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RESEARCH ARTICLE

Comparison of in-person and remote camera lek surveys for prairie grouse (*Tympanuchus* spp.)

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Abstract

In-person lek count surveys are commonly used for estimating population size and trends for prairie grouse. However, the emergence of noninvasive camera trap survey methods holds promise for more cost-effective and precise estimates of lekking species. To evaluate the efficacy of using camera traps, we deployed a remote camera study at lekking grounds over 3 years in conjunction with in-person surveys. Our objectives were to 1) develop an effective remote camera survey for greater prairie-chickens (GRPC; *Tympanuchus cupido*) and sharp-tailed grouse (STGR; *T. phasianellus*), 2) compare metrics of male detection, maximum male counts, and male abundance estimates derived from in-person versus remote camera surveys, 3) assess lek activity over the survey season to inform survey timing, and 4) evaluate costs for each survey type. We found that in-person surveys resulted in maximum male GRPC and STGR counts. The estimated number of male GRPC and STGR on leks were comparable between in-person surveys and camera monitoring when accounting for detection probability with N-mixture models. Camera traps constantly monitored leks over the season which provided daily and seasonal activity patterns of prairie grouse. Total cost of GRPC remote camera surveys was higher than in-person surveys, but hourly cost was less ($0.77 vs. $160 per hour). Remote camera survey costs for GRPC were high because of time classifying photos which could be reduced by decreasing the amount of time remote cameras were operated or using automated classification software to remove blank photos. We believe the use of remote cameras could supplement in-person surveys for future lek monitoring and aid future survey efforts by identifying yearly differences in activity and presence at leks inconsistently visited by birds.

KEYWORDS

activity patterns, cost analysis, detection probability, greater prairie-chicken, N-mixture models, population models, population trends, sharp-tailed grouse, trail cameras, wildlife monitoring

Accurate population estimates and trend data are foundational to the conservation and management of wildlife populations. For many species of conservation concern, long-term monitoring programs have been established to infer population dynamics in relation to management needs and to identify population declines (Blossey 1999, Brennan and Kuvlesky Jr. 2005). Annual monitoring of prairie grouse (*Tympanuchus* spp.) has allowed managers to assess population trends. *Tympanuchus* spp. were once widely distributed across North America in association with expansive shrub-steppe and grassland landscapes. Greater prairie-chickens (GRPC; *T. cupido*) and sharp-tailed grouse (STGR; *T. phasianellus*) have faced reductions to their historic range due to vegetation succession, fire suppression, and broad-scale loss and fragmentation of grassland and shrub ecosystems (Samson et al. 2004, Silvy and Hagen 2004, Fuhlendorf et al. 2017), especially in the Great Lakes region where abundance has continued to decline in recent decades (Maples and Soulliere 1996; Gregg and Niemuth 2000; Kardash 2022; Roy 2022a, b). Although habitat conservation and restoration has been the objective of numerous initiatives for both species, efficient monitoring efforts are needed as habitat management outcomes are often evaluated based on abundance estimates derived from monitoring.

Both GRPC and STGR are year-round upland game birds in Wisconsin, USA, and their presence indicates quality grassland and northern shrubland habitats (Gregg and Niemuth 2000, Johnson et al. 2020). During the breeding season, males of both species gather at display grounds known as leks where courtship and breeding occur, with males conspicuously displaying to females by vocalizing, fighting, and dancing (Connelly et al. 2020, Johnson et al. 2020). The aggregations at lek sites are generally the only time individuals are consistently seen, and thus provide an opportunity for surveying individuals that are otherwise elusive. Lek count surveys are the most widely used method for monitoring GRPC and STGR populations and trends and are often conducted in-person by viewing sites with binoculars or spotting scopes, or by counting from a blind immediately adjacent to the lekking grounds (Houts et al. 2022). Males are typically the focus of lek counts because they often maintain territories and display daily in early spring, which gives observers an access point for viewing and counting males on leks. Therefore, lek count data represent an index to population size, and the relationship between lek count indices and true population dynamics has been questioned (Applegate 2000, Anderson et al. 2001, Walsh et al. 2004). Nevertheless, lek count indices may remain useful for estimating annual and long-term abundance trends or to document the distribution or local occurrence of species (Applegate 2000, Engeman 2003).

The Wisconsin Department of Natural Resources (WIDNR) conducts in-person lek count surveys on an annual basis to provide an index to GRPC and STGR abundance to support informed management decisions (Hanson 2022, Kardash 2022). The surveys help to determine the distribution of GRPC and STGR by documenting the occurrence of leks and counting the number of male GRPC and STGR at each lek. Although lek surveys have a long history of use and have provided valuable historical datasets on statewide trends for GRPC and STGR, they may influence behavior and are time-intensive given the need to conduct multiple surveys to try and observe the maximum number of males at a lek site (Roy and Coy 2021). Monitoring techniques that can build on existing lek count data and provide robust estimates of abundance and trends that account for probability of detection are needed to advance management of these declining species (Fandel and Hull 2011, Wisconsin Department of Natural Resources 2022).

The use of remote trail cameras to monitor wildlife holds promise for prairie grouse lek monitoring as cameras can provide continuous and noninvasive monitoring of lekking grounds. Remote cameras have improved the spatial and temporal resolution for monitoring wildlife, and the gains are especially useful for species that are sensitive to other forms of monitoring (Caravaggi et al. 2018, Townsend et al. 2021). Remote cameras may be able to replace human observers at leks so that human presence does not disturb birds during their periods of peak activity (Roy and Coy 2021). Prairie grouse lek sites are often used annually, so remote cameras set up at lekking sites can provide consistent and repeatable lek monitoring.

