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Real-time thermal imagery from an unmanned aerial vehicle can locate ground nests of a grassland songbird at rates similar to traditional methods

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ABSTRACT

Monitoring songbird reproductive output is a well-established method for assessing population persistence, but reproductive studies on grassland songbirds often suffer from low sample sizes, high labor costs, and high levels of disturbance due to the difficulty of finding nests. However, technological advances in unmanned aerial vehicles (UAVs or drones) might improve our ability to locate these hidden nests with minimal intrusion. We compared the effectiveness and efficiency of locating grassland songbird nests with a thermal camera mounted on a UAV versus traditional nest searching techniques. We used a paired experimental design to determine whether UAV-assisted searches could replicate the results from traditional search methods. Two independent teams surveyed field sparrow (*Spizella pusilla*) territories with active ground nests for up to 2 h on consecutive days. Each team recorded the outcome and time it took to locate the nest. Both methods were highly successful at locating ground nests. UAV-assisted searches located nests 28% faster than traditional methods, but the results from a survival-style analysis indicated that the methods were not significantly different. Although UAVs may temporarily increase stress and alter the behavior of animals, UAV-assisted searches are generally less invasive than traditional methods because piloting the aircraft from the territory edge drastically reduces the need to traverse and trample vegetation within the territory. Thus, UAV-assisted nest searches represent a promising technique for locating grassland bird nests. Continued advances in UAV and thermal technology are likely to increase the efficiency of UAV-assisted nest searches and may eventually remove the need for humans to enter target territories when monitoring nest success.

1. Introduction

Songbirds have long been viewed as indicators of ecosystem health (Morrison, 1986). This is perhaps best embodied with the expression 'the canary in the coal mine', a situation where canaries were used as indicators of poor air quality. However, many environmental problems are not detectable through the immediate death of a caged bird. Rather, these processes are often identified through slow declines in population trends that remain undetectable until environmental impacts are near or beyond the thresholds required for population persistence. One reason it is difficult to detect population declines in songbirds is the use of abundance (i.e., the number of individuals) as the primary predictor of population trends (Bock and Jones, 2004). Yearly changes in abundance at any particular location may be due to a number of variables not associated with population trends, such as weather conditions, habitat selection, and irregular migratory behavior (e.g., Ballard et al., 2003). Thus, it may take years to establish clear patterns.

A more direct method of assessing population persistence is the quantification of reproductive output (i.e., the number of young produced; Vickery et al., 1992). Reproductive output, or birth rate, is one of the two fundamental measures (alongside death rate) used to develop population growth models (Wilson and Bossert, 1971). Yet, reproductive output is quantified far less than abundance in the scientific literature. One primary reason is the difficulty of locating bird nests. In forests, many species place nests > 20 m above the ground. Locating these nests is extremely challenging, and few biologists have the tools or time to access the canopy. In grasslands, nests are presumably more accessible since many species place their nests on the ground. In reality, locating these nests poses a significant challenge as these species are highly cryptic, placing nests deep within the grasses (Dion et al., 2000). In addition, adults often run to the nest under the cover of grasses, so simple observation of bird behavior may be unlikely to lead one directly to the nest location. As a result, assessing reproductive output in grasslands requires spending a substantial amount of time traversing

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target habitats. Traditional nest search methods in grasslands are highly intrusive and often damage vegetation. In addition, they often suffer from low sample sizes and high labor costs, causing investigators to second-guess their utility despite the wealth of knowledge that could be derived.

However, new technologies are revolutionizing ecological research in many dimensions, and hold much promise for improving our ability to locate and monitor songbird nesting activity (McCafferty, 2013; Horning, 2018). For example, handheld thermal imaging cameras that can detect the heat produced by thermoregulation in incubating birds or eggs have been used to locate the nests of grassland songbirds (Galligan et al., 2003), and unmanned aerial vehicles (UAVs, or drones) have been used to monitor forest nesting species (Mattsson and Niemi, 2006). UAV and thermal technologies have been paired previously for home inspections (Entrop and Vasenev, 2017) and search and rescue operations (Silvagni et al., 2016). More recently, UAV technology has been used to survey animal populations (Wilson et al., 2017; Gonzalez et al., 2016) and categorize habitats (Cruzan et al., 2016) in ecological research. But thermal imagery captured from a UAV has not been used previously to locate songbird nests.

