

Comparison of removal-based methods for estimating abundance of five species of prairie songbirds

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ABSTRACT. Estimating species abundance is important for land managers, especially for monitoring conservation efforts. The two main survey methods for estimating avian abundance are point counts and transects. Previous comparisons of these two methods have either been limited to a single species or have not included detection probability. During the 2012 breeding season, we compared and assessed the efficiency (precision for amount of effort) of point count time of detection (PCTD) and dependent double-observer transect (TRMO) methods based on detection probabilities and abundance estimates of five species of songbirds that use a range of habitats in a prairie system in Montana dominated by sagebrush and grassland vegetation. Our focal species included Vesper Sparrows (*Pooecetes gramineus*), a generalist species found in both shrub and grassland habitat, shrub-obligate Brewer's Sparrows (*Spizella breweri*), and McCown's Longspurs (*Rhynchophanes mccownii*), Horned Larks (*Eremophila alpestris*), and Western Meadowlarks (*Sturnella neglecta*), three species of grassland obligates that prefer different grass heights. Detection probabilities were significantly higher for TRMO surveys, with less variation for all five species and differences most pronounced for Brewer's Sparrows and Horned Larks. PCTD surveys required less field effort (~8–20 fewer people minutes per plot) than TRMO surveys because the TRMO surveys required two people. However, time spent on TRMO surveys provided between 0.38 and 87 times more precision per person minute than PCTD surveys. Our results suggest that TRMO surveys provide a more efficient (measured as time spent per unit of standard error) field-based technique in sagebrush prairie systems for the species we investigated, resulting in more precise detection and abundance estimates.

RESUMEN. Comparación de métodos basados en la remoción para estimar la abundancia de cinco especies de paseriformes de pradera

Estimar la abundancia de las especies es importante para los administradores de tierras, especialmente para monitorear los esfuerzos de conservación. Los dos métodos principales de censo para estimar abundancia de aves son puntos de conteo y transectos. Comparaciones previas de estos dos métodos han sido limitadas a una sola especie o no han incluido la probabilidad de detección. Durante la temporada reproductiva del 2012, comparamos y determinamos la eficiencia de métodos (precisión por unidad de esfuerzo) de tiempo de detección en el punto de conteo (PCTD) y transectos dependientes en doble observador (TRMO) basado en probabilidades de detección y los estimados de abundancia de cinco especies de aves paseriformes que usan un rango de hábitats en el sistema de praderas en Montana, dominados por artemisa y pastizales. Nuestras especies focales incluyeron *Pooecetes gramineus*, una especie generalista encontrada en ambos hábitats, un especialista de matorral *Spizella breweri*, y *Rhynchophanes mccownii*, *Eremophila alpestris* y *Sturnella neglecta*, tres especies obligatorias de pastizales que prefieren diferentes alturas de los pastos. Las probabilidades de detección fueron significativamente mayores en censos utilizando TRMO, con menor variación en las cinco especies y las diferencias más pronunciadas fueron en *Spizella breweri* y *Eremophila alpestris*. Monitoreos utilizando PCTD requirieron menor esfuerzo en el campo (~8–20 personas minuto menos por parcela) que monitoreos con TRMO porque el monitoreo con TRMO requiere dos personas. Sin embargo, el tiempo utilizado en monitoreos con TRMO fue más preciso entre 0.38 y 87 veces por persona minuto que monitoreos con PCTD. Nuestros resultados sugieren que monitoreos con TRMO proveen una técnica de campo más eficiente en sistemas de praderas para las especies investigadas, resultando en estimados de detección y abundancia más precisos.