Repeated surveys are a useful sampling strategy which allows for the estimation of detection probability and occupancy or abundance (Royle and Dorazio 2008). McCaffery et al. (2016) found that accounting for detection probability with N-mixture models on greater sage-grouse (*Centrocercus urophasianus*) lek count data from in-person surveys was preferred to using maximum male counts because of variation in detection probability across years. N-mixture models produce estimates of abundance in a hierarchical model structure that accommodates the incorporation of covariate effects on abundance and detection processes, allows for model building and selection, and produces estimates of uncertainty (Royle 2004, Kéry and Royle 2016). A challenge with N-mixture models is interpreting the area over which the abundance estimates are relevant. However, even if the area of inference is unknown, abundance estimates can be used as indices to abundance (Gilbert et al. 2021). Therefore, population trend information is easily derived from N-mixture model outputs. Both in-person and remote camera surveys can provide the repeated survey data structure needed for abundance estimates through N-mixture modeling.

Comparisons between in-person and remote camera survey methods for lek monitoring have not been thoroughly conducted. To investigate the potential for saving time, reducing costs, implementing more continuous monitoring, and increasing accuracy of GRPC and STGR survey efforts, WIDNR implemented a remote camera study at lekking grounds over 3 years in conjunction with in-person surveys. Our goal was to assess the feasibility, cost, and performance of remote camera lek surveys for GRPC and STGR as compared with in-person lek count surveys. Our objectives were to 1) develop and deploy an effective remote camera survey for GRPC and STGR, 2) compare metrics of male detection, maximum male counts, and male abundance estimates derived from in-person versus remote camera surveys, 3) assess lek activity over the survey season to inform survey timing, and 4) evaluate the cost of conducting each survey type.

STUDY AREA

In Wisconsin, remaining local populations of GRPC were found in relatively isolated state-managed wildlife areas in the Central Sand Plains ecological landscape (Wisconsin Department of Natural Resources 2015). In 2018, 2019, and 2021, we surveyed known GRPC lek sites on Leola Marsh Wildlife Area (1 lek), Buena Vista Wildlife Area (7 leks), and surrounding private land (2 leks; Figure 1A). The wildlife areas consisted of a diverse mosaic of grasslands, wetlands, shrublands, and isolated patches of forest cover (Niemuth 2000). Much of the land use in the surrounding private land was center-pivot irrigation and row-crop agriculture as well as dairy farming. Wildlife areas have been maintained as grassland-dominant landscapes and management to limit woody vegetation encroachment has included prescribed burning, mowing, and managed grazing with light to moderate stocking rates. Growing seasons averaged 135 days, with a mean minimum temperature of −16.4°C in January and a mean maximum