Our team recently paired the two technologies successfully to facilitate nest searching via a thermally equipped UAV in restored prairie grasslands at the Pierce Cedar Creek Institute (PCCI) near Hastings, Michigan, USA (unpublished data). Using small heat packs and active nests we determined that remote pilots were capable of locating heat-producing sources in grassland nests (i.e., eggs, hatchlings, and fledglings; Fig. 1). UAV-assisted nest searches are far less intrusive and destructive than traditional methods that include walking back-and-forth through known territories or grasslands in order to flush incubating adults. Inadvertently stepping on a nest or fledgling is also an unfortunate, but not uncommon, outcome of traditional search methods (Wells et al., 2007). UAV-assisted searches also allow observers to view otherwise inhospitable and inaccessible habitats, such as wetlands and dense shrub cover.

To be a viable alternative, UAV-assisted searches must be capable of detecting nests at a rate similar to that of traditional methods. To test this capability, we performed a quantitative comparison of outcomes from UAV-assisted and traditional nest searching methods for ground-nesting songbirds in three restored prairies in Southwestern Michigan, USA. Traditional search methods in grasslands range from targeted searches within the territory of a known breeding pair, often relying heavily on behavioral observation, to non-targeted surveys of expansive grassland tracts, often dependent on dragging mechanical devices such as ropes or chains to flush incubating adults off hidden nests (Winter et al., 2003). We used targeted nest searches in this study because it enabled us to standardize the search area and ensure that the same nest was active under both search methods. Specifically, we searched field sparrow (*Spizella pusilla*) territories with known active nests using both search methods, and recorded 1) whether a not a nest was located, and 2) the amount of time needed to locate the nest. Based on our pilot study, we predicted that UAV-assisted searches would be equal to or more efficient than traditional methods.

2. Materials and methods

2.1. Site and species selection

Research was conducted at the Pierce Cedar Creek Institute near Hastings, Michigan, USA, from 29 May to 26 July, 2018. We conducted nest searches in three grasslands at the Institute (42.534982° N, −85.301675° W) which were 29.8 acres (North prairie), 27.2 acres (Southwest prairie), and 22.2 acres (Jones' field; Fig. S1) in size. The North and Southwest parcels are restored prairies composed largely of warm-season grasses such as big bluestem (*Andropogon gerardi*) and switchgrass (*Panicum virgatum*), as well as raspberry (*Rubus occidentalis*), goldenrods (genus *Solidago*), and other native plants. The vegetation of the Jones field contains both cool and warm-season grasses. Grass height increased from ½ to 1½ m in height as the season progressed, and bare ground was rarely visible to the human observer from above the thatch.

The field sparrow was our target species because they place their nest on or near the ground, are semi-obligate to grasslands, native, and prevalent in our prairie sites (Carey et al., 2008). Field sparrows typically place small cryptic nests (85–210 mm) composed of woven grasses at the base of shrubs or grass clumps from May–July, and may raise multiple broods per season (Walkinshaw, 1968). Clutch sizes range from 2 to 5 eggs which are incubated for 11–12 days (Walkinshaw, 1978). Hatchlings remain in the nest for ~8 days before they fledge. Although not used for statistical analysis, we also searched for two song sparrow (*Melospiza melodia*; Arcese et al., 2002) and one common yellowthroat (*Geothlypis trichas*; Guzy and Ritchison, 1999) nests because these species possess similar nesting traits.

