus* spp. are unlikely to yield species-specific density estimates unless individuals can be identified by sight, without capture. Our results will be useful for informing the design of monitoring programs for *Bombus spp.* and other pollinators.

KEYWORDS
Bombus, detection probability, distance modelling, pollinators, surveys, transects

1 | INTRODUCTION

Native bees in North America are important pollinators of both crops and wild plants (Ashman et al., 2004; Garibaldi et al., 2013; Kremen, Williams, & Thorp, 2002). Indeed, bees, along with other pollinators, are considered keystone species that facilitate sexual reproduction for 85% of angiosperms worldwide (Allen-Wardell et al., 1998; Kevan, 1990). In agricultural portions of the United States, pollination services provided by native bees are valued at $3 billion USD, annually (Calderone, 2012). Even as the ecological and economic importance of native bees is recognized, there is a mounting evidence that many bee species are declining (Cameron et al., 2011; Goulson, Lye, & Darvill, 2008). These declines include not only managed species like *Apis mellifera* but also North American native taxa like bumblebees (*Bombus* spp.) and others (Cameron et al., 2011; Goulson, Nicholls, Botías, & Rotheray, 2015; Potts et al., 2010). For example, the rusty patched bumblebee (*Bombus affinis*) was listed as Federally Endangered under the Endangered Species Act in 2017, and several other *Bombus* species have been proposed for listing (Jepsen, Evans, Thorp, Hatfield, & Black, 2013). Although the drivers responsible for population declines vary among species, threats include pesticides, non-native pathogens and habitat loss/degradation (Goulson et al., 2015; Persson, Rundlöf, Clough, & Smith, 2015).

Still, while evidence is fairly clear regarding bee declines for some regions and/or species, the status of many bee populations remains unknown (Tepedino, Durham, Cameron, & Goodell, 2015). In 2015, the United States Pollinator Health Task Force proposed the development of national pollinator monitoring programs to estimate population trends and identify environmental stressors affecting native bees (Vilsack & McCarthy, 2015). Central to accomplishing these goals is the accurate estimation of bee population sizes across species, genera, morphospecies and functional groups to establish a reference benchmark for evaluating population trends, abundance across different habitats and assessing the outcomes of conservation interventions.

Although a variety of methods have been commonly used to sample wild bee populations (e.g., fixed-area aerial netting, bee bowls, vane traps), each is limited by inherent methodological biases that make inference of true densities difficult. In particular, few methods account for the bias caused by imperfect detection (e.g., Loffland et al., 2017) in that only bees captured or otherwise detected by an observer are counted and subsequently modelled. Regardless of sampling method, only a fraction of the individuals present at a location will be detected (Kéry & Schmidt, 2008). Raw counts, which fail to account for detection probability, will invariably generate estimates of abundance that are biased low if some individuals are present but not detected (Kéry & Schmidt, 2008; MacKenzie et al., 2002, 2005). Though such methods have merit under many circumstances, accurate estimate of abundance, or changes in abundance over space and time, requires consideration of methodological biases like those caused by imperfect detection (MacKenzie et al., 2005). In addition, failure to account for imperfect detection can obfuscate habitat associations, particularly when the habitat conditions that are attractive to the organism also make it more difficult for observers to detect the organism (MacKenzie, 2006). Consequently, researchers might be led to believe that certain habitat conditions (associated with low bee counts) are low-quality habitats while bees may, in reality, be of equal/greater abundance but less detectable or vice versa (MacKenzie, 2006).

Here, we demonstrate the utility of hierarchical distance sampling (HDS) for estimating habitat-specific density (i.e., abundance per unit area) and detection probability of bumblebees in deciduous forest of central Pennsylvania. Hierarchical distance sampling is an analytical technique that allows researchers to model habitat-specific abundance and heterogeneity in species detection within a unified framework (Hedley & Buckland, 2004; Kéry & Royle, 2015; Royle, Dawson, & Bates, 2004). It builds upon standard distance sampling, which is a widely used method for estimating animal abundance while for accounting imperfect detection (Buckland, Anderson, Burnham, & Laake, 2005). However, HDS differs from standard distance sampling in that it allows for spatial variability in abundance and detection across multiple sites to be explained as a function of covariates (Kéry & Royle, 2015). Although other methods exist for estimating abundance while accounting for detection (e.g., occupancy, *N*-mixture, etc.), most require multiple visits, with the assumption of population closure between surveys (Kéry & Royle, 2015; MacKenzie et al., 2005). Distance sampling may be particularly useful for insect studies because it requires only a single site visit to estimate detection probability and many short-lived insects (like some bee species) may not emerge long enough to allow multiple visits per site. Distance sampling has been routinely used by wildlife researchers to model abundance and detection functions for multiple vertebrate taxa (Hammond et al., 2002; Karanth & Sunquist, 1995; Marques, Thomas, Fancy, & Buckland, 2007). To our knowledge, no previous research has demonstrated the use of distance sampling to estimate bee abundance or habitat associations (Bendel, Hovick, Limb, & Harmon, 2018). Our goals were to: (a) use HDS to evaluate how *Bombus* spp. detection probability varies with distance, survey technique and habitat attributes; (b) compare abundance and density estimates generated from HDS to standard sampling approaches (fixed-width transects and fixed-radius net counts) that do not account for imperfect detection; and (c) identify site-specific habitat relationships for *Bombus* spp. across sampling methods.