Key words: avian monitoring, dependent double-observer, grassland, point count, removal model, sagebrush, transect

Abundance is the most widely used biological metric for avian monitoring programs (Kéry and Schmidt 2008). Use of abundance

to establish and achieve monitoring program objectives has led many authors to suggest that field efforts should include sampling that can account for the probability of detecting individuals (e.g., Rosenstock et al. 2002, Thompson 2002, Kéry and Schmid 2004). Failing to

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account for detection can lead to incorrect inferences about drivers of change in abundance. Observers may assume that differences in counts not corrected for detection represent true changes in abundance, when in fact they may be a result of changes in detection probability (Thompson 2002). Detection probability can be affected by numerous factors, including survey method, time of day, species, observer, distance from observer, ambient noise, vegetation, and time of season (Farnsworth et al. 2002, Rosenstock et al. 2002, Alldredge et al. 2007a, Simons et al. 2007, Pacifici et al. 2008). Recent advances allow researchers to quantify imperfect detection during surveys (Nichols and Williams 2006), making estimates of detection probability more reliable. Alldredge et al. (2008a) identified four commonly used methods to incorporate detection probability, including distance sampling, use of multiple observers, time of detection sampling, and repeated count measures (Table 1). Each method has its own assumptions associated with estimating detection probability, which is addressed through the survey method and/or statistical analysis.

The two most common avian survey methods used are point counts (46% of avian surveys), which depend primarily on auditory cues, and transect surveys (29% of avian surveys), which depend primarily on visual cues (Rosenstock et al. 2002). However, comparisons of survey methods that incorporate detection have largely been limited to different point-count methods (e.g., Alldredge et al. 2006, Forcey et al. 2006, Kissling and Garton 2006, Reidy et al. 2011). We know of only a single comparison between point counts and transects that incorporated detection probability. Bollinger et al. (1988) found that transects provided more precise detection probability estimates than point counts for Bobolinks (*Dolichonyx oryzivorus*) in two grassland systems in New York. Other investigators that compared point counts and transects did not account for detection probability, so it is unclear if the results, which varied (Verner and Ritter 1985, Dobkin and Rich 1998, Taulman 2013), were due to the field technique or other factors that affect detection probability (e.g., observers' abilities, species behavior, time of day, and weather).

Habitat can affect detection probability so is an important factor to consider when

deciding which survey method to use (Nichols et al. 2000, Ruiz-Gutiérrez and Zipkin 2011). In open habitats, such as grasslands, detections are often visual (Forcey et al. 2006, Alldredge et al. 2007b), whereas in heavily vegetated habitat, such as forests, detections are almost exclusively auditory (Alldredge et al. 2008b). As a result, transects may be a better survey method in open habitats because they increase the ability to make visual detections (Brewster and Simons 2009). Although Bollinger et al. (1988) found that transects provided more precise detection probability estimates than point counts for a single species, the extent to which these results might apply to other species or multi-species survey efforts, in open habitats is unclear. To address this, we compared and assessed the efficiency (precision for amount of effort) of point counts and transects based on their resulting detection probabilities and abundance estimates for five songbird species that use a range of habitats in a prairie system dominated by sagebrush and grassland vegetation. We compared point counts using time of detection sampling (PCTD) and transects using multiple observers (TRMO). Both methods use a removal model to estimate detection based on (1) availability, the probability that an individual is present in the survey area and signaling its presence (e.g., vocalizing or is in view), and (2) perceptibility, the probability that an animal is detected by the observer, given that it is available for detection (e.g., vocalizing or is in view) (Farnsworth et al. 2002). Individual birds are "captured" (i.e., counted) then removed from the population. PCTD treats the "captures" as individuals being removed (i.e., not counted again) during later sampling periods. TRMO treats the "captures" as individuals being removed by one of two observers in the observation team. Here we provide a general comparison of PCTD and TRMO by excluding factors that may influence estimates of detection and abundance.

METHODS

Study site. Our study was conducted in a prairie ecosystem on public land managed by the Bureau of Land Management near Roundup, Montana, during the breeding season (24 May to 18 June) in 2012. Vegetation

Table 1. Description of avian survey methods and the assumptions of each method.