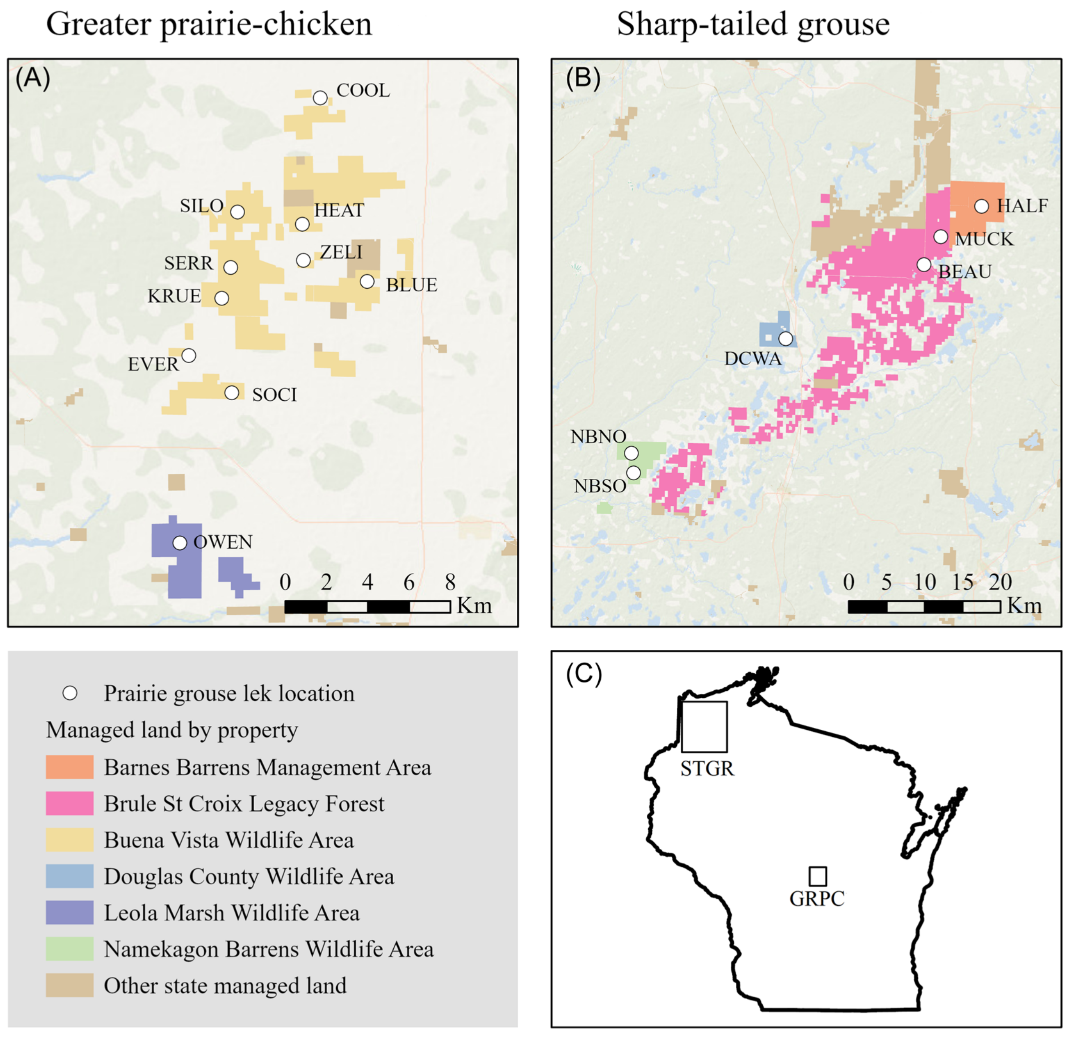

FIGURE 1 (A) Greater prairie-chicken (GRPC) leks surveyed in 2018, 2019 and 2021 along with their position on public land in central Wisconsin, USA, except for 2 on private land (EVER, COOL). (B) Sharp-tailed grouse (STGR) leks surveyed in 2019 positioned on public lands in northwestern Wisconsin. (C) Location of surveyed GRPC and STGR leks within Wisconsin, USA.

temperature of 27.1°C in August. Mean annual precipitation was 83.3 cm and winter snowfall ranged from 79.8–138.7 cm (Wisconsin State Climatology Office 2023).

The majority of STGR lekking in Wisconsin occurred on state- or county-managed wildlife areas in the Northwest Sands ecological landscape (Wisconsin Department of Natural Resources 2015). We conducted surveys of STGR in 2019 at Namekagon Barrens Wildlife Area (2 leks), Douglas County Wildlife Area (1 lek), Brule-St. Croix Legacy Forest (2 leks), and Barnes Barren Management Area (1 lek; Figure 1B). The study areas consisted of a mosaic of hardwood and conifer forests, pine-oak barrens, grassland, shrublands, wetlands, and limited row-crop agriculture. Historically, the Northwest Sands were characterized by frequent fires that maintained the barrens habitat often associated with STGR in Wisconsin (Curtis 1959, Radeloff et al. 2006). However, following decades of fire suppression, much of the contemporary early-successional habitat has been associated with clear-cuts, although wildfires and severe storms have occasionally created open patches. The growing season averaged

121 days, with an annual mean temperature of 5.1°C. Annual precipitation averaged 79.8 cm and snowfall totals ranged from 131.3–205.7 cm (Wisconsin State Climatology Office 2023).

METHODS

Lek selection, surveys, and trigger classification

We conducted our study in the spring seasons of 2018, 2019, and 2021. We did not survey in 2020 due to field work restrictions brought on by the Covid-19 pandemic. In late March to early April, we scouted established leks for fresh GRPC or STGR sign, including feathers and droppings. We prioritized sampling GRPC public property leks that were well established and monitored annually by WIDNR (Kardash 2018). We chose STGR leks based on the same criteria and selected active leks from major wildlife areas (Figure 1B; Hanson 2021). In fall, WIDNR staff mowed most known lekking grounds to help improve visibility for distinguishing sexes. Large, portable observational blinds (handmade from plywood or purchased from Primos, Overland Park, KS, USA) were deployed at some leks before birds congregated in spring.

In-person survey records for each repeat lek visit were not available for some STGR leks (season-long lek summaries of male detection and maximum counts were available) and therefore STGR was left out of analyses requiring repeated in-person surveys. In-person surveying for GRPC occurred in April through early May to overlap with peak breeding season when hen attendance at lekking grounds was highest. Surveying occurred 45 minutes before to 2 hours after sunrise on clear, calm mornings with winds <16 km/hr. An observer sat at the lek in either an observational blind or truck (using binoculars or a spotting scope) and counted numbers of male and female GRPC observed. Ideally, leks were surveyed ≥2 times per season (Kardash 2018).

Remote camera surveys were deployed on GRPC leks in 2018, 2019 and 2021 and STGR leks in 2019. We used 3 Bushnell Trophy Cam HD trail cameras (models 119836 and 119837; Bushnell Outdoor Products, Overland Park, KS, USA) at each lek deployed 45 cm above the ground to face north, west, and south. In 2021, only north and west facing cameras were placed on each GRPC lek to reduce photo processing workload. In 2018, distance between cameras varied at each site depending on size of the mowed lek. Detection range was determined by having a person crawl on the ground to determine the farthest movement detectable. Prior to 2019, we conducted trials with live, domesticated chickens to better understand camera detection distance and found reliable detection at ≤7.6 m. In 2019 and 2021, we scouted for the highest concentration of bird sign and measured 7.6 m out from that center east, north, and south to place 2 (2021) or 3 (2019) cameras.

All trail cameras were programmed to take a burst of 3 photos (hereafter, trigger) upon detection of movement with a 15-second rest period between triggers. Infrared images were taken at night. Each camera was fitted with a combination padlock to protect devices from tampering and deterrent strips to prevent predatory, avian species from perching on cameras. Cameras were placed using Stic-N-Pic trail camera mini ground mounts (Masterpiece Outdoors, Milton, IA, USA).

From late March to mid-May, we checked cameras every 1–4 weeks and collected photos for classification. Triggers were classified with tags of female, male, or unknown and counts for each tag. Additionally, a behavioral tag of a booming male (GRPC) or dancing male (STGR) was classified if a male's penne or air sacs were displayed (i.e., penne forward and air sacs enlarged). Any other species in photos were classified by species and count. We considered mammal predators as red foxes (*Vulpes vulpes*), coyotes (*Canis latrans*), wolves (*C. lupus*), domestic dogs (*C. familiaris*), domestic cats (*Felis catus*), and unknown canids (*Caninae*). Birds other than GRPC, STGR, eastern wild turkeys (*Meleagris gallopavo silvestris*), sandhill cranes (*Antigone canadensis*), or ruffed grouse (*Bonasa umbellus*) were classified as other bird. We used unknown tags for photos that were unidentifiable. Photos with humans or vehicles in them were labeled human and blank photos were marked as blank. We tested impact of camera orientation (facing north, west, or south), camera model, and year (GRPC only) on number of animal triggers per day, number of blank triggers per day, and proportion of triggers that were animals (Camera setup analysis and results S1 available in Supporting Information).