2 | MATERIALS AND METHODS

2.1 | Study area

We surveyed bees within the Pennsylvania Wilds region of northcentral Pennsylvania, focusing on Centre and Clinton Counties (Figure 1). This region lies within the Appalachian Plateau of the northcentral Appalachian Mountains and is characterized by a rugged series of high-elevation ridges (300–600 m.a.s.l.) punctuated by low valleys along the Allegheny Front (Shultz, 1999). Vegetation communities within the Pennsylvania Wilds are chiefly mature

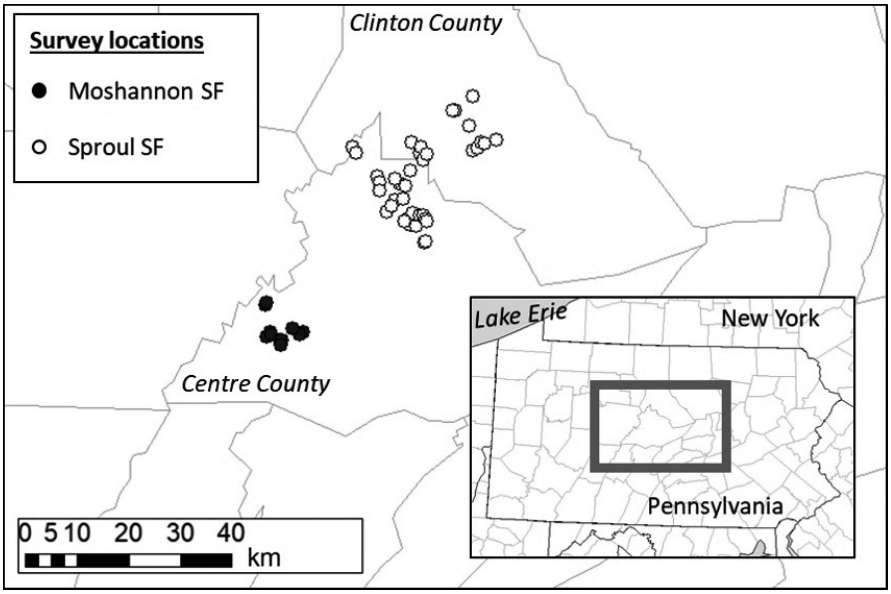

FIGURE 1 Survey locations within the Pennsylvania Wilds where we conducted surveys for *Bombus* spp. within regenerating timber harvests

deciduous- or mixed forest (80–100 years, post-harvest; McCaskill et al., 2009) with oak (*Quercus* spp.), hickory (*Carya* spp.) and eastern hemlock (*Tsuga canadensis*) among the most common species (Wherry, Fogg, & Wahl, 1979). We concentrated our efforts within deciduous forests of Sproul and Moshannon State Forests where oak silviculture aims to restore young forest age classes through timber harvest and regeneration. Because silvicultural practices within these two State Forests aim to restore habitat for forest wildlife, we focused our survey efforts within regenerating oak stands, 0–9 years post-management. During surveys, a variety of flowering plants were available to *Bombus* spp. including low-growing shrubs like hillside blueberry (*Vaccinium pallidum*) as well as herbaceous forbs like eastern teaberry (*Gaultheria procumbens*) and common cow-wheat (*Mellampyrum linerare*). Most tall woody plants were not flowering except for Devil's walkingstick (*Aralia spinosa*), which we detected only within a few of our sites.

2.2 | Site selection and survey placement

We randomly selected 47 timber stands within Sproul and Moshannon State Forests that had been recently treated with overstory removal (basal area: 2.3–9.2 m^2/ha). We attempted to maximize the distance between sites such that our average distance-to-nearest-site was 1,110 m (*SE*: 107 m; range: 464–4,516 m). This reduced the likelihood of individuals being detected at multiple sites (Redhead et al., 2016). Timber harvest units averaged 23.14 ha (*SD*: 18.62 ha; range: 2.54–103.92 ha) in size. A single survey point was located within each harvest using a random point generator tool in ArcGIS 10.2 (ESRI, 2011). We attempted to minimize edge effects by ensuring points were relatively consistent in their placement with respect to timber harvest edges; sampling was restricted to areas at least 80 m from the edge of timber harvests and our final sample of sites was a mean distance of 118.67 m (*SE*: 6.24 m).

2.3 | Transect surveys

At each point, we sampled *Bombus* spp. using three survey types: (a) distance transects; (b) transect counts; and (c) aerial netting counts. Both distance transects and fixed-width transect counts occurred simultaneously along 66 m transects oriented north-to-south and centred at each point location. Along each transect, observers walked forward at a constant rate (~1 m/min) such that the observer arrived at the transect end after 30 min. Prior to surveys, each observer (n = 2) was trained in distance estimation using dummy transects along which bees' distances were physically measured after each attempted estimate using a measuring tape. Once all observers were consistently estimating distances within ±0.25 m, field surveys were conducted with a 2 m long measuring stick for constant reference. While walking along each survey transect, the observer recorded *Bombus* spp. detections such that a final count (#) was generated for each survey coupled with the distances (±0.25 m) between each *Bombus* spp. and the transect. We did not attempt to identify species or sex for *Bombus* spp. detected in situ therefore counts were likely multiple species and sexes. Survey data for each point included a *Bombus* spp. count and their corresponding detection distances. We discerned between *Bombus* spp. and *Xylocopa virginica* by abdomen pubescence (Michener, McGinley, & Danforth, 1994). Distances were recorded as the perpendicular distance from the transect to each bee and noted as the distance at which the bee was *first* detected. While walking along each transect, observers attempted to keep track of previously detected *Bombus* spp. to avoid double-counting individuals that might be moving among floral resources near the transect. We anecdotally observed this method largely avoided double-counting, as *Bombus* spp. are generally large-bodied, conspicuous insects and easily audible in flight. All raw counts and detection distances constituted our "distance transect" data (a) and raw counts within 2 m of the transect constituted our "transect count" data (b).