Method	Description	Assumptions	Citation(s)
Distance Sampling (DS)	A single observer records the identity of the species detected as well as the distance to the species. Detection is assumed to be a function of distance and calculated based on distance from a transect or point	<ol style="list-style-type: none"> (1) Detection probability at the center of the survey is 1 (2) Birds do not respond to the observer (3) Distance to bird is accurately recorded (4) The population is a closed during sample period 	Buckland et al. (2001)
Multiple Observers (MO)	<p>Multiple observers conduct the same survey of a closed population. Both independent approaches (IMO) and dependent (DMO) methods exist:</p> <ol style="list-style-type: none"> (1) IMO approaches require that observers do not share data until the conclusion of the survey (2) DMO approaches require that the observers work together to note the order of observation <p>The difference in detection is used to create an encounter history. Mark recapture methodology is used to determine the probability of detection</p> <p>A single observer records the time at which birds are detected. Probability of detection is calculated using removal models with maximum likelihood estimators</p> <p>A single observer revisits the same site multiple times to measure heterogeneity in abundance. Because of the relationship between abundance and detection probability, this heterogeneity in abundance can be used to estimate detection probabilities</p>	<ol style="list-style-type: none"> (1) Independence or dependence is maintained (2) An observer's detection probability does not change with the role they play within DMO surveys (3) The population is a closed during the sample period 	Nichols et al. (2000) (IMO and DMO), Kissling and Garton (2006) (IMO)
Time of Detection (TD)		<ol style="list-style-type: none"> (1) Singing frequency is the main method of detecting avian species during the survey 	Farnsworth et al. (2002)
Repeated Counts (RC)		<ol style="list-style-type: none"> (1) The relationship between heterogeneity in abundance and detection probability is constant across repeated survey efforts (2) The population is closed during the sample period (including repeated visits) 	Royle and Nichols (2003)

was dominated by Wyoming big sagebrush (*Artemisia tridentata*) intermixed with western wheatgrass (*Pascopyrum smithii*), needle-and-thread grass (*Stipa comata*), blue grama (*Bouteloua gracilis*), and prairie Junegrass (*Koeleria macrantha*). The area is arid, with average annual precipitation of 0.34 m. Average temperatures range from -11°C in January to 30°C in July (US Climate Data 2016).

Survey methods. We randomly selected 40 sampling plots dominated ($>75\%$) by sagebrush and/or grassland vegetation. Sampling plots were $500\text{ m} \times 500\text{ m}$ (25 ha) following Tipton et al. (2009). On each of the 40 sample plots, we randomly selected a survey method, PCTD or TRMO, and used the other method the next day. All surveys were conducted between sunrise and 11:00, during periods of low or no wind ($<24\text{ kph}$), no or light precipitation, and temperatures $>0^{\circ}\text{C}$ and $<25^{\circ}\text{C}$.

We surveyed five species that represent a range of songbird habitat use in sagebrush prairie systems, including Brewer's Sparrows (*Spizella breweri*), a shrub-obligate species, McCown's Longspurs (*Rhynchophanes mccownii*), Horned Larks (*Eremophila alpestris*), and

Western Meadowlarks (*Sturnella neglecta*), grassland-obligate species with preferences for different grass heights, and Vesper Sparrows (*Poocetes gramineus*), a generalist species found in both shrub and grassland habitats. With the PCTD method, four 10-min point-count stations were placed 125 m from the two closest edges of sample plots (Fig. 1a, points A–D) and counts were conducted by a single observer. The observer waited 3 min after arriving at each count station to allow birds to acclimate to his/her presence. All birds observed $\leq 125\text{ m}$ from the point were recorded, along with detection type (auditory, visual, or both). New individuals, those not detected in previous intervals, were recorded at 1-min intervals. We limited the distance of the bird counts because $\geq 95\%$ of birds observed are within 125 m of observers (Ralph et al. 1995). Observers were trained to recognize 125 m at the beginning of the field season and used topographic maps on GPS units to confirm distances in the field. PCTD surveys lasted between 72 and 80 min per plot, including four 10-min point counts, three 3-min waiting periods, and $\sim 5\text{--}7$ min to move between points. The order of surveys at the four count stations in sample plots was A,