Metrics

For GRPC and STGR, we compared male detection, maximum male counts, and abundance estimates for in-person and remote camera surveys. Male detection was whether ≥1 male was detected anytime during the surveys. Maximum counts were the maximum number of male GRPC or STGR seen across all surveys (in-person) or weeks (camera) at each lek and in each year.

We estimated male abundance using single-season N-mixture models (Royle 2004). We used replicate counts for each lek-year. Each in-person survey was treated as a replicate and replicate counts were male counts from each survey. Remote camera survey replicates were weeks, and for each lek-year replicate counts were from the trigger that had the maximum number of males that week. Camera replicates for GRPC ran from week 13–22 and for STGR ran from week 16–21, though not necessarily for this entire time for each lek-year. We included weeks for lek-years that had ≥4 days of camera monitoring.

In GRPC models, we included lek (random effect) and year (fixed effect) in the abundance process and mowing (binary fixed effect) and year (fixed effect) in the detection process. We did not include additional covariates due to low sample size. We used this same model for STGR except we removed the year effect because all data were from the same year. Models were run in Program R (R Core Team 2021) with package ubms (Kellner et al. 2022). We used function stan_pcount to fit Bayesian N-mixture models allowing for random effects. We used reasonable weakly informative default priors (Kellner et al. 2022) and set K (upper index of integration for N-mixture) to 100. We ran 4 chains for 30,000 iterations after 5,000 iterations of burn-in and thinned by 3. We assessed model convergence by requiring all $\hat{R} < 1.05$ (Gelman and Rubin 1992) and through visual inspection of trace plots to see good mixing of chains. We conducted model checking with residual plots and goodness-of-fit tests (Kellner et al. 2022).

Activity pattern and timing of surveys

We used occurrence of GRPC and STGR males on remote cameras to assess diel and seasonal activity patterns related to time of day and day of year of when in-person surveys were conducted. For seasonal analysis, we used the date range when the majority of leks were being monitored. We found peaks of activity curves in each year by time of day and across season. We calculated proportion of male density functions that were within the time of day and day of year of when in-person surveys were conducted.

Cost comparison

We assessed the cost of GRPC in-person surveys and remote camera surveys in terms of total cost per lek (time and equipment), cost per day surveyed, and cost per hour surveyed during one lekking season. We assessed 2 in-person and 1 remote-camera survey scenarios. The in-person scenarios were based on the use of a blind versus spotting scope/binoculars. Blinds are placed on the edge of lek sites and require more survey time compared to spotting scopes/binoculars because observers stay in blinds for many hours to not disrupt lekking activity. Contrarily, surveys with spotting scopes/binoculars can be faster because observers can view leks from some distance and do not have the same concerns about disturbing birds on leks.

A set of equipment (i.e., blinds, spotting scope or binoculars, camera equipment) was purchased for each lek, and we assumed 2 remote trail cameras per lek. The hours surveyed were based on the average amount of time surveys took by equipment type. We also calculated costs without equipment to represent projected cost per lek once equipment had been purchased. We did not include time or costs of scouting, mowing, and report writing that were common to all methods. We calculated costs for GRPC leks and assumed these costs were very similar for STGR leks.

RESULTS

Lek selection, surveys, and trigger classification

There were 10 unique GRPC leks monitored, but not all leks were monitored in 2018, 2019, and 2021 by both survey methods. We monitored 26 GRPC lek-years with in-person surveys and most (77%) lek-years had 2 surveys (min–max = 1–8 surveys). We monitored 17 GRPC lek-years with remote cameras and most (71%) were monitored for 8 weeks (min–max = 5–9 weeks). Remote camera STGR surveys ran 4–6 weeks at 6 leks with most (67%) leks running for 6 weeks.

Remote cameras captured 133,253 triggers (5.3% of triggers contained GRPC) from GRPC leks and 77,077 triggers (13.0% of triggers contained STGR) from STGR leks, most of which were blank (Table 1). Across all 3 years, there were 5,057 triggers of GRPC males and 2,406 (47.6%) of the triggers had booming males. There were 1–8 GRPC males per trigger and 50.9% of triggers had just 1 male (Figure S1, available in Supporting Information). There were 8,817 triggers of STGR males and 7,656 of the triggers (86.8%) had males displaying. There were 1–15 STGR males per trigger and most often (22.2% of male triggers) there were 2 male STGR (Figure S1 and Data S1, available in Supporting Information). There were 15 mammalian species (5 of which were potential predators) and 25 avian species (other than GRPC and STGR) detected (Table 1).

TABLE 1 The number of photographic triggers by type from a remote camera study of greater prairie-chicken (GRPC) and sharp-tailed grouse (STGR) leks in 2018, 2019 and 2021 in Wisconsin, USA. Other animal triggers were any that contained animals that were not GRPC, STGR or mammalian predators.