We followed standard bee survey methods to avoid common causes of detection failure (Ward et al., 2014); Surveys were conducted only in bright light conditions, low wind, warm days (≥16°C), and only during late morning and afternoon (10:00–17:00). Though we attempted to use study design to reduce the potential impacts of these factors on *Bombus* spp. detectability, we also included them in detection modelling. At the time of each survey, we recorded: (a) surveyor ID; (b) cloud cover; (c) time of day; and (d) Beaufort Wind Index. Local temperature data were downloaded from Weather Underground from the KUNV weather station in State College, Pennsylvania (Weather Underground Inc., 2018). Cloud cover was estimated in the field to the nearest 25% (0%–100%). Beaufort Wind Index was measured on an incremental scale from 0 to 5 with 0 representing no wind at all (i.e., smoke would theoretically rise without drift) and 5 representing high winds such that entire trees sway in the wind (Hau & Von Renouard, 2006). We avoided surveying in wind indices > 3, and thus considered two categories of wind: 0–1: "low", 2–3: "moderate" in our analyses. All surveys took place from 10 to 25 July, 2017.

2.4 | Net counts

To measure *Bombus* spp. abundance within fixed-radius net counts, we created 15 m radius count surveys centred around each point location (the centre of each distance transect). Netted bee counts took place immediately upon the conclusion of transect surveys (described above). Within each fixed-radius plot, a single observer spent 30 min seeking- and attempting to capture all *Bombus* spp. detected with a hand net. We chose fixed-radius net sampling because it is a standard sampling technique for native bees (Persson et al., 2015; Potts, Vulliamy, Dafni, Ne'eman, & Willmer, 2003; Roulston, Smith, & Brewster, 2007) and would therefore serve as a basis for comparison to our abundance estimates generated from HDS. For each *Bombus* spp. detected, the observer attempted to capture each bee using a hand net (collapsible 15" diameter net, 17" handle, Bioquip Product #7115CP) and, once captured, all bees were held captive for the remainder of the survey. For each captured bee, the timer was stopped while the observer placed it into a plastic zipper bag and resumed immediately thereafter. This method prevented us from recapturing and double-counting bees within the same plot. After 30 min of survey time had elapsed, each *Bombus* spp. was removed from its bag with forceps, photographed for another project, and released unharmed. In the few occasions where *Bombus* spp. were observed but evaded capture, they were treated as all other *Bombus* spp. captured for the purposes of this study (i.e., included).

2.5 | Habitat surveys

We surveyed regenerating vegetation structure within timber harvest units from 15 June to 15 July 2017. Vegetation surveys shared their centroid with *Bombus* spp. surveys. Vegetation data quantified habitat structure of woody stems and herbaceous understory, rather than plant composition. All vegetation data were collected along three 50 m radial transects, each oriented at 0°, 120° and 240° from point centre. Along each transect, we recorded plant strata at 10 "stops" (10 m apart; $n = 30$/net count location). Vegetation strata recorded at each stop consisted of the presence/absence of sapling, shrub, forb and grass/sedge. Saplings were young trees <10 cm (in diameter breast height). This sampling regime gave us adequate resolution to assess vegetation structure (15 stops/site) while remaining of comparable scale to our bee sampling transects (33 m). We found vegetation structure to be highly correlated across scales as large as 100 m and therefore believe our 50 m vegetation plots represented site conditions reasonably well. Shrubs were woody plants with multiple primary stems (in contrast to single-stemmed saplings). Forbs were broad-leafed dicotyledonous plants (e.g., *Solidago* spp.). The plant category "grass" included any monocotyledonous plant (grasses, sedges, etc.). We recorded plant strata with an ocular tube such that only strata that intersected with crosshairs in the ocular tube were considered present (James & Shugart, 1970). While a single stop could include multiple strata types, each stratum could only be represented once per stop and thus each site could have a maximum of $n = 15$ occurrences for each stratum. We analyzed plant strata values as percentages. Prior to all analyses, we calculated Spearman's rho (ρ) for all pairs of covariates to be modelled. Because none were strongly correlated (Spearman's $\rho < 0.60$), no covariates were redundant and all were suitable for modelling.

2.6 | Hierarchical distance models

We analyzed distance transect data (bee counts and distances) using HDS models implemented in the R package "unmarked" (Fiske & Chandler, 2011; R Core & Team, 2018). The package unmarked fits linear models in a maximum likelihood framework and can be combined with an Information-Theoretic approach (Anderson, 2007) for the purpose of model selection (e.g., using Akaike's Information Criterion; AIC; Burnham & Anderson, 2002). Hierarchical distance models allowed us to create and rank candidate models, each of which contained independent model components for detection probability (p) and expected animal abundance (density; λ). HDS models assume (a) subjects are accurately identified (e.g., no false-presences); (b) that all subjects on the transect (distance = 0 m) are detected perfectly ($p = 1.0$); (c) subjects are detected at their original location (i.e., movement is not influenced by the observer); (d) distances are accurately measured; and (e) detection of each individual is independent of the detection of all other individuals (Thomas et al., 2010). Bumblebees appear to constitute good candidates for distance sampling as they can be easily identified (to genus) in the field (Michener et al., 1994), are easily approached by observers (Ward et al., 2014) and remain relatively still during pollination such that accurate distance estimations could be made for each worker. Although distances were measured in the field directly, we binned detections as recommended by Buckland et al., (2005): 0–1, 1–2, 2–3, 3–4 and 4–5 m. Moreover, to prepare distance-based transect data, we truncated the outer 10% of our data such that analyses were conducted using only the closest 90% of *Bombus* spp. detections, as recommended for distance analyses by Buckland et al. (2005). By truncating the data in this way, all detections were <5 m from the observer.