2.2. Territory delineation

We identified active territories containing field sparrow nests prior

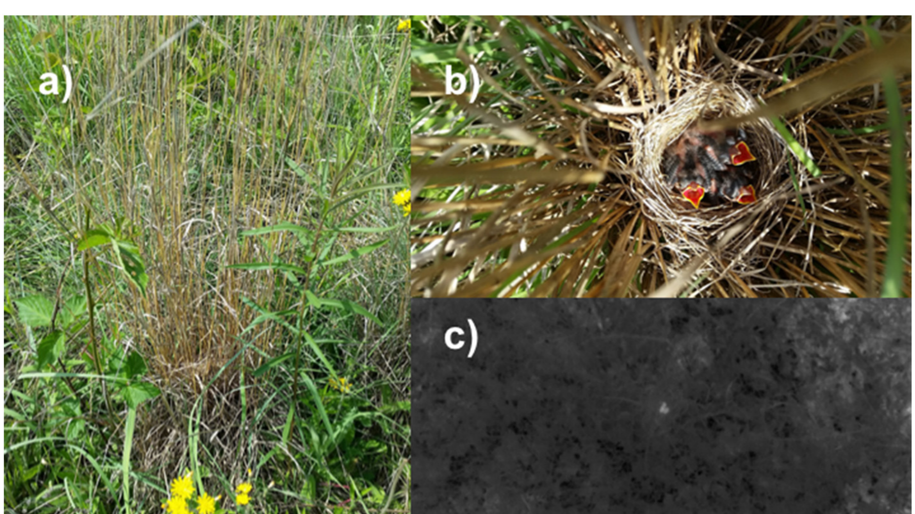

Fig. 1. Example field sparrow nest visualized from a) typical human observer perspective, b) close-up color imagery, and c) from ~4 m overhead with UAV-mounted thermal imagery.

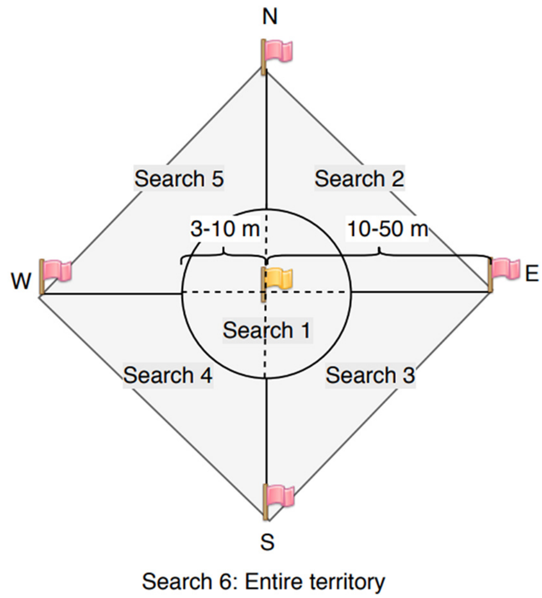

Fig. 2. Diagram of a territory search layout, with the yellow flag in the activity center and pink flags placed at edge of observed activity in the four cardinal directions. Segments were searched in the numbered order for both the UAV-assisted and traditional nest search methods. Search six included paying special attention to places where we had observed bird activity or thought the nest was likely to reside. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

to conducting UAV-assisted or traditional searches to ensure that data were not biased by nest absence during one or both searches. Active territories were located by scouting target fields; which included listening for vocalizations from target species, visually locating an interacting pair, and following behavioral cues to locate active nests (containing eggs or hatchlings). Behaviors used to indicate the presence of a nest included; provisioning, repeatedly returning to a particular location, flushing nearby, or demonstrating alarm at the approach of the scout. In most cases, scouting was conducted until a nest was located. Once a nest was located or provisioning was confirmed, territories were marked with five wire flags. The first flag was placed at the center of activity, where the bird pair spent the most time. If the nest was found, the center flag was placed within 3–10 m of the nest based on accessibility within grassy and shrubby habitat, but never closer than 3 m to avoid disturbing the nesting pair. Corner flags were then placed in the four cardinal directions from the territory center at a radius determined by the observed size of the nesting birds' territory. Territory size was determined for each site by measuring the distance from the center flag to the furthest point at which bird activity was repeatedly observed (Fig. 2). Territory radii ranged between 10 and 50 m with a mean of 22.15 ± 2.44 m (se). Because the scout was familiar with these territories and often knew the nest location, he or she did not participate in UAV-assisted or traditional searches conducted in the site. The scout was also responsible for monitoring nest activity to ensure the nest remained active during both search periods, but never relayed information regarding nest presence or contents to those conducting searches.

2.3. Nest searches

Once an active territory was established, teams conducted nest searches using traditional and UAV-assisted techniques on consecutive days. Teams consisted of two individuals, and the order of the search method was alternated to avoid bias due to any clues left inadvertently (although there was no visual indication that inadvertent clues, such as flattened paths leading to the nest location, were present). Because the ability to locate nests may vary between individuals, the membership of search teams was rotated to balance each member's participation in both search types. Information was not relayed between teams, ensuring the researchers were always blind to the search results from the other team.