Study area	Year	Cameras	Active days	Blank triggers	Human triggers	Other animal triggers[a]	Mammalian predator triggers[a,b]	GRPC or STGR triggers	Total triggers[c]
GRPC	2018	15	711	66,655	2,399	478	25	541	70,076
GRPC	2019	21	1,201	38,012	344	519	94	2,666	41,605
GRPC	2021	10	510	16,876	188	732	51	3,892	21,572
STGR	2019	18	625	66,248	644	155	13	10,037	77,077

[a]By percentage of combined other animal triggers and mammalian predator triggers: Other birds (39%; ≥23 species primarily *Passeriformes*, *Anseriformes*, and *Falconiformes* orders), white-tailed deer (*Odocoileus virginianus*; 32%), coyote (*Canis latrans*; 7%), striped skunk (*Mephitis mephitis*; 7%), sandhill crane (*Antigone canadensis*; 5%), eastern wild turkey (*Meleagris gallopavo silvestris*; 2%), unknown triggers (2%), eastern cottontail (*Sylvilagus floridanus*; 1%), domestic cattle (*Bos taurus*; 1%), domestic dog (*C. familiaris*; 1%), and raccoon (*Procyon lotor*; 1%). The following categories each made up <1% of triggers: red fox (*Vulpes vulpes*; 8 triggers), American badger (*Taxidea taxus*; 7 triggers), domestic cat (*Felis catus*; 7 triggers), snowshoe hare (*Lepus americanus*; 5 triggers), squirrels (*Sciurus* spp.; 4 triggers), gray wolf (*C. lupus*; 3 triggers), unknown canid (*Caninae*; 2 triggers), Virginia opossum (*Didelphis virginiana*; 1 trigger), North American porcupine (*Erethizon dorsatum*; 1 trigger), and woodchuck (*Marmota monax*; 1 trigger).

[b]Mammalian predators were red foxes, coyotes, wolves, domestic dogs, domestic cats, and unknown canids.

[c]Total triggers were less than the sum of triggers because there were triggers that had both the target species (GRPC and STGR) and another animal (other animal triggers or mammalian predator triggers) in them and were therefore counted in both columns.

Metrics

Detections of GRPC males were made in 24 out of 26 lek-years (92.3%) from in-person surveys and 16 out of 17 lek-years (94.1%) from remote camera surveys. There were STGR male detections at all 6 STGR leks from both in-person and remote camera monitoring. Across all years, maximum male GRPC counts ranged from 1–21 males per lek from in-person counts and 1–8 males per lek from remote cameras where GRPC males were detected. There were 14 GRPC lek-years that were monitored with both survey types, and the majority (8 lek-years, 57.1%) had higher maximum GRPC male counts from in-person surveys as compared with remote camera monitoring. Maximum male STGR counts ranged from 6–18 males per lek from in-person counts and 4–15 males per lek from remote cameras. The majority of leks (5 leks, 83.3%) had more STGR males counted from in-person surveys as compared with remote camera monitoring.

All N-mixture models converged as determined by all $\hat{R}$ < 1.05 (Table S3 available in Supporting Information) and good mixing of MCMC chains through visual inspection of trace plots. Model fit was adequate based on residual plots without trends and nonsignificant ($P > 0.10$) goodness-of-fit statistics (Kellner et al. 2022). There were no significant differences by year (i.e., nonoverlapping 95% credible intervals) in detection and abundance for GRPC from remote-camera or in-person surveys, although 2019 did have lower average detection and higher average abundance than the other years, for the remote camera surveys. The effect of mowing on detection was significant for GRPC remote camera surveys and although not significant in the other models, the mean estimates were consistently in the direction of leks with mowing having higher detection (Table S3 available in Supporting Information).

Mean per-survey detection estimates by lek were 0.57 (min–max = 0.41–0.75) from in-person GRPC surveys, 0.23 (min–max = 0.06–0.51) from GRPC remote camera surveys, and 0.66 (min–max = 0.53–0.72) from STGR remote camera surveys (Table S4 available in Supporting Information). The GRPC male abundance estimates by lek-year ranged from 2–28 males ($\bar{x}$ = 11.0 males) from in-person surveys and 3–36 males ($\bar{x}$ = 11.8) from remote camera surveys (Figure 2). The average coefficient of variation (CV) for GRPC abundance was higher ($\bar{x}$ CV = 0.70) in remote camera surveys as compared with in-person surveys ($\bar{x}$ CV = 0.45), likely due to the smaller sample size (fewer lek-years) in the remote camera model. The average difference between GRPC abundance estimates and maximum counts was greater for remote cameras (8.4 more males) compared to in-person surveys (4.1 more males). The STGR male abundance estimates by lek from remote camera surveys ranged from 9–16 males ($\bar{x}$ = 11.6 males) with an average CV of 0.34 (Figure 2). Detection and abundance estimates were not available from STGR in-person surveys because numerous leks were missing data for repeated surveys (Table S4 available in Supporting Information).

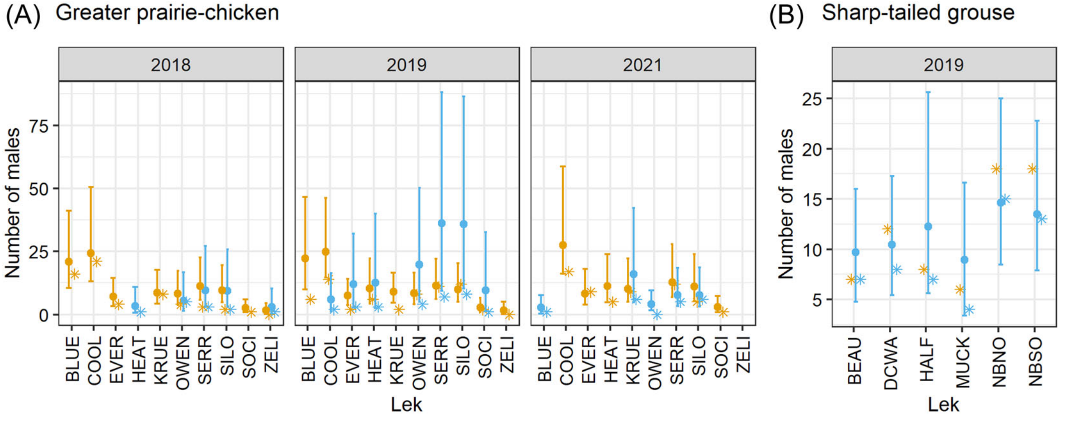

FIGURE 2 Male greater prairie-chicken and sharp-tailed grouse abundance estimates (solid dots) and maximum counts (asterisks) with 95% credible intervals from in-person (orange) and remote camera (blue) lek surveys in 2018, 2019 and 2021 in Wisconsin, USA.