Distance models provide robust estimates of abundance by adjusting animal counts by the probability of detection for given distances (Buckland et al., 2005). This is accomplished by fitting detection distance data to a "detection function" that describes a decay in detection probability as subjects are further from the observer (Buckland et al., 2005; Kéry & Royle, 2015). To evaluate an appropriate detection function, we evaluated models, each fit using one of the following detection functions: (a) exponential; (b) hazard rate; or (c) half-normal (Buckland et al., 2005). This was done prior to all covariate modelling. Each detection function is used to estimate the average probability of detection which is then used to adjust raw counts such that density predictions can be made (Buckland et al., 2005). Once the most appropriate detection function was selected based on AIC_c rank, it was used to model detection probability and density in consecutive models. We modelled detection probability in two tiers: detection tier 1 (survey covariates on detection) and detection tier 2 (habitat covariates on detection). Because our sample size was modest, we used only single-covariate detection models to avoid overfitting HDS models. Detection tier 1 included univariate models for (a) time of day; (b) surveyor; (c) temperature; (d) cloud cover; (e) wind index; and (f) a null (intercept-only) model. Detection tier 2 (fit independently of detection tier 1) included univariate models for (a) sapling cover; (b) shrub cover; (c) forb cover; (d) grass cover; and (e) a null model. Within both model tiers, we used a global habitat model (i.e., sapling + shrub + forb + grass) for density to ensure that variation in density was reasonably well explained while assessing detection probability. We considered covariates to be informative if they were both >2.0 AIC_c less than the null model and had β coefficient 95% confidence intervals that did not include zero. Using the informative covariates from detection tiers 1 and 2, we constructed a set of density models (habitat covariates on density) that accounted for imperfect detection: (a) sapling cover; (b) shrub cover; (c) forb cover; (d) grass cover; and (e) a null model. The null model contained only intercept terms and the informative parameters for detection. Prior to modelling, all continuous covariates were standardized using the *scale* function in base R. Model ranking was done using the "aictab" function of the package "AIC_cmodavg." All models were fit assuming a Poisson distribution in "gdistsamp" and model fit was assessed by calculating a variance inflation factor (ĉ\hat{c}\hat{c}\hat{c}) using the unmarked function "fitstats" (Kéry & Royle, 2015). We considered all models <2.0 AIC_c to be competing and equally supported by the data (Burnham & Anderson, 2002).

2.7 | Poisson generalized linear models

We used a Poisson generalized linear models in R (using the "glm" function) to model *Bombus* spp. abundance along fixed-radius transects and net counts. This allowed us to compare habitat-abundance relationships generated from HDS models to those generated from methods that do not account for detection probability. As with our HDS models, Poisson regression models allowed us to model bee counts as a function of habitat covariates: (a) sapling cover; (b) shrub cover; (c) forb cover; (d) grass cover; and (e) a null (intercept-only) model. We modelled our fixed-radius transect counts by truncating all HDS-transect data by 2 m of the transect line and treating the data as a raw count (Hanley, Awbi, & Franco, 2014; Scheper et al., 2015), which is a standard technique when conducting visual encounter surveys. Net count data were modelled in a comparable manner such that raw counts were modelled as a function of habitat covariates. We did not account for imperfect detection in either of these models but rather modelled *Bombus* spp. count/area interpreted as a density. We again used an information-theoretic approach (Anderson, 2007) with model ranking based on AIC_c considering models < 2.0 AIC_c to be equally supported by the data (Burnham & Anderson, 2002). We also used single-covariate models to avoid overly complex models and the inclusion of uninformative parameters within top models (Arnold, 2010).

3 | RESULTS

We detected 194 individual *Bombus* spp. within 5 m, of which 136 were within 2 m of the transect line. During aerial net counts, we captured n = 201 *Bombus* spp. workers. Of the bees captured during aerial net counts, over 50% were *B. impatiens*, with the remainder being a mixed community of less common species like *B. bimaculatus* and *B. vagans*.