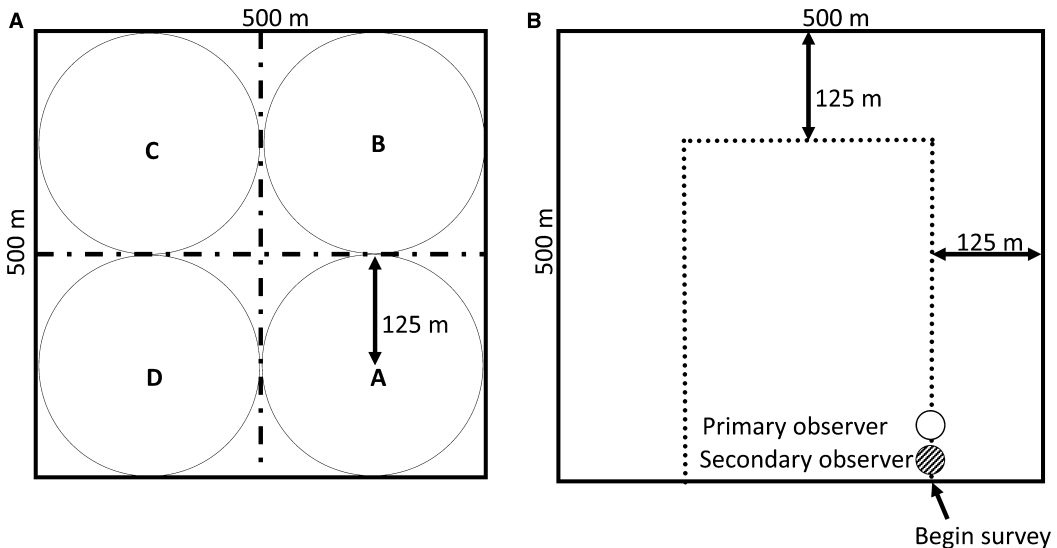


Fig. 1. Methods used to survey avian species in May–June of 2012 on public land outside of Roundup, Montana. (a) Point-count time of detection field method. A 10-min single-observer point count was conducted at four points (locations A–D) within plots so that 125 m around each point was surveyed. (b) Multiple-observer transect field method. The primary observer (open circle) and secondary observer (dashed circle) walked single file along the transect (dotted line), surveying up to 125 m on either side of the transect at all times. The survey was started at the bottom right hand corner of the transect.

B, C, then D (Fig. 1a), and covered a similar area as the TRMO method described below.

With the TRMO method, U-shaped transects in sample plots (Fig. 1b) were walked by two observers. Observers walked in a single line with the “primary” observer in front and the “secondary” observer 3–5 m behind. Following Nichols et al. (2000), the primary observer noted each bird observed including species, detection type, and approximate location. The secondary observer recorded the information on a data sheet that resembled the plot (Fig. 1b) to note the approximate location of bird observations. In addition, the secondary observer recorded birds not detected by the primary observer. To maintain independence of observations by the primary observer, the secondary observer randomly used false behaviors (e.g., focusing on a spot with no bird or pretending to write down an observation) to avoid cueing the primary observer of birds he/she had missed. The secondary observer, with the aid of the data sheet, evaluated observations to avoid double counting, misidentification, and appropriate survey of transect corners. The roles of primary and secondary observer alternated on consecutive transect surveys. TRMO surveys lasted 40–60 min per sampling plot.

Statistical analysis. We used a removal model in program MARK (White and Burnham 1999) to estimate detection probabilities and abundances for the five bird species using the PCTD and TRMO methods. Removal models require the assumption of closure during the time the population is sampled. Bird-count data from PCTD and TRMO were collected on consecutive days during the breeding season, minimizing violation of this assumption. We divided PCTD surveys into the following time intervals based on Farnsworth et al. (2002): min 0–3, min 3–5, and min 5–10. Encounter histories (100, 010, or 001) reflected the time interval during which a bird was first detected. For the TRMO method, we divided the TRMO surveys into encounter histories of the primary observer detecting a bird (10) or the secondary observer detecting a bird that the primary observer missed (01), following Nichols et al. (2000). For both methods, we used a Huggins closed-capture model (Huggins 1989, 1991) in MARK (White and Burnham 1999) to simulate a removal model. The probability of

initial capture (i.e., detection) (p) was set as constant in both cases because we assumed that a bird was equally available for detection during the entire survey. To simulate a removal model, we set the probability of recapture (i.e., observing in a different time interval for PCTD or observing by a different observer for TRMO) (c) to 0; once observed, the individual was effectively “removed” from the sampling population in the plot. For the PCTD method, detection probability for each interval was used to calculate the overall detection probability for each species across all surveys. Similarly, for the TRMO method, the detection probability for each observer was combined to calculate the overall detection probability for each species across all surveys.