There were 14 GRPC lek-years that had concurrent in-person and remote camera monitoring where abundance estimates from remote camera monitoring could be compared to maximum counts and abundance estimates from in-person surveys. The 95% credible intervals for male abundance from in-person and remote camera surveys overlapped in all lek-years. All in-person maximum counts for STGR fell within the 95% STGR male abundance estimate from remote camera surveys (Figure 2).

There were 3 GRPC leks that were monitored for consecutive years with concurrent in-person and remote camera surveys and could therefore be used to compare trend information among methods (i.e., in-person maximum counts, in-person abundance estimates, remote-camera maximum counts, and remote-camera abundance estimates). The remote camera abundance trends matched trends from in-person maximum counts in 2 out of 3 leks. Abundance estimates from in-person surveys did not match the in-person maximum count trends in any of the leks (Figure S2 available in Supporting Information).

Activity patterns and timing of surveys

We conducted in-person surveys from 0500 to 0930 between 2 April and 5 May for GRPC. Remote cameras monitored leks continuously from 31 March to 17 May (2018) or 29 May (2019 and 2021) for GRPC and from 19 April to 17 May 2019 for STGR on the majority of leks. Peak remote camera activity for male GRPCs fell between earliest and latest in-person GRPC survey in each year. On average, 64% (min–max = 59–70%) of the GRPC male activity was between 0500 and 0930 (Figure 3A). Peak STGR male detections were at 0620 and most (74%) detections occurred between 0500 and 0930 (Figure 3B). Peak GRPC male detections from remote cameras fell within the earliest and latest in-person surveys in all years, except peak male GRPC detections were prior to the first in-person survey in 2021 (Figure 3C). On average, 71% (min–max = 65–75%) of GRPC male activity was between 2 April and 5 May. Peak STGR male detections were on 6 May. The period of 2 April–5 May captured 57% of STGR male detections (Figure 3D).

Cost comparison

Total cost per GRPC lek was highest for remote-camera monitoring ($1,084/lek) and lowest for in-person monitoring with a spotting scope/binoculars ($160/lek; Table 2). Once equipment was purchased, surveying was still the least expensive with in-person surveys using spotting scopes/binoculars ($60/lek). The cost per day and per hour surveyed by remote cameras was $18.07/day and $0.77/hour, respectively, which was many times less expensive than in-person survey costs calculated per day or hour (Table 2).

DISCUSSION

We compared in-person surveys to remote camera monitoring of detection, maximum counts, and abundance estimates of GRPC and STGR males on leks and found benefits to each survey approach. Both survey methods reliably detected GRPC or STGR on leks, and in-person surveys were preferred for observing higher maximum male GRPC and STGR counts. We demonstrated that the estimated number of male GRPC and STGR on leks was comparable between in-person surveys and remote camera monitoring when accounting for detection probability with N-mixture models. Remote camera monitoring provided constant monitoring of leks over the season which allowed for discovery of other wildlife using lek sites and daily and seasonal activity patterns of GRPC and STGR on leks. The cost of in-person surveys was lower for the season, but higher when considering cost-per-hour monitored as compared with remote camera monitoring. Remote camera monitoring of leks should be considered for future lek monitoring, especially if activity pattern information is desired.