3.1 | Detection probability

Of three detection function models we ran, the best-ranked model included an exponential detection function where detection probability > 5 m from the transect was ≈0 (Figure 2). Using an exponential detection function, we found that detection probability varied as a function of time since 10:00 (the earliest possible start time)

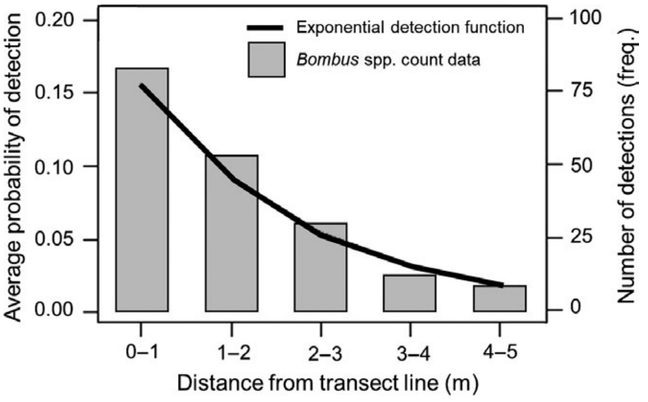

FIGURE 2 Frequency of detections (grey bars; right axis) for *Bombus* spp. within regenerating timber harvests. Detection probability (left axis) declined as a function of distance from transect and was fit to an exponential detection function (black line). *Bombus* spp. were only rarely detected further than 5 m from the transect line

TABLE 1 Hierarchical distance models of detection probability as a function of survey covariates (Tier 1; top) and site covariates (Tier 2; bottom)

Model name	K	AIC_c	ΔAIC_c	AIC_c Wt.	β estimate (95%CI)
Survey covariates on detection probability					
p (observer)	7	348.93	0.00	0.78	0.58 (0.21 to 0.95)
p (time)	7	351.56	2.64	0.21	−0.23 (−0.38 to −0.08)
p (.)	6	358.29	9.36	0.01	-
p (wind)	7	359.87	10.94	0.00	−0.16 (−0.44 to 0.13)
p (temp.)	7	360.64	11.72	0.00	−0.05 (−0.19 to 0.09)
Site covariates on detection probability					
p (grass)	7	352.67	0.00	0.85	0.35 (0.07 to 0.63)
p (forb)	7	358.27	5.61	0.05	0.17 (−0.04 to 0.37)
p (.)	6	358.29	5.62	0.05	-
p (shrub)	7	359.65	6.99	0.03	−0.13 (−0.35 to 0.09)
p (sapling)	7	360.48	7.82	0.02	0.10 (−0.16 to 0.36)

Note. Models are ranked in descending order of Akaike's Information Criterion adjusted for small sample size (AIC_c). Survey covariates included time since survey start time (continuous; "time"); temperature (continuous); cloud cover (% overcast; continuous), observer (categorical), and wind index (categorical). Site covariates included per cent cover as measured by 50 m radius vegetation surveys for vegetation structure: saplings, shrubs, forbs and grass. Both candidate model sets are ranked against a null: intercept-only model. Below, we report number of model parameters (k), ΔAIC_c, AIC_c weight (AIC_c Wt.) and β parameter estimates (95% confidence interval).

and observer ID suggesting that the latest surveys of each day had the lowest detection probability and that observers were unequal in their ability to detect *Bombus* spp. (Table 1; Figure 3a). Among models investigating the relationship between habitat covariates and *Bombus* spp. detection, the model that included grass cover (%) was the only supported model and suggested that *Bombus* spp. were more readily detected at sites with more grass cover (Table 1; Figure 3b). All other covariates modelled in tiers 1 and 2 were >2.0 AIC_c less than the null model and the β 95% confidence intervals overlapped zero.

3.2 | Habitat modelling

Models from all three analyses yielded discernable habitat associations with *Bombus* spp. abundance (Table 2; Figure 4). All three analyses indicated that *Bombus* spp. abundance during the survey period was negatively associated with per cent sapling cover and not associated with forb cover (Table 2; Figure 4). The importance of shrub cover and grass cover as predictors of *Bombus* spp. counts and estimated abundance varied across methods (Table 2); HDS and transect counts revealed support for shrub cover as an informative covariate being >2.0 AIC_c less than the null and having parameter 95% confidence intervals that did not overlap zero (Table 2). Only net counts suggested that grass cover was positively associated with *Bombus* spp. abundance while HDS suggested that grass cover was instead correlated positively with detection probability but not abundance (Table 2; Figure 4). In contrast, our net count analysis suggested no effect of shrub cover on bee counts, with the "shrub" model ranked lower than the null model and the shrub parameter 95% confidence intervals overlapping zero (Table 2). Our top-ranked HDS model ("sapling") showed evidence of minor overdispersion (ĉ\hat{c}\hat{c}\hat{c} = 1.33) while most other models did not appear overdispersed (ĉ\hat{c}\hat{c}\hat{c} < 1.0; with a mean ĉ\hat{c}\hat{c}\hat{c} = 1.01 across models in our final HDS model set). We considered this an acceptable level of overdispersion and did not use a variance inflation factor to adjust our parameter estimates (Burnham & Anderson, 2002).

3.3 | Density estimation

In addition to examining abundance as a function of habitat among the three methods, we compared their estimated mean densities of foraging *Bombus* spp. based on intercept-only abundance models (including detection covariates for HDS). Estimated *Bombus* spp.