RESULTS

We observed 1289 and 1407 individuals of the five bird species using the PCTD and TRMO methods, respectively (Table 2). Vesper Sparrows were the most frequently observed species and Horned Larks the least frequently observed (Table 2). We observed more McCown’s Longspurs and Western Meadowlarks using the PCTD method, and more Brewer’s Sparrows, Horned Larks, and Vesper Sparrows using the TRMO method (Table 2). Of 1289 detections using the PCTD method, 454 (35.2%) were auditory, 502 (39.0%) were visual, and 333 (25.8%) were auditory and visual. Of 1407 detections using the TRMO method, 96 (6.8%) were auditory, 1308 (93.0%) were visual, and 3 (0.2%) were auditory and visual. Across all 2616 observations, 82.0% (2146) had a visual component (i.e., either visual or auditory and visual detections; Table 2).

Estimates of detection probability were lower for the PCTD method than the TRMO method for all five focal species (Fig. 2a, Table 3). We found the greatest difference in detection (i.e., largest difference between non-overlapping confidence intervals) between the two methods for Brewer’s Sparrows and Horned Larks (Fig. 2a). In addition, the PCTD method provided less precise estimates (e.g., larger standard errors and confidence intervals) than the TRMO method for Brewer’s Sparrows and Horned Larks (Table 3). Differences (i.e., confidence intervals did not overlap)

Table 2. Number of observations of five species of songbirds using point count time of detection and dependent double-observer transect methods in 2012 on public lands near Roundup, Montana.

Common Name	Point count time of detection				Dependent double-observer transect			
	Auditory	Visual	Auditory/Visual	Total	Auditory	Visual	Auditory/Visual	Total
Brewer's Sparrow	92	63	68	223	33	267	3	303
Horned Lark	26	83	15	124	3	160	0	163
McCown's Longspur	26	137	33	196	2	174	0	176
Vesper Sparrow	157	140	90	387	33	523	0	556
Western Meadowlark	153	79	127	359	25	184	0	209
Totals	454	502	333	1289	96	1308	3	1407