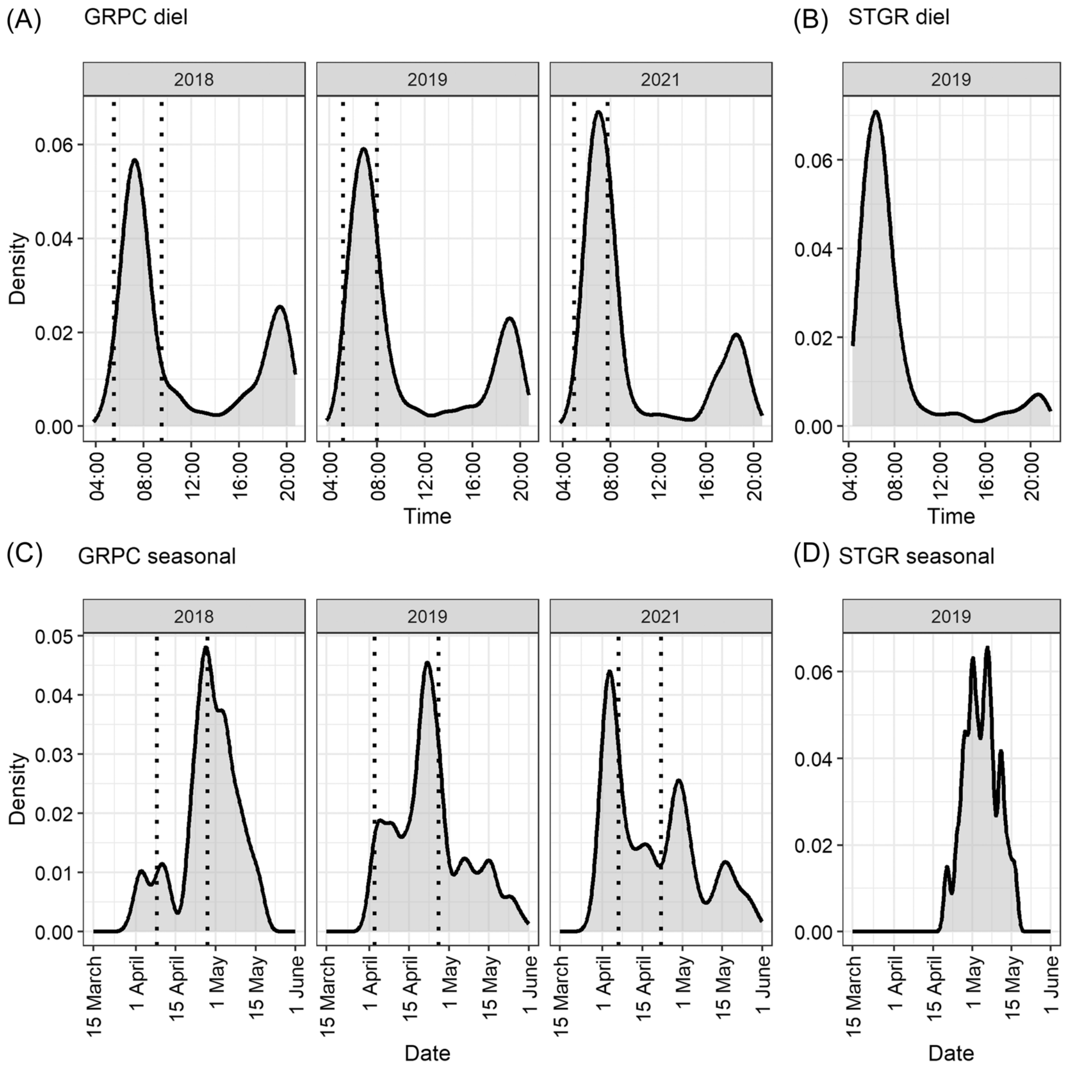

FIGURE 3 Diel and seasonal activity patterns from detections of male greater prairie-chickens (GRPC) and sharp-tailed grouse (STGR) on remote cameras placed on leks in 2018 (5 GRPC leks), 2019 (7 GRPC leks and 6 STGR leks) and 2021 (5 GRPC leks) in Wisconsin, USA. Dotted vertical lines denote earliest and latest times of day (diel) and day of year (seasonal) that in-person lek surveys were completed.

Remote cameras were less likely to capture maximum number of GRPC or STGR males as compared with in-person monitoring. Accurate counts for all birds using lekking grounds are understandably difficult to obtain from a stationary remote camera with its limited field of view, especially given that birds cannot be individually identified (Sollmann et al. 2013). The angle of a spotting scope or location of a parked vehicle can be changed by an in-person observer on a day-to-day basis, but remote cameras are fixed in place. Multiple cameras on each lek with nonoverlapping fields of view could take synchronized time-lapse photos to increase the total area sampled in each trigger. However, it's not likely necessary to optimize remote cameras for maximum male counts at leks because N-mixture models provide indices to abundance that also account for detection probability (McCaffery et al. 2016).

Our current method for counting maximum number of males on leks relied on birds being in a single photo together. The classification task of categorizing remote camera triggers into counts of GRPC and STGR males and

TABLE 2 Estimated cost of equipment and time for in-person and remote camera monitoring of a greater prairie-chicken (GRPC) lek in Wisconsin, USA, based on lek monitoring conducted in 2018, 2019, and 2021.

Category	In-person blind	In-person spotting scope or binoculars	Remote cameras
Equipment[a]	Blind - $500	Binoculars - $100	2 camera kits - $400
Time to set up	4 hours	0 hours	4 hours
Time to survey or check cameras[b]	8 hours (2 surveys at 4 hours each)	3 hours (2 surveys at 1.5 hours each)	4 hours (2 camera checks)
Time to tear down	4 hours	0 hours	2 hours
Time to classify photos[c]	NA	NA	24.2 hours
Number of days surveyed[d]	2	2	60
Number of hours surveyed[e]	6	1	1,416
Total cost with equipment[f]	$820.00	$160.00	$1,084.00
Total cost without equipment[f]	$320.00	$60.00	$684.00
Cost per day surveyed with equipment	$410.00	$80.00	$18.07
Cost per day surveyed without equipment	$160.00	$30.00	$11.40
Cost per hour surveyed with equipment	$136.67	$160.00	$0.77
Cost per hour surveyed without equipment	$53.33	$60.00	$0.48

[a]There was a range of costs for blinds depending on the type (hand-built plywood or pop-up). This was the average cost of a blind. Each remote camera equipment kit included a remote camera with 2 SD cards, rechargeable batteries and battery charger, security box with padlock, mounting stake, and avian predator deterrent strips.

[b]Travel time was included at 1 hour travel time per trip.

[c]The median number of triggers per GRPC lek was 8,713 and it took an average of 10 seconds to classify each trigger (approximately 1 second for blank photos with no wildlife and up to a minute for triggers with many GRPC).

[d]The median number of days for remote camera surveys was 60 days.

[e]The number of hours surveyed for in-person surveys did not include travel time. The average number of hours surveyed for remote cameras was 59 days × 24 hours because first and last day were not surveyed for a full 24-hour period.

[f]Time cost was estimated at $20 per hour.

females was time consuming and difficult (Photos S1, available in Supporting Information). It was often possible to detect individuals but not determine sex and therefore we classified them as unknown sex; these unknown classifications were not used in our analyses. Considering additional metrics that use total numbers of GRPC or STGR individuals may be a useful means to obtain more accurate total counts of birds on each lek. Photo classification was the most time-consuming portion of our study. Automated classification using machine learning could classify blanks and humans and these photos could be removed prior to a human classifying the triggers containing animals (Tabak et al. 2020). With >90% of triggers being blank or containing humans in our study, automated classification would lead to substantial time savings. It is less certain whether automated classification techniques could accurately count and categorize target species into males (with and without display behavior) and females, though these methods have improved (Vélez et al. 2023).