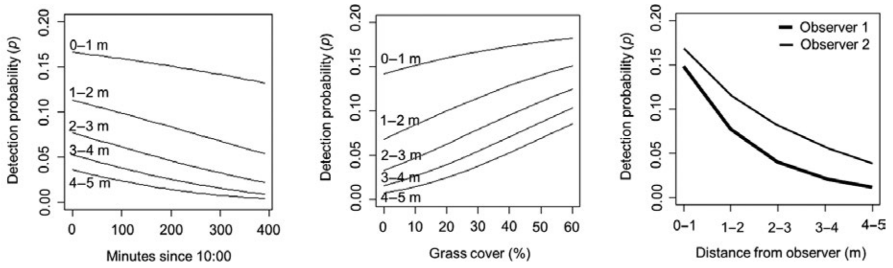

FIGURE 3 Models of *Bombus* spp. detection probability as a function of survey time (left), per cent grass cover (centre), and observer (right) while also being most detectable closest to the transect (all)

TABLE 2 Habitat models derived from hierarchical distance models (top), fixed-width transect models (centre) and linear models of net count data (bottom), all fit using a Poisson distribution

Model name	K	AIC$_c$	ΔAIC$_c$	AIC$_c$ Wt.	β estimate (95%CI)
Hierarchical distance sampling					
λ (sapling)	6	337.69	0.00	0.98	−0.30 (−0.45 to −0.14)
λ (shrub)	6	345.83	8.13	0.02	0.21 (0.05 to 0.37)
λ (.)	5	350.2	12.51	0.00	–
λ (grass)	6	350.41	12.71	0.00	−0.17 (−0.38 to 0.05)
λ (forb)	6	352.82	15.13	0.00	−0.01 (−0.16 to 0.14)
Transect counts					
λ (sapling)	2	277.63	0.00	0.96	−1.44 (−2.20 to −0.69)
λ (shrub)	2	284.48	6.85	0.03	0.85 (0.25 to 1.44)
λ (grass)	2	289.8	12.17	0.00	−0.93 (−2.14 to 0.28)
λ (.)	1	290.07	12.44	0.00	-
λ (forb)	2	292.16	14.54	0.00	0.133 (−0.74 to 1.01)
Net counts					
λ (sapling)	2	360.71	0.00	1.00	−1.63 (−2.26 to −1.01)
λ (grass)	2	384.38	23.67	0.00	0.85 (0.03 to 1.67)
λ (shrub)	2	385.65	24.94	0.00	0.41 (−0.09 to 0.90)
λ (.)	1	386.08	25.37	0.00	–
λ (forb)	2	387.09	26.38	0.00	0.39 (−0.31 to 1.09)

Note. Models are ranked in descending order of Akaike's Information Criterion adjusted for small sample size (AIC$_c$). Distance transect data included *Bombus* spp. detected from 0 to 5 m along 66 m transects. Transect counts included *Bombus* spp. detected from 0–2 m along 66 m transects. net count data were counts of *Bombus* spp. within 15 m radius plots. Site covariates included per cent cover as measured by 50 m radius vegetation surveys for vegetation structure: saplings, shrubs, forbs, and grass. Below we report number of model parameters (k), AIC$_c$, Δ AIC$_c$, AIC$_c$ weight (AIC$_c$ Wt.) and each covariate β parameter estimate and β parameter estimates (95% confidence interval).

forager density within timber harvests was highest for the HDS models (192 foraging workers/ha; 95% CI: 153–240) and lowest for net counts (21 foraging workers/ha; 95% CI: 19–23 Figure 5); an 89% difference between the two methods. Transect counts yielded intermediate estimates of density (40 foraging workers/ha; 95% CI: 34–47), and were 80% lower than density estimates from HDS. Site-specific HDS modelled densities and netting count raw densities were correlated (Pearson's $r = 0.31$; $p = 0.03$). though the relationship was not 1:1 (Figure 5).

4 | DISCUSSION

Our study provides the first empirical evidence that detection probabilities of *Bombus* spp. vary in ways that can affect abundance estimates and inferences about habitat relationships. Observation error caused by imperfect detection is one of the central challenges of ecological monitoring programs (Thompson, 2002; Yoccoz, Nichols, & Boulinier, 2001) but has yet to be widely applied to monitoring of many invertebrates, including pollinators (but see Bendel et al., 2018; Loffland et al., 2017; Mackenzie, 2003; Van Strien, Termaat, Groenendijk, Mensing, & Kery, 2010). Methods like distance sampling, while offering a potential solution to this challenge, are still under-utilized in entomological research. Meanwhile, distance sampling and similar methods have been a staple of vertebrate wildlife research for decades (Buckland et al., 2005; Burnham, Anderson, & Laake, 1980; Seber, 1986; Thomas et al., 2002), and have been expanded to estimate population size, habitat-specific abundance for individual species and communities (Sillett, Chandler, Royle, Kéry, & Morrison, 2012; Sollmann, Gardner, Williams, Gilbert, & Veit, 2016). Although our study is not the first estimate and account for detection probability of bumblebees (Loffland et al., 2017), no study before ours has described factors associated with detection probability and done so in a HDS framework.

We found that distance sampling transects were both a simple and effective survey method for estimating density and habitat relationships (Buckland et al., 2005). Hierarchical distance sampling models are one of the few available methods that allow researchers to model detection-adjusted abundance with only a single visit to each site (Buckland et al., 2005; Kéry & Royle, 2015; MacKenzie et al., 2005). The method uses only non-lethal sampling, unlike trapping/netting methods (Tepedino et al., 2015) which is especially desirable when sampling for species of conservation concern, or for common species in areas where capture-based sampling is not allowed. Additionally, HDS models are also useful because the output is an easily interpreted latent state: density with units in "animals/area". In our study, HDS models generated estimates of foraging *Bombus* spp. worker density.