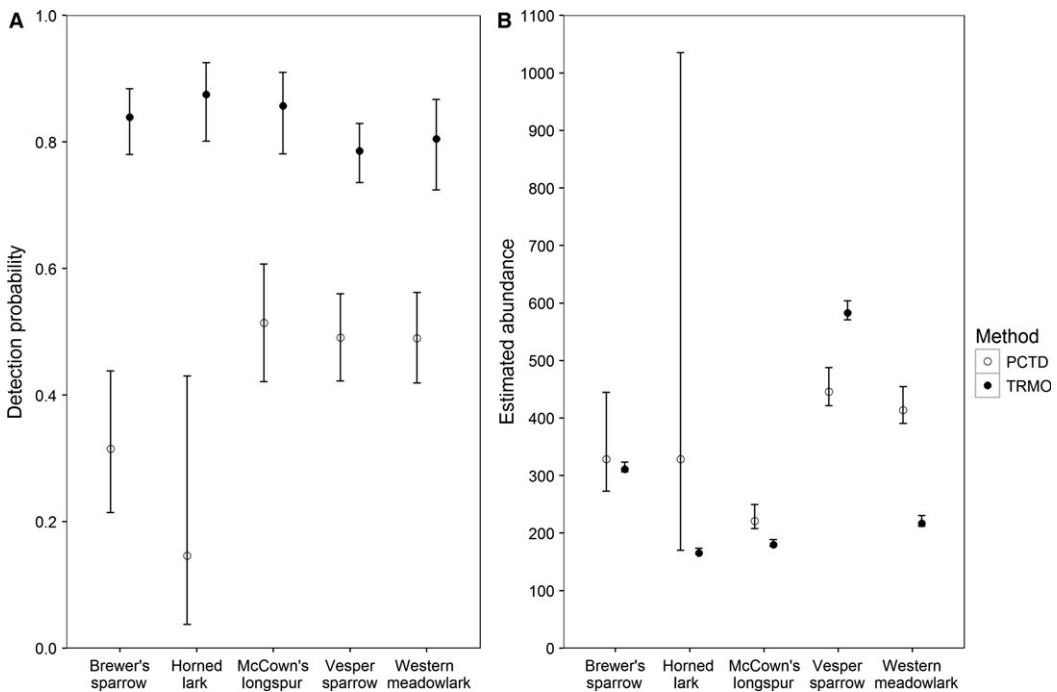


Fig. 2. Detection probabilities (a) and abundance estimates (b) for five species detected in a prairie ecosystem using the point count time of detection (open) and dependent double-observer (solid) methods in 2012 on public lands outside of Roundup, Montana. The 95% confidence intervals are represented with bars.

in detection probabilities between methods for McCown's Longspurs, Vesper Sparrows, and Western Meadowlarks showed similar patterns (Table 3).

In all cases, the PCTD method provided less precise estimates of abundance than the TRMO method (Table 3). Across all species

and both methods, the PCTD method provided the least precise estimate for Horned Lark abundance. In contrast, the most precise estimate was the TRMO method abundance estimate for Horned Larks. Abundance estimates based on the two methods were different for McCown's Longspurs, Vesper Sparrows,

Table 3. Detection probability and abundance estimates for five avian species detected using the point count time of detection (PCTD) and multiple-observer transect (TRMO) methods in 2012 on public lands outside of Roundup, Montana. Standard errors (SE) are shown in parentheses, and 95% confidence intervals (CI) are shown in each column to the right of the estimate.

Common name	Detection probability estimate				Abundance estimate			
	PCTD (SE)	PCTD 95% CI	TRMO (SE)	TRMO 95% CI	PCTD (SE)	PCTD 95% CI	TRMO (SE)	TRMO 95% CI
Brewer's Sparrow	0.315 (0.058)	0.214–0.438	0.839 (0.027)	0.780–0.884	328 (41.50)	273–445	311 (3.98)	306–323
Horned Lark	0.146 (0.095)	0.037–0.430	0.875 (0.031)	0.801–0.925	329 (181.55)	170–1035	166 (2.07)	164–173
McCown's Longspur	0.514 (0.048)	0.421–0.607	0.857 (0.033)	0.781–0.910	221 (10.05)	208–250	180 (2.58)	177–189
Vesper Sparrow	0.491 (0.035)	0.422–0.560	0.786 (0.024)	0.736–0.829	446 (16.37)	422–488	583 (8.17)	571–604
Western Meadowlark	0.490 (0.037)	0.419–0.562	0.805 (0.036)	0.724–0.867	414 (15.84)	391–455	217 (4.33)	212–231

and Western Meadowlarks (Fig. 2b, Table 3). These differences were the combined result of the different counts and detection probabilities. The PCTD method resulted in higher abundance estimates for McCown's Longspurs and Western Meadowlarks because more McCown's Longspurs (196 vs. 176) and Western Meadowlarks (359 vs. 209) were counted using the PCTD method than the TRMO method (Table 2). Similarly, the PCTD method resulted in fewer Vesper Sparrows counted during PCTD than TRMO (387 and 556, respectively).

PCTD surveys required fewer people (single observer) than TRMO surveys (two observers). TRMO surveys took ~80–100 people min (40–60 min total), and PCTD surveys ~72–80 people min. The time needed to train observers was similar for both methods.

DISCUSSION

We found that the TRMO method provided higher estimates of detection probability for our five focal species. In addition, abundance estimates with the TRMO method were more precise than those with the PCTD method. Differences in detection probability and precision of abundance were consistent across the five species, suggesting that the TRMO method provides similar benefits across the species we selected.