Nest searches began at either 0600 or 0900 h. Within each territory, both search types began at the same time on consecutive days to minimize differences in temperature or bird activity. Since birds are more active at 0600 h, priority was given to this timeframe. Later start times for a territory were used only when the number of active nests exceeded our ability to complete surveys during the 0600 time period. Nest searches were terminated when a nest was located or when search time reached 120 min.

Both UAV-assisted and traditional searches were divided into six active search segments with observational periods placed between each active segment. During the first active segment, teams limited the search area to within a 10 m radius of the center flag (Fig. 2). The second active search segment occurred in the northeast quadrant, bounded by the north, east, and center flags. Search segments then proceeded clockwise to the southeast, southwest, and northwest quadrants. The sixth segment was used to search the entire territory, paying special attention to places where we had observed bird activity. During observational segments, teams stationed themselves beyond the territory boundary and watched for behavioral cues (e.g., birds disappearing into the grass) which would assist in nest location. If the focal pair provided cues regarding nest location during any active or observational search period, the team immediately explored the likely nest location, returning to the established search pattern if no nest was located. This search design standardized site coverage for each search method when nest indicators were not available, but provided needed flexibility to follow cues when provided by the focal pair. At the completion of each search, we recorded the outcome (0 = nest not located, 1 = nest located) and the search time (0–120 min).

Both survey techniques began with an observational period and cycled between active and observational segments thereafter. The allotted time for active and observational segments differed between traditional and UAV searches to maximize the detection of cues needed to assist in nest location. Because traditional methods are highly dependent upon observing adult behavior, observational and active segments were divided equally into ten-minute periods. Since each territory segment could easily be traversed within a ten-minute timeframe, spending more time within these territories was unlikely to increase the odds of flushing an adult bird and could reduce the likelihood of observing adults returning to the nest site. However, UAV searches were less dependent upon the observation of adult behavior because heat-producing nests, the primary cue of interest, could be detected in the absence of cues from adults. Further, UAV searches were often unable to cover entire segments within the ten minute timeframe. Thus, UAV-assisted observation periods were 5 min, and corresponding active periods were 15 min.

During active segments for traditional searches, the team traversed the appropriate section of the territory in a lawnmower pattern, with parallel transects separated by approximately 2 m. Each individual searched visually for a nest or flushing adult while waving a 2 m plastic pole at or below grass height. The pole was used to encourage flushing and to part dense vegetation to increase visibility of grass stems and the ground below. Active segments for UAV searches used the same spatial search pattern as traditional searches. The search team was comprised of a pilot and a spotter. The spotter watched for bird activity and for obstacles in the flight path while the pilot flew the UAV and monitored the thermal feed. The pilot and the spotter switched roles after each search segment. UAV-assisted searches utilized a DJI Inspire 1 UAV (DJI North America, Los Angeles, California, USA) fitted with a FLIR XT Zenmuse thermal camera (640 × 512, 9 Hz, 9 mm; FLIR Systems, Nashua, New Hampshire, USA). Thermal imagery was relayed in real time to a handheld DJI remote control equipped with an iPad Mini 4 display for immediate visual feedback. The Inspire 1 was powered by six rechargeable intelligent batteries (DJI TB48, Los Angeles, California, USA), each providing ~15 min of flight time.

The UAV was launched from the edge of the flagged territory and elevated to a height of 20 m for its initial approach into the search area. The pilot then descended to a height of 2–4 m above the grass, rotated the thermal camera to point directly downward, and began to traverse the territory in a lawnmower search pattern. The spotter watched from the edge of the search area for adults to flush while the pilot monitored the thermal feed on the handheld controller. A red-hot color palette was used to identify hotspots indicating the presence of a potential nest. Wind from the UAV rotors enhanced thermal contrast by cooling grasses within the thermal field of view, and by parting longer grasses to reveal a view of the ground beneath. When a nest-sized hotspot was identified, the spotter walked towards the heat signature under the pilot's direction to confirm whether the thermal signature was a nest or a false positive. If the hotspot was not the target nest, the spotter returned to the edge of the territory area and the search progressed in the established search pattern. UAV-assisted search termination and recording procedures mirrored traditional searches. To maximize UAV performance, we conducted a compass calibration daily, IMU calibration weekly, and a deep-cycle charge of batteries every 10 discharges (*Inspire 1 User Manual V2.0,* 2017).