Our cost comparison demonstrated lower costs over the season using in-person surveys (2 days of effort) compared to remote camera surveys (60 days of effort). This is unsurprising because there was 30 times more effort from remote camera surveys as compared with in-person surveys. Each day of remote camera effort generated ~145 triggers, taking ~24 minutes to classify. Reducing the number of days surveyed to every second day (30 days of effort) would result in seasonal cost estimates comparable to in-person surveys with blinds. No amount of photo classification effort reduction would make the seasonal cost of remote camera surveys comparable to in-person surveys with spotting scope/binoculars because of differences in equipment costs. We recommend that reduced remote camera effort be achieved by sampling every second or third day rather than reducing the length of the survey season or the time of day surveyed. Remote camera data should still be collected ≥2 times/week and at a regular interval to provide information for activity pattern analysis and the repeated data needed for models that can account for detection probability; additional consideration would be needed to choose the length and number of survey replicate periods to ensure equal effort or that differences in effort are properly accounted for. Subsets of remote camera data could result in loss of maximum male counts (50% of leks saw their maximum male count on just one day), though remote cameras are already inferior at providing this metric as compared to in-person surveys.

Throughout our study we improved the protocol for remote camera placement and that resulted in a higher proportion of triggers of our target species. Standardizing camera placement and reducing the number of cameras at leks led to fewer total triggers and proportionally more triggers of GRPC and STGR, thereby reducing classification work without impacting quality and quantity of usable data collected. A change in camera model was important to decrease the proportion of blank triggers, further reducing time needed to complete trigger classification. Changes in remote camera set up protocols and camera equipment can impact detection probability and it is important to test and account for these changes in modeling (Hofmeester et al. 2019). Given our small sample size, we did not include these variables in our models after determining that triggers per day of our target species were not impacted by these variables. Future efforts with remote camera monitoring would benefit from keeping camera set up protocols and equipment consistent once study design is optimized for a particular species and lekking system.

We observed a vast difference in total number of triggers between the 2 species we studied. This may suggest that STGR exhibit more consistent and stationary lekking behavior, which could be more suitable for remote camera estimates (Baydack and Hein 1987). Also, higher numbers of STGR detections may reflect more birds on STGR leks as compared with GRPC and more birds lead to more opportunity to trigger remote cameras. Mowing of leks has been standard practice in Wisconsin to improve sightability and counting of birds. Birds were generally easier to sex and count in triggers from leks that were mowed, and mean detection estimates from N-mixture models were higher for mowed leks. The benefit for speeding up photo classification (and potentially in-person survey counts) and improving detection should be considered when deciding to mow leks.

N-mixture models allowed for inclusion of covariate effects in detection and abundance processes, and while accounting for detection probability, we generated trend information for GRPC leks monitored in multiple years. Trend information that properly accounts for detection probability is preferred to using maximum male counts alone (McCaffery et al. 2016). When detection rates differ among years and are not accounted for, observed interannual changes arise from both actual changes in abundance and changes in detection thereby potentially leading to appearance of a trend that is a relic of detection rate differences (Maunder and Punt 2004). Detection probability should always be accounted for as even small differences in detection probability can lead to erroneous results (Archaux et al. 2012). Both in-person and remote camera surveys can provide repeated surveys that are necessary for detection probability estimates within N-mixture or similar hierarchical models (Kéry and Royle 2016). Poisson models, for example, can also model abundance while accounting for detection probability. Researchers running any model relying on count data alone to estimate abundance should be cautious with interpretation as it is more appropriate to view estimates as indices to abundance rather than absolute abundance (Barker et al. 2018, Gilbert et al. 2021). Uncertainty in abundance estimates was high from both survey methods despite remote camera surveys having many more survey occasions than in-person surveys, on average. We expect that increasing sample size with more lek-years will decrease variability in detection and abundance estimates.

Maximum male counts of GRPC and STGR at leks have been the traditional metric used to track annual population trend of these species. Transitioning to other metrics, like male abundance estimates that account for detection probability, may complicate comparison with historical data. However, the raw data remain largely the same and multiple metrics, like maximum male counts and male abundance estimates, can be calculated annually from a dataset with repeated surveys. Calculating multiple metrics in tandem for several years would allow for correlation analysis among these metrics and could further our understanding of how well each metric tracks population abundance and trend of lekking species.

Remote camera monitoring is also useful given its ability to capture diel and seasonal activity information. A specific application of having detailed activity information is to direct in-person survey efforts to the time of day or week of year with the peak activity of target species. Remote camera monitoring of the same leks over numerous years can provide information for how to time in-person surveys. Furthermore, Wann et al. (2019) showed that 48% of subadult male and 36% of adult male greater sage-grouse visited ≥2 leks during a season. Remote cameras surveying the duration of a lekking season have potential to provide information on relationships between maximum counts and within-season lek-switching dynamics, but more work is required here given the need to relax closure assumptions of N-mixture and similar models.

MANAGEMENT IMPLICATIONS

Our work indicates that in-person surveys paired with N-mixture models offer the most cost-effective and scientifically valid means of reaching monitoring program goals. However, if the monitoring program comprises additional goals or broader scope, such as providing data for other species' abundance estimates, evaluating species' behavioral patterns, optimizing survey windows for future monitoring, maximizing survey hours, or engaging the public, then remote cameras may provide a higher return on investment.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHIC STATEMENT

We did not handle animals in this study and therefore did not require review through Wisconsin Department of Natural Resources Animal Care and Use Committee.

DATA AVAILABILITY STATEMENT

Data are available in supporting information and any additional data needs can be requested from the authors.

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