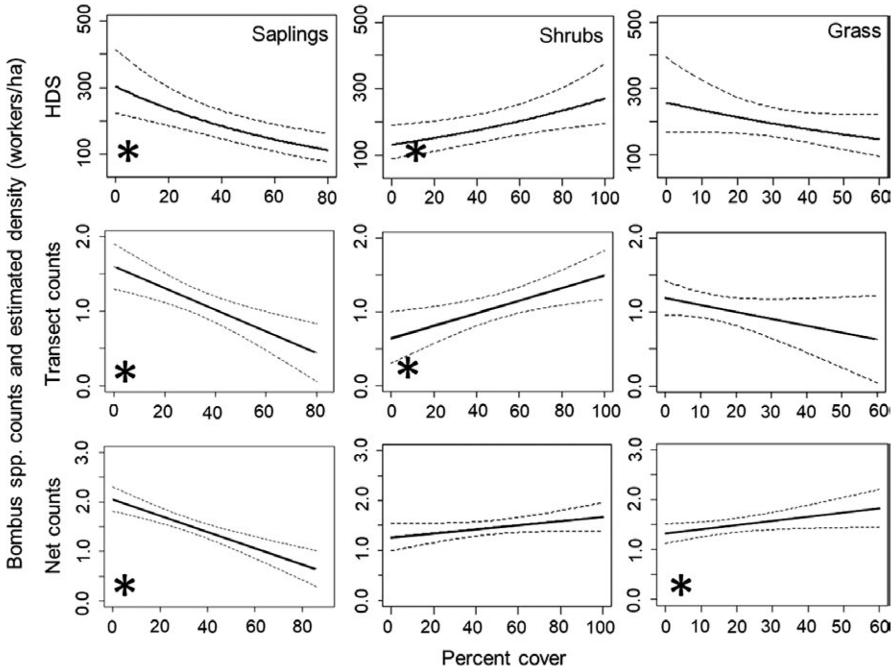

FIGURE 4 Modelled habitat associations between *Bombus* spp. and structural vegetation features within regenerating timber harvests as predicted by hierarchical distance models (top), fixed-width (4 m) transect counts (centre) and net counts (bottom). Variables shown are sapling cover (left), shrub cover (centre) and grass cover (right). Solid lines represent model predictions with dashed lines as 95% confidence intervals. Relationships marked with an asterisk were those with model support (i.e., more informative than a null model and β 95% CI non-overlapping zero)

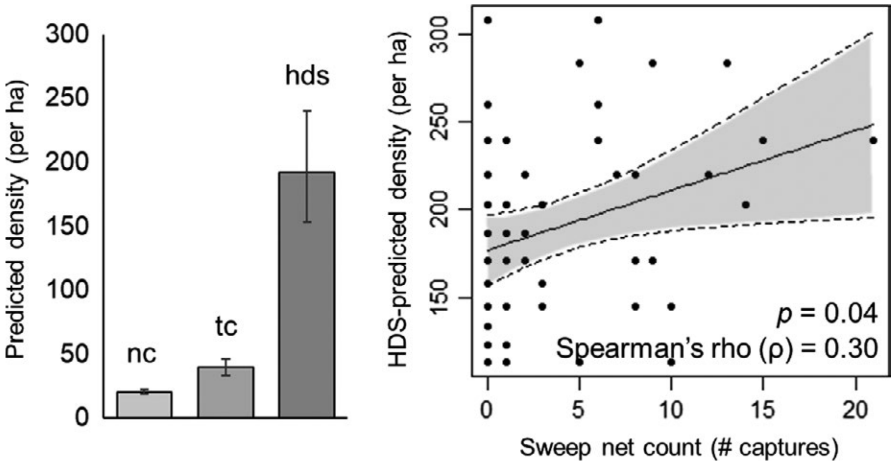

FIGURE 5 Left: *Bombus* spp. predicted mean density for models of net counts ("nc"), transect counts ("tc"), and hierarchical distance sampling models ("hds"). Right: Predicted density (workers/ha) generated from our top-ranked hierarchical distance model (p [observer + time + grass], λ [sapling]) regressed against count data from *Bombus* spp. net counts

Despite being among the largest and most conspicuous of North American bees (Michener et al., 1994), we found that detection probability of *Bombus* spp. was imperfect and declined markedly with distance from the survey transect, with almost no detections beyond 5 m. Detection probabilities in our study were influenced by survey-specific (e.g., time of day) and site-specific (e.g., grass cover) variables, with detection probability highest in the morning in mid-summer and in habitats with abundant grass cover. Within regenerating timber harvests in our study area, "grass" cover was typically low-growing monocotyledons like *Carex pennsylvanica*. Abundant low-growing sedge allowed observers to view *Bombus* spp. from greater distances than when sites were dominated by tall saplings, shrubs or forbs (e.g., *Solidago*). Consequently, studies within habitats dominated by low grass or other short vegetation might find detection probability for *Bombus* spp. to be reliable at distances >5 m. Although we are uncertain as to why *Bombus* spp. were less detectable during surveys conducted later in the afternoon, one plausible explanation is that longer shadows cast by late afternoon light made *Bombus* spp. more difficult to detect when foraging in low vegetation. Additional work exploring the drivers associated with *Bombus* spp. detection would prove valuable to monitoring regimes aimed at surveying bumblebees.