2.4. Statistics

The binomial variable search *Outcome* (nest located/not located) and the continuous variable search *Time* were combined into a binomial matrix for a survivorship-style analysis (Hazler, 2004). This analysis treated nest location as the event of interest, while also taking into account the 120 min cap on search time in cases where the nest was not located. Our generalized linear effects model with binomial errors (glmer, package lme4, Bates et al., 2011, R version 3.3.3; R Core Team, 2017) included fixed terms for *Treatment* (UAV-assisted/traditional), *Block* (0600/0900 start), treatment *Order*, territory *Radius*, and *Julian* date. Interactions between *Treatment***Block*, *Treatment***Radius*, and *Treatment***Julian* were also included. A random term was included for *Location* to account for the paired experimental design (two searches per location). Significance was assessed via Anova (package car, Fox and Weisberg, 2011) with a $p < 0.05$ considered to be a significant result. All means are reported with 95% confidence intervals.

3. Results

UAV-assisted nest searches located the target nest in 17 of 20 territories (85%; Fig. S2) and traditional searches located the target nest in 18 of 20 territories (90%). The methods were equally successful at 0600 h (13/15; Fig. 3). Fewer searches were conducted at 0900 ($n = 5$), but only the UAV-assisted search method resulted in any failed searches (located 4/5). UAV-assisted searches were 14.25 ± 17.98 min shorter on average than traditional searches (35.15 ± 18.14 and 49.40 ± 17.65 respectively). The efficiency gain for UAV-assisted searches was greater during 0600 starts (+17.6 ± 21.66 min) than 0900 (+4.2 ± 47.92 min). Despite these differences, neither *Treatment* ($\chi^2_1 = 0.63$, $p = 0.428$), *Block* ($\chi^2_1 = 0.17$, $p = 0.681$), nor the interaction between them ($\chi^2_1 = 0.30$, $p = 0.584$) were significant. Treatment *Order* was also non-significant ($\chi^2_1 = 0.26$, $p = 0.612$). *Radius* ($\chi^2_1 = 0.76$, $p = 0.382$) and the *Treatment***Radius* interaction ($\chi^2_1 = 0.05$, $p = 0.827$) were similarly non-significant. Finally, neither *Julian* ($\chi^2_1 = 1.07$, $p = 0.300$) nor *Treatment***Julian* ($\chi^2_1 = 0.01$, $p = 0.915$) were significant.

4. Discussion

For UAV-assisted nest searches to be viable, we hypothesized that they must be equal to or more efficient than traditional search methods. UAV-assisted searches located nests 14 min faster than traditional searches on average, but variability within each search type resulted in a non-significant effect between methods. Time and search success were not tested independently in our analysis. For example, if we remove the single territory where a nest was located with traditional methods but not found with a UAV-assisted search, the search time advantage for the latter method improves from 4.2 ± 47.92 to 20.0 ± 28.55 min for 0900 starts. But this result ignores that one less nest was located using UAV-assisted searches. To fully compare the effectiveness of these two methods, both time and success must be compared in tandem. As a result, we chose to report only the combined results.

Neither the order in which the searches were conducted nor territory size were significant predictors of nest search results. This indicates that research teams successfully avoided leaving inadvertent cues on the landscape that could influence the success of the following nest search, and that increasing territory radii did not influence the two search methods differentially. Search outcomes were also not significantly impacted by Julian date. This could indicate that increasing vegetation height did not impact search time. Alternatively, experience may have increased the efficiency of both search methods over time, obscuring the impact of growing vegetation. While we cannot disentangle the impacts of experience and habitat change, our situation is likely reflective of most field-based research initiatives.