Differences between the two methods in detection probability show a clear pattern, with more auditory detections with the PCTD method and more visual detections with the TRMO method. However, most detections, regardless of survey method, were visual, suggesting that habitat has an effect on the type of detection cues used by observers. Other investigators have also found that detections are primarily visual in open habitats (e.g., Bollinger et al. 1988, Forcey et al. 2006, Diefenbach et al. 2007). In addition, the quality of information gained from each method was similar to that reported in other studies. Bollinger et al. (1988) found that transects provided more precise abundance estimates than point counts for Bobolinks in an open prairie habitat.

Differences between the two methods in detection probability were likely a result of the different behavioral cues that observers relied on for each method. During TRMO

surveys, observers relied more on visual detections, likely because they flushed birds as they moved along transects (Table 2). Diefenbach et al. (2003) found that, in restored grassland habitats, observers of all skill levels were able to detect between 93 and 100% of birds within 25 m of transects. The flushing response of birds to the presence of observers is likely responsible for many of the detections close to transects. The greater reliance on detections with an auditory component (auditory or auditory/visual detections) in the PCTD surveys (32.8% of detections) compared to the TRMO surveys (7% of detections) may have contributed to the variability in the PCTD detection probability because counting and identification errors are more likely with auditory than visual detections. For example, Simons et al. (2007) recorded double counting and misidentification rates as high as 32% for auditory surveys in an open habitat. If there were more errors in PCTD method, this would likely lead to more variation in detection and abundance estimates, which is consistent with our results.

Differences among species in detection probability in our study may have been due to differences in perceptibility. Low perceptibility may introduce variation, which could increase the difference observed between the two methods. This pattern is consistent with our observations because the PCTD detection probability estimate for Horned Larks, a species reported to have low perceptibility (Leston et al. 2015), was the lowest and most variable for all species across both methods. In contrast, species reported to have high perceptibility either because of singing behavior, such as Vesper Sparrows and Western Meadowlarks (Leston et al. 2015), or because they form loose flocks during the breeding season, McCown's Longspurs (With 2010), had smaller differences in detection probability between the two methods.

There are potentially important trade-offs, primarily in the implementation process, in the amount of effort required for each method based on the field surveys. The PCTD method only requires one observer, whereas the TRMO method requires two. Bird identification training was the same for both methods and time to learn each method

was similar. However, training time for TRMO observers could possibly be reduced because observers can consult with each other about identification. To cover the same area, implementation of four TRMO surveys took ~8–20 people minutes more than four PCTD surveys on the same plot. However, the time spent on TRMO surveys resulted in more precise estimates of abundance. Considering the total people minutes for each method (an average of 76 people minutes for PCTD and 100 people minutes for TRMO) per unit of standard error, the TRMO method ranged from 0.38 to 87 times more efficient than the PCTD surveys, depending on species. Given this efficiency, the effort required to obtain the same amount of precision in information using PCTD surveys is consistently higher. Therefore, the TRMO method may provide an advantage over the PCTD method on private lands by minimizing observers activities (e.g., less sampling time per unit of standard error), which has been shown to increase participation in monitoring programs by private landowners (Hilty and Merenlender 2003).

We recognize that the number of observers can affect detection (Diefenbach et al. 2003). For example, Kissling and Garton (2006) found that the presence of two observers increased detection probability by an average of ~8%. In our study, we could not disentangle the effect of two observers from the effect of survey method on detection probability. We suggest that future cross-method comparisons include both single and double observers, as well as methods that provide information about how availability and perceptibility influence estimates of detection.

Our results provide investigators with a more comprehensive assessment of survey methods for monitoring birds in prairie systems. For tracking changes in abundance of multiple songbird species in open habitats, we suggest the TRMO method as an alternative to PCTD surveys. We found that the TRMO method provided more precise information for a similar amount of effort compared to point counts. However, PCTD and other point count survey methods may provide better estimates in more closed habitats or be the better method to use given logistical and financial constraints.

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