Though our study is not a comprehensive habitat assessment for *Bombus* spp. within regenerating timber harvests of eastern forests, our results provide a glimpse into the habitat dynamics of bumblebees in regenerating forests during mid-summer. Our findings that *Bombus* spp. were positively associated with shrubs and negatively associated with saplings can be explained primarily by flower phenology during our survey window. Regenerating saplings within the timber harvests we monitored were largely oaks, hickories, black cherry (*Prunus serotina*) and red maple (*Acer rubrum*; Wherry et al., 1979). These species do not flower as small saplings and do so in early spring as mature trees (i.e., outside the sampling period; Wherry et al., 1979). In contrast, several species of shrub were flowering during sampling including black huckleberry (*Gaylussacia baccata*), and hillside blueberry. In contrast, most forbs (e.g., goldenrod;

Solidago spp., snakeroot; *Ageratina* spp.) had not begun flowering yet. Future work should explore how *Bombus* spp. may track resources across a growing season to persist within eastern forest ecosystems.

Monitoring programs for *Bombus* spp. and other native pollinators can be improved by incorporating study design and model-based approaches for minimizing detection error. Although we included several design-based solutions for minimizing detection error (e.g., restricting survey times, only surveying in fair weather; Ward et al., 2014), detection probability remained imperfect and varied due to time of day, observer and vegetation cover. Consequently, methods that ignored detection probability generated density estimates 80%–89% lower than HDS. Past studies have shown the importance of using design-based approaches to minimize false negatives when sampling bees (Buchanan, Gibbs, Komondy, & Szendrei, 2017). Our study demonstrates the value of using both design- and model-based approaches for reducing sampling errors caused by imperfect detection. Other study systems with thick vegetation cover, such as prairies and forested wetlands, or obstructive objects, such as urban environments, are also likely to underestimate bee abundance even if multiple design-based approaches are used. While traditional sampling techniques that do not account for detection have numerous applications, our study highlights the importance of incorporating model-based approaches for accounting for detection probability within native bee surveys, particularly when attempting to estimate bee abundance or density.

Although our results suggest that HDS represents a promising tool for monitoring bumblebees, researchers wishing to employ the method should recognize its associated limitations. For example, distance models assume that all animals on the transect line are detected perfectly. Although it is likely this assumption was met with a large insect like *Bombus* spp., this assumption might be violated with smaller insects. Moreover, subjects are assumed to be uniformly distributed in a manner unaffected by the observer. While it is possible that *Bombus* spp. were frightened by observers, we took care to note the location of first detection for *Bombus* spp. apparently flushed and their loud flight made close detections almost certain. We note that this method would not work well for species-level identification because observations are made from a distance and some bee genera are exceedingly difficult to identify, even with a microscope (Michener et al., 1994). Misidentification of species would constitute a false positive which would violate an assumption of distance sampling.

Another consideration of this study design, and many methods of abundance estimation, is that animals may violate the closure assumption. In the case of *Bombus* spp., this likely occurred as foragers flew in- and out- of the effective survey area (~5 m from the observer for HDS). While this may constitute a problem for some study objectives and methods, we have no reason to believe that *Bombus* spp. movement was nonrandom with respect to the observer and an accurate density could therefore still be made when passive counting was used. Closure violation may be a more important problem when attempting to calculate density from a netting plot where animals may enter the plot and be unable to leave as they are captured and held until the survey has finished. In such cases, movement would be biased by individuals immigrating into the monitored plot but unable to emigrate and movement would be biased towards the plot. Although net-based sampling is often preferable for investigating species-specific habitat relationships, the potential for movement bias highlights the need for cautious interpretation of net-based density estimates for bees. Similarly, researchers should consider the potential for double-counting subjects. Although *Bombus* spp. in our study were apparently few enough and slow enough to avoid most double-counting, this may be a more important problem to consider for more abundant insects with reduced detectability (*e.g.*, Halictids).

We also advise caution with interpretation of habitat relationships reported here as our study should be interpreted as a small "snapshot" in time, and lacking species-specific habitat relationships (Olesen, Bascompte, Elberling, & Jordano, 2008). Full-season habitat associations are temporally dynamic for *Bombus* spp. and vary across species (Goulson, 1999; Jha & Kremen, 2013). Relative floral resource availability of different species changes across the season and future studies employing these methods at regular intervals from early spring when queens first emerge through late autumn would prove valuable. In fact, examination of queen bee densities would likely prove a better assessment of population density and habitat quality than worker density; when monitoring or researching colonial organisms such as bumblebees, estimating the true number of reproducing colonies is of more value than estimating the number of foraging workers, as we have done here. Conducting HDS during the spring and early summer, when queens are the only active bumble bee foragers, may prove a useful and non-lethal approach to estimating the abundance of reproductive individuals, and the expected number summer colonies for a given area. However, sampling queens would likely require additional sampling sites or repeat visit because counts would be much lower and HDS models may have trouble converging with relatively few sampling locations. Caution should also be exercised with interpretation of *Bombus* spp. density estimates reported here as our densities likely consist of multiple species of *Bombus* modelled and reported as one. We also recommend future studies explore how non-*Bombus* genera (or morphospecies, functional groups) perform as the focus of HDS models. Although HDS is not without limitation, we believe our study highlights the utility of HDS models for estimating densities and elucidating habitat associations of bumble bees when individuals are detected imperfectly.

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AUTHORS' CONTRIBUTIONS

DJM, CRVO, ELM and JLL conceived research. DJM and ELM collected field data. DJM, CRVO and ELM conducted statistical analyses. DJM, CRVO, ELM, KRUM, DEK, ADR and JLL wrote the manuscript. JLL secured funding. All authors read and approved the manuscript.

ORCID

Darin J. McNeil http://orcid.org/0000-0003-4595-8354

Clint R. V. Otto http://orcid.org/0000-0002-7582-3525

Amanda D. Rodewald http://orcid.org/0000-0002-6719-6306

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