The use of UAVs to locate nests potentially introduces a new source

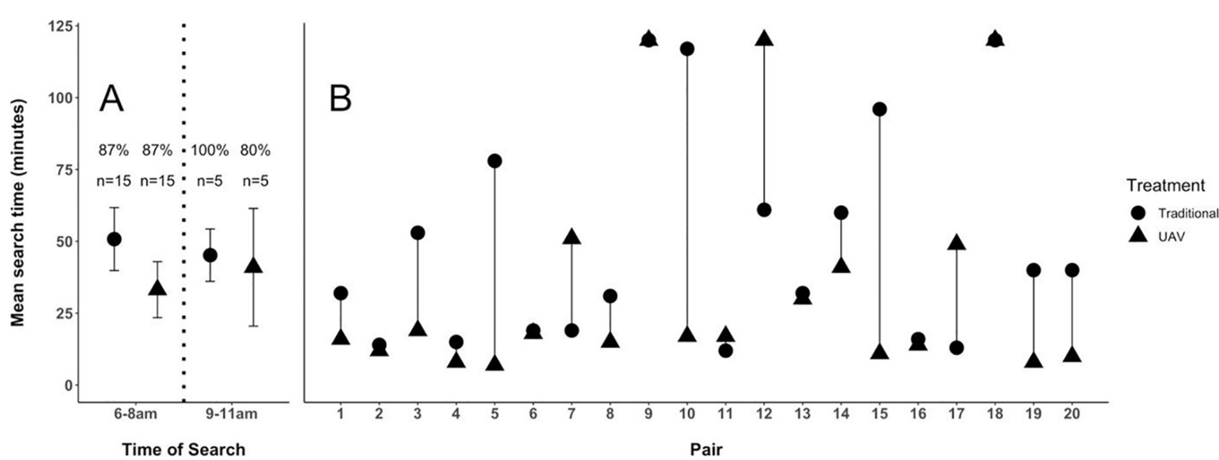

Fig. 3. Search time for territories containing an active field sparrow nest. A) Mean search times by treatment and time block. Error bars represent standard error (SE). The percentage of nests successfully located and the associated sample size (n) is indicated above each point. B) Pairwise comparison between traditional and UAV searches. Although territory size was not a significant predictor, the pairs are arranged by territory size (10 → 50 m). Search time was capped at 120 min.

of disturbance, but also alleviates much of the disturbance that typically characterizes traditional nest searches. Gillette et al. (2013) found that sage-grouse (*Centrocercus urophasianus*) regularly flushed at the approach of a fixed-wing UAV, and we observed similar behavior in field sparrows. Vas et al. (2015) documented stress behavior in waterfowl and shorebirds when a UAV approached to within 4 m, a distance generally greater than the separation between our UAV and sparrow nests. In a recent meta-analysis of wildlife response to UAVs, birds were some of the more likely organisms to show active responses to UAV activity, especially during targeted flights (Mulero-Pázmány et al., 2017). However, the extent and duration of these stress responses remains relatively unknown. It is plausible that the short-term interaction with a UAV that occurred during our nest searches produced only a temporary stress response similar to the presence of a known predator, although more lasting effects are also possible. Of the 20 territories utilized in our study, all nests were monitored until young fledged or the nest was predated. None of these territories were abandoned. Nonetheless, studies on the short- and long-term impacts of UAV activity on animal behavior and endocrinology are urgently needed.

Conversely, UAV-assisted searches create far less physical disturbance to grassland habitats than traditional methods. Regular disturbance of the vegetation within a target territory, which often occurs during traditional nest searches, can increase adult stress levels and decrease cover, ultimately heightening the likelihood of predation (Conkling et al., 2015). Repeatedly traversing active territories also increases the likelihood that predators will use human scent to locate a songbird nest (Dion et al., 2000). By dramatically reducing the need for human intrusion into grassland habitats, UAV-assisted searches may reduce predation that results indirectly from research activity. This is not trivial since predation is one of the primary causes of nest loss for grassland species (Patterson and Best, 1996). UAV-assisted searches may also reduce direct destruction of target nests, which can be inadvertently trampled by researchers.

Once nests are located, monitoring their survivorship could potentially be done through repeated UAV flights rather than return nests visits. The presence or absence of life in a known nest can be easily determined by a hotspot on the real-time thermal display. Counting individuals or deciphering between eggs and hatchlings is currently more difficult because the entire nest generally appears as a single thermal hotspot (Fig. S3). However, FLIR Systems has recently developed a dual-payload UAV imaging system (DJI Zenmuse XT2 or the more economical Duo) that streams thermal and visual video simultaneously. This new technology will likely increase the feasibility of using UAV-assisted search methods in more detailed nest monitoring protocols and could potentially eliminate the need to enter territories to examine hotspots, locate nests, or monitor survivorship.

Because UAV-mounted thermal imagery is still a relatively new technological pairing, hardware and software challenges can hamper the efficiency of UAV systems (Duffy et al., 2018). During several of our nest searches, the thermal feed lagged or became pixelated, making it difficult to distinguish hotspots on the live feed. This limitation was more severe and regular during searches starting at 0900, which appeared to correlate with increases in temperature and direct sunlight. Two searches were substantially impaired by this equipment limitation and were removed from the analysis (along with the paired traditional search). UAV-assisted searches that were not entirely impaired were retained, even though they may have been slowed by grainy imagery. These instances were retained to produce a conservative and realistic estimate of UAV-assisted search times under the current capabilities of UAV technology. In the future, improvement in thermal imagery and connectivity between the UAV and video feed are likely to increase the efficiency of UAV-assisted nest searches.

Although not tested empirically, UAV pilots consistently reported that increasing temperature and sunlight as the day progressed made it more difficult to distinguish hotspots from background vegetation, even without lagging or pixelation on the live video feed (Balick et al., 1981). While 0600 and 0900 searches did not differ significantly, equipment limitations alongside decreasing bird activity (Best, 1977) indicate that UAV-assisted searches might be most successful near or before sunrise. Testing this novel UAV-assisted search method at night might also prove to be beneficial, although the FAA currently prevents night UAV operations in the United States without a special permit.

Our search protocol was designed to occur in territories only after active nests were located and boundaries were marked. This design facilitated a highly-controlled comparison between search methods. However, delineating territories prior to conducting surveys likely facilitated more rapid nest location than is generally found in the literature. As a result, we make no attempt to compare our search results with other studies, focusing instead on comparative times between the two methods tested. Since most nest searches do not occur in 'pre-established' territories, we conducted three UAV-assisted searches on three separate mornings within portions of prairie grassland where territories had not been marked. We located three new nests during these flights (2, 1, and 0 nests, respectively), demonstrating that it is possible to locate grassland bird nests using UAV-assisted methods without first locating a nesting bird pair. Although our sample size in unmarked grasslands was small, it represents an important proof of concept because it indicates that scouting is not necessary for locating grassland bird nests. It also suggests that UAV-assisted surveys may be useful in larger scale, non-targeted grassland surveys. However, additional methodological comparisons are needed to establish the value of using UAVs in other grassland nest survey techniques.

For uniformity, our comparative searches were limited to nests from a single species, the field sparrow. However, during the course of the season we also located nests from song sparrows, common yellowthroats, dickcissels (*Spiza Americana*), and red-winged blackbirds (*Agelaius phoeniceus*) using UAV-assisted searches. In some cases, nests were located by accident. Others were targeted, although not in high enough numbers for statistical comparison. We were not successful at locating nests in two grasshopper sparrow (*Ammodramus savannarum*) territories, although it is not known if the territories contained active nests. Our multi-species success indicates that UAV-assisted nest searches could be applicable across a broader swath of ground-nesting species.

In summary, our comparison between UAV-assisted and traditional methods for locating grassland bird nests revealed that these two search methods are equally successful at locating nests and similar in their efficiency. UAV-assisted searches can provide tangible benefits by reducing the level of disturbance and destruction typically associated with traditional nest searching methods. Advances in UAV and thermal technology, such as simultaneous color video, will likely lead to more efficient UAV-assisted searches, and may eventually remove any need for human presence at nest sites during nest monitoring programs. We recommend that future nest studies using UAVs schedule sunrise or pre-sunrise flights when cooler ground and vegetation temperatures may increase the detectability of warm eggs and nestlings. The amount of time dedicated to observation and active flights might also be altered to optimize UAV-assisted search protocols. Nevertheless, our results indicate that a UAV equipped with a thermal camera can be used to locate the nests of grassland bird species, offering a promising new technique for enhancing our ability to monitor reproductive success in birds, and potentially other organisms, in grassland ecosystems.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2019.03.001.

Data accessibility

Data is available in the OSF repository at https://osf.io/5vh8u/.

Authors' contributions

D. Proppe developed the research objective and initial experimental design, trained research participants, directed data collection, and completed statistical analysis; K. Strydhorst-Lee and C. Scholten performed a pilot study to determine the viability of UAV-assisted nest searches, and collected data to compared UAV and traditional techniques; J. Atma, A. Kamphuis, O. Lamberg, C. Shea, and K. Vredevoogd finalized the methodology for comparing search techniques and collected corresponding field data; all authors contributed substantially to the composition of the manuscript. The authors have no competing interests to report.

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